

Organization, life, and systematics of trilobites

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Organization, life, and systematics of trilobites

JAN BERGSTRÖM

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The alimentary and vascular systems are discussed. The “alimentary prosopon” of polymerid trilobites is thought to show the course of the superficial dorsal vascular system. The arrangement of segments in the cephalon and thorax is investigated. Evidence of six cephalic segments is found. The articulation and enrollment mechanisms are scrutinized. Spiral enrollment evolved in Early Cambrian times and characterized a ptychopariid group which forms an evolutionary end line. Sphaeroidal enrollment is found in most other trilobites. An attempt at a new classification is made. The concepts of the Redlichiida, Phacopida, Odontopleurida, and Ptychopariida are profoundly changed, and the Illaenida are recognized as an order for the first time. Except for the Olenellida, all orders may have descended from the Redlichiina. The mode of life and feeding is discussed, arguments being drawn from features of dorsal and ventral morphology and from trace fossil evidence. The agnostids may have been parasitic, while there is evidence for carnivorous habits in other instances. The exites commonly assisted in the food search in burrowing trilobites. Most trilobites were benthic but a few may have been pelagic.

[Бергстрём, Ян: Строение, жизнь и систематика трилобитов.] Рассматриваются пищеварительная и сосудистая системы. Исследовано устройство сегментов в головном щите и туловище. Найдены доказательства присутствия шести головных сегментов. Рассматривается механизм сочленения и свертывания. Спиральное свертывание развивалось в раннекембрийское время и характеризует птихопариидную группу, которая образует слепую эволюционную ветвь. Сделана попытка предложить новую классификацию. На основании особенностей спинной и брюшной частей панциря и следов передвижения, обсуждается образ жизни и питание.

Jan Bergström, Department of Historical Geology and Palaeontology, Sölvegatan 13, S-223 62 Lund, 20th December, 1972.

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Introduction

The class Trilobita is unique among major arthropod groups in being extinct. Fortunately for the palaeontologists and stratigraphers the dorsal exoskeleton was well calcified and the dorsal morphology is therefore well known from many thousands of species. In many cases silicified specimens have added greatly to the knowledge of morphology and ontogeny. Unfortunately other aspects, including anatomy, ventral morphology, feeding methods, and mode of life are much more difficult to make out from the fossil record. This contribution is an attempt to criticize and systematize known data and to find new evidence primarily in these fields.

The treatment is based on an analysis of fossil material, comparison with extant arthropods, and a study of the literature. Only selected problems have been treated and many others, such as the function and evolution of ecdysial mechanisms, have been left aside. Even so the total amount of material is much too large to be studied. Exemplification is used as a way out of this dilemma.

The study was performed at the Department of Historical Geology and Palaeontology in Lund. I am most grateful to Professor Gerhard Regnéll, Director of the department, for suggestions, facilities, and collections put at my disposal. Drs. Valdar Jaanusson, Roland Skoglund and Mr. Fredrik Bockelie and Lars Karis assisted me with material housed in the Swedish Museum of Natural History and the Swedish Geological Survey in Stockholm. Professors Christian Poulsen and Valdemar Poulsen of Copenhagen assisted with nicely preserved olenellacean material from Greenland, Dr. Stanisław Orłowski of Warsaw with Cambrian trilobites from Poland, and Dr. David Worsley of Oslo with trace fossil material from Norway. Many other persons have aided greatly by discussing problems or yielding information. I would like to mention particularly Professor Erik Dahl and Drs. Rolf Elofsson, Sven Laufeld, Lennart Jeppsson, Bengt Nilsson, and Anders Edler of Lund, Dr. Sven Almquist of Malmö, Professor Anders Martinsson of Uppsala, Professors Gunnar Henningsmoen and Leif Størmer of Oslo, Professors Rolf Siewing and Wilhelm Stürmer of Erlangen, Dr. Andrzej Radwański of Warsaw, Dr. Sidney M. Manton of London, Professors Stig M. Bergström of Columbus, Ohio, and Richard A. Robison of Salt Lake City, Utah. Mrs. Siri Bergström finished the drawings and Mr. Sven Stridsberg made the photographs. Language correction was performed by Mr. Brian Holland, and Mrs. Ingrid Lineke assisted in typing part of the manuscript. Grants received from Kungliga Fysiografiska Sällskapet, Lund, and Matematisk-naturvetenskapliga fakulteten, Lund, made the work possible. I am grateful to the above institutions and persons, and still others, for all kinds of assistance.

Terminology

An alphabetic list of some more or less important terms used in the text is given below. The list generally

does not include terms which are used according to Harrington, Moore & Stubblefield (in Moore 1959: O117—O126). Where the term is new or redefined a page reference is given.

Acron. Most anterior part of cephalon carrying eyes, not considered to be true cephalic somite (Moore & McCormick in Moore 1969).

Anterior palpebro-ocular ridge. Anterior (outer) part of palpebro-ocular ridge, separated from posterior palpebro-ocular ridge by a longitudinal furrow (ocular striga of Öpik 1961b). (New term; p. 4; Fig. 1.)

Apodeme. Hollow exoskeletal process for attachment of muscle or apodeme (cf. Moore & McCormick in Moore 1969).

Caridoid facies. Aspect of primitive Eumalacostraca distinguished by enclosure of thorax by carapace, movably stalked eyes, biramous antennules, scaphocerite-bearing antennae, thoracopods with natatory exopods, elongate abdomen ventrally flexed and powerfully muscled, and caudal fan (Moore & McCormick in Moore 1969). The caridoid facies characterizes swimming and commonly pelagic forms.

Cruzianiform. Refers to the extended, band-like form of burrows of the type originally described under the ichnogenus name *Cruziana* d'Orbigny. (New term; pp. 52, 53.)

Diplichnitiiform. Refers to a superficial trackway of typically symmetrical shape, with or without trails produced by pygidial spines or cerci. (New term; pp. 52, 58.)

Dorsal furrow. Groove outlining rhachis in most trilobites. (*Syn.*: axial furrow.)

Dorsal furrow joint. Pivot joint in the dorsal furrow, consisting of a process facing anteriorly and fitting into a socket in the sclerite next in front. (New term; p. 14; Fig. 7.)

Fulcral joint. Pivot joint between adjoining sclerites and situated at the fulcrum. (New definition; p. 13; Fig. 7.)

Furrow joint, see Dorsal furrow joint.

Glabellar furrow. Sulcus separating glabellar lobes; as the number of lobes and furrows in the glabella is highly variable, the furrows are counted from behind: S1, S2 etc. (Symbols from Jaanusson 1956.)

Glabellar lobe. A glabellar lobe is generally a serially arranged lateral lobe of the glabella. As the number of lobes is highly variable, the lobes are counted from behind: L1, L2 etc. The anterior lobe or frontal lobe (La) of the glabella is medial. (Symbols from Jaanusson 1956.)

Hinge, hinge-line. Horizontal line of articulation between adjoining sclerites. (New term; p. 14; Fig. 7.)

Hypostome. Ventral sclerite roughly covering labrum. (New definition; p. 11.)

Labrum. Unpaired outgrowth arising just in front of mouth and more or less covering it (Moore & McCormick in Moore 1969); in trilobites covered by the hypostome.

Marginal connective device. Device for connection between adjacent pleurae at the most distal point of soft tissue connection, i.e. at the base of the pleural spine. In cases where the hinge-line extends to the pleural spines the marginal connective device may serve as a pivot joint. (New term; p. 13; Fig. 7.)

Miomeric trilobites. Trilobites belonging to the Order Agnostida (= Miomera Jaekel, 1909), characterized by the development of only two or three thoracic segments. (Term used e.g. by Öpik 1967.)

Occipital furrow. Transverse groove separating occipital ring

from glabella; symbolized SO (*sulcus occipitalis*). (Symbol from Jaanusson 1956.)

Occipital ring. Most posterior segment of the cephalic rhachis; shortened LO (*lobus occipitalis*). (Symbol from Jaanusson 1956.)

Palpebro-ocular ridge. Combined palpebral lobe and eye ridge; cf. Anterior and Posterior palpebro-ocular ridge. (New term; p. 4.)

Plectrum. A backward projection of the anterior border in front of the glabella (Öpik 1967).

Pleural spine. Part of pleura distal to a line between the anterior and posterior distalmost points of interpleural soft tissue connection. (New definition; p. 14; Fig. 7.)

Polymerid trilobites. Non-agnostid trilobites, generally characterized by the development of more than three thoracic segments. Corresponds to the Suborder *Polymera* Jaekel, 1909. (Term used e.g. by Öpik 1967.)

Posterior palpebro-ocular ridge. Posterior (inner) part of palpebro-ocular ridge in some early trilobites with a longitudinal furrow (ocular striga of Öpik 1961b) in the palpebro-ocular ridge. (New term; p. 4; Fig. 1.)

Prosopon. External markings and features in the exoskeleton that have been commonly classed as ornament, but signify the presence of organs. The prosopon may be characterized as a functional ornament. (Gill 1949; Öpik 1961b.)

Rhachis. Medial region of dorsal exoskeleton, outlined by dorsal furrow. (Syn.: axis.)

Rusophyciform. Refers to the concentrated form of burrows of the type originally described under the ichnogenus *Rusophycus* Hall. (New term; pp. 52, 53.)

Segment. One unit in a series of units (segments or metameres) occurring along the length axis of the body or an appendage and characterized by a repetition of a pattern of elements (e.g. organ elements). An appendage segment is sometimes called a podomere.

Serial similarity. A similarity in presence and morphology between corresponding elements in a series of segments. (Cf. Occipital similarity, Öpik 1958.) (New term; p. 9.)

Somite. One unit in a series of blocks, into which the mesoderm is segmented during the ontogeny.

Telson. Post-segmental part of arthropod body, bearing anus and commonly caudal furca or pair of cerci. Post-cephalic somites form successively at the anterior margin of the telson during ontogeny.

Morphological and anatomical features of the trilobite cephalon

Ridges, lobes and sulci have been interpreted in various ways by different authors. On the whole the explanations are of two main kinds. One of these interpretes lobes as segments or, to be more correct, the exoskeletal cover of segments. Linear elements are commonly explained as boundaries between segments. The second kind is based on attempts to explain the exoskeletal morphology as an expression of functional needs. These developmental and functional explanations need not necessarily exclude one another, but, in particular cases, one or the other may be the more reasonable one.

Genal prosopon

The genal prosopon ("functional ornament") includes at least three different kinds of structures, namely the palpebro-ocular ridges, the eye lines, and the radiating structures commonly thought to be the exterior expression of alimentary diverticula. The different kinds of

structures are found most commonly in early trilobites, particularly in olenellids, but the palpebro-ocular ridges are present also in many later forms.

In most olenellids and in a few other Early Cambrian trilobites, including *Bigotino*ps, *Termierella*, *Pruvostina*, and *Jalonella*, the palpebro-ocular ridge is wide and divided by a longitudinal furrow into an anterior (outer) and a posterior (inner) branch. In most other trilobites, where a palpebro-ocular ridge is developed, it is undivided and narrow.

Wanneria? lundgreni (Moberg) may serve as an example of an olenellid with typically developed palpebro-ocular ridges. The posterior palpebro-ocular ridge extends into the glabella, where it merges with the fourth lobe (L4) without any distinct delimitation. The anterior palpebro-ocular ridge turns forward at the lateral side of the glabella and may be distinguished as a weakly defined raised strip along the margin almost to the anterior tip of the glabella. Between the raised strip and L4 is an undifferentiated triangular field. The glabellar prolongations of the palpebro-ocular ridges and the intervening triangular section apparently are identical with the regions distinguished by Hupé (1953a:261—264, Figs. 60—63 and 67; 1953b:19, Fig. 14) as antennal, preantennal and X segments. *Fallotaspis* and *Callavia* are identical with *Wanneria?* in this respect. The so called preantennal segment is just a low triangular field, as hinted at above, and shows no similarity to normal glabellar lobes. Neither the preantennal nor the X segment is delimited by glabellar furrows.

The relationship between the palpebro-ocular ridges and the glabella in *Bigotino*ps and similar genera appears to be identical to that in olenellids (cf. Hupé 1953a, Figs. 47, 49, 50, 53, and 63 with 62).

In trilobites with an undivided palpebro-ocular ridge there is no direct connection between this ridge and the lobe L4 of the glabella. Actually the dorsal furrow separates the two elements and in many instances the ridge bends forwards just outside the dorsal furrow. The bending forwards is well seen in species of *Resserops*, *Longianda*, *Despujolsia*, *Gigantopygus* (cf. Hupé 1953a), *Redlichia* (cf. Öpik 1958), etc. From this morphology and from the position next to the eye facet on the palpebral lobe it seems probable that the simple palpebro-ocular ridge corresponds to the anterior ridge only of the bifid palpebro-ocular ridge found in early trilobites.

The significance of the palpebro-ocular ridge has been discussed by several authors. At least five interpretations have been forwarded. Lindström (1901:19) suggested that the ridge covered a trunk of the vascular system. Jaekel (1901:168—169) simultaneously suggested that the ridge housed a trunk of the liver or hepatopancreas, an idea opposed by Moberg (1902:299) but seemingly accepted by most trilobite students of today. Still earlier Beecher (1895:309) thought that the nerve of the lateral eye was lodged beneath the palpebro-ocular ridge and this idea was repeated by Öpik (1937:131). Richter (1926:93) suggested that the palpebro-ocular ridge served to stiffen the exo-

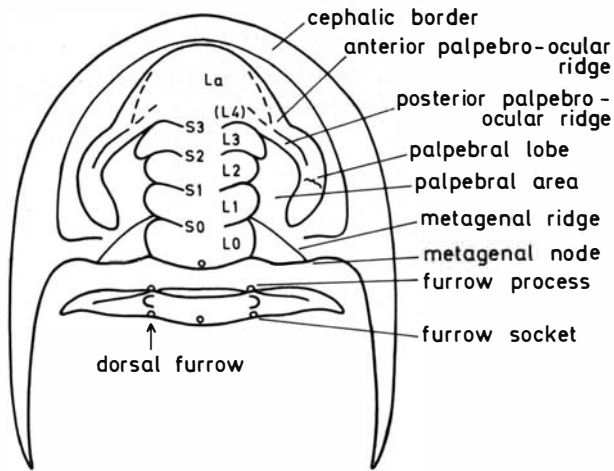


Fig. 1. Terminology of features in the dorsal exoskeleton in trilobites. The letter L signifies the occipital (LO), lateral glabellar (L1—L4) and anterior glabellar (La) lobes of the cephalic rhachis, while S denotes the occipital (SO) and lateral glabellar (S1—S3) furrows. The drawing is based on *Wanneria? lundgreni* (Moberg).

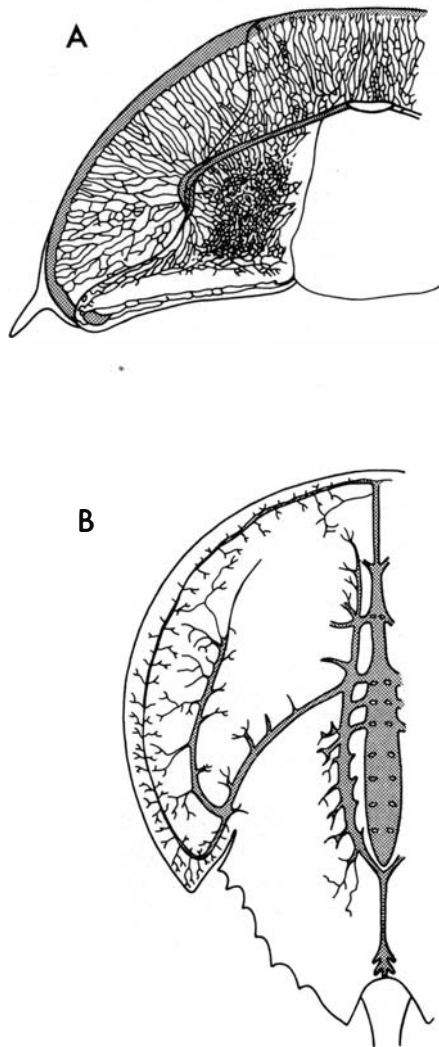


Fig. 2. The vascular system. A, cephalic prosopon in *Papyriaspis lanceola* Whitehouse, supposed to reflect the pattern of the dorsal vascular system. Shaded areas correspond to suggested vascular trunks. B, dorsal elements of vascular system in *Limulus polyphemus* (Linnaeus). Modified from Öpik (1961b) and after Grassé (1949) from Lameere, respectively.

skeleton, in addition to housing part of the hepatopancreas. Several authors, including Öpik (1937), Størmer (1942, 1944), and Palmer (1957) have suggested that the palpebro-ocular ridge represents part of a segment, a suggestion which is not in conflict with the four others. According to the two hypotheses put forward by Lindström and Jaekel, respectively, the palpebro-ocular ridge is part of a system in which the radiating ridge net of the cheeks is also included and it is therefore necessary to take account of that net before treating the ideas.

A radiating genal net of internal furrows, commonly associated with fine ridges on the external surface, is known from many different trilobites, including a variety of olenellids (e.g. Walcott 1910; Öpik 1961b), *Elyx* and *Conocoryphe* (cf. Lindström 1901; *Elyx* also in Jaekel 1901 as *Eurycare*), *Redlichia*, *Papyriaspis*, and various agnostids (Öpik 1961b), to mention a few examples. The agnostid pattern differs markedly from that of other trilobites and is treated separately here. It is particularly well seen in blind trilobites like *Elyx* and *Conocoryphe* that the palpebro-ocular ridge forms a proximal trunk from which the genal net radiates (Lindström 1901, Pl. 6:43, 44; Harrington in Moore 1959, Fig. 73 A and B). A second trunk may be present in the posterior part of the cephalon, as in *Elyx*, where it emerges opposite the lobe L1. There is no particular indication that the canals underlying the radiating ridges ended blindly. On the contrary, the morphology in *Papyriaspis* (Fig. 2A; cf. Öpik 1961b, Pl. 68:2) indicates that the canals recollected in a marginal trunk. It is noteworthy that the radiating ridges anastomose to a considerable degree in some trilobites.

Considering the obvious connection between the palpebro-ocular ridges and the radiating net, the anastomosing pattern of this net and the presence even in trilobites without lateral eyes, the idea that the prosopon shows the course of the eye nerve or of other nerves is simply impossible. A stiffening function is not impossible, but it is hardly probable that this is the primary function. In cases where the net is visible only as furrows in the interior surface the function is certainly not stiffening.

It is regarded almost as a fact that the genal pattern under discussion is an alimentary prosopon, the ridges covering alimentary caeca (e.g. Harrington in Moore 1959:O100—O101; Öpik 1961b). However, some features are not fully in accord with this interpretation. The anastomosing pattern and, in particular, the collecting marginal trunk obviously present in *Papyriaspis* would not be expected in a hepatopancreas. Furthermore, the (anterior) palpebro-ocular ridge originates in an anterior region which at least in the olenellids should be in front of the stomach, provided that the stomach is situated between the glabella and the hypostome as in phacopids (Stürmer & Bergström 1973). This means that the trunk probably originates far in front of the entodermal part of the alimentary canal. Contrary to the suggestions by Hupé (1953b) and Öpik (1961b) it is unlikely that the diverticula opened

into the ectodermal stomach. This would be as exceptional as Öpik's definition of the term oesophagus (Öpik 1961b:436: defined as proventriculum and stomach). Actually, in most extant chelicerates, all diverticula open into the entodermal midgut and it appears reasonable to assume that trilobites were organized in a similar way. Accordingly, it is highly improbable that the palpebro-ocular ridges and the connected net of radiating ridges represent an alimentary prosopon.

The pattern represented by the prosopon is what might be suspected of a vascular system, at least if this is not radically different from what is found in other arthropods including xiphosurids and arachnids. The vascular system of arthropods is said to be open, which means that the arteries do not split up into capillaries but discharge the vascular fluid into perivisceral sinus systems. However, this open condition is sometimes thought to be secondary and in xiphosurids and scorpions there is an actual splitting into fine vessels, some of which may recollect in a ventral sinus in the scorpions. The almost capillary size of the finest branches in the prosopon (*Paedumias*, *Olenellus*) and the commonly anastomosing pattern (species of *Olenellus* in particular) appears to be in better accord with a vascular system than with an alimentary one. The marginal cephalic vessel in *Papyriaspis* (cf. Öpik 1961b:423; Pl. 68:2) has a position corresponding to the marginal artery in limulids (Fig. 2B). The vessel beneath the palpebro-ocular ridge has also a counterpart in various chelicerates.

Functionally, a fine-meshed vascular net closely beneath the exoskeletal cover would seem to be of great value in the moulting process, both in breaking down parts of the old skeleton by resorption and in building the new one.

That the genal prosopon pattern, including the palpebro-ocular ridges, may be connected with the vascular system is also indicated by

- (1) the need of blood supply to the large eyes,
- (2) the consequent extension of the palpebro-ocular ridges (also found in other polymerid trilobites). The extension appears to be consistent with a vascular system idea, whereas it is difficult to imagine why an alimentary diverticulum should be strictly confined to a distinct path and end just at the lateral eyes.

The anterior eye line (Størmer 1942) found in olenellids and redlichiids is suggested by Hupé (1953a:268, ligne préoculaire) and Öpik (1961b:418—419, facial line) to reflect the course of an alimentary diverticulum. The anterior eye line seems to originate from the anterior palpebro-ocular ridge closely anterior to the palpebral lobe as seen in *Wanneria? lundgreni*. A special problem is the curved course of the anterior eye line in several olenellids such as *Holmia kjerulfi* (cf. Størmer 1942, Fig. 14), *Callavia* cf. *gilberti* (cf. Walcott 1910, Pl. 28:1), *Olenellus* cf. *gilberti* (cf. Walcott 1910, Pl. 41:1), *Kjerulfia lata*, *Fallotasps longispina*, and *Daguinasps ambroggi* (cf. Hupé 1953a, Fig. 68). In *Olenellus* cf. *gilberti* the anterior

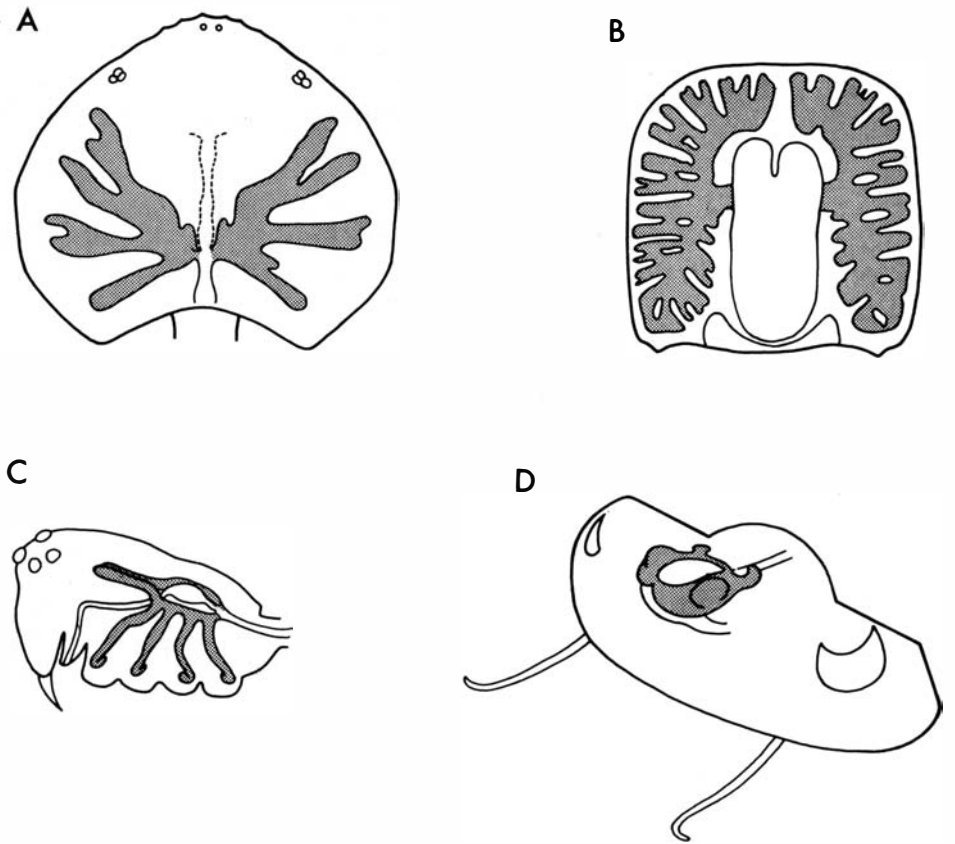
eye line appears to cross the radiating prosopon ridges angularly, which may mean that the two features represent independent entities. Apart from the anterior eye line there is also an additional fine ridge in some of the species mentioned, the posterior eye line (Størmer 1942). In some olenellids there is a similar ridge extending from the lateral side of the compound eye. This ridge may be called a middle eye line and is found in *Nevadia weeksi* (cf. Walcott 1910, Pl. 23:3) and *Olenellus thompsoni* (cf. Walcott 1910, Pl. 33:1). The functional significance of the different eye lines is not known with certainty but it is not impossible that they reflect part of the vascular system.

In some agnostid genera, including *Glyptagnostus*, *Corrugatagnostus*, *Ptychagnostus*, *Hypagnostus*, and *Tomagnostus*, there is a radiating pattern of prosopic ridges in the pleural region of the cephalon and in some cases in the pygidium (Fig. 3B; cf. Öpik 1961b). The pattern is superficially somewhat similar to the genal prosopon of polymerid trilobites. However, there are also distinct differences. First, the individual ridges are very much stronger than in polymerid trilobites in comparison to the size of the cephalon. Still, the absolute size may be similar, as agnostid trilobites are comparatively small, when the comparison is made with large or medium-sized polymerid trilobites. Small polymerids like olenids have a much finer prosopon pattern than agnostids (cf. Henningsmoen 1957, Pls. 13:1; 14:1, 3, 5, 9; 19:14; 24:3) and therefore the size difference may be important. A second distinguishing feature is the distal terminations, which in the agnostids look like blind sacks aligned just inside the cephalic border (cf. Öpik 1961b, Pl. 70:1—11). The termination is so distinct that there is no doubt that the underlying structures actually ended there. A third feature is the coverage. The prosopon in the agnostids fill the entire surface, the ridges being separated only by narrow grooves. In polymerid trilobites the ridges form a rope-like pattern on an otherwise smooth surface. Fourth, the main contributing stem connects further back on the glabella than in the polymerids, even if still in the anterior half of the glabella (cf. Öpik 1961b, Figs. 2, 4).

The bulk of evidence suggests that the prosopon of agnostids has another cause than in polymerids. I find Öpik's (1961b) comparison with *Burgessia* sound, and I concur with his idea that the agnostid pattern is an alimentary prosopon. The pattern has also much in common with the alimentary diverticula of extant chelicerates, pycnogonids and branchiuran crustaceans (cf. Fig. 3). These arthropod groups are not closely interrelated, but they all feed on fluid food. The development of the diverticula appears to be connected with the feeding manners, and it therefore seems likely that also the agnostids (at least the reticulated forms) and *Burgessia* ingested fluid food.

Although most of the prosopon of polymerid trilobites has been referred to the vascular system in the discussion above, there may be an alimentary prosopon as well. Öpik (1961b) described large swellings of the palpebral area in *Olenellus* (mentioned as *Paedumias*)

Fig. 3. Intestinal diverticula composing the hepatopancreas in extant arachnids (A, C) and presumed counterparts in trilobites (B, D). A. The amblypygan *Sarax*. B. The agnostid *Diplagnostus*, with diverticular pattern as deduced from prosopon arrangement. C. *Araneus*. D. *Phacops* with hepatopancreas as revealed by X-rays. Modified after Grassé (1949), Gerhardt & Kästner (1938), Öpik (1961b), and Stürmer & Bergström (manuscript).



and *Redlichia*. The evidence is fairly weak, but the explanation appears possible.

In conclusion it may be said that an alimentary prosopon is possibly found in the swellings of the palpebral area reported by Öpik (1961b) in *Olenellus* and *Redlichia* and most likely in the pleural ornament in *Glyptagnostus* and some other agnostids. The radiating genal prosopon of many olenellids, *Redlichia*, *Papyriaspis*, *Elyx*, olenids, etc. evidently branches from the (anterior) palpebro-ocular ridge which extends to a position obviously far in front of the entodermal part of the alimentary canal and therefore can not belong to the alimentary system. Instead, the configuration shows certain similarities with the vascular system of *Limulus* and scorpions and it is assumed that the ornament is a vascular prosopon. The eye lines are likely to represent some kind of prosopon but the arrangement in different olenellids indicates that at least the anterior eye line does not belong to the vascular prosopon.

Muscle attachments and cephalic appendages

Few detailed studies have been based on trilobite muscle scars. Moberg (1902), Størmer (1930), Öpik (1937), Sinclair (1947), Whittington (1950), and Jaanusson (1954) are among those who have treated appendage muscle scars. Cephalic muscle scars not referable to the appendage muscles were treated in detail by Eldredge (1971). Eldredge distinguished four

groups of muscle attachment sites after the morphologic appearance, namely (1) exoskeletal invaginations; (2) calluses, bosses or pads; (3) dark markings (with no relief); (4) pits or scars.

In this text the discussion is confined to the position and size of attachment sites of muscles extending to the appendages. It is suggested that the size of the attachment sites is roughly proportional to the strength of the muscle and thereby to the development of the associated appendage. It is possible that muscles from one attachment site extend to two or more appendages. This may distract from the reliability of the suggestion just made.

The even depth of the glabellar furrows indicates that there was a comparatively uniform series of muscles to the cephalic limbs in many trilobites. This is the case in many olenellid trilobites, in paradoxidids, many cheirurids, oryctocephalids, etc., where at least four pairs of fairly similar furrows may be discerned. In oryctocephalids even a fifth pair, S4, belonging to the antennal segment, may be included in the series of furrows with comparably similar strength (cf. Shergold 1969).

In many other instances this is not the situation. Even in the above mentioned trilobite groups there is commonly a weak tendency towards more pronounced furrows and probably progressively larger attachment areas backwards in the cephalon. Jaanusson (1954: 550) states that the two posterior attachment areas are generally larger than the two anterior ones in illaenids.

This is also the case in *Pharostoma* (cf. Öpik 1937, Pl. 15:4). Actually, a similar gradation is a rule in the entire trilobite class. The most plausible explanation for the gradation in size is that the limbs were successively weaker forwards in the cephalon (cf. Eldredge 1971:64, regarding Phacopacea).

In some cases the longitudinal change is not successive but abrupt. In *Dalmanites vulgaris* (a Gotland specimen housed in Lund) there are only three pairs of apodemes, corresponding to SO—S2, although S3 is distinctly developed. In the cheiruracean *Pliomerella* only three distinct furrows (SO—S2) are developed. In several phacopids, including *Phacops*, two posterior furrows (SO—S1) are quite deep while the anterior furrows are invisible from the exterior. The same condition is found in *Tretaspis*, some harpids and the cheiruracean *Hemisphaerocoryphe*, to mention a few examples. If the small size of the attachment area means that the muscle and corresponding limb was comparatively small, the absence of glabellar furrows and apodemes may indicate that the corresponding appendages were reduced or absent.

Results of X-ray studies

Radiographic techniques have been used in palaeontology for more than 70 years. Still, fossil arthropods have only occasionally been studied with the aid of X-ray examination. In most cases the material studied was derived from the Lower Devonian (Siegenian) Hunsrück Shale of the Rheinische Schiefergebirge. Published X-ray studies in trilobites include those by Størmer (1939, *Phacops*, *Triarthrus*), W. Lehmann (1932, 1938, 1956b, *Phacops*; 1934, *Asteropyge*), and Stürmer (1970, *Asteropyge*, *Phacops*).

The radiographic examination has been hampered by the scarcity of well preserved pyritized material and by the crudeness of the methods. Recently, however, Prof. W. Stürmer of Erlangen has brought together specimens from existing collections and collected much new trilobite material. Moreover, he has improved the X-ray technique considerably and shown that it is possible to obtain more morphological detail through the application of soft X-rays and through stereoscopic exposures. I was kindly invited to cooperate in the interpretation of the radiographs. A summary of the results is given here. The reader is referred to the original treatment (Stürmer & Bergström, in print) for a detailed account.

Three trilobite species are concerned here. Two of them have been found in the Hunsrück Shale. Of these, a species of *Phacops* is most common. The species may be *P. ferdinandi* Kayser. The other species is a dalmanitacean, which has been referred to as *Asteropyge* sp. Actually, the species does not belong to *Asteropyge* but probably to *Pseudocryphaeus* or *Rhenops*, but the former name is used provisionally as long as the correct assignment is not known with certainty. The third species is *Triarthrus eatoni* (Hall) from the Middle Ordovician Utica Shale near Rome, New York. The latter is an olenacean (suborder

Asaphina), while the two former belong to the Phacopida.

Cephalic appendages.—It is generally accepted that trilobites have four pairs of cephalic appendages apart from the antennae. This concept has been confirmed in *Triarthrus*, but *Phacops* and *Asteropyge* have both suffered appendage reduction from the front. The hypostome appears to have expanded correspondingly. In *Phacops* there are three pairs of cephalic appendages (corresponding to LO—L2) apart from the antennae. The two most posterior pairs of coxae are provided with powerful enditic prolongations, which are serrated and no doubt served as jaws. The posterior pair is stronger than the anterior one. The anterior pair of coxae (corresponding to L2) is concealed under the hypostome and not well enough preserved to show the presence or absence of serrated endites. The absence of corresponding apodemes (in the glabellar furrow S2; those of S1 and SO are well developed) may indicate that the coxae were comparatively weak. In *Asteropyge* there are three pairs of cephalic apodemes and a corresponding number of appendages (LO—L2). The coxae are not well enough pyritized to yield any information about the morphology. *Triarthrus* has four pairs of cephalic appendages (excluding antennae) with strong enditic prolongations, the posterior of which are larger than the anterior ones. The tendency to concentrate the strongest gnathobases posteriorly is a character shared with the merostomes and may be considered to be an arachnomorph feature.

Alimentary system.—The alimentary canal is fairly well visible in both *Phacops* and *Asteropyge* (Figs. 3D, 4). It is remarkably similar to the models suggested by Richter (1925, 1926a) and Eldredge (1971). The mouth lies above the posterior half of the hypostome (and labrum) and opens into a short oesophagus, which extends anteriorly to an expanded stomach (proventriculus). From the stomach a cylindrical narrow intestine extends backwards. The anus is at the doublural edge close to the posterior end of the pygidium. The stomach is surrounded by voluminous structures, which obviously represent the hepatopancreas (intestinal diverticula). These are morphologically different in *Phacops* and *Asteropyge*, but in both they are confined to the rhachial part of the cephalon. This means that the space between the frontal glabellar lobe and the hypostome is partially filled by the stomach and the hepatopancreas. In *Asteropyge* there may also be additional hepatopancreas lobes under the posterior glabellar lobes.

The hepatopancreas of the phacopids does not cover the stomach on the dorsal side, but leaves a window which is elliptical or rounded in *Phacops* but more triangular in *Asteropyge*. The shape and position of the window in the two trilobites corresponds roughly to the pattern of muscular markings of the glabella in phacopaceans and dalmanitaceans, respectively, as these are illustrated by Eldredge (1971). The window

apparently furnished a space where muscles connected the stomach with the tergum (cf. Eldredge 1971, Fig. 7). Other muscles apparently connected the alimentary system with the hypostome although some authors believed in a direct muscular connection between glabella and hypostome (cf. Brögger 1886; Richter 1925, 1926a; Eldredge 1971). These muscles are not distinctly visible in radiographs but may be represented by cloudy shadings.

Compound eyes.—Anatomical details belonging to the compound eyes were first discovered in radiographs by Stürmer (1970). Further studies have confirmed that the compound eyes of *Phacops* have very long ommatidia, while nothing similar has been observed in other trilobites (cf. Stürmer & Bergström in print).

Segmentation

The study of trilobite segmentation is greatly hampered by the general absence of soft tissues and the lack of information about the ontogeny, apart from the development of the exoskeleton. Therefore, the knowledge about the segmentation of the cephalon is based primarily on the existence of a repetition of certain characters along the axis of the trilobite. This feature may be termed *serial similarity*. The serial similarity is considerably more pronounced in the thorax, where each sclerite commonly is practically identical to its neighbours. The conclusions about the segmentation must depend on the supposition that the serial simi-

larity reflects a segmentation also in the soft parts of the animal. Apparently this supposition has never been questioned. There is also general agreement that the segmentation was simple, with but one pair of appendages and one set of serially repeated features in the exoskeleton pro segment. From our knowledge of extant arthropods it appears relevant to regard these suppositions as well justified. On the other hand there is considerable uncertainty as to the exact course of the segmental boundaries in the exoskeleton in the cephalon as well as in the thorax and pygidium, and different solutions have been presented. However, this uncertainty does not affect the principles of segmentation or the concept of serial similarity.

Cephalic segmentation

There is general agreement that the occipital ring and the posterior glabellar lobes represent cephalic segments. In the anterior part of the glabella the lobes and furrows may be weak or absent, or there may be features which are not necessarily homologous with the posterior lobes and furrows. Nevertheless, Hupé (1953a, b) stated that there are seven glabellar segments in various early trilobites. Other authors, including Jaekel (1901), Kiær (1916) and Palmer (1957), have suggested that even the frontal area and, according to some authors, the ventral rostrum and hypostome is of segmental origin, despite the

complete absence of what is here called serial similarity.

In considering the segmental composition of the trilobite head tagma, the following points may be important.

- (1) A presegmental complex or acron is present in all present-day arthropods and it is hardly probable that trilobites differed in this respect. The size of the acron may vary within wide limits.
- (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. Exceptionally, as in some agnostaceans, the anterior part of the glabella is indistinguishable from the surrounding pleural fields.
- (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 contribution; combined studies or comments have been made by Størmer 1930, Öpik 1958, 1961b, and others).

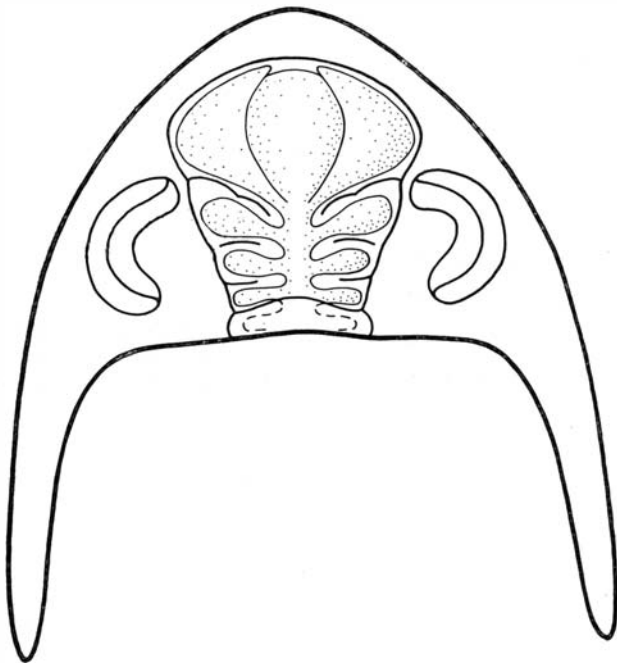


Fig. 4. "*Asteropyge*" sp. from the Devonian Hunsrück Shale in Germany. Stomach and hepatopancreas outlines as deduced from X-ray films made by Prof. W. Stürmer. The large anterior lobes of the hepatopancreas are well preserved, but the evidence for the lobes under the lateral glabellar lobes is not entirely satisfactory.

A simple counting of the occipital and glabellar lobes is not sufficient. As mentioned above, Hupé (1953a, b) found seven supposed segments in the rhachis. This result was based on some olenellaceans and some other early trilobites. On the other hand many illaenids exhibit no exterior signs of any cephalic segmentation. Most other trilobites are intermediate as far as this character is concerned. There is thus some morphological variation, and ideas about segmentation can not uncritically rely on the number of glabellar lobes in a single trilobite. Trilobite larvae would be suspected to show segmentation features more reliably as segmentation probably greatly influences the early ontogenetic development in all arthropods. However, the number of rhachial rings (including the anterior lobe) is five in *Olenellus gilberti* (cf. Palmer 1957, Fig. 6) but six in *Eccaparadoxides pinus*? (cf. Westergård 1936, Pl. 4). The explanation of this difference may be found in the composition of the palpebral lobe. In both species the undivided larval palpebral lobe extends to the anterior glabellar lobe. This condition remains throughout the development in *Eccaparadoxides*. However, in *Olenellus* the palpebral lobe divides into anterior and posterior palpebral or palpebro-ocular ridges in the fifth developmental stage (Palmer 1957, Fig. 7; Pl. 19:16, 19). The proximal ends of these palpebral ridges lie opposite to the anterior and posterior parts of the anterior glabellar lobe, respectively. In the same stage there is some diversification of the anterior glabellar lobe into a wide anterior and a narrow posterior part. The posterior part may be considered as a distinct glabellar lobe or ring, L4. The anterior palpebro-ocular ridge, therefore, has a position corresponding to that of the entire palpebral lobe of *Eccaparadoxides* and may be homologous with that lobe.

It has been shown in *Wanneria? lundgreni* (Moberg) and *Schmidtellus mickwitzii torelli* (Moberg) that the posterior palpebro-ocular ridge can be followed into the glabella, where it may be distinguished as a weakly defined glabellar lobe (L4) showing serial similarity backwards (Fig. 5; Bergström, in preparation). In the same species the anterior palpebro-ocular ridge was found to extend forward along the anterior glabellar lobe until it merges with this lobe anteriorly. An undifferentiated triangular glabellar field fills the area between the two ridges inside the glabella. The situation appears to be identical to that reported by Hupé (1953a:261—263) in *Fallotaspis tazemmour-tensis* and *Callavia crosbyi*. In these species 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. m. 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. Similar information may be gained from other olenellaceans, such as species of *Daguinaspis* and *Choubertella* (cf. Hupé 1953a).

Within the rhachial part of the cephalon there is,

therefore, evidence for the presence of five cephalic segments.

Genae or pleural areas.—In particular the studies by Kjer (1916) and Størmer (1942) on *Holmia kjerulfi* and by Palmer (1957) on *Olenellus gilberti* and “*Paedumias*” *clarki* show that the palpebral area of larvae 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 likely that this is 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 olenellaceans including the three species mentioned above. This serial similarity unites the lobes of the palpebral area opposite to LO—L3. In adult specimens of *Olenellus? curvicornis* (which may belong to the Wanneriinae) and “*Paedumias*” *tricarinatus* (cf. Poulsen 1932, Pl. 10:2, 3, and Pl. 11:13, respectively) the serial similarity in question in a very striking way also includes the posterior palpebro-ocular ridge. Similar conditions are found in many other olenellaceans, although generally the serial similarity is not so obvious.

Although there is common agreement about the presence of a segmentation in the palpebral areas, the course of the intersegmental boundaries has been discussed without a conclusive result. Størmer (1942, Figs. 14, 15, and 17) advocated the view that the occipital somite would have its central part under the occipital ring but its 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 spine to follow is the pleural spine of the first thoracic tergite, and this spine was therefore assigned to the occipital segment. Ross (1951:148—150) and Whittington & Evitt (1954:28), on the other hand, 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 the trilobites. This idea gains some support from *Redlichia*, where supposed 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 1961b, Fig. 8; the artery interpretation is mine).

Provided that the furrows of the palpebral area in larval trilobites show the position of somite boundaries, Palmer's (1957) material of *Olenellus gilberti* distinctly shows that the intergenal spine is connected with the preoccipital segment. I have 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. 4:13c; the furrow is hardly visible in the published figure). The same specimen has a deep bor-

der furrow similar to the pleural furrow of the thoracic tergites. At first glance the border furrow would seem to indicate the presence of an occipital segment extending to the intergenal spine. However, the border furrow is obviously important as a strengthening device and need not have anything to do with the segmentation of the animal. In this respect it is similar to the cheiruracean furrow treated by Ross (1951) and Whittington & Evitt (1954). On the other hand the faint furrow extending from S1 in *Eccaparadoxides* obviously lacks functional significance and closely resembles the supposed segmental boundaries of olenellid larvae. In *Eccaparadoxides*, as well as in olenellaceans, there is therefore evidence that the intergenal spine belongs to the preoccipital segment.

There is certainly no necessity for the occipital somite to end in a pleural spine. As the presumed vascular trunk originating from the occipital lobe in *Redlichia* is confined to the cephalon, it is simplest to regard the occipital segment as a laterally somewhat reduced segment, confined to the posterior margin of the cephalon.

It was said above that the lateral eyes belong to the non-segmental acron. There is no evidence for any segmentation of the genae lateral to the eyes, and it is therefore likely that also those areas belong to the acral complex.

Evidence from the ventral morphology.—The number of ventral appendages should give a minimum number of cephalic segments. It must be realized that there may be segments without typical appendages in trilobites as well as in modern arthropods. Actually, a loss of one pair of cephalic appendages appears to be a fact in *Phacops* (cf. Pl. 2:1, 2) and perhaps also in *Asteropyge* as compared with trilobites like *Olenoides*, *Triarthrus*, and *Ceraurus*. The latter three genera, which are the oldest of the five, have five pairs of

appendages including the antennae. This number seems to be “normal” and the condition in phacopids derived (cf. Stürmer & Bergström, in print).

This indicates the presence of at least five cephalic segments, the first of which is antennal. Evidence from extant arthropods shows that there may be more or less reduced segments in front of the antennal segment. The larval anatomy of trilobites is not tangible, but a study of the external expressions of preantennal segments in extant arthropods may reveal features which may be compared with skeletal structures in trilobites. In a review of head development in the arthropods, Manton (1960:274—278) states that the labrum may be formed in different ways. In the myriapod *Scolopendra* it forms ontogenetically out of a median labral rudiment. However, in insects preantennal limb rudiments develop at the sides of the median labral rudiment and fuse with this to form the ultimate labrum. Obviously there is some variation but the interesting thing is that the labrum may be partly formed by modified preantennal limbs.

Now it should be remembered that the trilobite hypostome is roughly the exoskeletal cover of the labrum, although sutural rearrangements are responsible for a somewhat variable delimitation of the hypostome. The so called anterior wings of the hypostome extend through the body to the fossular apodeme (or a corresponding spot where no apodeme is developed) on the dorsal side (see Whittington & Evitt 1954:19—20 for discussion and references). This connection is obviously found in very many trilobites, though not in all. A similar dorso-ventral connection in trilobites is indicated only between the rhachial apodemes or attachment surfaces and the ventral appendages. The dorso-ventral connection is therefore a feature shared by appendages and hypostome, indicating serial similarity and appendage character of the anterior hypostome wings. Turning to the dorsal exoskeleton, there may be serial similarity between the fossula and the glabellar furrows. This is particularly well seen in larvae, as for instance in *Peltura scarabaeoides* (cf. Whittington 1958, Pl. 38). There are generally modifications in adult trilobites, but exceptionally, as in *Oryctocephalites gelasinus* Shergold, a serial similarity is indicated. In the latter species there are five pairs of glabellar furrows or pits, the most anterior of which are more laterally positioned than the others. Still more lateral, antero-lateral to the most anterior glabellar furrow (S4) and in the dorsal furrow, is the spot where the fossula is found. Apart from the lateral displacement, it is similar to the dorsal furrows, particularly to S2 which is pit-shaped.

The indicated serial similarity both ventrally and dorsally in addition to the partly preantennal nature of the labrum in insects makes 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 (cf. Öpik 1958:30). I can not find evidence for any additional preantennal segments and therefore it seems possible that the total number of cephalic segments in trilobites is six, in-

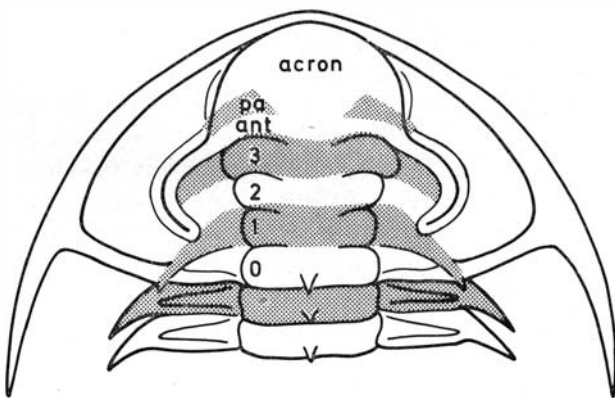


Fig. 5. Inferred segmentation in the anterior part of *Holmia kjerulfi* (Linnarsson). The anterior part of the cephalon is judged to be a presegmental acron, to which the extraocular cheeks also probably belong. The presence of a preantennal segment (pa) is suggested in the text. Five segments may have had appendages of “normal” appearance, viz. the antennal segment (ant) and the four posterior segments (3—0). Modified from Størmer 1942.

cluding one preantennal segment. In addition, the cephalon consists of the presegmental acron (Fig. 5).

Thoracic and pygidial segmentation

The question of thoracic segmentation is primarily a question of the course of segment or somite boundaries. First, it must be questioned whether the boundaries of the thoracic sclerites coincide exactly with the somite boundaries or not. Second, if the boundaries do not coincide, what is the relation between somites and sclerites in the trilobite thorax? When these problems are solved, the pygidial segmentation is no longer any problem.

It has been said that the sclerite and somite boundaries in extant arthropods do not coincide exactly (see e.g. Hessler 1962, referring to Snodgrass and to observations on *Hutchinsoniella*). However, in general, the amount of overlap seems to be small. Only in the case of modern xiphosurids is there a marked secondary segmentation at the junction between prosoma and opisthosoma. The xiphosurid type of secondary segmentation has been proposed to be present also in trilobites (Størmer 1942). The xiphosurid case shows beyond doubt that a secondary segmentation is possible, but it may be a highly advanced feature found only in Permian and later xiphosurids. In the secondary segmentation of modern xiphosurids the somites and sclerites are not parallel but cross at a fairly large angle in the pleural area. Somites and sclerites in other modern arthropods appear to have practically parallel boundaries even if they do not coincide.

In the following I will avoid the difficult question of coincidence or not between somites and sclerites in trilobites and concentrate on the eventual angle difference between the two features. I will only take the opportunity to stress that muscles, and hence muscle attachment spots and apodemes, are intrasegmental and not intersegmental. Muscle scars and apodemal pits (including glabellar furrows) therefore are not likely to mark the exact position of somite boundaries.

Previous authors have relied heavily on features in the cephalon (Størmer 1942; Ross 1951; Whittington & Evitt 1954; Palmer 1957; Hessler 1962) or in the pygidium (Hessler 1962) for the discussion of thoracic segmentation. However, it must be emphasized that particularly the cephalon is a specialized tagma with segmental modifications in all arthropods. Extrapolations backward from the cephalon are therefore not unconditionally advisable.

According to Størmer (1942, e.g. Figs. 14, 15, 17), Palmer (1957), and Hessler (1962) the pleural furrows mark the position of somital boundaries. In most trilobites the pleural furrow extends more or less distinctly from the anterior side of the pleura at the dorsal furrow posterolaterally to the pleural spine. Each somite would therefore have its central portion under the rhachial ring of one sclerital segment and the lateral tip in the pleural spine of the next succeeding sclerite. However, in many trilobites, the appearance of the pleural furrow does not fit with the given

model. Particularly in many trilobites belonging to the order Ptychopariida (as defined herein), the furrow is a wide depression absolutely parallel to the sclerital borders. A very similar arrangement is found in several corynexochids. Also in many cheiruraceans (*Reraspis*, *Cyrtometopus*, *Pseudosphaerexochus* etc.) the pleural furrow is parallel to the pleural borders. It seems easiest to regard the pleural furrows simply as strengthening devices.

In trilobites with prothorax and opisthothorax the boundary between these two tagmata is likely to coincide with an intersomital boundary. In *Elliptocephala asaphoides* (cf. Walcott 1910, Pl. 24:1) the rhachial rings have short and long spines and the pleurae have long and short spines, respectively, in the prothoracic and opisthothoracic tagmata. Both in the rhachis and in the pleural area the boundary between the tagmata is obviously between the 13th and 14th sclerites. In this case the somital boundaries therefore seem to be parallel with the boundaries between the sclerites.

Also the macrospinal development found in some olenellaceans (e.g. *Olenellus fremonti*, see Walcott 1910, Pl. 37:7) may be used as an argument for a conservative view as the excessive development is confined to one sclerite, not to two, which would be expected where secondary segmentation is present.

In *Redlichia* and *Papyriaspis*, Öpik (1961b, Fig. 49; 1961b, Figs. 8–12) demonstrated the structures herein considered to represent the vascular system. There is one vein along each of the anterior and posterior margins in each pleura and one vein along the adjoining cephalic and pygidial margins. No veins are seen to cross the sclerite borders. As the veins obviously must be considered as segmental, this condition is a very strong argument for a close correlation between somites and sclerites.

Hessler (1962) based much of his discussion on trilobite segmentation on features of the pygidium. One of his points in favour of a secondary segmentation is that pleural furrows are well developed throughout the pygidium in some Carboniferous trilobites while the interpleural furrows tend to be developed only anteriorly. If the pleural furrows acted as strengthening devices, then, this is reason enough for them to be developed throughout the pygidium (cf. Richter & Richter 1934). On the other hand, the interpleural furrows had a function only in the thorax and may have been preformed ontogenetically only in the anterior part of the pygidium. It is not certain that any of these structures mark the position of the intersomital boundary. In addition, the trilobites studied are phylogenetically late forms, and there is considerable variation.

I have no opinion about the developmental anomalies referred to by Hessler (1962:1308; Pl. 176:1, 2, 4), as his figures are out of focus and do not permit a close study.

In treating segmental features of the thorax and pygidium authors have commonly used the term segment more or less as a synonym to sclerite without really discussing the relation between somites and

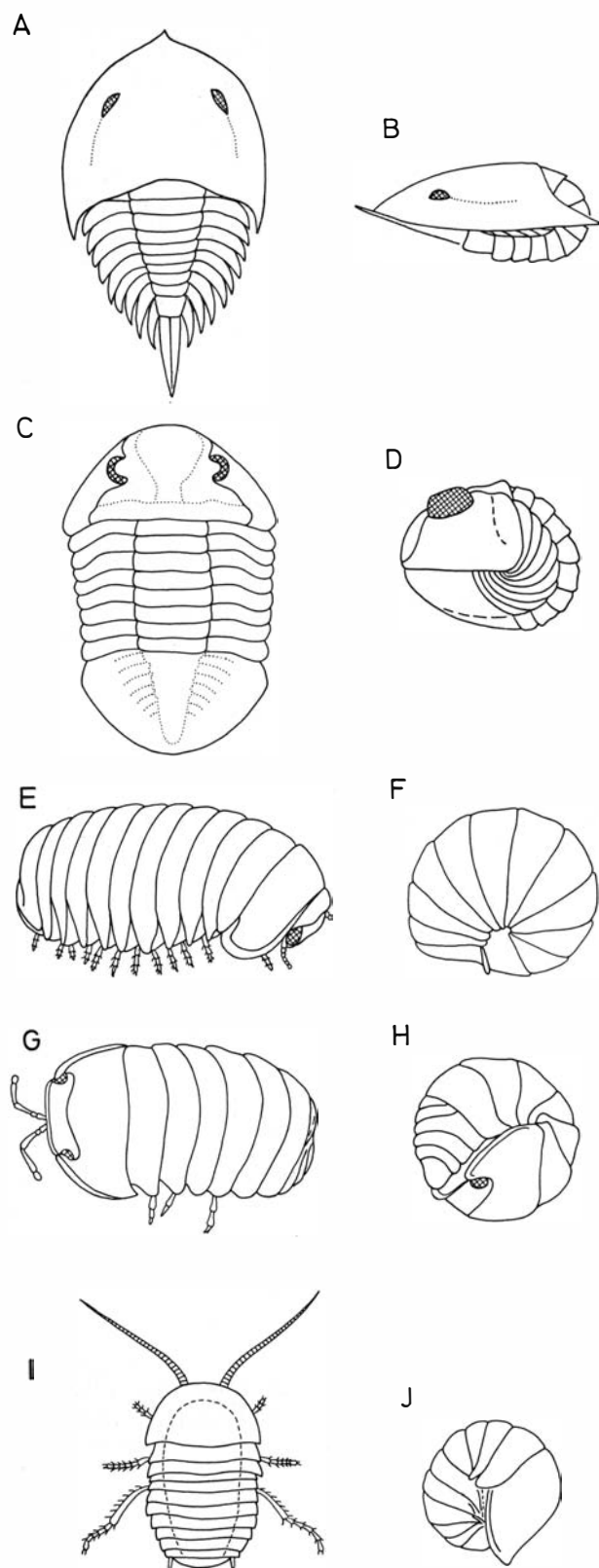


Fig. 6. Enrollment in different classes of arthropods. A, B. The Silurian xiphosurid *Pseudoniscus*. C, D. The Ordovician trilobite *Asaphus*. E, F. The extant milliped *Sphaerotherium*. G, H. The extant crustacean *Cubaris*. I, J. The extant insect *Perisphaera*. Note the general morphological similarity, no doubt caused by functional necessities connected with the enrolling ability. Partly from Moore (1959, 1969) and Lawrence (1958).

sclerites (e.g. Bohlin 1960; Erben 1967). Although the discussion may be sound it has little bearing on the question of secondary segmentation.

In discussions on pygidial segmentation as well as on cephalic segmentation, it is commonly forgotten that there is a non-segmental portion which has a position posterior to (anterior to in the cephalon) the segmental part of the body. The general arthropod term for this posterior non-segmental part is the telson although this term has also been used incorrectly for the partly segmental tail spine of xiphosurids. In most trilobites the telson, no doubt, corresponds to only the most posterior portion of the pygidium, but it is possible that it corresponds to the entire pygidium in some micropygous trilobites, e.g. many olenellaceans and ellipsoccephalids.

Articulation and enrollment

Relatively few studies have been performed on the enrollment and the mechanism of articulation in trilobites, despite the fact that enrollment is much more common in trilobites than in any other arthropod group. Notable exceptions are case studies by Pompeckj (1892), Kiær (1916), Öpik (1937), Størmer (1939), Kurtén (1949), Ross (1951), Jaanusson (1953), Whittington & Evitt (1954), Hupé (1954), Palmer (1958), and Robison (1964). More general reviews were given by Barrande (1852) and Harrington *et al.* (in Moore 1959).

It is not the aim of this contribution to review all the evidence presented in the literature, but only to chose some critical examples from the literature and from available collections. In doing so I hope to achieve a better understanding of the enrollment mechanisms and their evolution in the trilobites. As seen later on, the course of the early evolution of the enrollment mechanisms apparently has a distinct bearing on the evolution and classification of the trilobites, but this is basically a by-product of the study.

Articulation

The articulating half-ring is generally omitted from the study.

The nomenclature is basically that of Whittington & Evitt (1954) and Harrington *et al.* (1959). However, the structure in cheirurids called a fulcral joint by these authors commonly lies distal to the poorly defined fulcrum and the term therefore is not appropriate for this case. In other trilobites there may be a real socket and ball joint at the fulcrum, and the term *fulcral joint* is used in that case. The cheirurid structure differs from the true fulcral joint in its position at the inner margin of the doublure. It therefore marks the most distal point where successive segments are connected through soft tissues, and I have coined the term *marginal connective device* for the ball and socket connection. The marginal connective device may form a ball and socket joint if the pleural spine extends horizontally. In this case the device may be

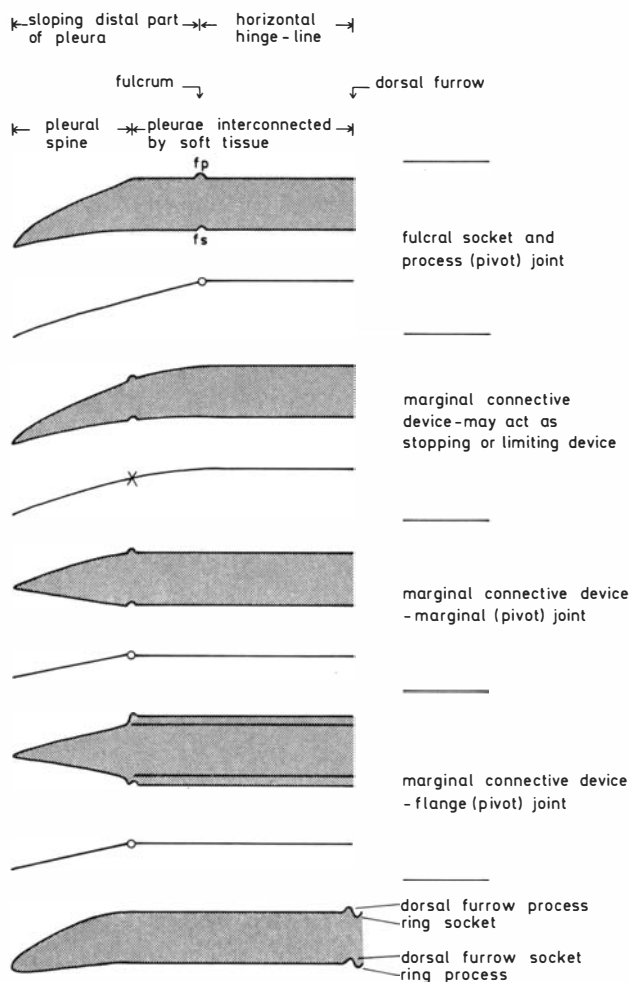


Fig. 7. Pleural morphology connected with interpleural articulation in trilobites with a horizontal hinge-line. Each type of pleura is schematically drawn as seen from above and from behind.

called a *marginal joint*, or in forms with a typical flange a *flange joint*. In forms with a fulcrum the marginal connective device is not aligned with the articulating hinge and can not act as a pivoting joint. In this case it may act as a *limiting device* in the enrollment.

As pointed out by Whittington & Evitt (1954) there may be two kinds of condyle-and-socket joints in the dorsal furrow. One process is directed backwards and is termed the *ring process*. This process fits into a socket on the anterior margin of the next posterior tergite. This socket is the *ring socket*. The other joint is positioned slightly lateral or dorso-lateral to the ring joint and the condyle faces forwards. Here the terms (*dorsal*) *furrow process* and *socket* are used as they lie in the dorsal furrow (axial process and socket and axial furrow of Whittington & Evitt 1954).

In very many trilobites the articulation between adjoining pleurae forms a straight and horizontal line between the dorsal furrow and the fulcrum. This linear articulation acts as a *hinge* (or hinge-line). The adjoining pleurae may meet edge to edge along the

hinge or they may be imbricated. In different groups a narrow area along the hinge is differentiated as a flat shelf, the *flange*.

Types of enrollment

It is certainly possible to distinguish almost any number of enrollment types among trilobites, if variation in detail is taken into consideration. I do not think that naming of a large number of types fills any purpose, but on the other hand it is convenient with terms for a few basic types. Three types were distinguished by Barrande (1852) and adopted by Harrington (in Moore 1959), namely *sphaeroidal*, *double* and *discoidal enrollment*.

The definitions of these enrollment types are based on a mixture of functional and habitual characteristics (cf. Harrington in Moore 1959:O102—O104). This mixture is unfortunate because it allows a considerable degree of subjective considerations. For instance, the closely comparable enrollment types of *Ellipsocephalus* and calymenids are classified as “double” and “sphaeroidal” respectively, mainly because of the size difference between the pygidia and possibly because of post-depositional compression of the ellipsocephalid. Herein the term *sphaeroidal enrollment* is used to designate a functional type of enrollment in which the pygidium rests with its ventral side more or less on the cephalic marginal doublure, not inside it, and in which the pleurae close the exoskeletal basket laterally. The thoracic tergites probably seldom had an exactly equal share in the flexure along the thorax, although this has been stated to be the main characteristic of the sphaeroidal enrollment. If the pleural spines fail to meet laterally the enrollment is termed *cylindrical*. An extreme type of sphaeroidal enrollment in which the pygidial spines reach the dorsal side of the cephalon may be called *inverted spiral enrollment*. An enrollment in which at least part of the tergal side of the pygidium abuts against the ventral side of the cephalon or thorax or the appendages of this region is called *spiral enrollment*, irrespective of the amount of doubling (Fig. 8). According to Treatise usage (Harrington in Moore 1959:O102—O104) spiral enrollment of the type found in ellipsocephalids was termed double enrollment, while the partly unrolled spiralling types found in calymenids and trinucleids were called sphaeroidal and discoidal enrollment respectively. The separation was based on the comparatively uninteresting variation in thoracic flexure. Öpik (1967:61) added the term spiral coiling for a spiral enrollment in which the amount of doubling is considerably larger than in *Ellipsocephalus*. Unfortunately this terminology does not take into account the profound difference between the sphaeroidal and spiral main types of enrollment but mixes the two under the sphaeroidal heading. Just as unfortunate is the splitting up of the types regarded here as belonging to the spiral group and the resulting neglecting of the functional similarity. When the spiral is partly unrolled, so that part of the pygidium was

visible even in the fully enrolled animal, the type is here called *unrolled spiral enrollment* (Fig. 8F). In some instances the part of the pygidium that was concealed under the cephalon was set off from the rest by a geniculation subparallel with the pygidial margin. This type which is well known from trinucleids and raphiophorids is here termed *basket and lid enrollment* (Fig. 8G). The geniculated border may be narrow or absent.

Undoubtedly a vast majority of trilobites were able

to enroll. The enrolling ability was secondarily lost in the Ordovician remopleuridid *Hypodicranotus* and in other cases as well, and its absence in some olenellaceans and redlichiaceans may be a primitive feature. Still, some of those trilobites that did not enroll completely were able to roll up to such a degree that the sclerites may have achieved a fairly good protection of the ventral side. This partial but still probably somewhat useful type of rolling up may be called *incomplete enrollment*.

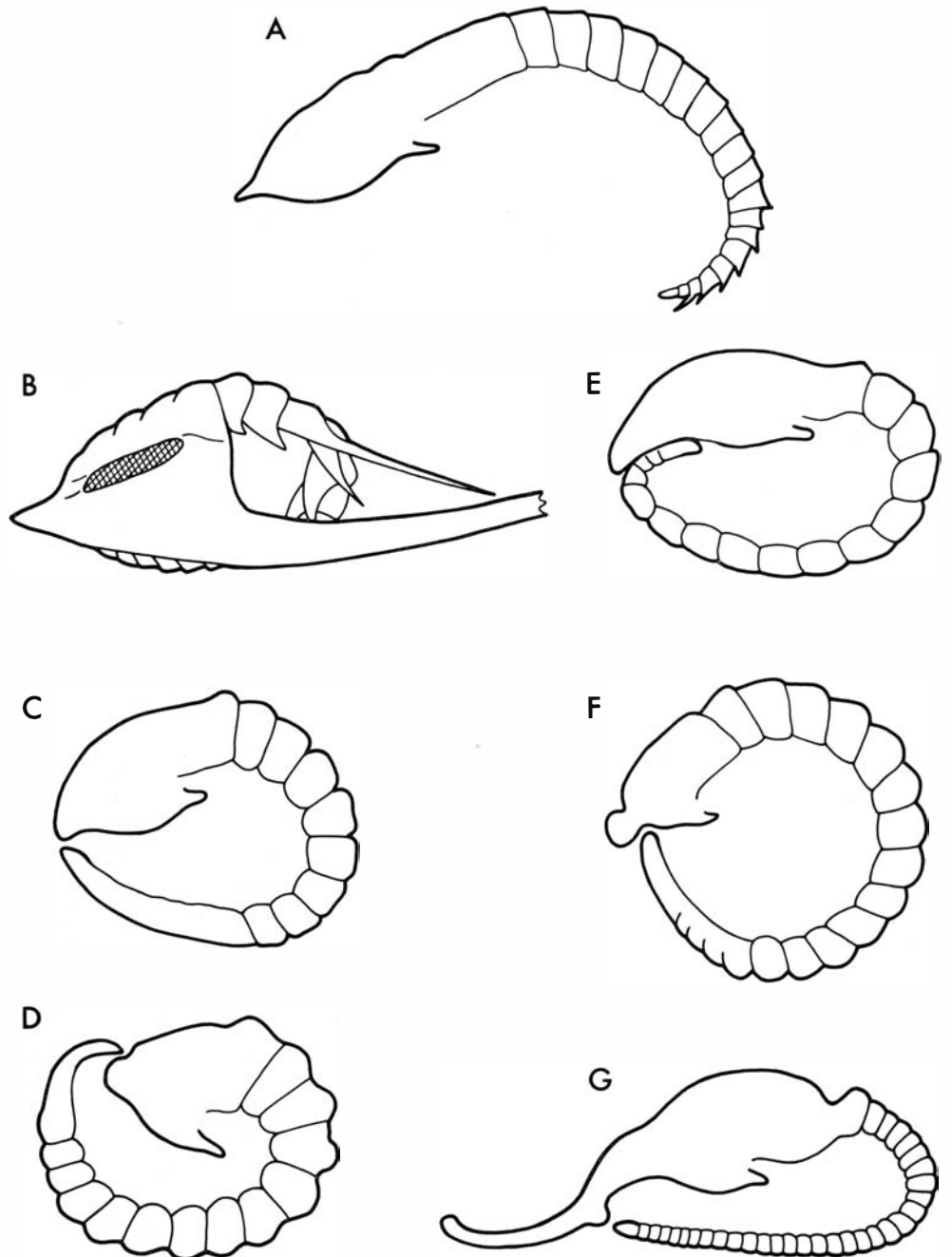


Fig. 8. Types of enrollment in trilobites. A. Incomplete enrollment (*Kjerulfia*). B—D. Sphaeroidal enrollment series: B, cylindrical enrollment without perfect closure laterally (this figure deviates from the others in not being a sagittal section) (*Fallotaspis*); C, sphaeroidal enrollment (*Asaphus*);

D, inverted spiral enrollment (*Placoparia*). E—G. Spiral enrollment series: E, spiral enrollment (*Ellipsocephalus*) (incorrect in detail; cf. text); F, unrolled spiral enrollment (*Flexicalymene*); G, basket and lid enrollment (*Harpes*). C, E and G modified from Moore (1959, others new).

Introduction to limiting and locking mechanisms

Several different mechanisms limited the movements in the rolling up action and kept the sclerites in exact positions in the fully enrolled trilobite. These are the *pleural devices*, positioned on the pleural spines and the adjoining margins of cephalon and pygidium, and the *vincular apparatuses*, which kept thorax and pygidium in position relative to the cephalon. Of the pleural devices the *panderian organs* are the most well-known. They generally consist of a *panderian notch* or a *panderian opening* in the pleural doublure and an adjoining limiting device, the *panderian protuberance*. The *articulating facets* on the antero-dorsal surface of the pleural spines are also well known. In some trilobites with conical encased pleural spines the spines limit the enrolling action by coming into contact with each other. This is the *abutting spine mechanism* (Fig. 9). These are the basic patterns of pleural devices. There is a great deal of variation in detail but this is still very poorly known. It is still more difficult to describe the vincular apparatuses within a few words. A common type consists of a furrow or a series of pits in the cephalic doublure in which the pleural and/or pygidial spines fit. A reversed type is found in agnostids, where a furrow in the pygidial doublure is called the *fibular furrow* (Robison 1964).

References to authors of families and subfamilies are not given, the reader is referred to Harrington *et al.* in Moore (1959) for these. In order not to put extra burden on the text, species names are given without author names when reference is given to publications where the species are treated. Headings are either families or subfamilies when these are considered to be natural entities or genera not easily referable to any higher category. Only the miomerid trilobites (Agnostida) are excepted from this rule and treated under subordinal headings.

The groups are treated in an order which is reasonably logical if the development of the articulation and enrollment mechanisms are taken into account.

Systematic review

Daguinaspidae.—This family is revised by Bergström (in preparation) and includes some of the subfamilies formerly included in the Olenellidae.

From *Kjerulfia lata*, Kiær (1916:79, Fig. 14; Pl. 12:4) described a dorsal furrow process which has a triangular shape. The corresponding socket is figured and described as a simple incision in the posterior margin. However, although this is not impossible it would be an outstanding exception, and I find it quite likely that a depressed socket floor is concealed by matrix and, accordingly, was not observed by Kiær. Although the proximal portion of the intertergal articulation outside the dorsal furrow is practically horizontal there is no fulcrum and no definable hinge. Most of the pleural length slopes outwards-downwards. The considerable length of the sloping part of the pleurae in the anterior part of the thorax

means that the possible angular movement between two adjoining pleurae was fairly small, reaching a maximum of only about 8° judging from experiments with a paper model (Pl. 1:2). This value may be compared with a maximum angular movement of 22.5° in *Asaphus expansus* according to Kurtén (1949: 8). As, in addition, the cephalon in *Kjerulfia lata* is long in comparison with the length of the thorax, it can not be doubted that this species was unable to enroll completely. This is also neatly shown by experiments with a paper model. The pygidium actually seems to have been turned upside down in maximum flexure, mainly because of the comparatively high flexibility in the rear part of the thorax where the pleurae are shorter than in front, but probably did not reach in under the cephalon at all. The under side of the cephalon therefore remained unprotected during maximal coiling, whereas the ventral side of the thorax was well protected.

Dr. S. Orłowski of Warsaw kindly allowed me to examine his Lower Cambrian trilobite collection during a visit to Poland in 1970. A specimen of *Kjerulfia lata* or a closely related species from a siltstone boulder collected at Ocieski in the Holy Cross Mountains, Poland (locality 9 in Samsonowicz 1959) comprises the coiled posterior part of a thorax, which confirms the information yielded from the paper model regarding the incomplete enrollment (cf. Pl. 1:2 with Pl. 2:8).

Holmiidae.—No completely enrolled olenellacean has been observed by me, nor has any been reported in the literature as far as I know. On the contrary, olenellaceans are generally thought to have been devoid of enrollment capacity (for instance Harrington in Moore 1959:O102: "... it is practically certain that the Olenellidae and other primitive Lower Cambrian micropygous forms lacked ability to enroll the carapace").

However, a specimen of *Holmia kjerulfi* figured by Størmer (1942, Pl. 2:4) exhibits a remarkable tilting backwards of the most posterior thoracic tergites visible indicating a considerable degree of articulation between the tergites. The same degree of bending along the thorax was probably much more than necessary for complete enrollment. Unfortunately I have not been able to see the specimen as Dr. David Bruton's kind efforts to find it in the collections in Oslo have been in vain.

Collections made by Dr. Hoffmann at Bukówka in the Holy Cross Mountains, Poland (locality 2 in Samsonowicz 1959) include one loosely coiled specimen belonging to *Holmia kjerulfi* or a closely allied species (Pl. 2:6). The pygidium and the posterior part of the thorax is missing but there is no doubt about the enrollment capacity in this case.

Dr. Reet Männil of Tallinn kindly informed me (personal communication, 1971) about the presence of an enrolled specimen of a *Schmidtellus* species, which will be described as a new species (Bergström in preparation).

Instances of enrolled olenellaceans are certainly exceptional but not lacking, though no tightly enrolled specimen has been found. There may be different reasons for the scarcity of enrolled specimens. One of them is apparently that much material has been found in shales, where trilobites in general are not found enrolled. Another reason is that at least the European material is commonly very fragmentary. Ultimately there may be anatomical reasons.

In contrast to several other olenellaceans, the dorsal furrow is strongly marked in holmiids, and the pleura bulges upwards close to the furrow. As a consequence of this the proximal part of the interpleural connection is suggestive of a horizontal hinge-line and may be regarded as an incipient hinge-line.

In *Holmia kjerulfi* (Linnarsson) and *Schmidtellus mickwitzii torelli* (Moberg) there is a strong dorsal furrow process and socket articulation (Pl. 2:5, 7).

Olenellidae.—Well preserved material, mostly in full relief, of olenellids and other olenellaceans from Greenland is preserved in the Mineralogisk Museum in Copenhagen, and I am grateful to Prof. Christian Poulsen and Valdemar Poulsen for giving me full access to these collections. Pleurae invariably lack a horizontal hinge (cf. Pl. 2:3, 4) and process and socket pivot joints (*“Paedumias” hansenii*, No. 3591, Poulsen 1932, Pl. 11:11; *Olenellus simplex*, No. 3576, Poulsen 1932, Pl. 9:10, 11; *O.* (s.l.) sp. indet, No. 2239, Poulsen 1932, Pl. 15:4; *O.* (s.l.) *kentensis*, Poulsen 1927 Pl. 14:32). The pleurae are more or less arched, giving the body a highly arched cross section. The base of the pleural spine is generally seen as a distinct angle of the anterior border. However, in No. 2239 (Pl. 2:4) there is a protruding flap which may be regarded as a marginal connective device. This device is far below a horizontal line through the indistinctly developed dorsal furrow, and it is therefore plainly evident that the successive tergites were almost immovably connected with one another. Any enrollment ability is therefore out of question. It was also shown by Raw (1957) on a paper model of *Olenellus thompsoni* that only a moderate bending of the body was possible (cf. Pl. 1:1).

Protolenidae.—A large majority of protolenids are known only from the cephalon and it is difficult to get a good idea of the thorax and its enrollment mechanism. An exception is *Lusatiops lusaticus*, of which the entire dorsal exoskeleton was described by Schwarzbach (1939). The pygidium is rounded and comparable to that of olenellaceans or redlichiids whereas it is completely unlike the short transverse pygidium of ellipsocephalids. The pleural spines are fairly long and pointed, particularly in the posterior part of the body. The pronounced dorsal topography of the pygidium and the long posterior pleural spines indicate that *Lusatiops* was unable to perform spiral enrollment. In one specimen (Schwarzbach 1939, Pl. 51:4) the presence of a distinct fulcrum and an ar-

ticulating hinge is clearly demonstrated. No ball and socket joints can be seen from the figures.

Protolenus elegans (cf. Matthew 1892, figure on second page) apparently has long pointed pleural spines, which should have made spiral enrollment impossible.

Redlichiidae.—*Redlichia idonea* and *R. forresti*, treated by Öpik in 1958, reveal some features of functional interest. The pleurae are more or less arched with the distal end pointing outwards-downwards, and there are no articulating hinges. The pleurae are of moderate length, but only a small portion falls on the pleural spines distal to the body margin and it appears fairly safe to conclude that these species did not enroll. There may be a dorsal furrow process and socket articulation (cf. Öpik 1958, Pls. 4:2; 6:6), but this suggestion needs confirmation.

Despujolsiidae.—This family with the junior synonym *Resseropidae* Chang, 1966, was considered to comprise *Despujolsiinae* and *Resseropinae* by Chang (1966). I agree that the subgroups are closely allied, probably too closely to be separated at the subfamilial level. *Resserops falloti* and *Despujolsia rochi* (cf. Hupé 1953a, Pls. 6:1; 8:3, 4) both have very short anterior pleurae without fulcral geniculations. A posterior macrospine is present in *R. falloti* and a series of long posterior pleural spines in *D. rochi*. A distal pleural process or ridge is present in *R. falloti*; this can not be a fulcral process but is better termed a marginal connective device. The long posterior spines and the short anterior pleurae made spiral coiling impossible, but it is possible that these trilobites were able to perform cylindrical enrollment.

Dolerolenidae.—Walcott (1912, Pl. 36) figured some specimens of *Dolerolenus zoppi* from the Middle Cambrian of Sardinia. The falcate pleural spines make up more than half of the pleural length and are completely covered ventrally by the doublure. The doublure extends some distance proximally along the inner pleura as a narrow band. The dorsal furrow is distinct. It is evident from the figures that there is no fulcrum or horizontal hinge and the entire pleura evidently sloped outwards-downwards, although only gently so close to the dorsal furrow. No ball and socket articulations are visible from the figures but it is only verified that the fulcral joint was absent. The thoracic morphology is remarkably similar to that of some olenellaceans such as *Kjerulfia*. It is safe to conclude that the long sloping pleurae made enrollment impossible.

Gigantopygidae.—*Gigantopygus bondoni*, *G. papillatus*, and *G. angustalatus*, figured and described by Hupé 1953a, exhibit a thoracic morphology very similar to that of *Dolerolenus* (cf. *Dolerolenidae*), and it is perfectly evident that these forms did not enroll (Pl. 1:9). Two figures of *G. papillatus* show structures in the dorsal furrow that may be furrow articulation processes (Hupé 1953a, Pls. 6:8; 7:1).

Bathynotidae.—The arched pleurae in *Bathynotus holopygus* lack hinge lines and fulcra (cf. Resser & Howell 1938, Pl. 12:6, 7). With comparatively narrow articulating half-rings in the strongly arched rhachis and with the arched pleurae this trilobite, no doubt, was unable to enroll.

Burlingiidae.—*Burlingia laevis* Westergård (see 1936, Pl. 12:8, 9) has a thoracic morphology, which except for the absence of distinct pleural furrows is quite similar to that of *Dolerolenus* (cf. *Dolerolenidae*). The pleurae slope consistently, although Westergård (1936: 32) states that they are flat (probably meaning that there is no pleural furrow), and the articulating half-ring seems to be extraordinarily narrow. The inability to enroll can not be doubted. Mr. M. J. Collins of Leigh, Lancashire, kindly lent me five specimens of *Burlingia laevis* collected in a boulder in Jämtland, Sweden. These specimens distinctly show that the dorsal furrow is poorly developed and that the pleurae slope downwards along their entire length. There are no ball and socket articulations, and the tergite margins overlap along their entire length.

Paradoxidinae.—From the general morphology paradoxidids would not be suspected of having had an enrollment ability. Still, already Pompeckj (1896, Pl. 16:1) figured a specimen of *Paradoxides gracilis* (Boeck) which was rolled up and flattened. Additional enrolled specimens have been met with in *Eccaparadoxides oelandicus* (cf. Orłowski 1964, Pl. 1:1a—b), *Hydrocephalus carens* (cf. Šnajdr 1958, Pl. 27:6), and *H. minor* (cf. Šnajdr 1958, Pl. 46:2). In the collections of the Palaeontological Department in Lund there is a specimen of *Hydrocephalus rotundatus* (Barrande) also rolled up. The pleurae do not close the enrolled exoskeleton laterally, and the enrollment is therefore cylindrical.

In *Paradoxides paradoxissimus*, Kurtén (1949, Fig. 13) found a broad and short flap forming a dorsal furrow process. This process extends slightly over a depression or furrow socket in the posterior edge of the neighbouring tergite. As in other species of *Paradoxides*, the pleural margins form a perfectly horizontal hinge-line which is ended by a fulcrum at the bases of the pleural spines. This feature has been observed in many museum specimens and is also visible from some of Barrande's figures (1852, Pl. 4:3, *P. gracilis*; 7, *P. minor*). The anterior border of the pleura has a narrow flange, that extends under the neighbouring pleura in front.

In *Eccaparadoxides* (including the indistinguishable *Acadoparadoxides*) and *Hydrocephalus* the construction of the thorax is somewhat different from that in *Paradoxides*. Specimens of *Hydrocephalus sjoegreni* (Linnarsson), collected on Öland, Sweden, and preserved in the collections of the Palaeontological Department in Lund show a short flap anteriorly in the dorsal furrow. At the posterior margin of the tergite the dorsal furrow is depressed, indicating the presence of a simple dorsal furrow process and socket articula-

tion like that in *Paradoxides paradoxissimus*. In *H. sjoegreni* there is a distinct fulcrum and only distal to this fulcrum is there a narrow anterior flange that extends to the spine base (Pl. 2:11). Distal to the fulcrum the anterior part of the pleura is slightly bent down to form what appears to be a poorly differentiated articulating facet. The features found in *H. sjoegreni* occur with some variation in different species of *Hydrocephalus* and *Eccaparadoxides*. It is possible that the hinge adaxial to the fulcrum is slightly curved in some species. In others, as in *H. carens* (cf. Pl. 2:9, 10) from the collections in Lund, the anterior flange extends on both sides of the fulcrum while there is no distinguishable facet. The marginal connective device consists of a small triangular flap at the distal end of the anterior flange and a rounded extension along the corresponding part of the posterior pleural margin. A posterior narrow strip of the spine doublure evidently extends under the extension of the posterior margin. Some good but slightly depressed transverse profiles through the thorax were given by Barrande (1852, Pl. 4:5, *Hydrocephalus rotundatus*; 6, *H. lyelli*; 11, *H. carens*; 8, *Eccaparadoxides sacheri*; 9, *E. pusillus*); it should be noted that the pleurae secondarily have been bent upwards to attain a roughly horizontal position for their entire length.

Centropleurinae.—The structures of the thorax are particularly well known in *Centropleura phoenix* Öpik from the detailed description given by Öpik (1961a: 119—22). There is a convex articulating half-ring, "allowing for a considerable amplitude of movement". Along the thorax are the dorsal furrow process and socket devices, providing stability in the articulation. From Öpik's figure 42 it appears that the furrow process is quite small. According to the description the pleurae are perfectly flat and horizontal without any trace of fulcral geniculation. Along the edges are anterior and posterior flanges which fit edge to edge. In the anterior ten or more tergites there are no fulcral joints. However, there is a weak fulcral process and socket articulation between the 12th and 13th tergites, and Öpik suggests that this may also be the case behind that point. In addition to these articulating devices there is a lateral flange on the pygidium distal to the fulcral point (characterized by the fulcral joint), in the doublural margin. This flange prevents the pygidium from sliding above the pleurae of the last thoracic tergite. In the larger part of the thorax the contact between two adjoining flanges form a straight and horizontal hinge. Between each of the most posterior three thoracic tergites and the pygidium the contact forms a curve and the axial and fulcral joints between any two tergites do not fall on a straight the morphologic gap between centropleurids and paradoxidids as well as between centropleurids and xystridurids.

Observations on *C. angelini* Westergård indicate that the position of the fulcrum is subject to ontogenetic shift. No very small forms seem to be known, and only cephalons with a length of about 15 mm and more

have been studied. On the smallest individuals in the collections in Lund (15–17 mm long) the distance from the dorsal furrow to the fulcral point on the posterior margin of the cephalon is about 0.25 of the length of the cephalon. In the cephalon figured by Westergård in 1950 as Pl. 1:8, with a length of 41 mm, the corresponding ratio is about 0.35, and specimens intermediate in size (for instance that figured by Westergård as Pl. 1:6, length 27 mm) are intermediate also in this character.

The functional reason for the ontogenetic shift is not well understood. One possible explanation is that the horizontal hinge formed phylogenetically from a sloping contact line, beginning close to the dorsal furrow and proceeding distally. We would then have a case of ontogenetic recapitulation of this process.

Xystridurinae.—Figures given by Whitehouse (1939, Pls. 21:2, 6, 11, 12; 22:1) of *Xystridura saintsmithi* reveal a distinct fulcrum approximately midway between the dorsal furrow and the inner edge of the pleural doublure. The detailed manner of articulation is not shown, but there is clearly a straight hinge extending to the fulcrum. Distal to the fulcrum is a pleural facet, that extends about halfway to the pleural tip. The articulation device is completed by an articulating facet on the ventral side of the pleura along the posterior edge (Whitehouse 1939, Pl. 22:1).

No enrolled specimen is reported, but details of articulation such as the development of facets makes it evident that *Xystridura* was able to enroll. The even shape of the thoracic margin and the relation between thoracic and cephalic width makes it probable that the enrollment was tight with the pleural spines fitting against the cephalic margin. This is also indicated by a paper model used to illustrate the mode of enrollment. Bending was probably fairly uniform in the six anterior segments or so, and then faded towards the pygidium. The angular movement required in each anterior joint appears to have been about 20°.

Crepicephalidae.—A specimen of *Crepicephalus* sp. line. Öpik (1961a:124) concludes that “curves have replaced straight hinge-lines, without which articulation between the tergites is impossible”, and he terms the stiffened rear end of the body “the pygidial unit”. As shown by Whittington and Evitt (1954:76) on *Acanthoparypha perforata*, a trilobite with curved contacts between adjoining tergites may even be able to enroll. Still Öpik is certainly correct that articulating movement in the pygidial unit of *Centropleura phoenix* must have been highly restricted because of the strong curvature. It should be added that any point on the curve is in the same horizontal plane.

Enrollment in *Centropleura phoenix* was probably complete and of the cylindrical type, as the pleurae did not close the space laterally (cf. Öpik 1961a:130). Bending was probably much centered on the joints approximately between the 3rd and 8th thoracic tergites, with an angular movement exceeding 20° in each joint (measured from a paper model, Pl. 1:3, 4).

Backwards, the angular movement decreased considerably until it ended completely in the pygidial unit. This supposed flexion in the middle part of the body would have caused the pygidial unit to press flat against the cephalon. The shape of the inner margin of the pygidial unit doublure and that of the rostral plate and doublure of the cephalon seem to correspond, and those two margins probably abutted against each other. Thus the enrollment may help to explain features in the pygidial unit morphology. In cylindrical enrollment the pleurae leave the ventral side with the appendages partly unprotected. In *Centropleura* this obvious drawback was partly counteracted by the long genal spines which extended outside the open ends of the exoskeletal cylinder.

In most respects *Centropleura angustata* Westergård is fairly similar to *C. phoenix*, as far as known. However, there is one marked difference in the pleural lobes, namely the presence of a fulcral geniculation in the former species. The fulcral geniculation on the holotype is best seen on the posterior pleurae of the left side and is about midway between the dorsal furrow and the pleural tips. The geniculation does not at all affect the pleural furrows but is quite distinct along the anterior and posterior borders although the geniculation angle is quite small.

The practical morphological difference between *C. angustata* and *C. phoenix* type pleurae is thus not very great. It is also interesting to note that the presence of a fulcral geniculation in *C. angustata* aids to bridge collected in the Conasauga Formation at Cedar Bluff, Alabama, and preserved in the collections of the Palaeontological institute in Lund is exposed from its ventral side. There is a kind of articulation in the dorsal furrow, although the details are not quite distinctly seen. However, the tergite borders seem to overlap in such a way that the result may be described as a ring socket and process articulation, although the structures are no doubt poorly developed. There is an articulating hinge extending to the fulcrum, which is midway between the dorsal furrow and the base of the pleural spine. There is no ball and socket joint at the fulcrum. The pleural edges appear to overlap along the hinges except in one or two instances where they abut edge to edge, but the overlap seems to be caused by compression. The edges are blunt and opposite edges correspond in their form, and it is therefore likely that the pleural edges actually met in the living animal. Distal to the fulcrum the pleurae are bent down slightly and overlap. The ventral side of the pleural spines is not preserved. The articulating half-ring is comparatively narrow, a feature that may indicate that this trilobite did not enroll. If it did, the presence of pygidial spines show that the enrollment must have been sphaeroidal.

Ceratopygidae.—*Ceratopyge forficuloides* and *Dichelepyge pascuali* exhibit a long straight hinge ended distally in what appears to be a fulcral process and socket joint (Harrington & Leanza 1957, Figs. 94:1 and 98:1b—d). Distally, the hinge margins in *D.*

pascuali are similar to the flanges of cheirurids. In this species the pleural spines can also be observed to be entirely sclerotized to a transverse line between the fulcral (or flange) joints and there is no panderian mechanism. Hutchison & Ingham (1967:54; Pl. 8:9, 10, 16) described and figured an identical morphology in *Dichelepyge phylax*. They state that there is a distal process and socket articulation, which is here termed a fulcral (or flange) joint, and a weaker proximal (i.e. furrow) joint, of which only the socket was actually observed. Other articulation or enrollment mechanisms are not mentioned. The pleural and pygidial spines show without doubt that the enrollment, if present, was of the sphaeroidal type.

Damesellidae.—A beautifully preserved specimen of *Damesella paronai* was figured by Kobayashi (1935, Fig. 18; reproduced from Airaghi). The specimen exhibits sphaeroidal enrollment, although it is slightly distorted. It is evident that there is a long articulating hinge adaxial to the distinct fulcrum.

Stephanocare richthofeni is generally very similar to *Damesella paronai* and is also characterized by sphaerical enrollment. As Öpik (1967:327) pointed out, the “wavy” appearance of the cephalic margin is due to the development of vincular sockets, which accommodate the tips of the pygidial and thoracic pleural spines.

Harpididae.—The articulating and enrolling mechanisms of this family are poorly known, but something can be deduced from the morphology. *Loganopeltis depressa* Rasetti, 1943, was described from comparatively complete material, including cephalon, most of the thorax, and pygidium. Abaxial to the distally placed fulcra there are long and pointed pleural spines, and the pygidium is longitudinally elongated. This morphology puts spiral enrollment definitely out of question. It seems probable that *Loganopeltis* was capable of spheroidal enrollment. Similar evidence is available from *Harpides* as far as the thorax is concerned. Functionally, the harpidids therefore differ fundamentally from the superficially similar harpids.

Isotelinae.—Panderian organs and locking devices were studied in silicified fragments of *Ptyocephalus declivitus* and *Lachnostoma latuclusum* by Ross (1951). In these species the lateral margin of the pygidium did not meet the cephalic margin during enrollment, but was received by one or two elevated ridges situated on the doublure. The posterior end of the pygidium abutted directly against the anterior cephalic doublure. In *P. declivitus* there is one longitudinal doublural ridge ending just in front of a “hooded” panderian opening. The margin of the parallel-sided pygidium may have rested on top of the ridge, while the panderian “hood” or protuberance was suggested to have limited the forward movement of the first thoracic sclerite (Ross 1951:93–94; Pl. 22:4, 5). The thoracic pleurae have panderian openings and protuberances (Ross 1951, Pl. 23:1).

Lachnostoma latuclusum has two cephalic doublural ridges, the inner one of which may correspond to that of *Ptyocephalus*. Ross concludes that the pygidium of the enrolled individual rested on the inner ridge and fitted with its margin against the outer ridge. The inner ridge ends abruptly in front of the panderian opening, and it is thought that the end prevented the pygidium from sliding forward (the exact mechanism is not mentioned). There is no panderian protuberance in the cephalon and the thorax is unknown.

Asaphinae.—The articulation and enrollment mechanisms of asaphine trilobites are well known from several different studies. Kurtén (1949) studied the articulation of the thoracic tergites in *Asaphus expansus* and some other trilobites. He sectioned his material and revealed the presence of a dorsal furrow process and socket articulation. This joint is invisible from above, and from the ventral side the bottom of the socket may be mistaken for a posteriorly projecting process, at least in poorly preserved material. There are no ring ball and socket joints. The anterior and posterior borders of the hinge are fairly blunt and abut against each other. Kurtén did not deal with the lateral parts of the pleurae. The articulating hinge ends abruptly in this species (as in many other asaphines), and the distal corner may be regarded as an initiation of a fulcral process. The pleural spine has a distinct sloping articulating facet. The ventral functional morphology was revealed by Siegfried in 1936 (see also Fig. 78 in Harrington *et al.* 1959). The ventral side of each pleural spine has a panderian notch, on the anterior side of which the border is elevated to the panderian protuberance. This border received the anterior edge of the next posterior pleural spine. The most anterior pleura was stopped by a panderian protuberance situated on the cephalic margin. The anterolateral corner of the pygidium forms a vincular hook, for the reception of which there is a vincular notch at the cephalic margin.

A similar arrangement is more or less well known from different asaphines including species of *Asaphus* (*Neoasaphus*) (cf. Pl. 2:12, 13), *Ogmasaphus*, *Plectasaphus*, and *Pseudomegalaspis* (all in Jaanusson 1953). In contrast to the condition in *Asaphus expansus* there appears to be an enclosed panderian opening with an adjoining panderian protuberance in all these forms.

No doubt, all species belonging to this subfamily were able to enroll. The cephalon and pygidia fitted together margin to margin and the outline of the two shields is nearly always identical in a species. Thus the enrollment is of the sphaeroidal type. An exception to the margin-to-margin fit is found in *Asaphus* (*Onchometopus*) *volborthi* F. Schmidt, 1898, in which the pygidium was received in a vincular furrow extending along the entire cephalic doublure. In addition there is a median hook in front of the vincular furrow.

Harrington *et al.* (1959:O104, Fig. 75A, B) distinguished a pseudomegalaspisid type from an asaphid type of sphaeroidal enrollment. However this is non-

sense. The pygidial doublure of *Pseudomegalaspis* is strongly flexed (as in *Plesiomegalaspis*, *Megistaspis* and *Basiliella*) and has no similarity to the flat structure shown in Fig. 75A. Moreover, the enrolled specimen of *P. formosa* figured by Jaanusson (1953, Pl. 10: 4—7) has no doubt suffered from distortion, and the cephalon has slid back from its normal position with its margin abutting the margin of the pygidium. Unfortunately the specimen has now disappeared, according to kind information by Dr. Jaanusson, but the figures and isolated shields are enough to reveal the situation.

Olenidae.—The family Olenidae is here considered to comprise the subfamilies Oleninae, Leptoplastinae, Pelturinae, and Triarthrinae, with a total range from the Late Cambrian to the Late Ordovician. To my knowledge the articulation and enrollment mechanism has not been studied within this family. No enrolled specimen has ever been reported in the literature, and Prof. Gunnar Henningsmoen, the prime student of the family, kindly informed me (verbal information, 1969) that he has never encountered any enrolled individual.

A flattened specimen of *Peltura scarabaeoides* found in a boulder at Gislövshammar, Scania, Sweden, by Mrs. Agnes Rodhe of Lund reveals some articulation details. The articulating half-ring has a longitudinal extension equalling the length of one tergal segment. The articulation in the dorsal furrow is not distinctly seen, but if there is any ball and socket joint, this must be very diminutive. There is a quite short articulating hinge formed by the pleural margins meeting edge to edge. There is no fulcral ball and socket joint. Distal to the fulcrum the pleura is divided into a proximal portion which has an antero-dorsal facet but lacks a ventral sclerite cover and a pointed distal spine which lacks a facet but is sclerotized ventrally. No panderian mechanism can be distinguished. The horizontal position of the articulating hinge is well seen in uncompressed material.

Two articulated pleurae of an *Olenus* species from Scania, Sweden (Pl. 2:14) show an example of the flat and long-hinged olenid, distinguished by Henningsmoen (1957) as the *Parabolina* type, whereas *Peltura scarabaeoides* (Pls. 2:15; 3:1, 2) represents the short-hinged and convex *Peltura* morphological type among olenids. The division of the pleura is the same as in *Peltura*, but the proportions differ; less than half of the pleura is distal to the fulcrum. The pointed spine is sclerotized ventrally. The proximal margin of the ventral sclerite cover appears to be thickened and the anterior end of this margin abuts against (a socket? at) the inner side of the posterior end of the corresponding margin in the sclerite next anterior. As this junction is some distance distal to the fulcrum it can not be regarded as a fulcral joint, but may be a limiting device similar to those occurring in the Cheiruridae.

The equipment of the above and other olenids indicate that many of them at least should have been

able to enroll. A specimen of *Ctenopyge* sp. from a stinkstone at Kiviks-Esperöd, Scania, Sweden, actually exhibits a distinct flexure of the thorax but not enough to warrant the designation "enrolled". A better example is provided by stinkstone material of three articulated tergites of a *Leptoplastus* species (*L. stenotus*?) from Andrarum, Scania. This short portion of a thorax is distinctly flexed along the hinge-lines and the specimen would have been partly enrolled if entire. The large articulating half-ring indicates that much stronger flexure was possible (Pl. 2:16).

Therefore, there is no doubt that at least some, and possibly all, olenids were able to enroll. However, the effectivity of the enrollment varied considerably. Paper models (Pl. 1:7) indicate that in *Peltura scarabaeoides* the long ventrally deflexed pleurae fitted against each other and against the cephalic margin to produce a perfect closure. In many species the pleural spines were only slightly deflexed, in some instances entirely flat (as in *Parabolina spinulosa*) or even deflected upwards (species of *Ctenopyge*). In these cases the pleurae did not close the enrolled body at the sides, and the enrollment is more cylindrical than sphaeroidal (cf. Pl. 1:8). The pleural and pygidial spines of most species preclude a spiral enrollment.

Remopleurididae.—The articulation is well visible on specimens of *Remopleurides* sp. from the Ashgillian Ulunda Mudstone at Skultorp, Västergötland, Sweden. Pl. 3:6 shows an enrolled specimen, in which the pleural spines slide under one another. Pl. 2:3—5 shows the exterior and interior of a straightened tergal skeleton. The pleurae are exceptionally short, and the pleural spines make up the largest parts of them. There is a small but distinctly developed ring socket and process articulation. At the lateral side of the ring joint there is an extraordinarily strong process and socket joint, which is directly followed laterally by the short pleural spine. There is no horizontal hinge line and it is not obvious from this material whether the strong ball and socket articulation is a furrow joint or a fulcral joint with regard to its origin. Functionally, and with regard to its position, it is both a furrow and fulcral joint. The pleural spine is entirely sclerotized on its ventral side, but it is not similar to that of cheirurids. The ventral side of the posterior margin has a curved shelf, in which the anterior margin of the next posterior pleura fits in the enrolled state. This shelf, bordered by a panderian ridge, was demonstrated in *R. nanus* by Öpik (1937, Pl. 24:5). It was also noticed and figured by Whittington (1959:397; Pls. 2:8; 9:4, 8; 12:17) in species of *Remopleurides*. In *R. eximius* and *R. similus*, Whittington (1959:397; Pl. 17: 10) noticed a similar shelf in the doublure of the free cheek. Because of the short pleural spines the enrolled exoskeleton was not closed at the sides (cf. figure of *R. rugicostatus* in Whittington 1959, Pl. 18:27); the enrollment was cylindrical.

Species of *Pseudokainella* and *Apatokephalus* figured by Harrington & Leanza (1957, Fig. 52:6, *P. keideli*; Fig. 54:3, *P. lata*; Fig. 55:1, *P. pustulosa*; Fig.

58:4 and 5, *A. exiguus*) exhibit an articulation hinge ended by a fulcral joint, while no axial joint is visible. Therefore, it seems plausible that the strong ball and socket joint in *Remopleurides* is the real fulcral joint. Whittington (1959:397) has expressed the opposite opinion.

Although most remopleuridids apparently were able to enroll more or less efficiently this is not the case with all members of the family. The enormous hypostome of *Hypodicranotus striatulus* extended back to the pygidium and made the body of this trilobite almost inflexible, as summarized by Whittington (1952:8).

Dorypygidae.—A specimen of *Olenoides serratus* (Walcott) preserved in Lund reveals the presence of a dorsal furrow process and socket articulation. The specimen is so flattened that no other details of importance for the articulation are observed. Resser (1939, Pl. 10:1—3) figured a specimen of *Kootenia convoluta* in sphaeroidally enrolled posture. A similarly enrolled specimen of *Bonnia bubaris* was figured by Rasetti (1948a, Pl. 4:22—24).

Corynexochidae.—Öpik (1967:180) mentions the presence of facets and a large articulating half-ring in *Corynexochus*. This indicates that an enrollment mechanism was developed.

Dinesidae.—I have not observed any enrolled dinesid but the development of the articulating mechanism indicates that *Dinesus arcticus* was able to enroll (cf. Palmer 1968, Pl. 1:1). There is a strong fulcral ball and socket joint to complement the transverse hinge. No other ball and socket articulation is visible on Palmer's figures. The facet of the pleural spine faces practically forwards and only slightly outwards-upwards.

Shumardiidae.—Pygidia assigned to "*Shumardia*" *alata* by Robison & Pantoja-Alor (1968, Figs. 17, 18) have a geniculated border, indicating basket and lid enrollment. Provided that this assignment is correct, "*S.*" *alata* would probably be a ptychopariid species. However, there is distinctly conflicting evidence from *Conophrys salopiensis* ("*Shumardia pusilla*"; cf. Whitworth 1972), well known from a study by Stubblefield (1926). *C. salopiensis* has a pair of thoracic macropleurae making spiral enrollment impossible. The pygidium has a narrow horizontal border with tubercles (Stubblefield 1926, Pl. 16:21), a development alien to spiralling trilobites but found in proetids and other groups with sphaeroidal enrollment. A figure given by Lake (1907, Pl. 4:1, in Lake 1906—1946) shows an enrolled specimen with the pygidium probably resting on the doublure. Lake (1906—1946:42) also reports the observation of many enrolled specimens. The spines of the fourth thoracic segment are said to be held in the same plane as the pygidium. As the long spines, no doubt, rest on the cephalic doublure in the

enrolled specimens, although this is not stated in the text or visible in the figure, this apparently was also observed to be the case with the pygidium. The three last segments and the pygidium were kept stiff in the enrolling action, and the flexure was confined to the anterior four joints of the thorax.

The observations indicate that the pygidia assigned to "*S.*" *alata* do not belong to any shumardiid trilobite, provided that *C. salopiensis* does.

Lecanopygidae.—Panderian notches have been observed in *Strigigenalis abdita* (cf. Whittington 1953, Pl. 67, pp. 672—673, Figs. 18—27). According to Whittington (*op. cit.*) the anterior edge of the notch is raised both in the free cheek and in the pleurae to form a limiting device during the enrollment.

Bathyruridae.—Whittington (1953, Pl. 69:16, 17, 19, 20, 21) illustrated a fully enrolled specimen of *Raymondites ingalli*. The margin of the cephalon is destroyed and the specimen, as a whole, somewhat distorted, but it is obvious that the enrollment is of the sphaeroidal type. The pygidium has a flattened border without spines, and it is probable that the pygidial and cephalic borders fitted margin to margin in the undistorted enrolled state. There is a fairly long horizontal articulating hinge adaxial to the fulcrum but no other details of the articulation are known.

Panderian notches are found in the doublure of the free cheek and the pleural spines in *Goniotelina williamsi* (cf. Whittington 1953:667; Pl. 68:14, 18). At least in the pleurae one edge of the notch was apparently used as a limiting device in the enrolling trilobite.

Holotrachelidae.—Warburg (1925:154; Pl. 3:16—18) reported two reasonably complete and partially enrolled specimens of the Late Ordovician *Holotrachelus punctillosus* and noted that the species undoubtedly was able to roll up completely. She also noted that the thin pygidium must have fitted against the terraced doublure of the strongly convex cephalon and it is evident from her figures that the tips of the pleural spines and the anterior margins of the most anterior spines abutted against the cephalic border. The enrollment therefore is sphaeroidal, and in its details it is closely comparable to the enrollment of some illaenids in particular. There is a horizontal hinge ended at the fulcrum. A study of the specimens figured by Törnquist (1884) reveals a straight hinge without any trace of sockets or processes at the ends in one specimen, whereas another one has a pit in the dorsal furrow that may be interpreted as a furrow socket. There is thus conflicting evidence regarding the presence or absence of furrow process and socket articulation, whereas other ball and socket joints obviously are missing. It should be emphasized that this study was made solely on the posterior border of the cephalon.

Proetidae.—In this family are here included the obviously related subfamilies Proetinae, Cornuproeti-

nae, Dechenellinae, Cyrtocymbolinae, Proetidellinae, Tropicocoryphinae, Phillipsiinae, and Griffithidinae. Barrande (1852, Pl. 16:4, 5) figured an enrolled specimen of *Proetus* (P.) *bohemicus*, in which the sphaeroidal type of enrollment is evident. The pygidium rests on the cephalic border, while the anterior pleural spines slide inside the free cheeks. The pleural spines have articulating facets and blunt tips.

Barrande (1852, Pl. 17:45) also figured an enrolled *Phaetonellus archiaci*, representing the Cornuproetinae. The enrollment is broadly similar to that of *Proetus*. The cephalon is flatter and the pleural and pygidial pointed spines developed in this form rest on the cephalic margin in the enrolled state and probably extend outside the cephalic margin. There is no articulating facet on the pleura.

A sphaeroidally enrolled specimen of *Paladin eichwaldi parilis*, representing the Griffithidinae was figured by Osmólska (1970, Pl. 18:8, 11). The enrollment is very similar to that of *Proetus bohemicus*. Hahn & Hahn (1968, Fig. 5) demonstrated the presence of a furrow socket and process articulation in *Kuhnella westfalica*. The figure appears to show a panderian notch and protuberance of the kind known also from *Paladin* (cf. Whittington 1954).

An enrolled specimen of *Kaskia chesterensis* was figured by Weller (1936, Pl. 95:4a—d). The enrollment is sphaeroidal, and pygidium and cephalon fit together margin to margin.

Thysanopeltidae.—Details of the articulating mechanism can be seen from material of *Eobronteus laticauda* (Wahlenberg). The articulating hinge is fairly long. The posterior articulating margin of one tergite slightly overlaps the anterior margin of the next posterior neighbour. The distal end of the articulating portion forms a distinct process, which corresponds to a socket under the posterior edge. It is not known whether there are additional ball and socket joints or not. There are no marginal flanges. The pleural spines are dorso-ventrally flattened. Their dorsal surfaces slope forwards in their anterior half, and it appears probable that adjoining spines slid over one another when the animal enrolled, although no typical facet is developed. I do not know of any enrolled specimen.

Many later thysanopeltids differ from *Eobronteus* in the development of articulating anterior and posterior flanges on the pleurae. This feature is shown for *Scutellum* (*Scutellum*), *S. (Planiscutellum)*, *S. (Paralejurus)*, *Decoroscutellum*, and others by Šnajdr (1960). As far as known the pleural spines are entirely encased ventrally (e.g. Šnajdr 1960, Pl. 28:13, showing *S. (Scabriscutellum) billingsi*) in a similar way as in cheirurids. Enrolled specimens of thysanopeltids are very rare; an enrolled *S. (Planiscutellum) planum* was figured by Šnajdr (1960, Pl. 1:2), and an enrolled *Paralejurus brongniarti* by Barrande (1852, Pl. 42:29). The enrollment is of the sphaeroidal type.

Illaenidae.—A specimen of "*Illaenus*" *angelini* Holm

collected in the Upper Ordovician Ulunda Mudstone at Skultorp, Västergötland, Sweden, exhibits articulating details (Pl. 3:7). The only ball and socket joint present is a ring joint, which is fairly well developed. The pleurae are slightly imbricated along the fairly long hinge-line. The doublure is smooth and extends half-ways to the fulcrum. The entire rhachis ring is smooth and there is no distinct articulating half-ring. Instead, the anterior part of the rhachis ring slides under a well developed doublure of the ring in front. The same morphology is seen in *Panderia megalocephthalma* (Linnarsson) and *Illaenus* sp. from the same locality and horizon. In the latter a panderian notch and protuberance is well visible (cf. Hupé 1954, Fig. 2d, e). The dorsal side of the pleural spine has a well developed articulating facet. A very similar morphology is seen in other illaenids, e.g. in *Illaenus sarsi* Jaanusson from the Lower Ordovician *Asaphus expansus* beds at Åketorp, Öland, Sweden.

Enrolled illaenids are fairly common. Specimens of *Illaenus sarsi* Jaanusson (RM Ar. 17624) and *Illaenus incisus* Jaanusson (RM Ar. 46655) from Östergötland, Sweden, illustrate how the tips of pleural spines may be visible or hidden by the free cheek. In both species, as evidently in all illaenids, the pygidium fits to the cephalic doublural border, which is convex and terraced. The enrollment is therefore sphaeroidal (cf. Pl. 3:8, 9).

Cyclopygidae.—Enrollment has been observed in different cyclopygids, including *Priscyclopyge binodosa*, *Microparia bergeroni*, and *M. princeps* (cf. Marek 1961). In *Priscyclopyge* the transverse flattened pygidium overlaps the terraced vaulted rostral field to the margin of the compound eyes. In *Microparia* there is a groove in the doublure for the reception of the pygidial border. The pleurae are truncated and abut against the cephalic doublure where they fit into small vincular pits. From the position of the hypostome it appears likely that there were no appendages in the posterior half of the pygidium; there is no space for any in the enrolled animal (cf. Marek 1961, Pl. 4:3).

Phacopidae.—Phacopids are among those trilobites which are most commonly found in an enrolled state. The ventral margin of the cephalon has a longitudinal vincular furrow (Pl. 3:10), the development of which in various phacopids was particularly noticed by Richter & Richter (1926). A short review is also given by Harrington (in Moore 1959:O105). The lateral parts of the vincular furrow may be differentiated into individual pits, each of which receives the blunt tip of one pleural spine (e.g. *Phacopidella hupei*, Henry & Nion 1970, Fig. 6; Pl. 5:B; *Acernaspis estonica* and *A.? konoverensis*, Reet Männil 1970a, Pl. 1:8, 9; 1970b, Pl. 1:4, 7, 8). To fit in the vincular furrow, the pygidium is invariably short and provided with an entire margin; this makes it resemble a ptychopariid pygidium. The pleural spines have well developed articulating facets. Much of this was shown already by Barrande (e.g. 1852, Pl. 20).

Specimens of the Devonian *Phacops rana* (Miller) from the Silica Shale, Ohio, have revealed details of the articulating mechanism. There is a well developed articulating hinge of a special construction. The posterior margin of the pleura forms an edge, which fits into a furrow on the anterior surface of the adjoining pleura behind it. The edge disappears close to the dorsal furrow where a shallow socket is formed to receive a blunt furrow process. There is no differentiated fulcral process and socket joint. Distal to the fulcrum there is a distinct articulating facet but no limiting device. The ventral side is not seen in this material, but in a specimen of the Middle Devonian *Phacops latifrons* (Bronn), collected at Gerolstein, Eifel, Germany there is a panderian protuberance in the shape of a long ridge anterior to a perfectly flat articulating facet of the doublure.

Pterygomotopidae.—Öpik (1937) figured and described specimens of *Chasmops wenjukowi*, *C. musei*, and *C. tallinnensis*, some of which reveal details of interest where enrollment is concerned. Fully enrolled specimens of *Chasmops wenjukowi* (cf. Öpik 1937, Pls. 8:5; 21:1, 2) show that the pygidial border rests on the cephalic border in front of the glabella, where it is practically horizontal. The pleural spine tips are hidden inside the downwards bulging margin of the cheek. There is a pleural stopping mechanism, the function of which is excellently revealed by Pl. 20:1 (*op. cit.*). The pleural spine is flattened dorsally to form an articulating facet. This facet is bordered posteriorly by a thick ridge, which acts as a stopping device when the animal is fully enrolled, as seen in the posterior part of the thorax. Functionally this mechanism is similar to the panderian mechanism, although the position is inverted.

An enrolled specimen of *Pterygomotopus sclerops* was figured by Whittington (1950, Pls. 68:17 and 69:1—3). The enrollment mechanisms cannot be seen in detail in this specimen.

Dalmanitidae.—Dalmanitids are rarely found enrolled, but there are known examples. One of these is *Kaysereps kocki*, an enrolled specimen of which was figured by Struve (in Moore 1959, Fig. 381:2, after Richter & Richter and Struve). Here the cephalic and pygidial borders abut against each other, and the pygidial spines extend outwards from the "commissure".

This mode of fitting means that the pygidial border is more flattened out than in phacopids. The pygidial spines together with the genal spines presumably acted as additional defence in the enrolled animal.

The opposing edges are somewhat thickened in the dorsal furrow in *Dalmanitina socialis* (Barrande) from the Middle Ordovician of Bohemia and *Dalmanites vulgaris* from the Middle Silurian of Gotland. However, there is no real process and socket joint in this or any other position. The adjoining edges are slightly overlapping along the hinge-line in the Gotland species (Pl. 3:11).

Monorakidae.—Specimens of *Evenkaspis sibirica* and *E. marina* figured by Maksimova (in Nikiforova 1955, Pls. 30:1a—d; 31:1a—d) show a sphaeroidal enrollment similar to that of phacopids. No functionally significant details are revealed.

Odontopleuridae.—The odontopleurids are known to have a sphaeroidal enrollment. This is the case even when there are strong ventrally directed spines as in *Ceratocephala verneuili* (cf. Barrande 1852, Pl. 38:1, 2; not entirely enrolled) and *C. vesiculosa* (cf. Bruton 1968, Pl. 8:1—3). The ventrally directed (anterior) spines (which are the original pleural spines because of the posture and of the similarity with the pleural spines) are concealed by the cheeks in the enrolled animal, while the principal (accessory) pleural spines and pygidial spines protrude. The hinge-lines are formed by the junction of anterior and posterior flanges, and there may be a flange process and socket joint (Bruton 1966:3—4; Fig. 1.) In *Ceratocephala laciniata* and *C. triacanthis* treated by Whittington & Evitt (1954) there is no sign of a furrow or ring ball and socket joint. The construction of the pleura shows some similarities with that of cheirurids; e.g., the ventral side is abruptly closed at the end of the flanges between the flange process and socket.

Glaphuridae.—Some details can be made out from the pictures of *Glaphurus pustulatus* and *Glaphurina lamottensis* given by Shaw (1968). Shaw's Pl. 8:10, 12, and 9:1, 2 show *G. lamottensis* partially enrolled. The pleural spine slides under its neighbour in front but there is no facet. There are well developed anterior and posterior flanges for the articulation in *Glaphurina*. The flanges seem to be horizontal. No similar arrangement is visible in *Glaphurus*, where the hinge is formed by raised anterior and posterior borders. There is no information about ball and socket joints.

Celmidae.—*Celmus granulatus* was revised by Jaanusson, who figured two enrolled specimens (Jaanusson 1956, Pl. 1:1—3, 4—5). These show a sphaeroidal enrollment, in which the anterior five pairs of pleural spines end beneath the cephalic margin, whereas the more posterior pleural spines and the pygidium rest on the lower and outer side of the cephalic margin. The pleurae (Volborth 1858:131; Jaanusson 1956, Fig. 2E, F) have well developed anterior and posterior flanges, and the ventral side of the pleural spine is sclerotized to the transverse line between the distal ends of the flanges. The pleural spine is devoid of facets. The pleural morphology and the reversed spiral enrollment (very similar to sphaeroidal enrollment) is closely comparable with that of the Glaphuridae, Odontopleuridae, Cheiruridae, Pliomeridae, and Encrinuridae. The peculiar pliomerid reversed spiral enrollment where the pleural and pygidial spines reach vincular pits on the dorsal side of the cephalon is easily derived from the celmid type of enrollment.

Cheiruridae.—The family is here delimited as by Lane (1971), and therefore includes the Cheirurinae, Eccoptochilinae, Sphaerexochinae, Deiphoninae, Acanthoparyphinae, Areiinae, and Pilekiinae. I regard the morphologic uniqueness and phylogenetic uniformity so impressive that a common treatment is motivated.

The enrollment has not been much treated in the literature, but many species of different subfamilies are known to enroll. The enrollment is always of the sphaeroidal type. The articulating device has been particularly studied by Ross (1951) and Whittington & Evitt (1954). *Sphaerexochus hapsidotus* was shown by Whittington & Evitt (1954, Pl. 33:8, 9; Fig. 27) to have an unusually complete set of articulating devices in the thorax. Apart from the articulating half-ring there are anterior and posterior flanges jointed in a hinge, ring socket and process, furrow process and socket, "fulcral" process and socket (here termed flange process and socket; see below), and anterior facet and posterior groove of the pleural spine. The underside of the pleural spines is completely encased distal to the flanges. The limiting device is formed by the spines themselves, which abut against each other in full enrollment (as judged from the text and from a study of other species, cf. Fig. 9; see also Dacqué 1921:617). In *S. hapsidotus* and also in *S. pulcher* (Whittington & Evitt 1954, Pls. 20:5; 21:2, 3; 32:33—35; Fig. 25) there is a notch in the outer side of the free cheek, thought to serve for the reception of pleural tips during enrollment. The most anterior pleural spine is short and passes under the cheek spine. The notch would seem to be in a good position to receive one of the succeeding pleural spines. As the notch is cut off from the underside by the margin (particularly in *S. hapsidotus*) the succeeding spines must be turned more outwards, but the exact arrangement is not known. The supposed nearly vertical posture of the hypostome presents another

problem, at least if the hypostome was immobile. The notch seems to be absent in related species. This is the case with *Sphaerexochus mirus*, of which Barrande (1852, Pl. 42:16, 17) pictures a partly enrolled specimen. It is evident from Barrande's figures that there is no notch in the free cheek and that the anterior pleural spines all fit in under the cheek.

Many cheirurines are known in an enrolled state, for instance *Paraceraurus aculeatus* (cf. Öpik 1937, Pl. 17:1, 2) and *Hadromerus subulatus* (Linnarsson, 1869), the latter found in the Ashgillian Ulunda Mudstone at Skultorp, Västergötland, Sweden. The structures connected with the enrollment are similar to those in *Sphaerexochus*. In *H. subulatus* as well as in *Ceraurinaella typha* (cf. Whittington & Evitt 1954, Figs. 3, 4) there are long hinge flanges, furrow process and socket (not well seen in the former species) and flange process and socket. There is no ring socket and process articulation. The pleural spines distal to the flanges are encased as in *Sphaerexochus*. In enrolled condition they abut against each other and against the doublure of the cephalon. The large pygidial spines project outside the cephalic margin.

The anterior and posterior hinge flanges are not exactly parallel in *Hadromerus subulatus*. A deviation from a parallel and horizontal condition is found in many different cheirurids; it is particularly well known in *Acanthoparypha perforata*. Whittington & Evitt (1954:76) concluded that the ring and furrow joints present in this species do not lie on the same transverse line as the "fulcral" joints and that the "fulcral" flange process must have been able to move fairly freely in and out of the socket. The hinge flanges are narrow and probably not visible in dorsal view.

The structure of *Sphaerocoryphe* of the Deiphoninae is partly shown by *S. dentata* Angelin, 1854 (collected in the Ulunda Mudstone at Skultorp, Västergötland, Sweden) and by various species figured by Lane (1971). The flanges are long and supplemented by a flange process and socket joint at the distal end. The material does not reveal any ball and socket joints. The pleural spines are bluntly pointed and entirely encased distal to the flanges, and evidently act as in *Sphaerexochus* and other forms in the enrollment (cf. Pl. 3:12).

The peculiar *Deiphon barrandei* was figured in a partially enrolled state by Lane (1971, Pl. 12:8). Lane states that there is no connection between adjacent pleurae but this is contradicted by the apparent presence of both posterior and anterior hinge flanges in at least the last thoracic tergite (Lane 1971:60 contra Pl. 12:5). Lane's Pl. 12:9 shows that almost the entire pleura consists of the wholly encased pleural spine. An analogous condition is met with in *Remopleurides*. Ball and socket joints are not visible, but the extremely short hinge flanges probably make the existence of strong ball and socket joints necessary.

The articulation mechanism in Eccoptochilinae is partly revealed by a specimen of *Skelipyx* cf. *cancrura* (Salter, 1853) from the Ulunda Mudstone at Skultorp, Västergötland, Sweden (Pl. 3:13). The flanges

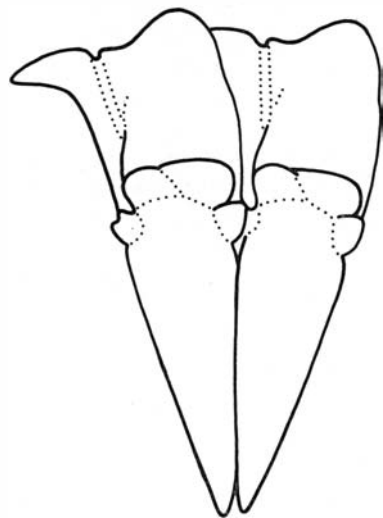


Fig. 9. Two thoracic tergites of *Ceraurinaella typha* Cooper in an enrolled animal. Note how the pleural spines abut edge to edge. Modified from Whittington & Evitt (1953).

are long and curved (cf. the discussion on *Acanthoparypha* above) and there is a distinct flange process and socket articulation in which firm contact was apparently achieved only in an enrolled state. The articulation in the dorsal furrow is poorly seen. Distal to the flanges the pleural spines are fully encased on the ventral side. A complete enrolled specimen of *Pseudosphærexochus orvikui* is figured by Männil (1958, Pl. 2:1—3).

Tesselacauda depressa, which may represent the Pilekiinae, is comparatively well known from a study by Ross (1951:145 and Fig. 4). The articulation device is comparatively simple. There is a curved anterior flange, which fits under the posterior margin of the pleura in front. The distal end of the flange is received in a notch. As this end lies beneath the main level of the hinge it is probable that the flange end abutted in the notch only when the animal was fully enrolled and therefore acted as a stopping device. There is no indication of any axial or ring joints.

Summarizing the evidence from the Cheiruridae, it may be said that the articulation mechanisms are generally very well developed. In the dorsal furrow there is generally a furrow process and socket articulation as well. These articulations serve as ball and socket joints. In most cases there is a set of pleural flanges, the anterior one fitting under the posterior flange of the proceeding tergite. The adaxial portion is horizontal, but the abaxial part tends to be bent downwards under the transverse articulation line. This means that the weakly defined fulcrum actually lies adaxial to the distal end of the flanges. It is very interesting to notice that the "non-spine" morphology of the pleurae, including the pleural furrow, also ends well adaxial to the ends of the flanges. This is particularly well seen in the Cheirurinae. Apparently then, in many forms at least there is no true fulcral ball and socket joint, and the "fulcral joint" at the end of the flanges is better termed the flange process and socket. The abaxial part of the flanged pleura tends to be slightly narrower than the adaxial part, and it is obvious that the abaxial portions of the flanges were in close contact only when the animal was enrolled. The flange socket and process therefore do not form a ball and socket joint but probably functioned only as a limiting device in the enrollment. The anterior and posterior sides of the pleural spines (distal to the flanges) may abut in the enrolled animal, thereby forming a limiting device. The enrollment is of the sphaeroidal type. There does not seem to be well developed vincular structures on the cephalon and the thoracic and pygidial spines just fit against the doublure under the cephalon or protrude out.

Pliomerinae.—Some aspects of the articulation and enrollment in *Pliomera fischeri* are presented by Öpik (1937:117—118; Pls. 19:4; 25:5; Fig. 32). A ring socket and process joint is distinctly visible (just above the letter "e" in Pl. 25:5). It seems probable that the thickening just at the outer side represents the furrow

joint, but this can not be seen with certainty. The nature of the hinge is obscure. Öpik's Pl. 19:4 shows that the pleurae slope outwards even adaxial to the fulcral(?) line and it is possible that there is no horizontal hinge. In the enrolled animal the pleural tips are received by sockets in the free cheek and the pygidial spines by a frontal vincular apparatus consisting of denticles and intervening sockets plus a furrow directly in front of the glabella.

Placopariinae.—The enrollment is well shown by Hammann (1971, Pls. 1:9; 2:13) in *Placoparia camabriensis* and *P. borni*. There is a well developed vincular apparatus on the cephalic margin with pits for the reception of the pleural and pygidial spine tips. The pygidial spines are curved through more than 90° and abut against the dorsal side of the cephalon. The pleurae seem to bear anterior and posterior flanges similar to those in Cheiruridae.

Encrinuridae.—Öpik (1937:118; Pl. 25:4) noticed the development of a pleural facet bounded posteriorly by a limiting ridge in *Encrinurus punctatus* and mentioned that the limiting ridge is absent in *Atractopyge*. *Encrinurus? moe* was figured completely enrolled by Ralph Männil (1958, Pl. 7:1—3) and *E. schmidtii* partly and fully enrolled by Reet Männil (1968, Pls. 1:1—6; 2:1—3). *Cybeloides girvanensis* was figured enrolled by Ingham (1968, Pl. 1:5), and enrolled specimens of many other species are known. In *Encrinurus* and *Cybeloides* the pleurae lie in an antero-posterior file without overlap in the enrolled animal. In *Atractopyge adornata* (Törnquist, 1884) the picture is quite different (LO 576T from Dalarna, preserved in Lund. Cf. Pl. 3:14, 15). The pleura at first extends laterally but then turns backwards and downwards to form a half volution when the animal is seen from the side. The distal part of the pleura next behind lies directly medial to the first pleura and the two abut with flattened sides. There is no limiting device. The most anterior pleura is neatly hidden just under the cephalic margin which has the same curvature. Only in front do the pygidial spines and the thoracic macrospine protrude. When the animal is seen from the side nothing is seen of the pleurae except the spines protruding anteriorly. A specimen of *Cybeloides loveni* (Linnarsson, 1869) collected from the Ulunda Mudstone at Skultorp, Västergötland, Sweden, shows the ventral side in an excellent way. There is a quite faint bulge which may be called a ring process and a corresponding shallow socket in the anterior side. There is no indication of any furrow process and socket. The pleura has a wide anterior flange but no posterior flange. In the anterior part of the thorax (nothing is preserved behind the seventh tergite) the fulcrum lies slightly less than half-way from the dorsal furrow to the distal tip of the anterior flange. Adaxial to the fulcrum the flange abuts against the posterior margin of the pleura next in front. Abaxially, the anterior flange is flexed slightly downwards and receives the edge of the anterior

pleura on its dorsal side. The anterolateral corner of the anterior flange ends in a straight angle but there is no corresponding socket on the posterior side. Instead, the dorsal ridges apparently serve as stopping devices in the enrollment. In the enrolling movement the posterior edge of a pleura obviously articulates with the inner part of the anterior flange but slides back over the abaxial part until it hits the dorsal ridge. The pleural spine outside the flange is entirely encased.

A specimen of *Encrinurus punctatus* (Wahlenberg) (probably from the Silurian of Gotland) reveals a vincular furrow along the cephalic doublure (Pl. 4:1). A few pleural tips are still in place in the furrow, but most of them have been pressed into the cephalon together with the pygidium, the margin of which was also received by the vincular furrow. The posterior tip of the pygidium still touches the anterior tip of the cephalic doublure, and it is evident that the closing up in this species was much more exact than in the long-spined *Atractopyge adornata*.

Lichidae.—Articulation devices seem to be poorly developed. In some species there is an articulating hinge-line (e.g. *Platylichas laxatus* (McCoy), Pl. 4:4, 5), whereas a similar hinge-line is not developed in other forms (such as *Amphilichas lineatus* (Angelin), Pl. 4:3). It has not been possible to reveal the presence of any pivot joints. Articulating facets and panderian organs are unknown. Probably the lichids could not enroll.

Ellipsocephalinae.—Spiral enrollment is known from *Ellipsocephalus ambiguus*, *E. polytomus* (cf. Westergård 1936:57; Pl. 11:9), and *E. (Ellipsostrenua) gripi* (cf. Kautsky 1945, Pl. 15:6, 7). As noted by Westergård, one of the most posterior tergites fits against the cephalic doublure in *Ellipsocephalus*. The *E. gripi* specimen is too damaged to show the exact fit (Pl. 4:9). In *E. polytomus* the pygidium and four or five thoracic tergites are concealed within the enrolled exoskeleton (Harrington *et al.* 1959, Fig. 76, erroneously shows only three concealed thoracic tergites). The pleural spines are blunt and the pygidium very small, possibly entirely post-segmental (telson). The pygidium is smooth except for terrace lines and has an entire margin. The hypostome is not fixed. The articulation mechanism is partly revealed by some of Kautsky's specimens of *E. gripi*, preserved in Naturhistoriska Riksmuseet, Stockholm (registered Ar. 9026, 9030, and 9042; the loan was kindly arranged by Dr. Fredrik Bockelie). There is a well developed horizontal articulating hinge, in which the posterior margin of each pleura overlaps the anterior margin of the pleura behind. The anterior border is distinctly bent at the fulcrum, but there is no fulcral ball and socket joint. There is also no ball and socket joint in the dorsal furrow, but just in this furrow the adjoining pleurae meet edge to edge instead of being imbricated as on both sides of the furrow. The pleural spines have distinct articulating facets. A specimen of *Ellipso-*

cephalus polytomus from the lower Middle Cambrian at Borgholm, Öland, Sweden, distinctly shows that the pleural margins are flattened at the fulcrum and in the dorsal furrow and that the pleurae meet edge to edge at these positions, whereas the edges are sharp and overlapping for the rest of their extension (Pl. 4:8).

Strenuellinae.—Thanks to Dr. S. Orłowski of Warsaw I had the opportunity to study the holotype of *Strenuella polonica* Samsonowicz, figured by Samsonowicz in 1959, Pl. 1:1a—e. The specimen is half-way enrolled and it seems likely that a continuation of the trend would lead to spiral enrollment. In contrast to the condition in *Ellipsocephalus polytomus* the pleurae meet edge to edge along the fairly long hinge-line. As far as can be seen from the exterior and the less preserved interior moulds there are no ball and socket joints.

Agraulidae.—Barrande (1852) noticed the spiral "double" enrollment in *Agraulos ceticephalus*. The pleural spines have blunt ends and the pygidium is smooth and very small. Hypostome not fixed.

Conocoryphidae.—The spiral "double" enrollment of *Conocoryphe sulzeri* is known from Barrande (1852, Pl. 14:20) and Šnajdr (1958, Pl. 33:5). Westergård (1936:57) also mentions double enrollment in *Bailiella emarginata*. In both species the pleural spines are blunt and the pygidium comparatively short, although comprising a few segments. The pygidium is smooth, with entire border. Hypostome not fixed.

Saoinae.—Spiral enrollment is known from *Sao hirsuta* (cf. Barrande 1852).

Crassifimbria.—This tiny trilobite was referred to the Antagminae by Palmer (1958), but to the Agraulinae by Öpik (1961:143—144). Palmer (1958:160; Fig. 5) reports that there is an articulating hinge extending from the dorsal furrow to the fulcrum, but there is no ball and socket joint. There is a stopping device consisting of a panderian crest in front of a wide panderian notch. The pleural spines are bluntly pointed and the pygidium is very small and transverse with an entire border. The hypostome evidently is not fixed to other sclerites (Palmer 1958:162). The enrollment is spiral (Palmer 1958, Pl. 26:14—15).

Ptychopariidae.—Double (probably unrolled spiral) enrollment was observed in *Ptychoparia striata* by Šnajdr (1958, Pl. 38:17). The pleurae end in sharp spines but these do not protrude much as they are inclined backwards. The pygidium lacks spines. It is possible that only part of the pygidium was concealed under the cephalon in the enrollment.

Solenopleurinae.—Double (spiral) enrollment has been reported in *Solenopleura canaliculata* by Westergård (1936:57). The pleural spines are blunt and the

transverse pygidium has an entire border. The hypostome appears to be free from other sclerites. In some forms there may be well developed articulating facets distal to the fulcrum, as in *Nilegna sigmata* (cf. Öpik 1967, Fig. 59 and Pl. 186).

Hystericurinae.—The pygidium in *Psalikius*? sp. (cf. Ross 1951, Pl. 30:1—3) exhibits a vertically deflected wide margin, suggesting an enrollment of basket and lid type. Pygidia referred to *Hystericurus* lack a similar deflexion and would indicate a more complete spiral enrollment.

Dimeropygidae.—In *Dimeropyge virginiensis* and *D. spinifera* the functional morphology is particularly well known after the treatment by Whittington & Evitt (1954). The pleurae have narrow anterior and posterior flanges along the hinge. There is a small ring process and a larger furrow (axial) process with corresponding sockets. No fulcral or flange ball and socket joint is developed. The pleural spine has a distinct articulation facet. In the narrow doublure there is a panderian notch with a raised edge (panderian protuberance) on the anterior side which acts as a limiting device during enrollment. In the cephalic doublure there is a pit ("p" in Whittington & Evitt 1954, Fig. 7; p. 42) which was believed to receive the pleural spine of the first thoracic tergite. However, the pit appears to be badly positioned to receive the pleural spine in question and the shape is also not adapted to that of the spine. Beneath the spiny rim of the pygidium there is a strongly inclined smooth margin; the margin appears to fit against the inner side of the cephalic doublure with the anterior end of the pygidial doublure in the cephalic doublure pit. The pygidium may have been sunk down into the cephalon till the level of the rim spines. Whittington & Evitt (1954:39—40) suggest that the hypostome was not fixed to the doublure in the holaspide cephalon (although it was connected by a stalk in early stages). The resulting picture is that of a basket and lid enrollment which is typical in almost all respects. An unusual feature is the spinosity of the pygidium. However, the fitting border is typically smooth.

Nepeidae.—*Bolaspidella* was moved from Menomoniidae to the closely related Nepeidae by Öpik (1967). *Bolaspidella housensis* was restudied by Robison who figured two enrolled but incomplete specimens (Robison 1964, Pl. 89:8, 9). What is seen from the specimens strongly suggests a spiral enrollment, although this cannot actually be observed as the cephalon are missing. The thoracic tergites appear to overlap along the horizontal hinge.

Menomoniidae.—Öpik (1967:61) remarks that the exceptionally long thorax in some menomoniids "is capable of coiling into an involute spiral (an extreme form of the 'double enrollment' . . .) of about one complete revolution". These enrolling forms are devoid of

fulcra according to the same author and the entire pleura is steeply inclined.

Plethopeltidae.—*Stenopilus elongatus* has an unrolled spiral enrollment with pleural spines and the pleural part of the pygidium concealed under the cephalic border (cf. Rasetti 1945b, Pl. 1:10—16; Hupé 1955, Fig. 99). In *Plethometopus dubius* (cf. Harrington *et al.* in Moore 1959, Fig. 313:5e) only the posterior border slants under the cephalic margin; this border has terrace lines. *Leiocoryphe transversa* has a flattened pygidium with an abruptly deflexed border (cf. Rasetti 1959, Pl. 53:28—30) and no doubt has an enrollment of basket and lid type.

Harpidae.—The enrollment was studied in *Harpes ungula* already by Barrande (1852, Pl. 9:3). Barrande distinguished the enrollment type as discoidal. The pygidium and thorax fits against the lower lamella as a lid in a box, though functionally the enrollment is better described as a basket and lid type. The horizontal thoracic hinges are very long, and distal to the fulcra there are only short and blunt pleural spines. The pygidium is transverse and smooth. The enrollment is known from several other harpid species and is uniform in type. The hypostome abuts against the lower lamella at least in some species, but is raised considerably above the level of cephalic-pygidial contact (cf. Moore 1959, Fig. 76).

Entomaspididae.—This small family is known only from disarticulated cephalon and pygidia. According to Rasetti (1952) the pygidium of *Entomaspis* has a vertical marginal slope beneath a submarginal ridge or line of spines. At least in *E. radiatus* (cf. Rasetti 1952, Pl. 117:1—11) the outline of the pygidium seems to correspond to the inner flexure (margin?) of the doublure (belonging to the free cheeks) and it is reasonable to suppose that there was an enrollment of basket and lid type.

Aulacopleuridae.—"Otarion" *burmeisteri* was figured by Barrande (1852, Pl. 18:70, 71) in an enrolled state. It is clearly seen that the pygidium projects in under the cephalic margin and, as only the pygidial margin is concealed, it is appropriate to consider the enrollment as belonging to the unrolled spiral type. In the collections of the Riksmuseum in Stockholm there are hundreds of enrolled specimens of *Cyphasps eleganta* (Angelin) from the Mulde Marl of Djauvik, Eksta, Gotland. Here the spiral enrollment is more complete and the entire pygidium is concealed under the cephalon in the enrolling. In both species the pygidium is transverse and without marginal spines and the pleurae have a blunt termination. The pleural tips are concealed under the lateral cephalic margin when the animal is enrolled.

Double enrollment and a morphology similar to that of the above mentioned species has been observed in several other aulacopleurids, for instance *Aulacopleura konincki* (cf. Barrande 1852, Pl. 18:19).

Phillipsinellidae.—The enrollment is well shown by a specimen of *Phillipsinella parabola* figured by Whittington (1950, Pl. 75:3) and by a specimen of *P. parabola aquilonia* figured by Ingham (1970, Pl. 5:20). As noted by Whittington the pygidium fits inside the inner margin of the cephalic doublure. The hypostome is fixed (cf. Whittington 1950:561), but there is a wide shallow depression in front of the anterior lobe to receive the margin of the pygidium. The enrollment is therefore of the basket and lid type. The pleural spines are short with well developed facets. There seems to be a fulcral process and socket joint at the end of the horizontal hinge and there is a quite strong ring socket and process joint (Kielan 1960, Pl. 5:1 and 2 respectively).

Calymenidae.—Calymenids are among those trilobites which are most commonly found in an enrolled state. Important contributions include the treatments by Kurtén (1949) and Evitt & Whittington (1953). In *Calymene* sp. Kurtén described the ball and socket articulation which is now called the ring joint, and stated that there is no furrow joint. Furthermore, he showed that along the articulating hinge the anterior margin of each pleura extends slightly under the neighbour in front. My own observations on *Flexicalymene meeki* and undetermined species of calymenids indicate that the overlap of pleural margins along the hinge may be much more distinct than in the material sectioned by Kurtén. The distal end of the anterior hinge margin tends to be slightly swollen (undetermined calymenids) and to rest in a shallow pit in the next anterior pleura; in this way a simple process and socket articulation may be formed. The doublure is typically very narrow and there is hardly reason to distinguish any panderian notch. The pleural spine just posterior to one tergite slides under the latter in the enrollment and is stopped at the thickened anterior border of the doublure that serves as a panderian ridge (Pl. 4:11 showing *Diacalymene* sp.). The pleural spines are blunt, the pygidium without spines and commonly transverse, and the enrollment is of an unrolled spiral type. The fit and amount of overlap in the enrolled exoskeleton of *Flexicalymene* (Pl. 4:10) is well demonstrated by Evitt & Whittington (1953, Fig. 1; Pl. 10:2—4).

The calymenids differ from most other trilobites with spiral enrollment in having a fixed hypostome (cf. Whittington 1941; Evitt & Whittington 1953). However, the hypostome is fixed to the inner end of a highly flexed rostrum, and, moreover, the anterior part tends to be flattened or concave to provide space for the pygidial margin. A similar situation appears to be present in *Phillipsinella* (cf. section on Phillipsinellidae).

Homalonotidae.—In advanced members like *Homalonotus* and *Trimerus* the hinge-line is completely lost, while it may be present in early representatives of the group. Material of *Trimerus delphinocephalus* Green, preserved in Lund, shows backwards directed processes

which probably are ring processes, and corresponding sockets. No other pivot joints are developed.

Trinucleidae.—Several trinucleids have been found in an enrolled state. The mechanism is well seen in material of *Tretaspis granulata* from the Ulunda Mudstone at Skultorp in Västergötland, Sweden (Pls. 4:12—16; 5:1). The enrollment is of the basket and lid type. The pygidium is transverse with a steeply inclined posterior facet which fits against the lower lamella below the hypostome. The thorax is similar to that of harpids, with a distally placed fulcrum, long articulating hinges with opposing pleural margins, and short rounded pleural spines. The safe articulation is secured by well developed ring ball and socket joints. There are no other ball and socket joints. The hypostome is withdrawn into the cephalic shield and probably not fixed to the lower lamella, an arrangement necessary for the accommodation of the pygidium in the enrolled trilobite (cf. Whittington 1959:442—443).

Dionididae.—A single specimen of *Dionide euglypta* (Angelin) from the Upper Ordovician Ulunda Mudstone at Skultorp, Västergötland, Sweden, is represented by external and internal casts. The articulation hinge is formed along adjoining pleural margins almost in their entire length and there is no fulcrum. The margins do not overlap but meet edge to edge. No ball and socket articulations are visible. However, the tergite is bent down slightly in the dorsal furrow and an inconspicuous process and socket articulation may be concealed here. No enrolled specimen of any dionidid is known to the author but there is no reason to doubt the capacity of enrollment.

Raphiophoridae.—A specimen of *Ampyx nasutus* Dalman (RM Ar. 8881, from an unknown locality in Östergötland) neatly exhibits a basket and lid enrollment. The triangular pygidium fits well inside the correspondingly shaped cephalic border and there is only a slight distortion (Pl. 5:2).

Details of the articulating mechanism is revealed in the related *Lonchodomas portlocki* (Barrande, 1846), of which specimens have been collected in the Upper Ordovician Ulunda Mudstone at Skultorp in Västergötland (Pl. 4:17). The hinge is very long, the fulcrum being close to the distal end of the pleurae. The pleurae probably abut edge to edge along the hinge. The only ball and socket articulation is a moderately strong ring joint. The broadly triangular pygidium has a ventrally deflexed border, indicating a basket and lid enrollment, a type of enrollment also seen in a specimen collected at the same locality by Mr. Sven-Erik Magnusson. In his description of *Lonchodomas chaziensis* Shaw (1968:34—35) mentions the presence of ring (although referred to as axial) and poorly defined fulcral ball and socket joints. Following Whittington (1959) he places the hypostome on a level well dorsal to that of the doublure and concludes that "this allows the pygidium to fit snugly to the

ventral side of the cephalon during tight enrollment, the median notch in the pygidium accommodating the median body of the hypostome". The notch is situated in the ventrally flexed border. Obviously the enrollment is of the basket and lid type.

Hapalopleuridae.—Enrolled but unfortunately distorted specimens of *Hapalopleura clavata* and *H. longicornis* were figured by Harrington & Leanza (1957, Figs. 110:5 and 112:1e). The morphological and functional details are poorly known. Harrington & Leanza claim that there is a short thorax (with 6 segments in both species) and a large pygidium (with 20 to 21 and 11 segments respectively) but I suspect that the proportions may be somewhat different. It may be seen from their figures 112:1c and 1e that there is a morphological unconformity behind the tenth segment in *H. longicornis*. Notably, pleural furrows are only seen in front of this limit. Therefore it is possible that there was a fairly small triangular pygidium more like that of other trinucleaceans than previously suspected, and the enrollment mechanism may also have been somewhat similar, at least in *H. longicornis*. In Fig. 110:6 of Harrington & Leanza 1951, the body of *H. clavata* is cut off behind the 20th(?) tergite and the rear end obviously is turned upside down. I find it entirely unlikely that the pygidium would disintegrate along the segmental boundaries and prefer to believe that there are some 20 segments in the thorax and fairly few in the pygidium. This is compatible with the presence of individual blunt pleural spines along the lateral margin in a large number of segments. The faceted most anterior pleura indicates that there was a strong bending in the most anterior segments during enrollment, and this is also born out by the enrolled specimen, in which only the first thoracic tergite seems to be visible from the dorsal side. If the rest of the body was held more or less straight, the rear end would reach beyond the anterior end of the cephalon, as seen in the enrolled specimen of *H. longicornis*. I suggest that the narrow posterior part of the body was folded in on itself so that the pygidial tergum was pressed towards the ventral side of the cephalon in complete enrollment. This would give a functional meaning to the peculiar sinuous shape of the lateral side. This type of enrollment must be termed spiral, although it is probably more like a folding along two lines.

Agnostina.—Agnostacean trilobites (excluding the condylopygids according to Dr. R. A. Robison, personal information) obviously form a natural unit and are here treated under one heading. The articulating mechanism has been studied in part by Öpik who concentrated on the axial portion. Here Öpik distinguishes an articulating half-ring, bordered posteriorly by an articulating furrow, and an axial recess and this combination is termed the articulating device (e.g. Öpik 1963:31). Three or four morphological types of articulating devices are recognized (e.g. Öpik 1967:53,

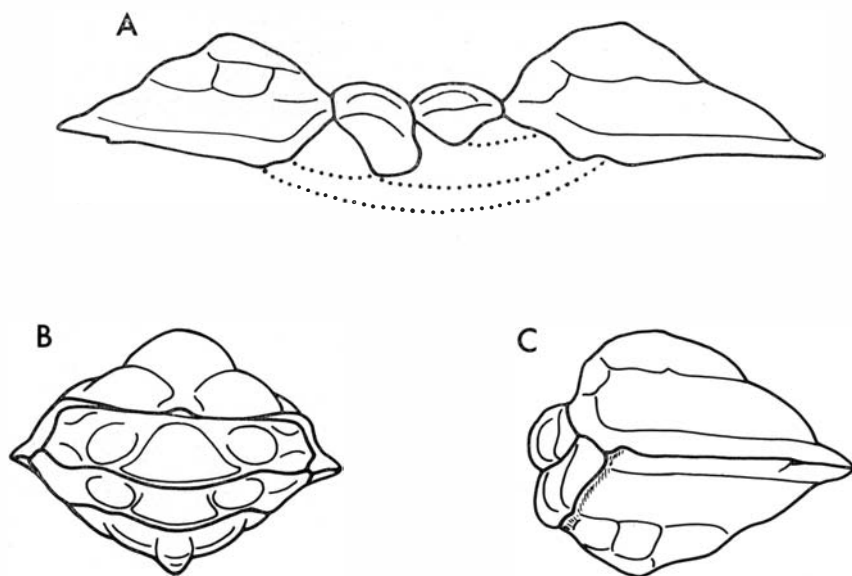
71, 72; table opposite p. 66), but functionally they seem to be fairly similar to each other. Öpik also found a "shoulder" as the fulcrum, and distal to this tip, an articulating facet, which may be flat or concave (Öpik 1967:55).

Less weight has been put on the horizontal articulating hinge and other pleural characteristics. Drs. Roland Skoglund and Lars Karis kindly assisted me in a study of the agnostid material described by Westergård in 1936 and mainly housed at the Geological Survey in Stockholm. Unfortunately the material is commonly painted in order to obtain photographic contrasts and details in the articulation are therefore difficult to discern. However, it is obvious that there is an articulating hinge in at least most species, irrespective of systematic position. It is difficult to see in the available material if the pleural edges are imbricated or if they abut edge to edge along the hinge. According to R. A. Robison (verbal information) there is normally an edge to edge articulation. The fulcral corner may be angular, but as far as can be seen there is never any real process for the articulation, neither in this position nor in the dorsal furrow.

Agnostids are not commonly found enrolled although the morphological fitting between cephalon and pygidium makes it virtually certain that all were able to enroll in the sphaeroidal way. Agnostids found in an enrolled state include *Hypagnostus metisensis* (cf. Rasetti 1948c, Pl. 45:21—26), *Peronopsis interstricta* (cf. Robison 1964, Fig. 3; Pl. 81:29), *Phalacroma glandiforme* (cf. Lindström 1901, Pl. 1:7; Westergård 1946, Pl. 15:13a—c), and *Trinodus tardus* (specimen from the Ulunda Formation at Skultorp, Västergötland, Sweden). Robison (1964:514—516) reports the presence of a longitudinal furrow on the pygidial doublure of agnostids like *Baltagnostus* and *Peronopsis*. The furrow, which is referred to as a fibular furrow, according to the description received the inner edge of the cephalic doublure in the enrolled trilobite. However, as the fibular furrow joins the lateral edge of the pygidium anteriorly I would not be surprised if actually the outer edge of the cephalon was received in the fibular furrow. A similarly strengthening mechanism is a vincular mechanism found in *Trinodus* (cf. Hunt 1966, Fig. 1; 1967, Pl. 22:25, 43, 47; Robison 1972b). Posteriorly on the cephalic doublure there are two pairs of sockets for the accommodation of the pleural tips of one thoracic sclerite and a pair of bosses on the anterior pygidial doublure. This kind of vincular apparatus is suggestive of the vincular apparatus found in the eodiscid *Serrodiscus*.

The lack of an articulating half-ring in the anterior thoracic tergite, demonstrated by Robison (1964:514—515; Pls. 80:4; 81:7, 29; 82:4, 5, 6) in many genera, means that there is a cephalothoracic aperture in the enrolled trilobite. It is probable that the aperture was covered by flexible membrane in the living animal just as in modern xiphosurids. The significance of the aperture is not known; it will be treated further by Dr. Robison.

Fig. 10. Enrollment of the agnostid *Trinodus erraticus* (Jaekel). A, lateral view of straightened specimen with cephalon to the right; B, posterior and C, lateral view of enrolled specimen. Modified from Jaekel (1909).



Eodiscina.—The articulating mechanism of eodiscine trilobites is poorly known. As in agnostines there is a distinct articulating hinge, which may end in an angular fulcral corner at the anterior edge. I am not able to tell if the articulating margins abut against each other or are imbricated. No distinct articulating processes or sockets have been observed, but the available material is very small. The enrollment is sphaeroidal. In some forms there is apparently a vincular apparatus consisting of marginal spines in the pygidium and corresponding submarginal pits in the cephalon. This is hinted at, for instance, in figures of *Serrodiscus griswoldi*, published by Rasetti (1967, Pl. 4:13–16), where dorsal submarginal tubercles on the cephalon mark the position of the probable ventral submarginal vincular pits. In *Bathydiscus dolichometopus* (cf. Rasetti 1966, Pl. 1:3) the pygidial border is faceted, obviously to fit inside the cephalic border in the enrolled animal. As far as known, only *Hebediscus cobboldi* has been found enrolled (cf. Kobayashi 1944:25).

Evolution of interpleural articulation

The simplest type of articulation between successive tergites is found in burlingiids and some olenellaceans. Here the pleural margins overlap along their entire margins. There is no horizontal hinge-line, nor any ball and socket articulations. Although this is the normal condition in most extant arthropods, it is exceptional and primitive within the trilobite class.

In some cases, as in paradoxidaceans, the overlap was changed only in the dorsal furrow with the evolution of a (dorsal) furrow joint. In paradoxidaceans the dorsal furrow process consists of a simple triangular flap extending into a socket on the posterior side of the neighbouring tergite. Generally the process is a hollow condylus, which probably, in some way, evolved out of the simple flaps. A furrow ball and socket joint is not the only way to achieve a firmer

articulation in the dorsal furrow. In ellipsocephalids two flat surfaces abut against each other and prevent telescoping of the tergites. In other instances, notably in ptychopariids and cheiruraceans, there may be a ball and socket articulation in which the socket is on the anterior side of the tergite, i.e. a ring joint. In members of Sphaerexochinae and Dimeropygidae furrow and ring joints may both be present.

The evolution of the articulation distal to the dorsal furrow depends to a great extent on the development of a horizontal hinge between adjoining tergites. Primarily the margins overlap along the hinge, but in systematically widely scattered groups the adjoining tergites secondarily abut margin to margin. In this respect there is thus an obvious parallel evolution, and there is reason to believe that this is the case with most of the evolutionary changes in the functional mechanisms. The hinge ends at the point where the pleural margin is deflexed downwards, i.e. at the fulcrum. The fulcrum may be vaguely defined or absent. In many cases the articulation at the fulcrum is strengthened by fulcral ball and socket joint. The formation of this articulation was probably possible only in those cases where the fulcrum was positioned close to the junction between the pleural spines and the body. In forms like paradoxidids and cheiruraceans the fulcrum tended to form far adaxial to the lateral body wall and a connective device formed at the junction between the pleural spines and the body wall. This connective device commonly is situated on the distal edge of a marginal flange which connects the tergite with its neighbour. As long as the connective device is distal to the fulcrum it is below the hinge and the transverse line of articulation and does not form a ball and socket pivot joint. Contact between process and socket is probably achieved only when the trilobite is fully enrolled, and the connective device, therefore, may act as a limiting or stopping device. However, in many instances, the fulcrum has probably either disappeared or moved to the base of the pleural spine,

Table 1. Synopsis of articulation and enrollment features in trilobites. The sign + indicates that a character was found in most or all of the species treated, while □ indicates that the character is fairly uncommon and — that it was not met with. Additional material may change these indications in many instances. a—b, dorsal furrow pivot joints: a, ring joint, b, dorsal furrow joint; c—g, hinge-line morphology: c, hinge-line not developed (indication only where missing), d, adjoining pleurae slightly imbricated, e, adjoining pleurae abutting edge to edge along hinge-line, f, hinge-line present but edge features unknown, g, hinge-line with flanges developed.

oped; h—j, distal junction: h, fulcral (pivot) joint, j, distinctly developed marginal connective device (position with regard to fulcrum is evident under letter h); k—m, limiting or locking mechanisms: k, panderian organ, l, abutting pleural spines, m, vincular mechanism (fibular mechanism in agnostids); n—t, type of enrollment: n, typical spiral enrollment, o, unrolled spiral enrollment, p, basket and lid enrollment, q, enrollment ability missing or incomplete, r, cylindrical enrollment, s, sphaeroidal enrollment, t, reversed spiral enrollment; u—v, hypostome: u, isolated from other sclerites, v, in contact with other sclerites.

	a	b	c	d	e	f	g	h	j	k	l	m	n	o	p	q	r	s	t	u	v	
Daguinaspididae	—	—	+				—	—	—		—	—	—				+	?			<input type="checkbox"/>	<input type="checkbox"/>
Holmiidae	—	+	+				—	—	—		—	—	—					?				+
Olenellidae	—	—	+				—	—	+		—	—	—				+				<input type="checkbox"/>	<input type="checkbox"/>
Protoleninae						+	—		—		—						?		?			
Redlichiidae	—	?	+				—	—	—		—						+	?	?			+
Despujolsiidae			+				—	—	+		—						?	?				
Dolerolenidae			+				—	—	—		—						?					
Gigantopygidae		?	+				—	—	—		—						+					
Paradoxidinae	—	+		+					+		—	—	—					?				+
Xystridurinae						+					—	—	—					?	?			+
Centropleurinae	—	+			+				+		—	—	—				+					+
Bathynotidae			+				—	—	—		—						?					+
Burlingiidae	—	—	+				—	—	—		—						+					
Ceratopygidae		+				+	<input type="checkbox"/>	+	+		+	—						?				+
Damesellidae						+	—				—	—	<input type="checkbox"/>					+				
Harpidae						+	—		—		—	—						?				
Crepicephalidae	?			?			—	—	—		—	—					?					
Asaphinae	—	+			+		—	<input type="checkbox"/>	—		+	—	<input type="checkbox"/>					+				+
Isotelinae	—					+	—				+	—	<input type="checkbox"/>					+				+
Olenidae	—	+					—		<input type="checkbox"/>		—	—	—				?	<input type="checkbox"/>	+		?	+
Remopleurididae	<input type="checkbox"/>	—	+				<input type="checkbox"/>	+	—		+	—					<input type="checkbox"/>	+	<input type="checkbox"/>			+
Dorypygidae		+				+	—		—		—							+				+
Corynexochidae						+	—		—		—							?				+
Dinesidae				?			—	+	—		—			?				?				+
Shumardiidae						+	—				—							+				
Lecanopygidae						+	—				+	—						?				
Bathyuridae						+	—				+	—						+				+
Holotrachelidae	—	?				+	—	—	—		—	—						+				
Proetidae	—	+				+	—	—	—		+	—	—					+				+
Thysanopeltidae				+			<input type="checkbox"/>	+	+		—	—						+				+
Illaenidae	+	—		+			—	—	—		+	—	—					+				+
Cyclopygidae							—		—		—	—	<input type="checkbox"/>					+				+
Phacopidae	—	+			+		—	—	—		+	—	+					+				+
Chasmopinae	—					+	+				—	<input type="checkbox"/>	—					+				+
Dalmanitidae	—	—		+			—	—	—		—	—	—					+				+
Monorakidae						+					—	—	—					+				
Odontopleuridae	—	—					+	<input type="checkbox"/>	<input type="checkbox"/>		—	?						+				+
Glaphuridae							<input type="checkbox"/>				—	—						?				
Celmidae							+				—	+								+		

	a	b	c	d	e	f	g	h	j	k	l	m	n	o	p	q	r	s	t	u	v
Cheirurinae	—	+		+			+	+	+	—	+							+			+
Eccoptochilinae				+			+	—	+	—								+			+
Sphaerexochinae	+	+		+			+	—	+	—	+	□						+			+
Deiphoninae							+	+	+	—	+							+			+
Acanthoparyphinae	+	+		+			□	—	+	—								+			+
Areiinae								—		—								+			+
Pilekiinae	—	—		+			+	—	+	—								+			+
Pliomerinae	+	?				+		—		—		+							+		+
Placopariinae							+	—	+	—		+							+		+
Encrinuridae	□	—			+		+	—	—	—	□	□						+			+
Lichidae	—	—	□	+			—	—	—		—	—	—								+
Ellipsocephalinae	—	—		+			—	—	—		—			+							+
Strenuellinae	—	—			+		—	—	—		—			?							
Agraulinae						+	—	—	—		—			+							+
Crassifimbria	—	—				+	—	—	—	+	—			+							+
Ptychopariidae						+	—	—	—		—			?	?						?
Solenopleurinae						+	—		—		—			+							+
Saoinae						+	—		—		—			+							
Conocoryphinae						+	—		—		—			+							+
Nepeidae				?			—		—		—			?							
Menomoniidae			+				—		—		—			+							
Plethopeltidae			+				—		—		—				+	+					
Harpidae						+	—		—		—					+					
Entomaspidae						+	—		—		—					?					
Aulacopleuridae						+	—		—		—			+	+					?	
Phillipsinellidae	+	—				+	—	+	—		—					+					+
Calymenidae	+	—		+			—	□	—	+	—				+						+
Homalonotidae	+	—	+			□	—		—		—				+						+
Trinucleidae	+	—					—		—		—				+						+
Dionididae		—			+		—	—	—		—				?						
Raphiophoridae	+	—		?			—	□	—		—				+						+
Hapalopleuridae						+	—		—		—			?							
Agnostina	—	—			+			—	—	—	—	□						+			+
Eodiscina										—	—	□						+			

and in those cases the connective device may actually function as a ball and socket joint. However, the change is gradational and it is commonly difficult to judge if the connective device at the tip of a flange is in a true fulcral position or not. Therefore I have decided to use the term *marginal connective device* (Fig. 7) for this device in order to get an objective designation. A flange may also be formed in trilobites in which the fulcral line and the bases of the pleural spines coincide, as for instance in thysanopeltids, and the term *flange joint* has been used in this case as well although the structure is also (and primarily) a fulcral joint.

Secondary simplifications may have occurred in many cases. The most conspicuous case is the disappearance of the horizontal hinge in various evolutionary lines, for instance, within the Redlichiidae, Remopleurididae, Illaenidae, Nileidae, Plethopeltidae, and Homalonotidae. The olenids yield an instructive example of the variation in the position of the fulcrum; it may shift to a position close to the dorsal furrow or beyond the pleural spines. In *Remopleurides* the fulcrum has shifted adaxially from the position seen in *Pseudokainella* to the elimination of the horizontal hinge, but the fulcral joint has not disappeared. On the contrary it followed the shift almost to the dorsal furrow and grew stronger than any other ball and socket joint known from any trilobite.

The articulating half-ring has not been studied in detail because the variation seems to be comparatively uninteresting from the point of function. It is generally comparatively large in forms with enrolling capacity and fairly few thoracic segments. Exceptionally it may be reduced or absent, as in the most anterior thoracic tergite in *Cryptolithus tessellatus* (see Whittington 1959:443) and in agnostids.

Limiting and locking mechanisms

Under this heading are treated mechanisms that limit the movement of the tergites in the enrolling animal.

In trilobites devoid of enrolling capacity the swing around the transverse axis through the dorsal furrows was apparently limited by the membrane between the rhachial rings and between the (extra-fulcral) pleural margins of adjoining tergites. The enrollment is mainly controlled by other means. It is easily understood that there is a need for a limiting mechanism in a spiralling trilobite, but the sphaeroidally enrolling animal would seem to be effectively stopped when the cephalon and pygidium come together. Yet there are different kinds of limiting mechanisms also in this array of trilobites. Actually, in a majority of the enrolling trilobites, the pleural spines close the enrolled "basket" very tightly laterally. In order to achieve this close fit it is necessary that the spines are perfectly shaped and that their relative movements are exactly regulated. The movement of the pygidium relative to the cephalon need also be regulated.

Regulating or limiting mechanisms are poorly developed in the earliest enrolling trilobites. This means

that there is no general inherited pattern but a wide variety of solutions which have been reached independently in various phylogenetic lines. Two main groups of limiting mechanisms may be distinguished after the position. One is restricted to the thorax and adjoining margins of cephalon and pygidium and directly regulates the movements between neighbouring tergites. The other consists of devices on the cephalon for the reception of thoracic pleural spines and the pygidial margin or spines. In rare cases a reception device may be formed on the pygidium.

In the first group the most well-known limiting device is the *panderian protuberance*. The panderian organs of trilobites have been studied by several trilobite students, including Siegfried (1936) and Hupé (1945, 1954). The panderian organs consist of the panderian protuberance and of the panderian notch or opening. These organs are situated on the cephalic and thoracic pleural doublure in many trilobites.

There is general agreement that the panderian protuberance constitute a limiting or stopping device onto which the anterior edge of the pleural spine abuts in a fully enrolled trilobite. A panderian protuberance is known from trilobites belonging to several different families. It is always absent in cases where there is a marginal connective device serving as an alternative limiting device, as in many cheirurids. The present investigation fully confirms previous observations on the functional significance of the panderian protuberance.

The panderian notch or opening is an invagination in the margin or a hole in the sclerotized doublure. It is generally present where there is a panderian protuberance and lies directly posterior to this protuberance. The panderian notch or opening has been regarded to represent a real opening in the ventral integument (e.g. Raymond 1920, Siegfried 1936), being a tracheal opening or nephridial pore. The notch or opening has also been supposed to have been covered by soft integument and supplied with a sensory organ to tell when the enrollment was (nearly) completed (Hupé 1945, 1954).

It is difficult to understand why a nephridial opening would be connected morphologically with a limiting device and be absent in all those trilobites in which the panderian protuberance is absent. Tracheal openings are still more impossible in the marine trilobites. It is, perhaps, more reasonable to suppose a functional connection between a panderian limiting protuberance and a sensory organ reporting of the concluded enrollment. However, sensory organs need not large openings in the sclerites, nor would the need for a sensory control of the enrollment be largest in the trilobites with the best developed stabilizing mechanisms. Therefore I suppose that the functional significance of the panderian notches and openings is different from what has been suggested in the literature.

There is an obvious connection between the panderian protuberance on the one hand and the panderian notch or opening on the other. The protuberance is accompanied by a notch or an opening in a vast majority of known instances, and there is probably

never an opening where there is no protuberance (excepting the cephalon, where conditions may be somewhat specialized). The notch or opening is directly posterior to the panderian protuberance. This means that the notch or opening is directly in contact with the anterior edge of the next posterior pleural spine in the fully enrolled trilobite. This series of circumstances may indicate that the panderian notch or opening is connected functionally with the protuberance and with the enrollment.

The articulation between two adjoining thoracic tergites is along a line passing through the horizontal hinges. Only muscles lying above the plane of this line may straighten the enrolled trilobites. This means that only muscles in the dorsal part of the rhachial lobe could be used, and with comparatively little mechanical advantage, particularly in trilobites with a low rhachis. There may have been a risk that muscle power was not enough to unroll the enrolled animal, particularly if it was partly entombed by sediment or if mineral grains were trapped between the tergites. A "pushing" organ in the position of the notch or opening would have greatly aided the animal to overcome similar difficulties. This organ may have been in the shape of a hydrostatically powered expansible bladder. Hydrostatic mechanisms are actually employed by some extant arthropods, e.g. in the jumping apparatus of collembols and in the legs of arachnids. However, a serious difficulty is the lateral position in the pleural field where no muscles able to power the hydrostatic mechanism would be expected. The function of the panderian notch and opening is therefore still unexplained even if it seems likely that it is connected with the enrollment.

In trilobites without a panderian protuberance there may be a counterpart on the dorsal side of the pleura. In this case the anterior part of the upper surface is a smooth articulating facet, and this is bounded posteriorly by the ridge. This kind of limiting device has been noticed in *Chasmops* and in some encrinurids and it is obvious that it developed at least twice. Nothing similar to the panderian notch or opening has been noticed in connection with the *dorsal pleural limiting ridge*.

In the above instances the pleural spines are more or less dorsoventrally flattened. In some groups such as the cheirurids the spines may have a more or less rounded or anteroposteriorly flattened cross section. The morphology makes a sliding movement relative to neighbouring pleural spines impossible (cf. Dacqué 1921:617). In this case neighbouring pleural spines may abut posterior surface to anterior surface. There may also be a ridge or row of processes on one side and a receiving furrow on the opposite side, but this is exceptional. The pleural spine tips all tend to meet in one point. There are commonly flanges along the hinges in trilobites with this type of pleural spine. The flanges tend to be connected distally by a flange joint or marginal connective device as mentioned above. As this device is commonly distal to the hinge it is in those cases below the axis of swing and may act as a

limiting device. *Abutting pleural spines* are mainly confined to a cheirurid-odontopleurid group which may form a natural unit.

Limiting mechanisms in the cephalon are commonly referred to as *vincular apparatuses*. One type is particularly well known from the phacopids and consists of a *vincular furrow* on the cephalic doublure for the reception of the pygidial margin and the pleural spine tips. There may also be individual *vincular pits* for the spine tips. In Placopariinae and Pliomerinae the pygidial spines are received in vincular pits on the dorsal side of the cephalon in front of the glabella. This condition, which is foreshadowed in the Celmidæ, probably evolved only once. Odd mechanisms are known from the Isotelinae where one or two doublural ridges may regulate the position of the cephalon. The mode of reception of the pygidium in spiralling trilobites is poorly known. In *Dimeropyge* with basket and lid enrollment (derived from typical spiral enrollment) the anterolateral corners of the pygidium are obviously received in sockets formed by the cephalic doublure. In some members of Cyrtosymbolinae the pygidial border is deflexed downwards and the cephalon, which has an upwards deflexed border, probably fits against the pygidial doublure inside the border. A reversed mechanism is found in agnostids, where a *fibular furrow* in the pygidial doublure accommodates the cephalon. No doubt the vincular mechanisms like the pleural limiting mechanisms have evolved in several different branches of the phylogenetic tree and a similarity in one respect need not implicate that two trilobites are closely related.

Evolution of enrollment

There are strong reasons to believe that the enrollment capacity in trilobites was not inherited from a common ancestor but evolved inside the class. The olenellaceans have preserved primitive characters lost in most other trilobites and it is obvious that the enrollment was not yet evolved in some forms and of a primitive imperfect type in others. Among trilobites with facial sutures the redlichiaceans occurred early in Early Cambrian times. The most primitive members, the protolenids, are poorly known with regard to enrollment. In later trilobites, most of which were probably protolenid derivatives, there are two main series of enrollment types. One of the series begins morphologically in the earliest members with the full spiral enrollment in which the pygidium is entirely hidden under the cephalon and inside the enrolled "basket". The other (sphaeroidal) series is characterized by the complete exposure of the dorsal side of the pygidium and the ventral sides of pygidium and cephalon tend to face each other. A derived type of the spiral enrollment series, the basket and lid enrollment, may come close to the sphaeroidal enrollment, but a comparison between early and primitive forms reveal an important *functional discontinuity* between the two series. The margin of the pygidium has to pass over the cephalic doublure in order to get the type

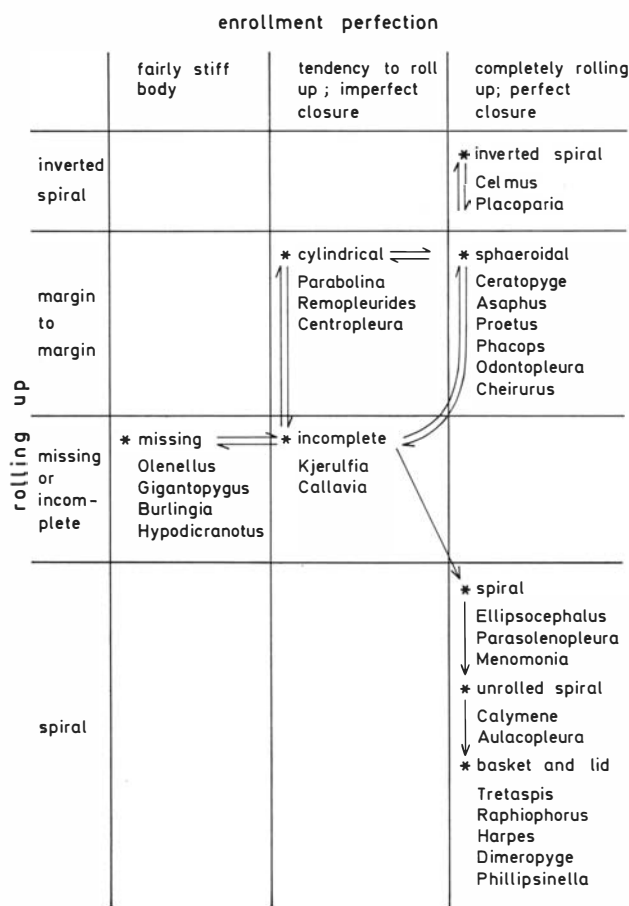


Fig. 11. Types and evolution of enrollment in trilobites. Arrows indicate possible directions of evolutionary changes of the enrollment.

of enrollment to change from one series to another. Observations on the morphology and considerations of functional possibilities indicate that this never happened. Therefore the spiral and sphaeroidal series each must have evolved out of incomplete enrollment. *Spiral enrollment* (Figs. 8, 11) was well developed in the Early Cambrian *Ellipsocephalus* and its allies. To achieve a tight closure the exterior was commonly notably smooth, the pleural spines were blunt and the pygidium small and transverse. The pygidium and a few posterior thoracic tergites were completely hidden inside the spiral. To allow space for the spiral the hypostome was not connected with the rostrum. In some later forms, like *Menomonina*, the spiral is still more complete, but the general trend is toward a loosening. The anterior part of the pygidium ultimately became visible and this marks the change where the spiral enrollment is judged to become an *unrolled spiral enrollment*. The step actually may have been a gradual change. This is also the case with next step leading to the *basket and lid enrollment*. The pygidium became a "lid" when the margin hidden in the enrolled animal was marked off from the exposed part by a geniculation. In all three stages the margin of the pygidium stayed entirely inside the inner edge of the cephalic doublure, as far as known. In forms

like *Calymene* and *Phillipsinella*, where only a narrow pygidial border was concealed in the enrolled animal, the hypostome was secondarily united with the doublure, but the connection was conspicuously flexed to accommodate the pygidial border.

The sphaeroidal series (Figs. 8, 11) is less regular than the spiral series. There is great variation in detail in the enrollment achieved, for instance, in asaphids, illaenids, proetids, phacopids, odontopleurids, and cheirurids. There is also no definite trend. By reduction or upward flexure of the pleural spines the *sphaeroidal enrollment* could evolve into a *cylindrical enrollment*, in which the enrolled box was not fully closed at the sides, as in some olenids and remopleuridids. It is probable that evolution could also go in the opposite direction. A kind of spiralling was performed by placopariids and celmids, in which the pygidial spines secondarily(?) reached vincular pits or a vincular furrow in the dorsal side of the cephalon. This *inverted spiral enrollment* may be regarded as a kind of sphaeroidal enrollment.

Ultimately, it should be noted that evolution could go backwards and produce forms which secondarily had lost their enrolling ability, like the remopleuridid *Hypodicranotus*, the enormous hypostome of which made enrollment impossible.

Attempt towards a classification of the trilobites

In trilobites the exoskeleton apparently was in existence before the enrollment capacity. The enrollment therefore may be considered as of secondary importance in distinguishing phylogenetic lineages. Certainly, a particular enrollment type may have evolved independently within different lineages and the enrollment mechanisms definitely were subject to evolutionary changes. In addition, the evolution of enrollment types has little bearing on the classification of early trilobites with a primary absence of enrolling power. However, the identification of the spiral enrollment and derived types as a distinct functional group seems to be useful for evolutionary and systematic distinctions among more advanced trilobites (Figs. 11, 12). Once the spiral main type of enrollment was evolved, there was a functional and morphological discontinuity between the spiralling group and other enrolling trilobites. It is important to note that this discontinuity was caused by the indispensable interaction between functional needs and a number of morphological features. Evolution among trilobites with full enrollment capacity would not bridge this gap. Therefore lineages characterized by the two enrollment types must have been isolated already in Early Cambrian times when the earliest representatives occurred. It is possible that one particular enrollment type evolved more than once. Certainly, this is a difficulty in the systematic treatment. On the other hand, it is now evident that the Ptychopariida, as commonly understood, includes a mixture of groups with and without enrollment of spiral type, which definitely means that

this group is a technical, polyphyletic one. This recognition is particularly important as the Ptychopariida has been recognized as one of the most central trilobite groups (e.g. authors in Moore 1959). Glabellar homeomorphy has even resulted in the inclusion of forms with different enrollment types within particular families.

It seems reasonable to suggest that the trilobites with spiral enrollment and derived types of enrollment form a phylogenetically uniform group or, at least, that they were derived from different but very similar and closely interrelated protolenid trilobites. This group may be distinguished as an order. As *Ptychoparia* belongs to this group, it is here called the Ptychopariida. Even if only one presumably natural group is distinguished by this comparatively easy method, the phylogenetic discussion regarding the remaining trilobites will be considerably less complicated than formerly because the ptychopariids may be left out of consideration. Still, the operation to sort out phylogenetic groups is no easy task.

In the Treatise on Invertebrate Paleontology (Harrington *et al.* in Moore 1959), olenellaceans were included in the order Redlichiida. With the delimitation presented, Redlichiida certainly has no natural basis or foundation and the groups included must be rearranged into separate orders. Olenellaceans constitute one of those trilobite groups which is most easily distinguished and morphologically most isolated. The ontogeny (morphogeny) is clearly different from what is found in other trilobite groups. There has been some speculation about the absence of facial sutures, resulting in the "recognition" of "fused sutures" in several olenellaceans. However, the anterior and posterior eye-lines do not represent fused ecdysial sutures but certainly belong to the prosopic pattern. They may reflect the course of vascular trunks. There is no ontogenetic or morphologic evidence of the earlier existence of facial sutures. On the contrary, there seems to be remnants of the olenellacean submarginal suture in other trilobite groups and a tendency to return to marginal or submarginal sutures in connection with the loss of eyes. Arachnomorph groups other than the trilobites, such as emeraldellids, strabopids, aglaspidids, merostomes, and arachnids, lack facial sutures and there is nothing similar to the facial sutures in any other arthropod group. Where the ecdysial suture is known, it is closely comparable in position with that of the olenellaceans (cf. Pl. 5:4). Therefore there is firm basis for the presence of a marginal or submarginal suture in olenellaceans as a primitive (protoparian according to Størmer 1942) condition. If orders are to be recognized at all in the Trilobita, the Olenellida is perhaps the most obvious group deserving order status. The first appearance of various trilobites shows that the known olenellaceans were not ancestral to other trilobites, but they obviously had a common origin.

The order Agnostida is also known from the Early Cambrian. Even the earliest members were functionally and morphologically advanced. The facial suture

indicates that the miomerids (agnostids and eodiscids) do not belong to the olenellid line. The articulation and enrollment type point at protolenid-like trilobites as ancestors. The most characteristic feature is the presence of only two or three thoracic segments. A similar reduction in segment number is exceptional in other trilobites and so far is only known from the proetacean *Pseudotrionodus aenigma* Kobayashi & Hamada, 1971, which is reported to have only three thoracic segments.

Among other trilobites occurring in the Lower Cambrian two groups are comparatively easily distinguished, whereas a number of forms are more difficult to place. The two groups may be called the protolenid-redlichiid and corynexochid groups.

The most primitive members of the protolenid-redlichiid group appear to be protolenids like *Termierella*, *Bigotinops*, and *Pseudolenus*. Typical characters include a long palpebro-ocular ridge divided into anterior and posterior ridges and, in some cases, merging with the glabella (as in olenellaceans), a forwards narrowing glabella with distinct furrows, a wide cranidium, and a short posterior branch of the facial suture. In addition, there is a distinctly developed horizontal articulating hinge-line in the thorax. Isolated cranidia may be difficult to distinguish from early ptychopariids, such as the ellipsocephalids. Where other parts of the exoskeleton are known the protolenids generally differ from the ptychopariids in having comparatively long and pointed pleural spines and pygidia of other shape than the short transverse and smooth type characteristic of the spiralling ellipsocephalids and their allies. Still, the similarities are so striking that I believe that the ptychopariids have their origin within the protolenid group or very close to it.

A large number of intermediate forms connect the most primitive-looking protolenids with the comparatively advanced redlichiids. The redlichiids have a long more or less undivided palpebro-ocular lobe that extends less outward and more backward than in the protolenids, a comparatively narrow cranidium and a long posterior branch of the facial suture. The horizontal articulating hinge was comparatively short and obviously lost in some species. A plectrum may be developed.

Early and Middle Cambrian genera such as *Drepanuroides* (Drepanopyginae), *Mayiella* and *Dolerolenus* appear to be morphologically intermediate between *Protolenus* and *Redlichia* except in pygidial characters. On the other hand they also show similarities with later trilobites. For instance, the three genera mentioned have a plectrum which is also found in some papyriaspids, ceratopygids, mapaniids, plectriferids, rhyssometopids, damesellids, auritamids, and still other groups. Many of these have spinous pygidia similar to those of *Drepanuroides* and its allies. *Dolerolenus* is actually so similar to some papyriaspids that it may be included in the Papyriaspididae. The entire group as outlined above appears to be morphologically relatively uniform and many genera have been referred to at least two families within this

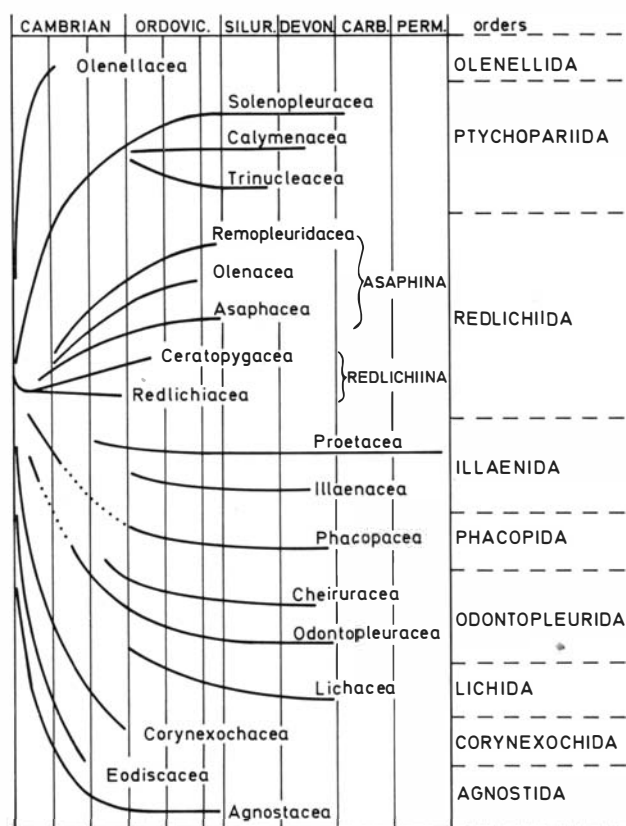


Fig. 12. Summary of the discussion in the text on trilobite phylogeny and systematics.

group by various authors. I suggest that the group be distinguished as the suborder Redlichiina. The subdivision is difficult. Here the early protolenid-redlichiid group is distinguished as the superfamily Redlichiaceae and the late diversified group as the superfamily Ceratopygaceae. This may be a horizontal classification as it can not be excluded that the ceratopygaceans were polyphyletically derived from the redlichiaceans but, at the present stage, it seems better to stress the uniting characters than the diversifying ones which tend to dominate the systematic treatment and lead to chaotic splitting.

The emuellids, paradoxidids, centroleurids, bathynotids, and burlingiids all have characters of their own which may merit a superfamily rank. However, except for the burlingiids they all are close to the protolenids. The burlingiids are probably close to the redlichiids, the main difference lying in the proparian condition of the former.

Henningsmoen (1957:26–31; Fig. 3) ably discussed the relationships of the olenids and concluded that they may be related to the andrarinids, elviniids, anomocarids, asaphids, ceratopygids, richardsonellids, and remopleuridids. With the exception of the ceratopygids and perhaps the elviniids I fully concur with this view and suggest the suborder Asaphina to contain the above and still other groups. Early members may have long palpebral lobes, transversely extended posterior facial sutures, anteriorly tapering glabella,

and pleurae sloping from the dorsal furrow or with poorly defined fulcra and hinge-lines (see e.g. Westergård 1950, Pl. 3, 4 with *Anomocare*, *Anomocarina*, *Anomocarioides*). These features are also found in the comparatively advanced members of the Redlichiaceae and it is probable that the Asaphina stems from this group. The asaphine group is more clearly distinguished from the Redlichiaceae than is the ceratopygacean group. This probably indicates a monophyletic derivation of the Asaphina.

The corynexochid group is primarily characterized by the anteriorly expanded glabella and by the fused hypostomal suture, two features which probably are partly interdependent. The palpebro-ocular ridges commonly are long and backwards directed. The pygidium is medium-sized to large except in the oryctocephalids and dinesids. There is a wide variation in other characters and it is not certain that the group is phylogenetically uniform. The shape of the glabella may be a paedogenetic character (cf. Robison 1967). If so, it is quite likely that a glabella of the general type found in the corynexochids was developed more than one time. The dinesids may prove to have spiral enrollment in which case they should be transferred to the Ptychopariida. The oryctocephalids are also habitually dissimilar from other corynexochids and may have a different origin. For the entire group, the ordinal name Corynexochida is retained. Monophyletic or not, the corynexochids probably had protolenid ancestors.

The Early and Middle Cambrian edelsteinaspidids share some characters with the corynexochids, probably because of convergent evolution. Remarkably enough, the morphologically stable pygidia are almost indistinguishable from dalmanitid pygidia from the Ordovician and Silurian. This may be due to convergent evolution. However, the morphology of the cephalon shows exactly the features that would be expected in Cambrian ancestors of the dalmanitid-phacopid group. The glabella is long and elevated, bounded by semiparallel dorsal furrows and provided with three pairs of deep glabellar furrows (S1–3). The anterior lobe is fairly large, without a trace of additional furrows. The anterior divergence of the dorsal furrows in phacopaceans is obviously an advanced character. The other glabellar furrows are shared by at least primitive members of the Phacopaceae (as defined herein). The eye ridges found in edelsteinaspidids have been lost in the phacopaceans, as in most late groups. The anterior branch of the facial suture is laterally positioned in the edelsteinaspidids as compared with the situation in phacopaceans, but the condition in the latter is secondary. The posterior branch extends to the base of the genal spine. This condition would also be expected in the ancestors of proparian trilobites. Analogous conditions are met with in other examples of probably related opisthoparian-proparian couples, e.g. redlichiids-burlingiids, odontopleurids-cheirurids, *Bavarilla*-calymenids/homalonotids, etc. Therefore I find it natural to unite the edelsteinaspidids with the phacopaceans

in one group, the order Phacopida. Cheiruraceans and calymenaceans are entirely unrelated to this group.

Illaenids, styginids, cyclopygids, bathyurids, and proetids share some characters and may form a monophyletic group. The hypostome is of the same general type, the rostrum tends to disappear, the enrollment is sphaeroidal, and there are well developed terrace lines ventrally and commonly on the cephalic margin. It is difficult to separate this group from some others, particularly the asaphaceans, and trilobites like the pterocephalids and elviniids may belong to either of the Illaenida or Asaphina. It seems likely that the two groups had separate origins within the Redlichia-cea and that the similarity between some members is due to parallel or convergent evolution.

Of the Phacopida as defined in the Treatise (cf. Moore 1959), the Calymenina have here been referred to the Ptychopariida and the Phacopina to the Phacopida. The third group, the Cheirurina, does not fit into any of these orders. Well developed flanges are common to most subgroups and the exoskeleton is generally ornamented. Inverted spiral enrollment occurs in some groups. The same characters, probably including the inverted spiral enrollment, are found in the Celmidae and Hammatocnemidae. *Hammatocnemis* has schizochroal eyes, a feature typical for the phacopaceans but also found in some cheiruraceans and a few other trilobites. The thoracic articulation and pleural morphology of the cheiruraceans is closely comparable with that of odontopleurids and glaphurids (*Glaphurina*), and these groups share a marked surface ornamentation with cheiruraceans, celmids and hammatocnemids, and some glabellar characters with celmids and some cheiruraceans. Glaphurids and odontopleurids are markedly spinose. The remarkable fulcral spines of glaphurids and odontopleurids (principal pleural spine of Bruton 1966) has no known counterpart except in *Gelasene* Palmer, 1968, which is remarkably cheirurid-like despite its Early Cambrian age. The cheirurid-like characters include the type and size of pygidium, the glabellar morphology, the palpebro-ocular ridges, and the course of the posterior branch of the facial suture, although *Gelasene* is technically opisthoparian. All the groups mentioned are either proparian or have the posterior end of the facial suture close to the genal spine, and the pygidia have distinctly developed pleural ridges or spines, if not telsonic (as possibly in Celmidae). The entire group is considered to be a monophyletic unit, for which the existing ordinal name Odontopleurida is used. The order appears to be closer to the Redlichia-cea than to any other group in its general morphology and may have redlichiid-like ancestors.

A last problematical large group is the Lichida. There are no obvious similarities with any of the advanced trilobite groups. It appears plausible that the lichids evolved from some group of redlichiaean trilobites.

In the following, I have tried to recognize groups of order, suborder and superfamily rank, which may be natural, while the lower categories are more schemat-

ically listed. Detailed systematics needs further study. However, a drastic diminishing of the number of families and subfamilies, based on comparatively uninteresting technical characters, is obviously necessary. When possible, the idea of the systematic position of each family group is based primarily on the type genus and its type species, as many families recognized in the Treatise (Harrington *et al.* in Moore 1959) in my opinion are terribly heterogeneous.

The list of groups is not complete. I have been unable to reach an opinion regarding a number of groups, most of which are poorly known in some respects. No doubt, I am also unaware of many pertinent publications or have been unable to obtain them. In many respects this attempt to a classification is based on the results of previous attempts, e.g. those by Richter (1933), Henningsmoen (1951) and Hupé (1953b, 1955). It should be mentioned that the classification by Hu (1971:71–72) is based on a single character (the sutures of the librigeno-rostrum) which is known to vary even inside particular genera (e.g. *Panderia*; cf. Bruton 1968a).

Class TRILOBITA Walch, 1771

Order OLENELLIDA Resser, 1938

Trilobites primitively lacking ecdysial facial sutures; eyes generally large; pygidium generally very small; dorsal furrow process and socket joint may be present, but other condyle and socket joints and horizontal hinge-line lacking; enrollment ability lacking or poorly developed. (Classification according to Bergström in preparation.)

Superfamily Olenellacea Vogdes, 1893

- Daguinaspididae Hupé, 1953
- Daguinaspidinae Hupé, 1953
- Fallotaspidinae Hupé, 1953
- Nevadiinae Hupé, 1953
- Neltneriinae Hupé, 1953
- Callaviinae Poulsen, 1959
- Holmiidae Hupé, 1953
- Olenellidae Vogdes, 1893

Order REDLICHIIA Richter, 1933 (emended herein)

With few exceptions, trilobites with opisthoparian sutures and medium-sized non-swollen glabella; eyes large in early forms but tend to be smaller in many later members; hypostome commonly connected with rostral plate, rarely fused; rostral plate tends to disappear; thorax commonly with pointed pleural spines; horizontal hinge-line present in early forms but disappears in some instances; flanges almost invariably absent; ring joint and dorsal furrow joint common; pygidium small to large, commonly with flattened border and marginal spines; enrolling capacity lacking in forms without hinge-line, sphaeroidal or cylindrical in others; panderian organ or vincular apparatus may limit enrolling action, in which pleural spines slide over one another.

Suborder REDLICHIIA Richter, 1933

Redlichiid trilobites mostly without panderian organ and vincular apparatus; where medium-sized or large, the pygidium has more commonly than not marginal spines.

Superfamily Redlichiacea Poulsen, 1927 (emended herein)

Redlichiiine trilobites commonly with tapering glabella having simple parallel glabellar furrows; palpebro-ocular ridge simple except in some early members, either fairly transverse or inclined strongly backwards; posterior

branch of facial suture short and longitudinal to long and transverse; pygidium commonly small.

- Protolenidae Richter & Richter, 1948
 - Bigotiniinae Hupé, 1953
 - Termierelliniinae Hupé, 1953
- Protoleninae Richter & Richter, 1948
- Myopsoleninae Hupé, 1953
- Palaeoleninae Hupé, 1953
- Lermontoviinae Suvorova, 1956
- Bergeroniellinae Repina, 1966
- Aldonaiidae Hupé, 1953
- Metadoxididae Whitehouse, 1939
- Jakutidae Suvorova, 1958
- Redlichiidae Poulsen, 1927
 - Neoredlichiinae Hupé, 1953
 - Abadiellinae Hupé, 1953
 - Wutingaspidiinae Chang, 1966
 - Pararedlichiinae Hupé, 1953
 - Redlichiinae Poulsen, 1927
- Despujolsiidae Harrington, 1959 (= Resseropidae Chang, 1966)
 - Despujolsiinae Harrington, 1959
 - Resseropinae Chang, 1966
- Dolerolenidae Kobayashi, 1951
- Yinitidae Hupé, 1953 (= Drepanopygidae Lu, 1961)
 - Yinitinae Hupé, 1953
 - Drepanopyginae Lu, 1961
- Mayiellidae Chang, 1966
- Gigantopygidae Harrington, 1959
- Emuellidae Pocock, 1970
- Paradoxididae Hawle & Corda, 1847
 - Paradoxidinae Hawle & Corda, 1847
 - Xystridurinae Whitehouse, 1847
 - Centropleurinae Angelin, 1854
- Bathynotidae Hupé, 1953
- Burlingiidae Walcott, 1928

Superfamily Ceratopygacea Linnarsson, 1869 (emended herein)

Redlichiine trilobites generally with tapering glabella; glabellar furrows tend to divide or get complicated in other ways; plectrum commonly present; posterior branch of facial suture long, transverse; hinge-line present; pygidium medium-sized to large, commonly with marginal spines; enrollment sphaeroidal, if present.

- Papyriaspidae Whitehouse, 1939
- Ceratopygidae Linnarsson, 1869
- Mapaniidae Chang, 1963
- Asaphiscidae Raymond, 1924
 - Asaphiscinae Raymond, 1924
 - Blountiinae Lochman, 1944
- Tsinaniidae Kobayashi, 1933
- Erixaniidae Öpik, 1963
- Plectriferidae Öpik, 1967
- Rhyssometopidae Öpik, 1967
- Chanshaniidae Kobayashi, 1935
- Damesellidae Kobayashi, 1935
- Polycyrtaspididae Öpik, 1967
- Auritamididae Öpik, 1967
- Liostracinidae Raymond, 1937
 - Liostracininae Raymond, 1937
- Doremataspidinae Öpik, 1967
- Harpidae Whittington, 1950
- Kaolishaniidae Kobayashi, 1935
 - Kaolishaniinae Kobayashi, 1935
 - Manuyiinae Hupé, 1955
 - Tingocephalinae Hupé, 1955
- Marjumiidae Kobayashi, 1935
- Crepicephalidae Kobayashi, 1935
- Tricrepicephalidae Palmer, 1954

Suborder ASAPHINA Salter, 1864 (emended herein)

Redlichiid trilobites commonly with long posterior branch of facial suture; rostral plate commonly disappeared,

doublure repeatedly fused over median suture; well developed hinge-line if not secondarily lost; commonly with panderian organ; pygidium generally medium-sized to large, with or without marginal spines; if spine-less commonly fitting cephalon margin to margin in enrollment and of identical outline; enrollment sphaeroidal, secondarily cylindrical or ability lost.

Superfamily Asaphacea Burmeister, 1843 (emended herein)

Asaphine trilobites with a fixed hypostome, commonly with a median incision or spine in the hypostomal margin; genal spines commonly strong.

- Anomocaridae Poulsen, 1927
 - Anomocarinae Poulsen, 1927
 - ?Conokephalininae Walcott, 1913
- Andrarinidae Raymond, 1937
- Parabolinoidea Lochman, 1956
- Loganellidae Rasetti, 1959
- Idahoidae Lochman, 1956
- Dikelocephalidae Miller, 1889
 - Dikelocephalinae Miller, 1889
 - Saukiinae Ulrich & Resser, 1930
- Dikelocephalinidae Kobayashi, 1936
- Asaphidae Burmeister, 1843
 - Taihungshaniinae Sun, 1931
 - Asaphinae Burmeister, 1843
 - Isotelinae Angelin, 1854
 - Niobinae Jaanusson, 1959
 - Ogygiocaridinae Raymond, 1937
 - Promegaspidiinae Jaanusson, 1959
 - Thysanopyginae Jaanusson, 1959
 - Griphasaphinae Öpik, 1967
 - ?Symphysurininae Kobayashi, 1935
 - Nileidae Angelin, 1854

Superfamily Olenacea Burmeister, 1843

Asaphine trilobites with hypostome probably disconnected from doublure; genal spines needle-like.

- Olenidae Burmeister, 1843
 - Oleninae Burmeister, 1843
 - Leptoplastinae Angelin, 1854
 - Pelturinae Hawle & Corda, 1847
 - Triarthrinae Ulrich, 1930
 - Rhodonaspidinae Öpik, 1963
 - ?Talbotinellinae Öpik, 1963
- Hypermecaspididae Harrington & Leanza, 1957

Superfamily Remopleuridacea Hawle & Corda, 1847

Asaphine trilobites with subquadrate hypostome fixed to doublure; anterior wing process obviously extending from doublure, not from hypostome; palpebral area narrow, tends to merge with glabella; hinge-line tends to disappear completely and strong fulcral process and socket pivot joint takes the position of the dorsal furrow joint; pygidium small to medium-sized, generally with marginal spines.

- Remopleurididae Hawle & Corda, 1847
 - Remopleuridinae Hawle & Corda, 1847
 - Rickardsonellinae Raymond, 1924
- Hungaiidae Raymond, 1924
- Bohemillidae Barrande, 1872

Order CORYNEXOCHIDA Kobayashi, 1935 (emended herein)

Trilobites with opisthoparian suture in most cases; hypostome generally fused with rostral plate; paired eyes commonly long but may be short or absent; glabella generally expanding forwards or parallel-sided; glabellar furrows on each side commonly converging outwards; horizontal hinge-line generally developed in thorax; dorsal furrow joint and fulcral joint may be present; pygidium generally medium-sized or large, with entire or spinous border; sphaeroidal enrollment at least in some members.

Superfamily Corynexochacea Angelin, 1854

- Hicksiidae Hupé, 1953
- Dorypygidae Kobayashi, 1935
- Ogygopsidae Rasetti, 1951
- Granulariidae Lermontova, 1951
- Zacanthoididae Swinnerton, 1915
- Corynexochidae Angelin, 1854
- Dolichometopidae Walcott, 1916
- ?Saukiandidae Hupé, 1953
- ?Oryctocephalidae Beecher, 1897
 - Oryctocephalinae Beecher, 1897
 - Oryctocarinae Hupé, 1955
 - Lancastriinae Kobayashi, 1935
 - Cheiruroidinae Kobayashi, 1935
 - Tonkinellinae Reed, 1935
- ?Dinesidae Lermontova, 1940

Order ILLAENIDA Jaanusson 1959 (*nom. transl. ex Illaenina* Jaanusson, 1959)

Trilobites generally with terrace lines on doublure, hypostome and cephalic border; glabella of variable outline; glabellar furrows generally weak or absent; facial suture opisthoparian; rostral plate tends to disappear and librigenae may fuse medially; thorax with comparatively few segments, exceptionally only three; horizontal hinge-line generally present; ring joint and dorsal furrow joint may occur, fulcral joint developed as flange joint exceptionally present; panderian organ may occur; pygidium large, generally with entire border; enrollment sphaeroidal.

Superfamily Proetacea Salter, 1864 (emended herein)

Illaenid trilobites commonly with medium-sized or large eyes; glabella parallel-sided or tapering, generally distinctly delimited in front.

- ?Leioestegiidae Bradley, 1925
 - Leioestegiinae Bradley, 1925
 - Pagodiinae Kobayashi, 1935
- ?Kingstoniidae Kobayashi, 1935
- ?Ptychaspidae Raymond, 1924 (? = Missisquoiidae Hupé, 1953)
- ?Catillicephalidae Raymond, 1938
- ?Eurekiidae Hupé, 1955
- ?Illaenuridae Vogdes, 1890
- ?Shumardiidae Lake, 1907
- Lecanopygidae Lochman, 1953
- Bathyuridae Walcott, 1886
- Holotrachelidae Warburg, 1925
- Proetidae Salter, 1864
 - Proetinae Salter, 1864
 - Cornupretinae Richter & Richter, 1956
 - Cyrtocymbolinae Hupé, 1955
 - Griffithidinae Hupé, 1955
- Brachymetopidae Prantl & Přibyl, 1950

Superfamily Illaenacea Hawle & Corda, 1847

Illaenid trilobites generally with small eyes; glabella generally expanding and faintly delimited anteriorly; pygidial rhachis commonly short; doublure wide.

- Thysanopeltidae Hawle & Corda, 1847 (= Scutellulidae Richter & Richter, 1925)
 - Thysanopeltinae Hawle & Corda, 1847
 - Stygininae Vogdes, 1890
 - Goldillaeninae Balashova, 1959
 - Theamataspidinae Hupé, 1955
- Illaenidae Hawle & Corda, 1847
 - Illaeninae Hawle & Corda, 1847
 - Bumastinae Raymond, 1916
 - Panderiinae Bruton, 1968
 - Ectillaeninae Jaanusson, 1959
- ?Cyclopygidae Raymond, 1925

Order PHACOPIDA Salter, 1864 (emended herein)

Trilobites with long posterior branch of facial suture extending laterally, opisthoparian or proparian; glabella distinctly delimited, slightly narrowing or parallel-sided to expanding

forwards; generally three pairs of glabellar furrows with deep apodemal invagination some distance from the dorsal furrow; pygidium medium-sized or large, with pleural and interpleural furrows and entire or spinous margin.

Superfamily Edelsteinaspidacea Hupé, 1953 (*nom. transl. ex Edelsteinaspididae* Hupé, 1953)

Phacopid trilobites with opisthoparian suture; glabella narrowing forwards or parallel-sided, with deep and regular glabellar furrows; ocular ridge present; ventral features poorly known; thorax with more than 11 segments; articulating facets probably not developed.

- Edelsteinaspididae Hupé, 1955
 - Edelsteinaspidinae Hupé, 1955
 - Nodicepinae Suvorova, 1964
 - Laticephalinae Suvorova, 1964

Superfamily Phacopacea Hawle & Corda, 1847 (emended herein)

Phacopid trilobites with facial suture proparian or lacking; glabella expanded anteriorly, commonly with somewhat irregularly arranged glabellar furrows; ocular ridge absent; eyes schizochroal; large rostral plate separated from hypostome by suture; thorax with 11 tergites with well developed articulating facets; enrollment sphaeroidal.

- Phacopidae Hawle & Corda, 1847
 - Phacopinae Hawle & Corda, 1847
 - Bouleinae Hupé, 1955
 - Phacopidellinae Delo, 1935
 - Andreaspinae Struve, 1962
- Pterygomotopidae Reed, 1905
 - Pterygomotopinae Reed, 1905
 - Chasmopinae Pillet, 1954
- Dalmanitidae Vogdes, 1890
 - Dalmanitinae Vogdes, 1890
 - Zeliskellinae Delo, 1935
 - Asteropyginae Delo, 1935
- Calmoniidae Delo, 1935
 - Calmoniinae Delo, 1935
 - Acastinae Delo, 1935 (= Acastavinae Struve, 1958)
- Monorakidae Kramarenko, 1952

Order ODONTOPLEURIDA Whittington, 1959 (emended herein)

Trilobites generally with strongly marked glabellar furrows, small eyes, surface ornamentation with tubercles or pits but without terrace lines, and opisthoparian to proparian facial suture; postero-laterally directed palpebro-ocular ridge commonly developed; hypostome in contact with rostrum; thorax with entirely encased pleural spines which abut against one another in full enrollment; pleurae generally with imbricating flanges, which extend to or beyond the fulcrum and end with a marginal connective device, either functioning as a fulcral pivot joint or as a limiting device in the enrollment; horizontally directed accessory pleural spines may be present; pygidium commonly fairly small, with marginal spines; enrollment sphaeroidal or reversed spiral; marginal and pleural spines may be accommodated by vincular groove or pits.

Superfamily and family not erected: Odontopleurid trilobites with opisthoparian facial suture; glabella tapering anteriorly, with regularly arranged glabellar furrow and lobes; small accessory pleural spines may be present; pygidium short.

- Gelasene* Palmer, 1968

Superfamily Odontopleuracea Burmeister, 1843

Odontopleurid trilobites with opisthoparian facial sutures; palpebro-ocular ridges well developed; eyes may be on elevated sockets; pleural spines projecting downwards; strong accessory pleural spines projecting laterally; pygidium short, with two or three segments.

- Odontopleuridae Burmeister, 1843
 - Odontopleurinae Burmeister, 1843

Miraspidae Richter & Richter, 1947
 Selenopeltidae Hawle & Corda, 1847
 Apianuridae Whittington, 1956
 Eoacidaspidae Poletaeva, 1957
 ?Glaphuridae Hupé, 1955

Superfamily Cheiruracea Salter (emended herein)
 Odontopleurid trilobites generally with proparian or gonatoparian facial suture; no accessory pleural spines; pygidium short or long.

?Telephinidae Marek, 1952
 ?Raymondinidae Clark, 1924
 Carmonidae Kielan, 1960
 Celmidae Jaanusson, 1956
 Hammatocnemidae Kielan, 1960
 Cheiruridae Salter, 1864
 Cheirurinae Salter, 1864
 Eccoptochilinae Lane, 1971
 Sphaerexochinae Öpik, 1937
 Deiphoninae Raymond, 1913
 Acanthoparyphinae Whittington & Evitt, 1953
 Areiinae Prantl & Přibyl, 1947
 Pilekiinae Szűz, 1955
 Pliomeridae Raymond, 1913
 Pliomerinae Raymond, 1913
 Placopariinae Hupé, 1955
 Pliomerellinae Hupé, 1955
 Diaphanometopinae Jaanusson, 1959
 Encrinuridae Angelin, 1854
 Encrinurinae Angelin, 1854
 Cybelinae Holiday, 1942
 Dindymeninae Henningsmoen, 1959
 Staurocephalinae Prantl & Přibyl, 1947

Order LICHIDA Moore, 1959

Medium-sized to large trilobites generally with tuberculate ornament; glabella with longitudinally elongated glabellar furrows; eyes small; facial suture opisthoparian; hypostome subquadrate, fixed to unpaired rostrum; thorax with horizontal hinge-line short or missing; flanges, ring joint, dorsal furrow joint, fulcral joint, and panderian organ not developed; pygidium large with generally three pairs of pleural segments; probably not enrolling.

Superfamily Lichacea Hawle & Corda, 1847
 Lichidae Hawle & Corda, 1847
 Lichinae Hawle & Corda, 1847
 Homolichinae Phleger, 1936
 Tetralichinae Phleger, 1936
 Ceratarginae Tripp, 1957
 Lichakephalidae Tripp, 1957

Order PTYCHOPARIIDA Swinnerton, 1915 (emended herein)

Small to medium-sized, seldom large trilobites, as a rule with opisthoparian or gonatoparian suture; compound eyes generally small or absent; glabella commonly trapezoidal, with glabellar furrows undifferentiated or absent; hypostome either not in contact with rostrum or with a transverse depression for the reception of the pygidial margin in the enrolled trilobite; thorax with blunt pleural spines; horizontal hinge-line present in most members, rarely secondarily lost; flanges only exceptionally developed; ring joint commonly present, dorsal furrow joint and fulcral joint usually absent; pygidium generally small to medium-sized, with entire border, which may be geniculated; spiral enrollment or derived type.

Superfamily Solenopleuracea Angelin, 1854 (emended herein)
 Ptychopariid trilobites generally with tapering glabella; palpebro-ocular ridges commonly visible; commonly long thorax and short pygidium; generally typical or unrolled spiral enrollment.
 Ellipsocephalidae Matthew, 1887
 Ellipsocephalinae Matthew, 1887
 Strenuellinae Hupé, 1953

Antatlasinae Hupé, 1953
 Kingaspidae Hupé, 1953
 Agraullinae Raymond, 1913
 Ptychopariidae Matthew, 1887
 Ptychopariinae Matthew, 1887
 Antagminae Hupé, 1953
 ?Nassoviinae Howell, 1937
 Solenopleuridae Angelin, 1854
 Solenopleurinae Angelin, 1854
 Acrocephalitinae Hupé, 1953
 Saoinae Hupé, 1953
 Hystricurinae Hupé, 1953
 Dimeropyginae Hupé, 1953
 Conocoryphidae Angelin, 1854
 Conocoryphinae Angelin, 1854
 Pharostomatinae Hupé, 1953
 Periomellinae Rasetti, 1955
 Bolaspidae Howell, 1959
 Nepeidae Whitehouse, 1939
 Menomoniidae Walcott, 1916
 Aulacodigmatidae Öpik, 1967
 Eulomatidae Kobayashi, 1955
 Plethopeltidae Raymond, 1924
 Harpidae Hawle & Corda, 1847
 Entomaspidae Ulrich in Bridge, 1930
 Aulacopleuridae Angelin, 1854
 Aulacopleurinae Angelin, 1854
 Otariinae Richter & Richter, 1926
 Cyphaspidinae Přibyl, 1947
 Phillipsinellidae Whittington, 1950

Superfamily Calymenacea Burmeister, 1843

Ptychopariid trilobites with trapezoidal glabella; palpebro-ocular ridges usually absent; facial sutures generally gonatoparian; hypostome fixed to rostrum; pygidium generally long and triangular.

Calymenidae Burmeister, 1843
 Homalonotidae E. J. Chapman, 1890
 Homalonotinae E. J. Chapman, 1890
 Portagininae Lépérance, 1968
 Bavarillinae Szűz, 1957
 Eohomalonotinae Hupé, 1955
 Colpocoryphinae Hupé, 1955

Superfamily Trinucleacea Hawle & Corda, 1847

Ptychopariid trilobites generally with forwards expanding and convex glabella; paired eyes generally absent; facial suture opisthoparian, submarginal or marginal anteriorly and anterolaterally; librigena in one piece, rostrum absent; genal spine long; thorax generally short and flat; generally basket and lid enrollment.

Trinucleidae Hawle & Corda, 1847
 Trinucleinae Hawle & Corda, 1847
 Tretaspidae Whittington, 1941
 Cryptolithinae Angelin, 1854
 Novaspidae Whittington, 1941
 Incainae Hughes & Wright, 1970
 Orometopidae Hupé, 1955
 Dionididae Gürich, 1908
 Raphiophoridae Angelin, 1854
 Raphiophorinae Angelin, 1854
 Ampyxininae Hupé, 1955
 Ampyxellinae Koroleva, 1959
 Bulbaspidae Kobayashi & Hamada, 1971
 Endymioniidae Raymond, 1920
 Alsataspidae Turner, 1940
 Hapalopleuridae Harrington & Leanza, 1957
 Myindidae Hupé, 1955

Order AGNOSTIDA Salter, 1864 (= Miomera Jaekel, 1909)

Small trilobites with thorax consisting of two or three segments; generally without dorsal eyes and then lacking ecdysial facial sutures; horizontal hinge-line developed; intestinal diverticula excessively developed, commonly traceable in exterior reticulation, filling genal regions.

Superfamily Agnostacea M'Coy, 1849

Agnostid trilobites without facial sutures and dorsal eyes; two thoracic segments with rhachis distinctly different from pygidial rhachis; rhachis on pygidium with a maximum of three well defined segments, but segments commonly not distinguishable.

Agnostidae M'Coy, 1849

Agnostinae M'Coy, 1849

Ptychagnostinae Kobayashi, 1939

Quadragnostinae Howell, 1935

Diplagnostidae Whitehouse, 1936

Diplagnostinae Whitehouse, 1936

Oidagnostinae Öpik, 1967

Tomagnostinae Kobayashi, 1940

Ammagnostinae Öpik, 1967

Pseudagnostinae Whitehouse, 1936

Glyptagnostinae Whitehouse, 1936

Clavagnostidae Howell, 1937

Clavagnostinae Howell, 1937

Aspidagnostinae Pokrovskaja, 1960

Trinodidae Howell, 1935 (= Geragnostidae Howell, 1935)

Discagnostidae Öpik, 1963

Sphaeragnostidae Kobayashi, 1939

Phalacromidae Hawle & Corda, 1847

?Condylipygidae Raymond, 1913

Superfamily Eodiscacea Raymond, 1913 (*nom. transl.*, ex Eodiscidae Raymond, 1913)

Agnostid trilobites with dorsal eyes and proparian facial sutures, or without dorsal eyes and facial sutures; thoracic and pygidial rhachis of similar morphology; long pygidial rhachis generally with more than three distinctly visible segments.

Eodiscidae Raymond, 1913

Pagetiidae Kobayashi, 1935

Gross morphology related to life habits

Convergent evolution commonly has produced animals so similar mutually in one respect or another that the similarity has been taken to indicate a close relationship. The trilobites do not form any exception, although the convergent couples are mostly found within the class while a close similarity with other arthropods is exceptional. It may be suspected that the development of the same morphological characteristics along different phylogenetic lineages is due to an adaptation to a particular mode of living or particular environmental factors. Exactly those morphological features which are least interesting from a systematic point of view may therefore be particularly important for the interpretation of trilobite biology. It is unfortunate that in most cases only the dorsal exoskeleton is known, but even so some deductions may be made. An attempt is made here for a few selected cases.

Wide rhachis and smooth exterior

Some trilobites combine a wide rhachis with a smooth exoskeleton and, in some cases, with small eyes. This combination is found notably in genera like *Homalonotus*, *Bumastus*, *Illaeus*, *Nileus*, *Illaeonurus*, *Leiocoryphe*, and *Plethometopus*, to mention a few examples.

Few observations with a bearing on the life of trilobites of the discussed morphological type have been made. A notable and excellent exception is the report by Finch (1904) of about 15 specimens of *Ptyocephalus vigilans* found in one limestone bed and in an area roughly 0.3 m². The specimens retain their free cheeks and undoubtedly were dead individuals. Remarkably enough, each of them has its cephalon straightened out horizontally while the thorax and pygidium extend vertically downward. Cephalons of different sized individuals do not rest at the same level. Instead, they are buried to the same relative extent under a marked surface with only the upper part extruding. Finch suggested that the trilobites burrowed actively backwards to reach the observed position, although his efforts to trace the burrows in the rock were in vain. Still, the suggestion was based on sound discussion of the facts and is no doubt correct.

In a collection of *Illaeus sarsi* Jaanusson from the lowermost Middle Ordovician at Råpplinge, Öland, south Sweden there are six more or less complete individuals. Of these, one is enrolled and one lies extended on one side. The other four rest in a position with the cephalic margin and the palpebral lobe approximately parallel to the bedding and with the thorax and pygidium held in a position strongly inclined to the bedding, but not fully vertical (Fig. 14; Pl. 5:5, 6). The entire body posture is closely comparable to that shown in a specimen of *Illaeus crassicauda* by Jaanusson (1954, Pl. 1:4), but in this case the orientation relative to the bedding is not known. In the case of *Illaeus sarsi* there actually is a stratification, although it is poorly developed in the homogeneous limestone. The texture of the limestone also probably causes the lack of a visible burrow around each specimen.

Illaeids with a habitus similar to that of *I. sarsi* and *I. crassicauda*, i.e. species included in genera like *Illaeus*, *Nanillaenus*, *Stenopareia*, *Ectillaenus*, *Platillaenus*, and *Panderia*, generally occur in various types of sediments, except very fine-grained ones, that indicate an originally soft-bottom environment. Moreover, many species are abundant in reef deposits and may be confined to these. For instance, the Middle and Upper Ordovician Kullsberg and Boda Reef Limestones in Dalarna, central Sweden, contain some 13 species of the genera listed above (count from Warburg 1925; cf. Lane 1972). Contemporaneous Swedish bedded limestones, marlstones and mudstones have yielded considerably fewer species of the listed genera. Of these species, only one (*Illaeus roemeri* Volborth) is shared by the two main types of environments.

A preference for reef habitats would perhaps seem to be contradictory to a suggested burrowing habit. However, Dr. Valdar Jaanusson informed me (1971, personal communication) that the primary reef builders in Dalarna occupied comparatively small areas in a growing surface, whereas the areas in between must be considered to have formed more or less soft bottoms. The constricted soft-bottom areas of the reefs

were not inhabited by trilobites like calymenids and trinucleids, which are known or supposed to have had burrowing habits. Asaphids are also absent (except for one questionable pygidium). However, the morphology of the illaenids and the evidence from *Illaenus sarsi*, as well as from the morphologically similar asaphid *Ptyocephalus vigilans*, definitely indicates that the illaenids sat with the posterior part of their bodies hidden in narrow burrows and the area needed for burrowing, therefore, may have been quite small.

Clarkson (1966a, b) concluded that the elongated visual surface of phacopid eyes must have been held horizontally in life in order to give all-round vision in the horizontal plane. This conclusion seems to be very reasonable and there is no reason to restrict it to the phacopids. To show the orientation used for photographing, Bruton (1968a, Fig. 1B) drew a cephalon of *Panderia* oriented with the visual surface and the palpebral lobe in a horizontal position. He did not use the resulting posture for any discussion of body posture. However, it is evident from Bruton's figure that the posterior part of the cephalon slopes very strongly backwards when the cephalon is drawn in supposed life posture with the palpebral lobe horizontal. This means that the anterior part of the thorax must have extended more downwards than backwards from the cephalon. This was apparently the case with the rear part of the body as well, as there is no morphological reason to believe that this part was flexed upwards. This orientation indicates burrow-dwelling habits. One obstacle is that the cephalic margin is strongly inclined to the horizontal plane in the suggested posture, but an inclined cephalic margin is not obviously disadvantageous to a burrow-dwelling trilobite (Fig. 13).

A very similar relation between the palpebral lobe and the slope of the posterior part of the cephalon is seen in *Stenopilus* which is not closely related to the illaenids.

In other illaenids, such as *Illaenus crassicauda*, the posterior part of the dorsum and the lateral margin of the cephalon remains horizontal when the palpebral lobe is oriented horizontally. Siegfried (1939) discussed the mode of life of the illaenids with this general morphology. He concluded that they must have lived and moved in a horizontally extended posture in which the margin of the cephalon extended far beneath the thorax and pygidium (cf. Siegfried 1939, Fig. 1). The lack of the inclination typical for *Panderia* indicates that Siegfried is at least partially correct, but it is difficult to see what function the enormous cephalon would have had in a purely walking and swimming trilobite. I suppose that the cephalic shield has some function in burrowing, although it is possible that illaenids of *I. crassicauda* type burrowed in a more horizontal posture than did *Panderia* species.

Regarding the mode of burrowing, the extended vertical anterior part of the cephalon must have hindered the animal from scratching with the appendages in front of the cephalon. Burrowing head first was

therefore not possible. Two postures for burrowing remain possible. Either the animal may have burrowed vertically from an extended horizontal posture, or it may have burrowed pygidium first. The evidence from specimens *in situ* and from morphological features discussed above indicates that the second method may have been employed by species of *Panderia*, *Ptyocephalus* and *Stenopilus*, to mention a few representative examples. It is difficult to tell if *Illaenus crassicauda*, *I. sinuatus* Holm, and similar forms burrowed in the same way or if they employed the former method. Anyway, they did not produce repichnial burrows.

Modifications of the appendages may be suspected in trilobites with specialized burrowing habits. Among the trilobites discussed or mentioned, none are known from the ventral side. However, *Ptyocephalus* is related to *Isotelus*, one of the few trilobite genera in which the appendages are known (cf. Raymond 1920:10). Unfortunately, however, the appendages are too poorly preserved to yield much useful information. It is known that the thoracic appendages have very long and massive coxal portions. Contrasting to the thoracic condition, the pygidial appendages are more closely set and have considerably shorter and weaker coxae. The boundary between the two sets is sharp and it is fair to speak of distinct tagmosis. The morphological differences indicate some functional difference between the tagmata. The thoracic coxae were probably fixed along most of their length to the ventral membrane. The extended connection made it possible for muscles to attach to very long margins, and these muscles may have provided the coxae with a strong rolling ability. As the coxae are situated under the rhachis, very long coxae are necessarily combined with a wide rhachis, as in *Isotelus*. Conversely, a wide rhachis may indicate the presence of long coxae and powerful muscles leading to the coxae although this is not necessary. In *Isotelus* the strong connection and the probably powerful muscles leading to the coxae of the thoracic appendages indicate that these were ideally suited for burrowing, at least as far as the power is concerned.

Although the appendages are unknown in the illaenids and other trilobites treated in this section other than *Isotelus*, these trilobites are suggestive of *Isotelus* in the width of the rhachis and it is tempting to suggest that the coxae were similarly constructed and powered. The presence of powerful muscles leading to the appendages of the cephalon is suggested by the large areas for muscle attachment in illaenids like *Ectillaenus katzeri* and *Stenopareia oviformis* (cf. Jaanusson 1954, Fig. 3B, D). There is a possibility that the cephalic appendages were exceptionally strong and used for rapid burrowing and grasping of prey or for chewing, but this can only be a matter for speculation at present. In illaenids, as in *Isotelus*, the pygidial rhachis is narrower than the thoracic rhachis. The difference in width may be conspicuous, as in *Illaenus crassicauda*. The pygidial rhachis is also fairly short. It seems likely that the pygidium formed a distinct tagma with comparatively small appendages

also in *Illaenus*. The thoracic rhachis is wider in front than posteriorly if it is not delimited by sub-parallel dorsal furrows. This is certainly a normal feature in trilobites but it may be remarked, in this connection, that the opposite may be true as in *Eobronteus laticauda* (Wahlenberg), which is a thysanopeltid and not regarded to belong to the morphological group discussed here. However, it ought to be stressed that the backwards widening rhachis may mean that the posterior appendages were longer or stronger than the anterior ones.

Among the trilobites treated above, *Isotelus* differs from the others in having a cephalon of "ordinary" general appearance instead of the extremely vaulted cephalon of illaenids and the others. A smooth exterior combined with a wide rhachis and a moderately vaulted cephalon is also found in many other trilobites, notably in various isotelinids, nileids, and homalono-

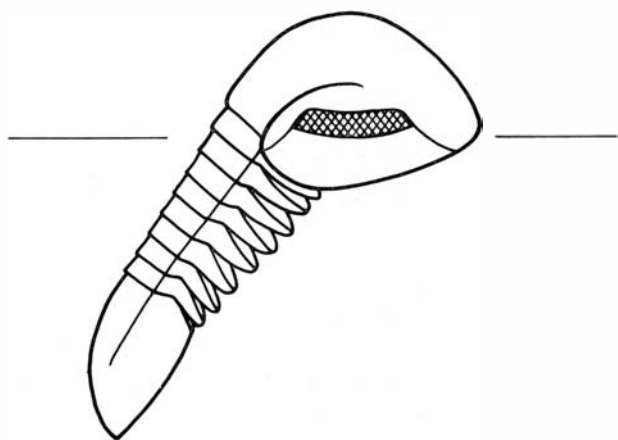


Fig. 13. The illaenid *Panderia megalophthalma* Linnarsson in inferred life position. The sediment surface is indicated as a horizontal line.

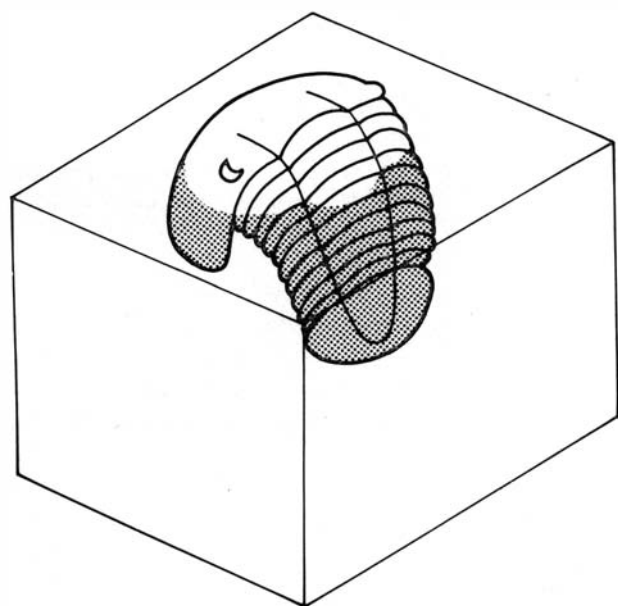


Fig. 14. The Ordovician illaenid *Illaenus sarsi* Jaanusson in its burrow. Hidden parts are shadowed.

tids. Osgood (1970, Pls. 57:1; 58:7, 8; 59:6; 71:1, 6; 72; 73:1, 2, 5, 6, 7; 74:6, 7; 75:2) figured scratch marks and vertical shallow burrows (cubichnia), of which at least the latter are referable to *Isotelus* without much doubt. Particularly the homalonotids have also been supposed to have had burrowing habits, e.g. by Richter (1920), Schevill (1936), and Sdzuy (1957), and I see no reason to doubt this conclusion. As in the illaenids, the eyes commonly lie on a high level and may be conspicuously elevated, as in the isotelinid *Ectenaspis* and the homalonotid *Homalonus*. A similar elevation is found in species of *Asaphus* which is very similar to isotelinids in general aspect. An elevated eye position is very likely in animals burrowing shallowly.

Still other characters are found in all or many of the trilobite forms discussed above and may be related to burrowing habits in one way or another. It is commonly seen that the body is strongly vaulted and, in some instances, its cross-section is nearly semicircular. If so, the horizontal hinge-line may have disappeared completely and the dorsal furrow may be obliterated. This condition is found more or less distinctly in genera such as *Anataphrus*, *Homalopyge*, *Nileus*, *Bumastus*, *Illaenurus*, *Homalonus*, *Trimerus*, *Stenopilus*, and *Leiocoryphe*. Practically without exception the pleural spines are rounded or bluntly pointed. In addition, the thoracic tergites show an exceptionally tight closure: there are no furrows or openings at any stage of enrollment which could be filled with sediment or propped by grains and hinder the normal movements between adjoining tergites. This tightness is supposed to be an almost necessary feature in a burrowing arthropod with a stiff exoskeleton.

Olenid morphology

The olenids are morphologically quite varied. Following Henningsmoen (1957) it is possible to distinguish three main types, the *Peltura*, *Olenus* and *Ctenopyge* types. The *Peltura* type is distinguished by a highly vaulted body and short pleural spines. *Ctenopyge* is flattened, with wide pleural areas and long pleural spines. The *Olenus* type is intermediate between the other two (Henningsmoen 1957:78).

Henningsmoen (1957:78–82, 87–89) discussed the mode of life of the different types. He concluded that the *Peltura* type suggests vigorous and active swimming, the *Olenus* type less vigorous swimming, and the *Ctenopyge* type a more passive planktic life. As pointed out by Henningsmoen, the *Peltura* type corresponds to Richter's (1919:229) agile *Phacops-Calymene* type, characterized by a vaulted body. However, what determined the swimming power of the trilobite was the appendage muscles, which, no doubt, were confined to the volume under the rhachis.

The convexity of the pleural areas is therefore fairly uninteresting as far as the muscular power is concerned. Richter (1919:229–230) was actually aware that the convexity of the body is not a safe guide to life activities. However, the volume available for append-

age muscles under the rhachis is interesting. *Peltura* actually has a wide and vaulted rhachis, while the rhachis of *Ctenopyge* is comparatively narrow but still strongly vaulted. However, *Jujuyaspis*, judged by Henningsmoen to belong to the *Ctenopyge* type, has a voluminous rhachis of *Peltura* type (cf. Harrington & Leanza 1957, Fig. 34), indicating that the pleural spines and the over-all convexity can not alone be used to characterize the morphological type.

It is important to stress the similarities between different olenid types. An important feature is the delicacy and smoothness of the exoskeleton. The genal spine, if present, is a needle-like structure. Exceptionally it may be as wide as in *Ctenopyge fletcheri* (cf. Henningsmoen 1957, Pl. 22:1, 3—6), but in that case it is very flat, the flatness only being interrupted by a strengthening rib on each side. Also, long pleural spines tend to be extremely flattened, as in *Boeckaspis mobergi* (cf. Henningsmoen 1957, Pl. 29:12). Another notable feature found in all olenids is the small size of the eyes. The appendages are known in *Triarthrus eatoni* (cf. Raymond 1920, Figs. 10, 42, 43, and Pls. 1—6; Størmer 1939, Figs. 21—23). The telopodite is invariably held straight to the side together with the long, feather-like exite. The size of the appendages indicates that *Triarthrus* was only capable of imperfect enrollment.

All the above features, except for the small eyes, indicate that the olenids were swimming animals. The delicateness of the exoskeleton made the body less heavy than in most other trilobites, as the exoskeleton consists largely of heavy CaCO_3 . The pleural spines were so flattened that they probably did not hinder swimming very much, but they certainly hindered the animal from fast sinking (cf. Henningsmoen 1957:79). They probably also protected the animal from predators. This effect seems to have been particularly well exploited by *Parabolina argentina*, which must have looked like a five-spined star when enrolled (cf. Harrington & Leanza 1957, Fig. 25:1, 2, 5). This kind of star-like spinosity may be particularly important in planktic forms in order to increase the size and to ward off attacks from all directions. The appendages, particularly their posture, indicate use in swimming. The mode of enrollment, probably imperfect in *Triarthrus* (cf. Dacqué 1921:274) and certainly cylindrical in flattened genera like *Boeckaspis*, *Ctenopyge* and *Leptoplastus*, is also suggestive of a swimming life. Perfect enrollment as protection against predators needs exoskeletal refinements which are likely to be a weight burden on a swimming animal.

Furthermore, the sedimentological and faunal conditions in the Cambrian Olenid Series of Scandinavia indicate that the alum mud bottom of the sea was practically barren, except for sojourning trilobites and perhaps a few brachiopods (cf. Henningsmoen 1957:79—89; Öpik 1963:27—28; Whittington 1966:704; Bergström, Laufeld & Christensen 1972:115). Trilobite trails in the Tremadocian *Dictyonema* Shale have been referred to the activity of a *Boeckaspis* species (Holm 1887; Henningsmoen 1957:74—76; Birken-

majer & Bruton 1971), but this is an exceptional case which may or may not have been correctly interpreted. Anyway, it does not prove anything regarding the Cambrian olenids, which lived in a different habitat, despite lithologic similarities. Cambrian trilobite trails from Poland and Wales, previously thought to have been made by olenids, were probably made by solenopleuraceans, as suggested in the chapter on trilobite trails.

The evidence is hardly entirely conclusive but it seems very likely that most olenids led a pelagic life (cf. Öpik 1963:27; Whittington 1966:704). The small eyes indicate that they were probably not great hunters. This suggestion is strongly corroborated by the appendage construction. It is possible that they fed on planktic algae.

A morphology somewhat similar to that of flattened olenids is found in the Middle Cambrian genus *Centropleura*. Öpik (1961a), from morphological, faunistic and sedimentological evidence, concluded that *Centropleura* led a swimming life. In contrast to olenids, *Centropleura* had large eyes, indicating that the way of living may not have been identical.

Remopleuridid and cyclopygid morphology

Remopleuridids and cyclopygids share a few characters, including exceptionally large eyes with a wide visual field and a wide rhachis. In addition, the pleural area is generally fairly narrow and the exterior surface of the exoskeleton smooth. Spines, if present, are posteriorly directed (except for a median anterior spine in the remopleuridid *Tetrarhynchus* and the cyclopygid *Symphysops*). The two trilobite groups are probably entirely unrelated and the shared characters, therefore, are best explained as the result of convergent evolution, presumably toward a particular kind of adaptation.

The remopleuridids differ from the olenids in the construction of the exoskeleton, which is fairly thick and strong in the former but delicate in the latter. However, the remopleuridids reduced the weight in another way. In advanced forms the pleural areas are much reduced. In *Remopleurides* and *Hypodicranotus* (cf. Whittington 1952 for the latter), for instance, the entire pleura consists of a short pleural spine and the rhachis has taken enormous proportions. This means that the "muscle capsule" is extremely spacious while non-muscular parts have been reduced as "superfluous". Evidently this condition may indicate extraordinarily powered appendages which may be expected in both burrowing and swimming trilobites. There is nothing indicating a burrowing capacity. On the contrary, the reduction of the pleural areas and the presence of large eyes distinctly indicates a swimming life. The presence of remopleuridids in graptolite shales practically devoid of benthic elements (cf. Bergström 1968a:233, regarding *Remopleurides* cf. *lata*) also strongly corroborates the interpretation of certain remopleuridids as swimmers. The large eyes may indicate that the remopleuridids were predators. Some

forms may have been pelagic, others benthic or nekto-benthic.

Conditions in cyclopygids are generally comparable with those in remopleuridids. In one respect the specialization has gone even further, *viz.* in the development of the lateral eyes, which are larger than in any other trilobite and may be confluent in front. The visual field includes much of the ventral hemisphere, a condition which has suggested swimming upside down to some authors, but dorsal side up to others (cf. Dollo 1910; Marek 1961). Apart from the morphological similarities, cyclopygids commonly are found in the same beds as remopleuridids. It is tempting to suggest that the two trilobite groups shared the same general mode of life.

Trinucleid and harpid morphology

A large cephalon with a wide fringe is found in both trinucleids and harpids. In details, however, the structures are fairly dissimilar. An ecologically probably significant difference is found in the spatial orientation of the fringe, which is horizontally flattened in the harpids but steeply inclined in the trinucleids.

The significance of the characteristic trinucleid morphology has been treated by several authors, e.g. recently by Bergström (1972) who stressed the similarity between the trinucleid cephalon and the xiphosurid prosoma and suggested a similar function in shallow burrowing. The comb-like or rake-like exite (in *Cryptolithus*) was found to have very long and strong spines which were probably used to work through the superficial layer of sediment (cf. Dacqué 1921:279–280). The telopodites have a fringe of setae, making strong pushing possible even on a soft subsurface.

Richter (1920) and Dacqué (1921) concluded that the cephalic fringe of harpids had no function in an animal moving on the bottom. The shape, no doubt, makes burrowing entirely implausible. Richter (1920:27) suggested that the large cephalic shield was well balanced in a swimming harpid. He obviously thought of the harpids swimming with their dorsal sides up. However, it seems plausible that the cephalic shield would have had a considerable lifting effect because of the more or less conical shape only if the animal turned upside down during swimming.

The real significance of the cephalic shield in harpids is not obvious. The animal must have rested on the margin of the fringe when enrolled, but this does not explain the morphology. Harpids are commonly found in reefs, where trinucleids do not normally occur (cf. Lane 1972). A possibility is that the morphology of the cephalon aided the animal in clinging to rock surfaces. Another possibility is that the fringe markedly added to the size of the animal and made it more difficult to be swallowed by carnivores of moderate size.

Agnostid morphology

Agnostid trilobites of the suborder Agnostina are characterized by a dorso-ventrally flattened shape, a

short thorax consisting of only two segments, and an absence of dorsally situated compound eyes. They have also other characters in common which are considered less interesting in this discussion, as for instance an isopygous condition. Some forms have a characteristic reticulated prosopon in the cephalon. The unique combination of characters typical for agnostids makes it impossible to make a close comparison with any other trilobites.

Opinions about the agnostid mode(s) of life are disparate. They have been regarded as pelagic, planktic, pseudoplanktic, nektic, epifaunal, or even infaunal. Furthermore, Robison suggested that they occasionally swam in rolled-up posture by clapping cephalon and pygidium together, much like a pectinid bivalve. For a review and treatment of these opinions see Robison (1972b).

Obviously agnostids are comparatively widespread and found in a variety of sediment types (cf. Howell & Resser 1934). This distributional feature has generally been taken as indication that the agnostids were planktic, pseudoplanktic or pelagic. However, a wide distribution in itself is not evidence for a planktic existence but rather indicates that feasible living conditions for the species in question prevailed over large areas. In modern seas this would indicate either a pelagic or a soft-bottom habitat. These two habitat types differ from one another in their distribution mechanisms, as distribution by means of eggs and larvae is much more important in the latter than in the former. This difference is very difficult to recognize in fossil faunas, however. Another difference is that particular soft-bottom animals are generally closely connected with particular types of sediments, whereas pelagic animals are not. Although complications may occur, this condition is much more likely to be recognized in fossil material. One of the possible complications is that the animals' choice of sediment may not correspond to the sedimentologist's idea of a lithology. Indeed, this commonly appears to be what happened when benthic trilobites are said to be independent of facies, which certainly is not true.

Some information about the agnostid mode of life may be gained from a study of the Upper Cambrian alum shale of Scandinavia where there is a fauna consisting of more than 150 known animal species. There is no evidence of any benthic life in most horizons. There is never any trace of bioturbation, as far as known, and only in a few levels are there stray individuals of comparatively large and clumsy trilobites which may have been benthic. The fauna is strongly dominated by olenid trilobites of small size and with thin exoskeletons. There are also agnostids, bradoriid crustaceans, small brachiopods, and sponges. At least some of the brachiopods may have been epiplanktic and there is no particular reason to suppose that any of the other forms apart from the stray elements mentioned above were benthic. Presumably, almost the entire fauna was pelagic.

It is possible that the lack of known agnostid protaspids may have some significance. In serolid isopods

the smallest larvae have entirely organic exoskeletons and calcium carbonate is introduced suddenly in one of the later moults (Bastida & Torti 1970). It may be that agnostids, if planktic, were able to shorten the larval development by reducing the amount of energy and material necessary to form the exoskeleton. A reduction of the pelagic larval phase is more common in pelagic animals than among benthic forms. The odd agnostid hypostome found by Robison (1972a) is particularly characterized by its light construction. A lightening of the exoskeleton is certainly compatible with a pelagic life. Unfortunately, not one of these characters prove that agnostids were either benthic or pelagic, although much speaks for a pelagic life. It may well be that different agnostids had different habitats.

As argued in the chapter on morphological and anatomical features of the trilobite cephalon the characteristic type of prosopon indicates that the agnostids had a morphological type of alimentary diverticula characteristic of arthropods feeding on fluids. Among extant arthropods with this mode of feeding and type of diverticula the branchiurans are particularly interesting because they resemble agnostids also in other respects. Morphologically, the agnostids are as far removed as possible from the pelagic and swimming type of crustaceans, exhibiting the caridoid facies. The agnostids, therefore, seem to be particularly poorly adapted to a free swimming mode of life. Actually, the flattened shape is shared with the branchiurans, where it is obviously an adaptation to an ectoparasitic mode of life. It is tempting to explain the shape of agnostids in a similar way. The distribution of agnostids may therefore be governed by the distribution of the eventual hosts.

The agnostids are generally supposed to have been blind. This may be true but there is also a possibility that they possessed ventral eyes. Branchiurans are unique among crustaceans in having well developed ventral eyes. If the mode of life of the two groups is so similar as tentatively suggested above, ventrally placed eyes may have been an advantage for the agnostids as well. Actually, the eyes are located quite close to the lateral border in several members of the Eodiscina, a group considered to be ancestral to the Agnostina, and it is easy to picture a transfer over the margin to the ventral side. This is hard to prove, but it may be wise to remember that there is no conclusive evidence to support the assumption that the agnostids were actually blind.

It may be noted in this connection that Öpik (1963: 55–56; Pl. 2:14, 15) described two pairs of nodes interpreted as eyes in *Discagnostus spectator*. However, there is no particular evidence in favour of the interpretation.

Some of the conditions discussed above in connection with a possibly pelagic mode of life may be examined also in relation to suspected ectoparasitic habits. For instance, the lack of known agnostid protaspids may indicate that the young hatched at a comparatively mature stage of development, a condi-

tion also found in various branchiurans, where it may be an adaptation to the ectoparasitic life. Furthermore, the peculiar hypostome reported by Robison (1972a, b) indicates that the mouth was elevated over the general ventral surface. It is tempting to suggest that there was a proboscis perhaps similar to that of branchiurans. Ultimately, it may be added that the branchiurans are considered to be good swimmers (cf. Hessler in Moore 1969:R203) and that they have a small number of trilobite-like appendages, a condition also supposed to be relevant for agnostids.

However, there are also features seemingly not fitting well with an idea of an ectoparasitic life. I am grateful to Dr. R. A. Robison of Salt Lake City for pointing out a number of such features. First, many communities in Utah and Nevada are said to contain five or six species of agnostids, which seems to be an unexpectedly high diversity if the species were ectoparasites. It may be added that Westergård (1946) found great diversities in the Middle Cambrian in Sweden, for instance 32 agnostid species in the Andrarum Limestone (with an unknown number of communities). Second, Robison points out that there is a size dispersal in sympatric agnostid species similar to that found in modern sympatric species adapted to feeding on different sizes of food. Third, the enrollment in agnostids has no counterpart in modern ectoparasites. However, the enrollment capability is characteristic of the trilobite group as a whole, whereas it is more or less exceptional in modern arthropods. Fourth, the large ventral flange on the pygidium of *Phalacroma glandiforme* (see Westergård 1946, Pl. 15:10b) and the absence of a similar flange on the cephalon would seem to prevent a good “fit” against a potential host. Robison also adds that the shape of the body behind the “head” is entirely unlike that of the branchiurans, but this can not be regarded as an argument in any direction.

Possible faunal evidence against an ectoparasitic mode of life is also found in the Upper Cambrian of Scandinavia. After the olenids, the agnostids are the most common preserved animals. In many cases they are found in such numbers that they almost cover the sediment surfaces. Ectoparasitic animals in general would not be suspected to be found in such numbers. However, extant ectoparasitic acarids may be abundant and represented by many species, a condition that throws considerable doubt on the faunistic evidence presented above (personal communication from Dr. Anders Edler, Lund). There is a difficulty in finding possible hosts in the poorly diversified fauna, but it must be remembered that we know nothing about the faunal constituents lacking hard skeletal parts.

The rich agnostid faunas in the Cambrian of Scandinavia are found in black limestones and shales with a high content of organic material which may have been derived from pelagic algae (seaweed). It is possible that the agnostids lived among the algae. It may be questioned whether they also fed on the algae. Extant acarids generally have alimentary caeca with well developed diverticula. However, acarid species

feeding on plants are exceptional in lacking diverticula (oribatids) or even caeca (Tetrapodili). Herbivorous habits therefore seem to be incompatible with strongly developed diverticula. Provided that the reticulated prosopon of many agnostids is correctly interpreted as evidence of alimentary diverticula the ectoparasitic mode of life obviously is the only real alternative, at least for the reticulated species.

Despite the presence of agnostids in the Middle Cambrian Burgess Shale of British Columbia the appendages are unknown. Many ectoparasitic arthropods have particularly strong legs for clinging to the host, while others may have comparatively weak legs in combination with sucking organs. The latter type is found within the Branchiura. The absence of preserved appendages in the Burgess agnostids may indicate a similarity to the branchiurans with respect to the development of appendages and suckers.

It may be concluded that the agnostids, or at least some of them, appear to have paralleled branchiurans and acarids in certain respects, notably in the comparably small and externally poorly segmented body, well developed alimentary diverticula and ectoparasitic habits. The enrolling ability proves that the agnostids were only temporarily attached to their hosts. The peculiar shape of the hypostome may be connected with a development of a suctorial mouth. Compound eyes, if present, may have been ventral. The appendages may have been weak and supplemented by sucking discs for the attachment to the host. Some species probably were pelagic while others may have been benthic. The larvae probably hatched at a fairly mature stage, which is an advantage in animals living free but with ectoparasitic habits.

Spinous trilobites

Strong exoskeletal spines are found in many trilobites but no single group is so characterized by spinosity as the odontopleurids. Following Dollo (1910), some authors believed that the spines kept the odontopleurids suspended in the water. They would therefore have been planktic. However, Whittington (1956) stressed that the ventrally directed spines appear to be adapted for resting on the bottom and Seilacher (1959) indicated that the spines were quite insufficient to keep an animal the size of an odontopleurid suspended. The odontopleurid case has been further discussed and elaborated by Clarkson (1969). There is not much to add to this discussion. It may be worth remembering, however, that the length of the pleural spines (but not of the accessory spines) was not only determined by the benthic habits but, more distinctly, by the demands on exact fit in the enrollment. The accessory horizontal spines, unique to the odontopleurids, must have had a protective significance. No doubt, this was also the case in many other spinous trilobites, such as *Ctenopyge*, raphiophorids and many lichids.

Larval spines

Paradoxidid larvae may provide the material for a case study (Pl. 5:7, 8). Larval stages of paradoxidids have been described by different authors, including Barrande, Matthew, Raw, Šnajdr, Størmer, and Westergård. The protaspides are characterized by fairly long spines formed by pleural extensions and generally regarded as genal, metafixigenal (intergenal), and first thoracic pleural spines (Størmer 1942:75; Whittington in Moore 1959:O131). Apart from the three pairs of large spines the test seems to be smooth.

In the early meraspis the second thoracic pleurae are also drawn out into long spines, and, with the exception of the metafixigenal extensions, the spines grow even stronger than in the protaspides. This development is seen in *Eccaparadoxides pinus* (Westergård)?, *E. pusillus* (Barrande), and *Hydrocephalus carens* Barrande (according to Westergård 1936 and Šnajdr 1958).

When the first thoracic segment was detached from the transitory pygidium the three main pairs of spines (excluding the successively more reduced metafixigenal spines) came to belong to three movably articulated tergites (see e.g. Whittington in Moore 1959, Fig. 93C, D). Later on the macropleural spines degenerated. This process began in the first thoracic segment in the three species mentioned and resulted in a stage with two pairs of spines, the genal and the second thoracic spines. This stage is illustrated for instance by Westergård (1936, Pl. 5:7, 9) for *E. pinus* and by Šnajdr (1958, Fig. 24:7, 9; Pls. 24, 25, several figures) for *H. carens*. This two spine stage is also found in other paradoxidids in which the earlier stages are unknown. This is the case in *Hydrocephalus sjögreni* (cf. Westergård 1936, Pl. 9:12), *H. minor* (cf. Šnajdr 1958, Pl. 23, several figures; the macrospine is retained in the early holaspides), and *Paradoxides gracilis* (cf. Šnajdr 1958, Pls. 12, 13, several figures of meraspides and early holaspides).

Why are the larvae of paradoxidids (and many other trilobites) provided with long spines? Many answers may be proposed, among the more plausible or popular are the following:

- (1) The spines have no special function. This is possible but not very plausible. It was probably optimal for the larvae to grow as fast as possible. Unnecessary devices would lay an extra burden on growth economy and could hardly be permitted.
- (2) The spines would retard sinking in pelagic larvae. This has often in the past been used as an argument for pelagic life even of spiny adult trilobites. However, the physical explanation only applies to microscopic objects and spiny paradoxidid larvae may be more than 10 mm long.
- (3) The spines had a balancing or steering function in swimming. This is entirely possible, but this explanation does not exclude others.

(4) The spines were used for defence. It has been found that extant pelagic carnivores commonly swallow their prey without chewing it. Many types of potential prey avoid being eaten in this way by enlarging their radius by means of long spines (cf. Thorson 1968:366–368). The spines in extant planktic larvae seem to have an exclusively protective function in many instances. This is shown by the arrangement in swimming forms such as the polychaete *Disoma*, in which the spines are turned backward in active swimming, and the decapod crustacean *Porcellana*, in which one large spine points forwards in the swimming direction and two backwards. Apparently spines are a hindrance in swimming if not longitudinally directed. At the same time, spines are obviously more effective as a protection against predators if spread out in a star-like manner as in many echinoderm larvae.

It seems reasonable to assume that paradoxiid larvae led a free-swimming life, as has been suggested by several authors for trilobite larvae in general. As seen in extant larvae, the backward orientation of spines is normal for an actively swimming animal. However, the radius or total volume occupied by the animal is increased comparatively much less in straightened trilobite larvae than in the modern larvae with which comparison can be made. This may mean either that the spines did not have a protective function, that the protective function was comparatively unimportant or that the spines were capable of diverging in some way to obtain the most efficient protective capacity.

The last explanation is very tempting for two reasons. First, the spines grew large in the early meraspis stages when the spine-bearing tergites were separated from one another by transverse articulations. This may indicate that the spiniferous larva was able to enroll and spread its paired spines in a star-like pattern. Second, enrollment is known to have a protective function in extant arthropods and is reasonably thought to have had the same function in trilobites. The possible enrollment capacity may also explain the seemingly odd and meaningless parallel and adjoining arrangement of the two macropleural spines (e.g. Westergård 1936, Pl. 4:21, 22; Whittington in Moore 1959, Fig. 93C, D). In the enrolled state the macropleural spines of the two first thoracic tergites may have diverged approximately 60°, provided that the enrollment flexure was equal and restricted to the most anterior three articulations. In larger meraspides, with a longer thorax and a larger number of articulations, the enrollment flexure was spread out over a larger number of segments, resulting in a smaller angular movement between adjoining tergites. This must mean that the advantage of macropleural spines on the two anterior-most thoracic segments was successively lost, as divergence between the spines during enrollment was diminished. This seems to explain why one of the spine pairs was reduced in late stages. Furthermore, it is natural that the spines of the second thoracic segment are retained longer as these spines diverge more

from the genal spines than those of the first thoracic segment.

The above discussion is purely theoretical as long as enrollment is not proved by actual enrolled specimens. However, enrolled larvae actually have been found. Šnajdr (1958, Pl. 24:35) figured a meraspis of *Hydrocephalus carens* in which the first thoracic tergite with its reduced spines is in contact with the cephalon. The second tergite is not seen but on the left side of the cephalon there is a forward-pointing spine which apparently belongs to the second segment. Anyway, the length indicates that it is not the genal spine of this individual. This means that there is probably a thoracic tergite below the visible remains, turned over and in a position indicating enrollment.

A second instance of probable enrollment is provided by a small holaspis of *Paradoxides gracilis*, figured by Šnajdr (1958, Pl. 12:12, 19). In this case four thoracic tergites are visible, the last of which is markedly tilted backwards, as indicated by the convexity of its rhachial part. This individual seems to have been about 12 mm long, and the fourth thoracic segment ought to be, in this case, approximately in the middle of the animal, which fits with the enrollment explanation. At this stage the thoracic macrospines are comparatively little inclined during enrollment as compared with the genal spines. The functional effectivity is therefore less than in earlier stages and this seems to be the stage where the macrospines begin to degenerate during ontogeny.

A third case of enrolled paradoxiids is found on the piece of rock yielding the original of one of Westergård's larvae of *Eccaparadoxides pinus*(?) (cf. Westergård 1936, Pl. 4:13c, Swedish Geol. Surv. orig. C394). One unfigured specimen on the slab has one thoracic macrospine pointing forward. Unfortunately this is all that can be seen from the thorax. A second specimen on the same slab exhibits the rhachis of the most anterior thoracic tergite turned upside down under the occipital ring. Both thoracic macrospines of one side are preserved and turned forwards. This is a plain case of rolling up.

To sum up, it is evident that paradoxiid larvae were able to enroll. In the enrolled state the large spines of the cephalon and the two most anterior thoracic tergites diverged strongly, increasing the volume of the individual as a protection against predators. The protective function decreased in effectivity when the enrollment flexure came to be shared by successively more thoracic tergites, added during ontogeny, and the spines were accordingly reduced. It may be added that a similar series of events is found in other trilobite groups, for instance among redlichiids and ellipsocephalids.

Trilobite appendages

The bifid appendages of trilobites have recently been restudied (Bergström 1969, 1972) and a treatment of the appendages of the Devonian *Phacops* and *Asteroptyge* is in preparation (Stürmer & Bergström). A sum-

mary of the results may be motivated here, particularly as the interpretation of the trace fossils depends on the state of knowledge of the appendages.

One pair of uniramous multisegmented antennae appears to be universally present, if it is possible to make an extrapolation from the approximately 20 species with appendage remnants which are known today. Pygidial cerci similar to the antennae are known only from *Olenoides serratus* (Rominger) and were certainly not developed in several other forms.

The biramous appendages have two subequally strong rami, a condition similar to that in crustaceans where the rami are called endopod(ite) and exopod(ite). However, the bifurcation is obviously comparatively closer to the body in trilobites than in crustaceans, indicating that the rami in the two groups are not homologous structures. When the walking leg (inner ramus) of a trilobite is considered as the only main ramus, the outer ramus has a position corresponding to that of an exite in crustaceans (Størmer 1939:156; Størmer in Moore 1959:O8; Manton in Moore 1969:R7; Bergström 1969, 1972). The term exite has therefore been used. Although I have not been able to see any precoxa in well preserved material of *Phacops* sp. it can not be stated that trilobites lacked this podomere or that the exite is an epipodite and not a pre-epipodite. The trilobite exite is probably not homologous with crustacean exites. Anyway, the term appears better than the term exopodite, which leads to a false comparison between the bifid appendages of trilobites and crustaceans. The inner ramus is called a telopodite in accordance with common usage.

The telopodite may be comparatively straight, as in *Olenoides*, *Kootenia*, *Isotelus*, and *Triarthrus*, or provided with a more or less pronounced "knee", as in *Phacops* and *Cryptolithus*. In the two latter forms the telopodite is provided with a fringe of bristles, which evidently acted as a "snow-shoe" in the muddy environment in which these two trilobites lived. As far as known the telopodites of different trilobites had from one to three distal spines. In *Phacops* sp. the medial side of the telopodite is also provided with

spines, which probably were used to catch and keep hold of a prey (Seilacher 1962:220; Bergström 1969:408). Spines are found in the same position in *Cryptolithus* (Fig. 15).

The exites exhibit even wider morphological variation. In principle an exite has a shaft from which long and thin structures, formerly thought to be gill filaments, extend at least on one side. The "gill filaments" were found to be strong spines, which were only slightly distorted by post-mortem and diagenetical processes and in some cases were used for raking the sedimentary surface (Bergström 1969, 1972). In *Cryptolithus* the exite is rake-like, with very long pendent spines, arranged parallel with one another and with the tips on a straight line. In *Phacops* and *Ceraurus* the spines are also pendent but radiate from a flattened shaft. The tips of the spines lie on a curve, and the entire exite is fan-shaped. While the rake-like exite is likely to be responsible for the observed scratching of the sedimentary surfaces, there is no easy functional explanation of the fan-shaped exites. However, it is possible that they were primarily used for swimming and perhaps also for generating a current of oxygenated water over the gills, which may have been situated on the soft ventral side of the body, lateral to the appendages.

A morphologically very different type of exite is found in *Olenoides*. The shaft consists of a very long blade-like segment and a smaller triangular distal plate. The posterior side of the long segment carries fairly long sub-parallel spines which are not pendent but directed backwards and upwards over the neighbouring exite shaft. The distal triangular segment carries no spines but a posterior row of long setae. The arrangement was compared with that of the filtering appendages of crustaceans like *Branchinecta* and *Daphnia*, and a similar function was suggested (Bergström 1969:404—408). The supposed lateral position of the coxae and the supposed absence of trilobite jaws caused me to propose that the filtered food was transported forwards to the mouth along two lateral paths. However, new evidence regarding the presence of jaws in trilobites and regarding the position of the coxae in trilobites no longer necessitates the two-path explanation. It therefore seems reasonable to suppose that the food was transported to the mouth medially in filter-feeding trilobites.

The exite of *Triarthrus* is fairly similar to that of *Olenoides*. The main difference lies in the extreme slenderness of the shaft in the former. I find it difficult to judge if the *Triarthrus* exite was used for filtering or not. Probably the exite of both *Triarthrus* and *Olenoides* played an important role in swimming. The exite of the former may be characterized as feather-like, that of the latter as comb-like.

Appendages are known also from olenellids, asaphids and odontopleurids (cf. Harrington in Moore 1959:O76), but the remains are poorly preserved. Remains described by Moberg (1907) may represent trilobite appendages, but the interpretation is not reliable.

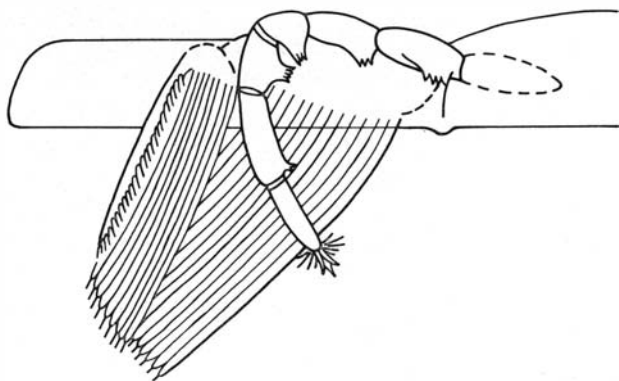


Fig. 15. Right half of a thoracic segment in *Cryptolithus bellulus* (Ulrich) showing an appendage with telopodite and rake-like exite branches. Modified from Bergström (1972).

Trilobites and trilobite trails

Attribution of trace fossils to trilobites

Today it cannot be doubted that many Palaeozoic burrows of the bilobite type as well as surface trails were made by trilobites. The assignation can be made with a high degree of probability in many cases and with objective certainty in one case. In other instances, particularly in small bilobites without claw marks, it is possible that trilobites were the actors, but it may equally well have been other arthropods or perhaps gastropods. There is no reason to believe that all trace fossils of one particular morphological type was made by closely related animals, and this further complicates the case. Future studies will probably bring out many new facts, which may provide a sound basis for a discussion.

As is well known, it is nearly axiomatic that trilobite trace fossils are not found together with abundant trilobite remains. The general attribution to trilobites is therefore in most cases based on indirect evidence. The main points are listed below:

(1) The stratigraphic distribution of supposed trilobite trace fossils corresponds roughly to the distribution of trilobites. The trilobites are actually known from younger strata than their supposed traces, but this is explainable by the scarcity of the last representatives.

(2) Osgood (1970) reports three instances of *Flexicalymene meeki* in burrows of *Cruziana pudica* type. *C. pudica* is regarded to be a "typical" bilobite of the type generally attributed to trilobites.

(3) Burrows are commonly broadly oval in outline like many trilobites but unlike most other arthropods. In some cases the burrows show impressions of genal and pleural spines fitting only with the trilobite morphology.

(4) Burrows as well as surface trails show serial homopody with a fairly long file of appendages. This condition fits with the leg arrangement in trilobites, aglaspids, some crustaceans, myriapods, and some early arthropod groups.

(5) In surface trails the individual tracks are typically arranged in one row on each side, the two of which diverge forwards. This divergence is consistent with the knowledge of appendage morphology in trilobites but may also be expected in aglaspid trails. It is possible that some trilobites deviated on this point. In thysanopeltids like *Eobronteus* the rhachis as well as the entire thorax widens backwards which may indicate that the posterior legs were longer than the anterior ones. The small and triangular pygidial rhachis indicates that the pygidial appendages were reduced, an explanation that would fit well with the reversed size trend in the thorax. Anyway it is wise

to remember that track sets diverging backwards must not necessarily be rejected as trilobite trails.

(6) Both surface trails and burrows commonly show marks from at least two claws or in some trails from a ring of spurs. Identical arrangements may be found among trilobites and chelicerates but are alien to crustaceans in general.

(7) The scratches from an outer set of appendage branches in some burrows indicate the presence of an exite of the type found in *Cryptolithus* and some other trilobites.

Trilobite trails

Knowledge of trilobite trails has greatly increased in recent years particularly by the systematic work by Professor A. Seilacher. An important trigger to this research was also the trace fossil conference in Liverpool in 1970, largely organized by Dr. P. T. Crimes.

Trail types which may be wholly or partly referred to the activity of trilobites may be grouped according to ethological characters. One important group of trails is the burrows, treated particularly by Seilacher in several publications. The burrows have been divided into several ethological subgroups. The concentrated domichnia and subichnia (ethological terms from Seilacher 1953) include the ichnogenera *Cruziana* d'Orbigny, 1842, *Rusophycus* Hall, 1852, and to some extent *Iso podichnus* Bornemann, 1889. Band-like trails (repichnia and pascichnia) include *Cruziana* d'Orbigny, 1842, *Crossopodia* M'Coy, 1851, *Roualtia* de Tromelin, 1877, *Crossochorda* Schimper, 1879, *Iso podichnus* Bornemann, 1889. Subsurface burrows (fodinichnia) are regarded to include *Trichophycus* Miller & Dyer, 1878, *Teichichnus* Seilacher, 1955, and *Cruziana ancora* Seilacher, 1970. Of these ichnogenera *Crossopodia* and *Crossochorda* are generally considered as synonyms. *Cruziana* and *Rusophycus* have been united by Seilacher (1970), who actually referred all trilobite burrows to *Cruziana*. This fusion has not been unanimously accepted (cf. Orłowski, Radwański & Roniewicz 1971:344).

A second group of trails which at least partly can be assigned to trilobites is the surface crawling, walking, or swimming trails. These include the following ichnogenera: *Protichnites* Owen, 1852, *Diplichnites* Dawson, 1873, *Asaphoidichnus* Miller, 1880, *Petalichnus* Miller, 1880, *Teratichnus* Miller, 1880, *Trachomatichnus* Miller, 1880, *Merostomichnites* Packard, 1900, *Incisifex* Dahmer, 1937, *Dimorphichnus* Seilacher, 1955, *Monomorphichnus* Crimes, 1970, and *Allocotichnus* Osgood, 1970. It appears unnecessary to retain all these form genera, several of which are based on mere individual anomalies. *Protichnites* is generally reserved for walking trails (trackways) with imprints of trailing pygidial spines (or possibly cerci). Other walking trails including those with asymmetry caused by current action or by a slope, and including those with tracks arranged in neat rows or in disorder,

may be called *Diplichnites* (synonyms: *Asaphoidichnus*, *Petalichnus*, ?*Teratichnus*, ?*Trachomatichnus*, and ?*Merostomichnites*). *Dimorphichnus* includes asymmetrical grazing trails. There is no name available for trails composed of only exopodite tracks. If there is any particular need, *Monomorphichnus* may be used for trails in which currents are the dominating moving agents. *Incisifex* is poorly known.

In summary, trilobite trails may be concentrated more or less deep burrows, extended superficially burrowed trails, or superficial trackways. The trackways were produced by the telopodites, while the burrowed trails were made either with the telopodites or with the exites, or with both telopodites and exites.

The orientation of burrows as compared with the orientation of the burrowing trilobites has been discussed recently by Crimes (1970a) and Birkenmajer & Bruton (1971). The authors agree that an individual V in the herringbone pattern in cruzianiform trails has its open side facing in the same direction as the cephalon of the burrowing trilobite. However, Birkenmajer & Bruton occasionally propose the opposite direction for the same type of trail (1971, Fig. 8, right extremity). In the same trail the tail spines made impressions offset to the lower part of the trail as this is figured. This means that the current active when the trilobite was moving came from the upper side of the figure, i.e. in a direction opposite to that proposed by Birkenmajer & Bruton. The new interpretation provides that the trilobite was turned slightly more towards the current than was the resulting trail. This is a hydrodynamic necessity as long as the animal moved head first. When the animal made the rusophyciform burrow to the left it still had the same current caused inclination to the axis of the trail behind. The relation between the rusophyciform burrow and the pygidial spine scratches does not provide any clue to the order of events. The deepest marks are preserved irrespective of the relative age. It should be added that the individual tracks of the *Protichnites* trail in the middle indicate that the animal was actually pulled towards the left by the appendages. In my opinion the entire trail therefore shows that the trilobite was constantly facing towards the left. This means that the wide portion of the rusophyciform burrow corresponds to the anterior end of the trilobite, a view held by Crimes (1970a) but partly opposed by Birkenmajer & Bruton (1971). Also the additional evidence given by the latter authors seems to be questionable and I prefer to accept the view given by Crimes as a general rule.

The trails and their morphology ought to be connected with particular trilobites and their functional morphology as far as possible. Correlation between particular trail types and their producers is difficult and successful only in exceptional cases, for instance where a trilobite is found in its burrow or morphological details of the trail are particularly elucidating. A few selected cases will be studied below.

Cruziana dispar, a burrow made with telopodites.—

The trace fossil *Cruziana dispar* Linnarsson, 1869, was originally reported from the Lower Cambrian *Eophyton* sandstone (= *Mickwitzia* Sandstone) of Kinnekulle, Billingen and Lugnås in Västergötland, Sweden. The burrow, considered by Linnarsson as a trilobite trail, was figured for the first time in 1871 by the same author. Of Linnarsson's figures, one (Fig. 19) shows the relatively rare band-like cruzianiform trail, whereas two (Figs. 17, 18) show concentrated rusophyciform trails.

The Västergötland *Cruziana dispar* has been repeatedly figured and discussed, for instance by Seilacher (1959, 1970) and Bergström (1968). Similar trails, which may be referred to under the same name, have been described from the Lower Cambrian of the Holy Cross Mountains, Poland, by Radwański & Roniewicz (1963), and Orłowski, Radwański & Roniewicz (1970) and from Digermul Peninsula at Tanafjord, northern Norway, by Banks (1970). Finds have also been made in the Lower Cambrian Norretorp Formation at Röstånga in Scania, Sweden, by Dr. S. Laufeld, and at Simrislund in Scania by me.

Because of the association in Västergötland with *Strabops hamiltoni*, the only arthropod known from the *Mickwitzia* Sandstone, Bergström (1968) suggested that this animal was the trail-maker. However, this suggestion is contradicted by conditions in Poland, where *Cruziana dispar* occurs together with species of *Holmia*, *Schmidtellus*, *Kjerulfia*, and possibly also other olenellids, and there are also other and smaller trilobites. Orłowski, Radwański & Roniewicz (1970, pp. 350, 354) take the Polish association as an indication that the trails were made by olenellids (the other trilobites are too small). At the new locality in Simrislund the trails are associated with *Schmidtellus mickwitzii torelli* (Moberg), and the two species *Wanneria? lundgreni* (Moberg) and *Holmia* n.sp. (Bergström, in preparation) are found at a distance of a few kilometres in the same formation. As the divergent views regarding the origin of the burrows in both cases are based only on the associated fauna and as the trails also bear evidence of large prey hunting otherwise not reported from trilobite trails, the matter cannot be solved without additional analysis.

Cruziana dispar is included in Seilacher's (1970) *dispar* group, which is said to be characterized by a dominance of resting tracks (cubichnia) or nests (domichnia) which were formed by bidirectional scratching with the telopodites. In this way the eroded material was transported out of the track both backwards and forwards at the same time. Furthermore, the division between the anterior proverse scratchings and the posterior retroverse markings is said to be obvious. The telopodites are said to have two main and two small anterior claws.

A well preserved specimen was illustrated by Bergström (1968, Fig. 7; cf. Pl. 5:12–14). In this specimen the anterior individual tracks reveal two strong distal claws, possibly with a small one in between. A series of up to five or more fine parallel scratches in front of each main pair indicates the presence of a

number of setae on the anterior side of the telopodite. It is noteworthy that this morphology of the track appears to be typical for the *fasciculata* group of Seilacher (1970). The telopodite was inclined strongly backwards and digging was performed not only by the distal claws but also by the anterior setiferous (or spinous) side. The inclination is probably intimately connected with the proverse direction of the anterior scratches and with the strong backward arching of the body (cf. Seilacher 1970, Fig. 5c). Which one of these two features is dependent on the other is difficult to judge. The posterior telopodites were held comparatively vertically, with the result that only scratches from the distal claws can be seen. The spacing of individual tracks is fairly even, and it is difficult to distinguish the exact boundary between proverse and retroverse scratchings (Pl. 5:12). This is also the case in many other specimens, although there tends to be some crowding of scratches in the deepest part of the burrow.

Regarding the excavated sand and mud, Seilacher (1959, 1970) appears to believe that it was transported out of the burrow in two directions. This may be correct, but there may also be other possible explanations. First, the proverse direction may be connected with feeding on relatively large animals which were brought towards the mouth with the aid of the telopodites. Second, it is tempting to suggest that there was a consequent water current from one end of the body to the other regardless of the direction of the telopodite tips. This would be more effective both for breathing and for sediment transport than a bidirectional water current.

It is particularly interesting to note a common close association between *Cruziana dispar* and various other burrows in Västergötland (Martinsson 1965:211; Bergström 1968:499–500). Thanks to Drs. Orłowski, Radwański and Roniewicz of Warsaw I have been able to satisfy myself that this is also the case with Polish *Cruziana dispar*. The association is not restricted to occurrence in the same beds. Conspicuously common is that even when the ichnofauna is sparse the deepest part of the *C. dispar* burrow ends in another trail. In many cases the digging arthropod has turned around during the burying procedure, so as to form an irregular hole similar to that of *Cruziana navicella* Fenton & Fenton (1937). Commonly also the associated trail ends just beneath the *C. dispar* burrow and the trail-maker has disappeared without a trace. In one case the cause of the disappearance is particularly obvious (Fig. 16; Pl. 5:10; cf. Pl. 5:9). Here the burrowing arthropod has obviously located its prey, burrowed down to it, and caught it. The trail of the prey is abruptly ended, and the irregular manipulation of the arthropod legs around the end is neatly recorded. There can hardly be any doubt that the arthropod localized its prey actively. This is the only possible explanation to the common position of the *Cruziana* burrow exactly over the other burrow. Interestingly enough, the burrows of the hunter and of the prey are, more often than not, more or less

parallel with the head end in the same direction. This indicates that the localization was performed with the aid of sense and not with smell or taste.

It is evident that the rusophyciform *Cruziana dispar*, at least in some instances, is a hunting or feeding burrow rather than a resting burrow. This is suggestive of Glaessner's (1957) idea that *Cruziana*, *Rusophycus* and bean-shaped *Isopodichnus* forms all are feeding burrows.

Cambrian homopod arthropod groups are few and, in practice, most cruzianiform and rusophyciform trails are believed to be produced by trilobites, without much discussion. However, in this particular case the type of trail is associated only with the enigmatic *Strabops hamiltoni* (Størmer) in one area and with a number of trilobites in other areas.

Strabops hamiltoni is commonly thought to be an aglaspidid, although this was by no means taken for granted by its author. New research (Bergström 1971) indicates that *Strabops* may be distinct from chelicerates and trilobites, though still an arachnomorph. With the apparently fairly uniform homopod construction of the appendages of early chelicerates as well as of trilobites (cf. Bergström 1969), there is reason to suspect that also *Strabops* had a similar uniform series of legs. This makes *Strabops* a potential producer of "trilobite" trails. However, the curved bottom of the deep *C. dispar* burrows shows that the producer must have been able to bend backwards into an arch (cf. Seilacher 1970, Fig. 5c). Owing to the high convexity and the fairly narrow tergites without any trace of hinge lines or socket and process joints, it is safe to conclude that this was impossible for *Strabops*. This rules out *Strabops* as a possible producer of the deep *C. dispar* burrows (although not of shallow burrows).

Among early Cambrian trilobites outside the *Redlichia* realm practically only olenellids were large enough to make burrows of the size of *Cruziana dispar*. Burrowing for shelter is an attractive idea as long as the burrows are regarded as resting tracks and the olenellaceans are thought to be devoid of enrolling capacity. This purpose may be correct in *Redlichia* with a presumed ability to make a shallow rusophyciform burrow (cf. Seilacher 1955:363–364; Fig. 5:3) and lack of enrolling capacity. However, *C. dispar* was shown above to be at least partially a hunting-burrow rather than a shelter. Moreover, many olenellaceans were able to enroll more or less completely. The most elucidating evidence comes from a study of articulation mechanisms. Among species of *Wanneria*?, *Kjerulfia*, *Schmidtellus*, and *Holmia*, the four olenellacean genera known from Poland and Scania, only *Holmia kjerulfi* (Linnarsson) is known to have rhachial rings which are distinctly narrower in the medial part than at the sides and also moderately vaulted. This morphology indicates an ability to bend backwards far beyond the straightened body posture, an ability characteristic to the animal which produced the *Cruziana dispar* burrow. Certainly this is not conclusive evidence that the tracks were made by *Holmia kjerulfi*, but they must have been made by a trilobite

with the same kind of rhachial specialization. *C. dispar* is commonly wider than any known specimen of *H. kjerulfi* and may fit better with the size of *H. grandis* Kær or *H. n.sp.* Bergström, 1973 (in preparation), but these species are comparatively poorly known.

Lower Cambrian telopodite and exite trails.—In 1937 the Fenton sisters described three kinds of burrows from Alberta under the names *Cruziana jenningsi*, *C. irregularis*, and *C. navicella*. The two latter ichnospecies were found in the Lower Cambrian Lake Louise "Shale", while *C. jenningsi* was found in a moraine boulder which is thought to have come from the same formation. After an analytical discussion the three forms were suggested to have been made by species of *Olenellus* and *Mesonacis* (the latter is now regarded as a junior synonym of the former). A burrow referred to *C. cf. irregularis* was described from the Lower Cambrian of Pakistan by Seilacher (1955). Seilacher (1970) provisionally united the three rusephyciform burrows under the name *C. jenningsi*.

Another interesting trail was described by Cowie and Spencer 1970, Pl. 1b and 2d, e) from the Lower Cambrian Ella Island Formation of East Greenland. This trail is similar to the specimen from the Middle Cambrian Flathead Formation figured by Walcott (1918, Pl. 39:3, 4) and referred by Seilacher (1970: 460) to *C. arizonensis* Seilacher. However, as no type specimen of this ichnospecies has been selected and the other specimens figured by Walcott (1918, Pls. 39:1, 2; 41; these specimens are from the Middle Cambrian Tapeats Sandstone) are rather dissimilar, the name is not very useful. As the Tapeats Sandstone trails were listed first by Seilacher and as these trails fit best with the original diagnosis of *C. arizonensis* Seilacher, 1970, the specimen figured by Walcott (1918) as Pl. 39:1, is here chosen as lectotype. I prefer to refer to the specimen from the Flathead Formation as *Cruziana cf. semiplicata*. This name may also be used provisionally for the Lower Cambrian trail described by Cowie & Spencer (1970). Needless to say,

the similarity in name does not imply that the trails were made by the same or even closely related trilobites.

The trails discussed below belong to Seilacher's (1970) *C. semiplicata* group, which is particularly characterized by exite "brushings" lateral to the telopodite lobes of the trail.

Of the burrows named by Fenton & Fenton (1937) *Cruziana jenningsi* was by far the best illustrated and described. Distinct imprints appear to have been caused by movements of the anterior border of the cephalon and of the genal spine, as suggested in the description. An impression of the thoracic macropleura is also mentioned but is hardly evident from the drawn figures. The authors stress the distinction between relatively coarse anterior scratches, of which there are four within five mm, and finer posterior scratches, of which five to seven may be counted within five mm. From the original Fig. 2 it appears that there is no gradation between the two areas. Instead, there is obviously a fairly sharp boundary between them. This indicates that the telopodites may be responsible for the anterior tracks, while the posterior scratches were probably made by the exites. In addition, it is seen from Fig. 2 (Fenton & Fenton 1937) that the anterior scratches are arranged in bunches which narrow distinctly towards the midline. The narrowing may indicate that only a few scratches were made by the end of the telopodites, while additional ones were made by setae or spines of podomeres proximal to the distal tip. A similar condition is seen in *Cruziana rugosa* and was discussed in connection with that burrow.

The Greenland Lower Cambrian *Cruziana cf. semiplicata* described by Cowie & Spencer (1970, Pls. 1b; 2d, e) is a band-shaped trail with a pair of telopodite lobes bordered laterally by comparatively smooth lobes of variable width. In the specimen on Pl. 2d the fine lineation of the smooth lobes may be seen between the coarse telopodite scratches on the right side. Here the exites have touched the bottom surface but the action was not strong enough to sweep away the telopodite imprints. Evidently the exites were not digging but merely touching the bottom.

Both the trails from Alberta and those from East Greenland are associated with olenellaceans, though not in exactly the same beds. *Olenellus* species were supposed by Fenton & Fenton to have made the Albertan burrows, while Cowie & Spencer state that species of *Olenellus* and *Wanneria* match the Greenland trails in size. No known trilobites in either region except olenellaceans reach the size necessary for making the trails in question. If actually the imprints of a macropleural spine is visible, as stated by Fenton & Fenton in one case, the olenellacean explanation appears even more convincing. With regard to the faunas of the regions, I believe that it is fairly probable that the Albertan burrows were made by olenellids belonging to the Olenellidae, while the Greenland trails may have been made by olenellaceans belonging perhaps to the Olenellidae or Holmiidae. Though the trails

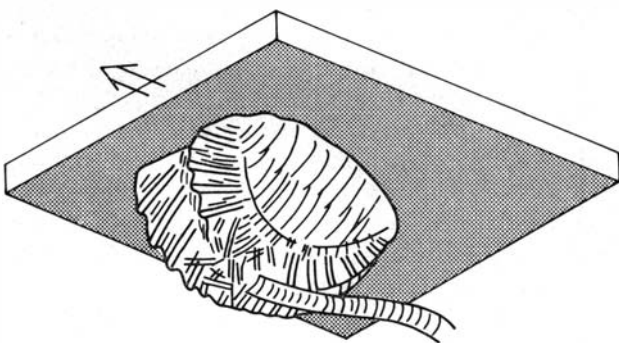


Fig. 16. Cylindrical burrow ended at the bottom of trilobite hunting burrow (*Cruziana dispar* Linnarsson) from the Lower Cambrian of Sweden. Irregular telopodite tracks in front of the cylindrical burrow indicate where the trilobite caught its prey. Both animals had their heads oriented in the direction of the arrow.

are of different types, probable exite tracks in both instances indicate the presence of long exite spines, which were strong enough to stir up the sediment surface.

Upper Cambrian telopodite and exite trails.—The rusophyciform burrow *Cruziana polonica* (Orłowski, Radwański & Roniewicz), as defined by Seilacher (1970), has been found in the supposed Upper Cambrian of the Holy Cross Mountains, Poland and of north Wales. Descriptions are given by Radwański & Roniewicz (1963), Orłowski, Radwański & Roniewicz (1970), and Crimes (1970a, b). In both areas *C. polonica* occurs together with *C. semiplicata* Salter and the two trails have been supposed to have been made at least partially by the same animal. That this may be the case, in some instances, is conclusively shown by Crimes (1970a, Pl. 12:a, b; 1970b, Pl. 5:e). Both in Wales and in Poland, the trails are regarded as produced by olenid trilobites.

Cruziana polonica was included in Seilacher's *C. carleyi* group, whereas *C. semiplicata* was included in the *C. semiplicata* group. The most distinctive character of *C. polonica* is the central field, which is divided into quadrangular paired areas, which apparently mark the position of the coxal parts of the appendages. In burrowing, the trilobite could hardly avoid moving the coxae together with the telopodites. The coxal imprints are therefore, in all probability, both longer and wider than the coxae themselves. This is particularly evident in cases where the quadrangles meet one another both medially and longitudinally; the coxae of a corresponding size would have been blocked against one another and unable to move. The most important conclusion that can be drawn from this kind of morphology is that the trilobite coxae or coxal chewing processes were evidently able to meet along the midline. Actual trilobite material has not been conclusive on this point (cf. Raymond 1920; Størmer 1939, 1944; Bergström 1969). Another important conclusion is that the rusophyciform *C. polonica* burrows actually are resting or hiding burrows rather than feeding burrows as the animal definitely was not able to feed efficiently with compact sediment filling the space up to the coxae and even intruding between them.

The cruzianiform *Cruziana semiplicata* and similar trails were certainly formed by a variety of trilobites, but what is particularly interesting is that *C. polonica* and *C. semiplicata* may grade into one another and, therefore, sometimes was made by one and the same animal (Crimes 1970a, b). *C. semiplicata* is distinguished by a pair of inner bands with coarse telopodite scratchings surrounded by an outer pair with fine longitudinal striation and a marginal line, probably formed by genal or pleural spines. The conclusion that the appendage exites of at least some trilobites were stiff structures rather than soft gills (Bergström 1969, 1972) has made it easy to accept ichnological markings as being made by exites. A corresponding division of exite and telopodite tracks is not visible in *C. po-*

lonica burrows and it is possible that the telopodites alone were used for burrowing in that case (Crimes 1970a:63). However, the evidence for this is not entirely conclusive. Remarkably enough, clear telopodite scratchings are not typical to *C. semiplicata* trails in the same sediment surfaces. Furthermore, imprints of genal spines can commonly be seen without any cover of exite imprints (Radwański & Roniewicz 1963, Pl. 2, Fig. 8; Crimes 1970a, Pl. 11b; 1970b, Pl. 5c; Orłowski, Radwański & Roniewicz 1970, Pl. 3b, e, f). As the exites are long enough to reach to the ground in the shallow trails, it is reasonable to suppose that their tracks are also represented in the rusophyciform burrows. It is even possible that the exite activity is responsible for the relatively smooth surface over the whole of the two paired bands, particularly if the series of exites embraced the telopodites like a mantle as they appear to have done in phacopids (cf. Broili 1930; Stürmer & Bergström, in preparation) and cryptolithids (Bergström 1972). This suggestion is strengthened by a specimen figured by Orłowski *et al.* (1970, Pl. 3:f). Here, obviously, telopodite scratch marks are present medially on the right side of the burrow, whereas the lateral sides are smooth. In the anterior end there is an isolated ridge just on the inside of the main right lobe of the specimen. The isolated ridge may be a remnant of telopodite activity and the main lobe, or at least its surface, may be formed by the exite "mantle". One Polish specimen in the collections in Lund has distinct fine longitudinal striation over the pleural spine imprints and the side of the adjoining burrow lobe, actually indicating exite sweeping. However, the striae over the pleural spine imprints can not have been formed until after the trilobite left the deepest position in the burrow.

In Poland, *Cruziana polonica* and *C. semiplicata* are accompanied by surface trackways of *Diplichnites* type. *Dimorphichnus* has also been reported (Radwański & Roniewicz 1963; Orłowski *et al.* 1970) but the fragmentary specimens thought to belong to this type of feeding trail probably are only casual asymmetric imprints. Thanks to kind guidance by Drs Orłowski, Radwański and Roniewicz, I have been able to collect some *Diplichnites* specimens from Wielka Wiśniówka. These specimens indicate the same size order of the trail-maker as *Cruziana polonica* and it is quite possible that the trails were made by the same trilobite species.

The trail-maker may be recognized with some degree of confidence. In the supposed Upper Cambrian of Poland, rusophyciform burrows are dominantly of two sizes, a small one being up to a few cm long (cf. Radwański & Roniewicz 1963, Pl. 3:2) and a large one measuring about ten cm in length (cf. Radwański & Roniewicz 1963, Pl. 2; Orłowski *et al.* 1970, Pl. 3; 1971, Pls. 1—6). In contrast to the large rusophyciform burrows, the small ones appear to be feeding burrows with distinct tracks of the telopodites. The profound difference makes it very probable that the producers were not small and large individuals of one species but individuals belonging to different species.

The large rusophyciform burrows, *Cruziana polonica*, match the trilobite "*Olenus*" *rarus* Orłowski in size, whereas the only other trilobite present at Wielka Wiśniówka, "*Protopeltura*" *olenusorum* Orłowski, matches the small burrows in size. The approximate shape of *C. polonica*, including the imprints of pleural spines, appear to be the same as that of "*Olenus*" *rarus*. I therefore agree with Orłowski *et al.* (1970, 1971) that there are strong reasons to suspect that "*Olenus*" *rarus* made the *Cruziana polonica* burrows and possibly also *C. semiplicata* trails. However, a crucial point is the generic and suprageneric identification of the two trilobite species occurring with the trace fossils. The pleurae of "*Olenus*" *rarus* as well as of "*Protopeltura*" *olenusorum* indicate that these trilobites belong to the Ptychopariida (as defined herein) (cf. Orłowski *et al.* 1970, Pl. 3a, d; Orłowski 1968:276 and Pl. 7:12, 13). The cephalic characters, including the blunt anterior end of the glabella, indicates that "*O.*" *rarus* belongs to the Acrocephalitinae, probably to one of the Upper Cambrian genera *Pesaia*, *Cliffia* or *Paracrocephalites*. Also "*P.*" *olenusorum* appears to be a solenopleuracean.

In Wales the beds with *Cruziana polonica* and associated *C. semiplicata* are devoid of body fossils. On the basis of exoskeletal impressions, Crimes (1970a:67 and Pl. 11b; 1970b:119 and Pl. 5c) suggested that the trails were made by one or more species of olenid trilobites. However, whereas the trace fossils indicate that the genal spine of the trail-maker was fairly strong, Henningsmoen (1957) pointed out that a slender needle-shaped genal spine is particularly characteristic of olenids. Thus, also in Wales the suggestion of olenids as burrowers is unwarranted and solenopleuraceans is a more plausible alternative.

Exite trails.—*Cruziana rugosa* and *C. furcifera* were both named by d'Orbigny in 1842. The Lower Ordovician *C. rugosa* is considered as generotype of the ichnogenus *Cruziana*, and its morphology and mode of formation is therefore of particular interest. Most recently the *C. rugosa* and *C. furcifera* have been treated by Crimes (1968, 1970b), Seilacher & Crimes (1969), Seilacher (1970), and Bergström (1972).

Cruziana rugosa is characterized by scratches organized into sets or bunches of up to about ten or more. The scratches are identical morphologically through the set and, contrary to the definition of the *C. rugosa* group (Seilacher 1970), the scratches within each set appear to be almost parallel with only a small divergence in some instances. Moreover, the beginning and the end of each set form straight lines. The uniformity is a constant feature in all trails I have seen and provides a strong indication that the individual sets were formed by a single comb-like organ and not by isolated but coordinated appendages. The latter alternative is also excluded because the serially arranged appendages in trilobites could definitely not be put down to form straight transverse lines of tracks.

As the known trilobite appendages seem to consist of two rami it must not be taken for granted that the scratch sets were made by the telopodites. The exites were shown by Bergström (1968, 1972) to have been fairly tough structures with probably a function in moving, feeding and aerating the gills, at least in some trilobites, but possibly without gill function. The reconstruction of the appendages of *Cryptolithus* (Fig. 15) shows a comb-like exite, with the long spines ending at a constant level. An exite of this type would be a perfect organ for producing sets of scratches like those seen in *C. rugosa*. The bristles at the end of the long spines would be responsible for the distal keel in the individual tracks (cf. Seilacher 1962, Pl. 25:4). On the other hand the telopodite morphology needed to produce the scratches would be quite aberrant and unlike anything seen among arthropod walking legs (cf. Seilacher 1962, Fig. 2, *Iliaenus*). There is nothing *a priori* saying that telopodites must have been used in all trilobite burrowing, and distinct evidence from *C. semiplicata* and other trail types shows that exites actually left impressions in some cases. It is therefore necessary to consider the attractive possibility that *Cruziana rugosa* trails were formed exclusively with the aid of the exites.

If the trail was made by the exites of a forwardly inclined trilobite, two main possibilities exist. Either burrowing was performed by only one pair of exites, which at first would appear plausible from the regular morphology of the trail, or several pairs of anterior exites worked together. The latter alternative would create by far the more effective burrowing and it is still probable that the persistent morphology of the trail would be due mainly to the activity of one exite pair, namely the most posterior one digging last and deepest. In some cases imperfect sets between the main ones indicate persistent scratches formed by other exites than the most posterior ones, as in Seilacher's (1962) Pl. 25:4. The numerous sets of scratches indicated in the deep burrow figured by Seilacher (1970, Fig. 2b) also indicate that several pairs of anterior appendages cooperated in burrowing. Thus the evidence is uniform, so far. The divergence of tracks within a set found in some instances is easily explained as the result of a rotating movement of the exites in relation to the scratching direction. Regarding the telopodites, there is no positive evidence in the trails. If not reduced, they may have been kept inside the exite mantle, at least during burrowing.

According to Seilacher (1970) the ichnospecies *Cruziana furcifera* and *C. goldfussi* can be safely coupled with *C. rugosa* in such a way that the same animal could produce the former two trails posteriorly and the latter anteriorly under specific conditions. It is therefore natural to question if the former trail types were really formed by telopodite activity, as argued by Seilacher, or by exite movements. *C. furcifera* is much more irregular than *C. rugosa* and it is commonly difficult to recognize distinct sets of scratches. However, in a Welsh trail figured by Seilacher & Crimes (1969, Pl. 1:5) and Crimes (1970b,

Pl. 2a) there is a distinct set of at least seven short scratches in the front end of the left side. This set looks convincingly similar to sets in *C. rugosa*. The irregularity of the scratchings is obviously caused by the overlapping work of the exites, which worked shallower than in *C. rugosa*, without extinguishing completely the pattern formed by the exite pairs just in front.

In the case of *Cruziana rugosa*, Seilacher (1970) suggests that the trail was made by a trilobite keeping the anterior part of the body in a low position. The evidence for this procline posture is not affected by the change in interpretation of the burrowing appendages. Evidently the burrowing trilobite worked fairly deep into the sediment, probably with much of the body below bottom surface level. In order to reach the sediment in the front end of the burrow with the appendages the cephalon must probably have been raised along its anterior margin. This is not the case in *Illaenus* which has been suggested to be the trail-maker. On the contrary, when an *Illaenus* individual is in a horizontal position the front side of the cephalon forms a steep wall reaching far beneath the level of the ventral side of the trilobite (cf. Siegfried 1939, Fig. 1). Pushing away the sediment with this large flattened wall (morphologically very different from the shield of a xiphosurid) must have been impossible except in very loose sediment. Moreover, the front forms a shield beyond which it must have been impossible to reach with the appendages. Therefore it appears safe to conclude that *Illaenus* was not able to burrow deep in the sediment head end first. This manner of burrowing is also unlikely for a trilobite thriving in reef environments, which is the case with many illaenid species. Still morphological details, including the broad rhachis and the smooth shell surface, indicate that at least many illaenids were burrowing animals, as concluded in another place.

Instead, the *Cruziana rugosa* trails may have been made by a trilobite with the general shape of a calymenid or homalonotid trilobite. Great strength in the muscles working on the coxae is indicated by the well developed appendifers in calymenids and by the wide rhachis, allowing a large attachment area of the coxae in homalonotids. Moreover, the surface is smooth, particularly in homalonotids. Another strong argument is the shape of the cephalon which, when seen in anterior view (cf. Harrington *et al.* in Moore 1959, Fig. 360:3b), has a small surface with little resistance in burrowing and is arched, which would make it possible for the appendages to grasp sediment at the front edge for further transport backwards.

Another corollary is the morphology of the exites in trilobites. Exites with a distal comb-like fringe of spines are found in *Flexicalymene*, *Ceraurus*, *Phacops*, and probably in *Asteropyge*, as well as in *Cryptolithus* (Fig. 15). Exites of different morphology are found in *Olenoides*, *Kotenia*, *Triarthrus*, and *Elrathina*. This evidence is scanty but it is obvious that an exite of the general type needed for burrowing the *C. rugosa* trail was present, for instance, in the Calymenidae-

Homalonotidae group, whereas it is absent in some other trilobites.

Trails of the *C. furcifera* type do not add much to the evidence from *C. rugosa*. The distribution of *C. furcifera* as shown by Seilacher & Crimes (1969, Fig. 1) indicates that the trail-maker was a member of the *Selenopeltis* fauna (cf. Whittington 1966, Fig. 2). However, this is probably not the whole story. In the Iberian Mountains in north-central Spain *C. furcifera*, *C. rugosa*, and *C. goldfussi* occur together in the apparently Tremadocian *Scolithus* (sic) Quartzite, whereas *C. furcifera* and *C. goldfussi* (but not *C. rugosa*!) are also present in the probably Arenigian Armorican Quartzite (Scheuplein 1970). The *C. rugosa* group of trails is therefore probably of Tremadocian-Arenigian age and not exclusively Arenigian. The earliest (Tremadocian) trail-makers therefore appear to belong to the Tremadocian *Pharostomina* fauna of Whittington (1966). Among trilobite families common to the *Pharostomina* and *Selenopeltis* faunas are calymenids, homalonotids, asaphids and dikelokephalinids.

Particularly interesting is the find (Sheuplein 1970) in the *Scolithus* Quartzite of the trilobites *Geragnostus* sp.; indeterminable olenids, *Asaphellus* sp., and *Dikelokephalina* sp. No doubt only the comparatively closely related asaphaceans *Asaphellus* and *Dikelokephalina* would attain a size necessary for the trail-maker. The probable presence of a pair of pygidial spines in the trail-maker (Seilacher 1970, Fig. 2a) is particularly consistent with the asaphacean alternative at the same time as it tends to exclude calymenids and homalonotids. A number of asaphaceans belonging to the *Pharostomina-Selenopeltis* faunas are provided with a pair of pygidial spines, e.g. *Taihungshania*, *Omeipsis*, *Asaphellina*, *Asaphopsis*, and *Dikelokephalina*. As with the trails of *C. rugosa* and similar types those spine-bearing asaphaceans are not found in rocks of Middle Ordovician or later age, whereas the calymenids and homalonotids persisted to much later times. There is therefore zoogeographical, stratigraphical and morphological evidence indicating that the Early Ordovician trail type variously designated as *Cruziana rugosa*, *C. furcifera*, and *C. goldfussi* was produced by asaphacean trilobites of taihungshaniid-dikelokephalinid type, provided with spinous exites. The coexisting calymenids and homalonotids may have preferred comparatively more fine-grained or muddy sediments.

A trilobite trackway.—A nice specimen of a diplichniform trackway (walking trail) was found by Dr. D. Worsley *in situ* in mudstones belonging to Stage 6a β in the Lower Silurian sequence south of Oslo. The locality is a shore cliff in the southwestern part of Malmøya, an island in the Oslo Fiord. The trail is about ten cm long, and the animal has moved approximately against a current. According to Dr. Worsley, the modal current direction at the locality is from the west or southwest. A similar current direction is indicated by structures on the trail surface.

The entire trail is visible on one surface and with good preservation of even the smallest tracks (Pl. 5: 11). This indicates that the now exposed surface is very close to, if not identical with, the bottom surface on which the trail was made. The initial part of the trail extends directly against the current direction. Here only few individual appendage imprints are preserved. These appear to be further apart than in the succeeding part of the trail. They are also longer, indicating a sliding movement on the sediment surface. It is therefore probable that the trilobite came swimming close to the bottom and touched only occasionally with the appendage tips. After making this initial swimming trail, the animal began to walk on the bottom and turned to some 45° from the current direction. Here the stride was small, as seen from the closely packed tracks. Also the individual tracks show signs of sliding sideways and backwards. While other surface marks tell the direction of the current, these two facts tell that the current was really in action when the trail was made. The individual tracks are rounded, without indications of large claws. No doubt the appendages moved in waves, which were transplanted forward along the body. According to Manton and others this is a necessity in arthropods with a long series of closely placed appendages. It is known from many extant arthropods and deduced from one trilobite trail, *Dimorphichnus obliquus* (cf. Seilacher 1955). In the Malmøya trail the tracks of each wave form a "V" with the open end directed forwards. On each side there are about 14 tracks which grade in size from small ones in the rear to larger ones in front. When walking the animal thus used about 14 pairs of legs, the tips of which were coarser and wider apart in the anterior part of the body than further back.

The homopody with a large number of closely set legs arranged in a forward open "V", in all probability, excludes all arthropods except trilobites and merostomoids from the position as possible trail-makers in this case. The merostomoids are very few and poorly understood, and none are known from the Silurian. Most known trilobite appendages and trilobite trails indicate the presence of a few strong distal claws which made distinct scratches in the trails. Only two known appendages indicate the presence of a ring of bristles which may have produced rounded tracks like those found in the track-way from Malmøya. These appendages belong to the Ordovician trinucleid *Cryptolithus bellulus* (cf. Raymond 1920, Fig. 45; Pl. 7:2, 4; Bergström 1972:94) and to a Lower Devonian *Phacops* species (Størmer 1939, Fig. 26; Seilacher 1962, Pl. 24:2). Round tracks with signs of a bristle ring were pictured by Seilacher (1962, Pl. 25:1) who assigned them to the above mentioned phacopid occurring in the same beds. The Upper Cambrian ichnofossil *Protichnites loganensis* Marsh also exhibits rounded individual tracks. The evidence from this kind of material is thus very scanty. The *Protichnites* producer is unknown and the lack of markings made by the cephalic shield makes it improbable that the trail was made by any trinucleid-like trilobite.

A few trilobites are known from the beds with the Malmøya trail. According to Dr. Worsley, these include species of *Phacops*, "*Calymene*" and *Encrinurus*. No one of these can be excluded with certainty although the encrinurid may have been too small to produce the trail. The presence of a bristle ring in species of *Phacops* and *Cryptolithus* is associated with a knee in the telopodite. Neither of these two features is known with certainty from any other trilobite. Together these two features indicate a pushing ability. The telopodites in *Flexicalymene senaria* are not well known but appear to lack distinct knees (cf. Walcott 1918, Pl. 27:11, 13, 14). If this was also the case with the Norwegian calymenid and if there is a casual relation between a ring-shaped bristle "snow-shoe" and the presence of a knee, the calymenid is not likely to have made the trail.

Although the above discussion contains weak links, the phacopid present in approximately the same beds as the *Diplichnites* trail appear at present to be the most likely trail-maker.

Raking trails.—*Dimorphichnus obliquus* from the Lower(?) Cambrian of Pakistan is well known from the original description and discussion by Seilacher (1955). The trail type is unique in showing that some trilobites were able to rake the bottom surface apparently for food with the two-clawed telopodites of one side, while the telopodites of the other side pulled the animal sideways. The best known specimen shows a gradation into a walking trail of *Diplichnites* type, ending where the trilobite is supposed to have swum away.

In beds of Eocambrian or Cambrian age in northern Norway crucial scratchings were found by Banks (cf. Banks 1970, Pl. 3d). Thanks to Dr. Banks I had the opportunity to scrutinize this trace fossil from a good photograph where considerably more details can be seen than in the published picture. This photograph shows (personal communication to Dr. Banks in 1969) that there are two completely different types of track sets, which are closely comparable with the two track set types found in *Dimorphichnus obliquus* and arranged in a spacially similar way. The main differences from the later trail are the comparatively shorter scratches and the enormous size of the trail, showing that the trail-maker, if a trilobite, must have been half a metre long and possibly twice or three times that size.

The only trail at all comparable with the Norwegian trail is *D. obliquus*. As that trail appears to be made by a redlichiid trilobite, this may possibly have been the case also in Norway. Associated trails may be classified as *Cruziana dispar* (cf. Banks 1970, Pl. 3c), indicating that olenellaceans and redlichiaceans may have lived together in northern Norway in Early Cambrian times.

Summary

Anatomy

Previously ideas on the anatomy of trilobites were based on muscle scars and the prosopon (functional ornament) of the exoskeleton and on the probable interior mould of the intestinal canal in *Onnia ornata* (Sternberg). A noticeable step forward was the article by Stürmer (1970) announcing the find of the alimentary system and internal parts of the compound eyes in a Devonian *Phacops* species from the Hunsrück Shale. I was offered the possibility to use all of the original radiographs in order to prepare a more detailed treatment in cooperation with Prof. Stürmer. Additional material of *Phacops* and *Asteropyge* yielded more detailed information regarding the construction of the intestinal system in these genera. The tubular pharynx leads forward and upward to a pear-shaped stomach which is situated under the frontal lobe of the glabella. The stomach appears to be divided into an anterior and a posterior part by an interior constriction. Behind the stomach the intestine forms a narrow straight tube extending almost to the posterior end of the pygidium. The stomach is surrounded on both sides by a compact hepatopancreas or liver, the fine tubules of which have a diameter of approximately 0.11 mm in *Phacops*. The hepatopancreas is confined to the space beneath the glabella. In addition to the main parts of the hepatopancreas, there seems to be smaller paired hepatopancreas compartments occupying the lateral glabellar lobes at least in *Asteropyge*. The hepatopancreas does not cover the dorsal surface of the stomach. Instead, this surface is obviously connected with the dorsal exoskeleton by muscle strands, as suggested by some authors.

Contrary to the opinion in several previous reports the hepatopancreas can not be traced in the exoskeleton of the pleural parts in polymerid trilobites, except questionably in a few cases and only close to the glabella (*Olenellus*, *Redlichia*). However, there is still reason to believe that the coarse reticulation covering the entire pleural surface inside the margin in cephalons (and in some instances in pygidia) of many agnostid trilobites actually reveals the course of intestinal diverticula (the hepatopancreas). The agnostids, therefore, seem to be significantly different from polymerid trilobites with regard to the development of the hepatopancreas.

The genal prosopon of polymerid trilobites consists of the palpebro-ocular ridge and a radiating net of comparatively fine external ridges. The ridges correspond to internal furrows in the dorsal exoskeleton. This pattern, generally supposed to show the path of the hepatopancreas diverticula, is entirely different from the configuration of the hepatopancreas in *Phacops*, *Asteropyge*, *Limulus*, and land arachnids. Instead, it shows similarities to the circulatory system of *Limulus* in particular and it can not be doubted that it reveals the pattern of the dorsal vascular system outside the glabella.

Segmentation

The segmentation of the cephalon has been discussed many times in the literature. Generally, the acral complex, present in all extant arthropods, has been forgotten with the result that even the anterior tip of the animal has been regarded as segmental. Even this view is not extreme. In some instances counting has proceeded over the margin and the hypostome has been regarded to represent the most anterior segment.

In the present treatment two criteria for a cephalic segment have been found practicable on the fossil material. First, a segment should show some morphological similarities to its neighbouring segments. This kind of similarity is called serial similarity. Second, the presence of appendages or appendage remnants signifies the existence of a segment. In addition, information from the larval development may be used.

The maximum number of typically developed cephalic appendages is five, including one pair of antennae. In many instances there are also five pairs of glabellar lobes and furrows. The furrows mark the position of apodemes to which, no doubt, appendage muscles were attached. In a few cases with particularly uniform cephalic segmentation, the fossula conforms with the glabellar furrows both in morphology and, more approximately, in position. The anterior wing of the hypostome is connected with the fossular apodeme. The labrum (with its sclerite, the hypostome) therefore seems to be formed, partly or entirely, by a pair of preantennal appendages. In addition to the acron, the trilobite cephalon therefore probably includes six segments, namely preantennal, antennal, and four segments with walking legs, at least one pair of which may be lost in some species.

The question of the boundary between the cephalon and the thorax is not definitely settled. However, the "secondary segmentation" of xiphosurids apparently is a comparatively late innovation in that group and there is no convincing phylogenetic or morphological evidence for somites similarly crossing the cephalo-thoracic boundary in trilobites. I am therefore inclined to believe that this boundary approximately conforms with a segmental boundary.

Ventral morphology

As far as known, trilobite appendages are biramous except for the antennae and cerci. The outer ramus is fixed basally to the inner ramus which is termed the telopodite. There is probably no precoxa in *Phacops* and the outer ramus would therefore be termed an epipodite. As there is no general agreement on this point I prefer to use the more neutral term exite. Neither of these terms is perfect as the outer ramus is a major appendage branch like the crustacean exopod rather than merely an outgrowth like the crustacean exites.

The cephalon is generally said to have four pairs of biramous appendages. This is true in some instances. However, there is a general tendency towards

a reduction of anterior muscle apodemes in the cephalon and in *Phacops* and *Asteropyge* the fourth appendage pair from behind is completely lost. The two posterior pairs in *Phacops* have coxae provided with strong enditic outgrowths which are denticulated and obviously served as jaws. The third pair from behind is basally hidden by the hypostome and the coxae are poorly preserved. The identification of strong jaws is judged to be of importance in the study of trilobite feeding and mode of life.

The telopodite consists of cylindrical podomeres generally with a somewhat flattened cross-section, as far as known. There may be a "knee" in the middle. The podomeres may carry strong spines on the medial surface. The spines were probably used for holding prey. Distally, the telopodite may have modifications for burrowing or for walking on a soft substratum.

The "gill filaments" of the exite branch obviously were quite strong spines in some trilobites and were used for scratching in the sediment surface, as shown by numerous trilobite trails. Where this is the case the exite has the shape of a comb or a rake. In trilobites like *Triarthrus* the exite is featherlike and may have been used in swimming. In still other instances, as in *Ceraurus*, the exite is fan-shaped.

The gills have not been identified. There is a possibility that the entire ventral surface between the appendages and the lateral doublure served the gas exchange or that the gills were situated on this surface, as is the case in the distantly related merostomes (excepting the xiphosurids with a secondary gill position on the appendages).

Articulation, enrollment, and evolution

The articulation between adjoining sclerites has been studied in some detail. Apart from the axial articulating half-ring there may be a horizontal hinge-line and pivot joints, each consisting of a condyle and a corresponding socket. Three types of pivot joints are recognized after their position, viz. dorsal furrow joint and ring joint, both in the dorsal furrow but in opposite directions, and fulcral joint at the fulcrum. The most distal connection between successive pleurae, at the base of the pleural spines, may be strengthened by a marginal connective device. The connective device, in some instances, acts as a limiting device in the enrollment. In other cases, where the connective device is in level with the hinge-line, it may act as a (fulcral) pivot joint. Where a flange is developed it invariably extends from the dorsal furrow to the marginal connective device.

Limiting and locking mechanisms regulate the relative position of the sclerites in the enrolled animal. One group of mechanisms regulate the relative posture of neighbouring tergites and include pleural facets and the panderian protuberance, possibly the entire panderian "organ". Other solutions occur, e.g. pleural spines which abut abruptly with their vertical anterior and posterior sides, or limiting ridges on the dorsal side of the pleurae. A second group of mechanisms

regulate the reception of pleural tips and the pygidial margin in the cephalon or the cephalic margin in the pygidium. These are the vincular and fibular apparatuses, respectively. Most or all types of mechanisms seem to have evolved independently in different phylogenetic lineages. To some extent, independent evolution also effected the enrollment. Many olenellaceans were unable to enroll but the ability evolved in some forms. Most non-olenellid trilobites did enroll. However, the enrollment is of two fundamentally different types. In the sphaeroidal main type, the ventral side of the pygidium faces the ventral side of the cephalon. In the spiral main type, the dorsal side of the pygidium faces the ventral side of the cephalon or thorax. The difference and functional discontinuity is particularly striking in Early Cambrian trilobites and it is evident that the two enrollment types have a common origin only in an imperfect enrollment type.

The identification of phylogenetically stable enrollment types yields a new insight in the evolution of the trilobites. The ptychopariids have hitherto been regarded as a stem group from which most advanced trilobites evolved. However, *Ptychoparia* has an enrollment of the spiralling main types and the Ptychopariida as a whole must therefore be considered as an end line with spiralling trilobites. The earliest members are ellipsocephalids of Early Cambrian age. The ellipsocephalids are strikingly similar to the protolenids, imperfectly enrolling early members of which probably are the ancestors. It can not be entirely excluded that the spiral type of enrollment evolved more than once, but the earliest members of eventual separate spiralling lines probably must have been quite close to one another both morphologically and phylogenetically. I therefore see no possibility at present to distinguish more than one main group of spiralling trilobites.

Most other trilobite groups appear to have evolved from redlichiaceans of either protolenid-like or redlichiid-like appearance. Even the miomerid trilobites show similarities with the protolenids and their allies in the sphaeroidal enrollment, horizontal hinge-line and facial sutures. The same characters distinguish them from the olenellaceans which obviously represent a more primitive stage in trilobite evolution. No doubt, the miomerids were very specialized animals but this secondary condition can not be used as an argument against a phylogenetic affiliation with early trilobites of generalized protolenid-like character.

The study of articulation and enrollment have given less clues to the evolution of smaller trilobite groups, but much more can certainly be done in this respect. The distinction herein of a cheiruracean-odontopleuracean group may serve as an example of the usefulness of the method, provided that the distinction is warranted.

Classification

A combined study of morphological features and functional mechanisms led to the distinction herein of

nine orders. Of these, the Olenellida and Redlichiida appear to have a common origin in the Early Cambrian or Late Precambrian. All other trilobites appear to be descendants of the redlichiids. The Order Agnostida is therefore placed at the end of the list of orders which has the following appearance: Olenellida, Redlichiida, Corynexochida, Illaenida, Phacopida, Odontopleurida, Lichida, Ptychopariida, and Agnostida. The concepts of the Redlichiida, Phacopida, Odontopleurida, and Ptychopariida are radically changed in comparison with the Treatise concepts (Moore 1959).

The lumping of unrelated groups in previously recognized orders and suborders, based on characters commonly without phylogenetic significance, led to an uncontrolled and uncontrollable swelling of the number of superfamilies, families and subfamilies. It may seem that there is a tendency in some instances to make a superfamily for each family just because it has been impossible to recognize larger natural units. Herein, the families are lumped in comparatively few large superfamilies which are supposed to be more or less uniform phylogenetically. A higher systematic level would not make much difference although it would split closely related and similar trilobites further apart. For instance, it is difficult to see what can be won by separating Ordovician phacopids into different superfamilies.

Many small trilobite groups are omitted from the systematic list because of lack of information regarding enrollment or thoracic and pygidial construction, making an evaluation of the phylogenetic position too difficult. Therefore, the presented classification is to be regarded as an outer frame and much detailed work remains to fill the holes and to correct mistakes.

Mode of life and feeding

Up till now only one trilobite species, *Flexicalymene meeki* (Foerste), has been found in its own burrow. A number of other burrows and surface trails have been assigned to the activity of trilobites, commonly with a high degree of confidence. However, in many cases it is almost impossible to tell what particular kind of trilobite may have been active. It is probable that different trail types have been correctly assigned with olenellaceans, redlichiaceans, asaphaceans, phacopids, solenopleuraceans, trinucleaceans, and homalonotids, except for those of calymenids.

The trace fossils indicate that some trilobites were able to walk over the substratum and that others were able to rework the substratum in one way or the other. In reworking the substratum the different trilobites were able to behave in different ways. The trace fossil *Dimorphichnus* Seilacher, 1955, tells about a trilobite which pulled the body sideways with the telopodites of one side, while the telopodites of the opposite side raked the surface systematically in search for food. The movements of the appendages followed regularly in waves which began posteriorly and moved forwards. Other trilobites burrowed along the sediment-water interface, also in this case in search for organic

material, living or dead. In some trails there is evidence that the telopodites were used for burrowing, while the exites and and telopodites or the exites alone were obviously used in other instances. The extended superficial burrow is here called a cruzianiform burrow or trail. A rusophyciform burrow is not extended horizontally and the trilobite may have burrowed more or less deep. New evidence shows that some of these burrows are actually hunting-burrows, made after careful locating of the burrowing prey. Similar burrows may indicate passive resting or hiding. Also these kinds of burrows were made either by telopodites or exites or by both appendage branches. More complicated deep burrows have been ascribed to trilobite activity, but the evidence is so far tenuous.

Some trilobites seem to have burrowed backwards in a more or less vertical posture. No burrows corresponding to this behaviour have been found, but some illaenids and asaphids have been found in a vertical life position. The spectacular morphology of many illaenids obviously is an adaptation to the vertical posture in the burrow.

The smooth exterior and the wide rhachis found in illaenids and asaphids seems to be an adaptation to burrowing habits. The same characters are found in other trilobites, notably homalonotids, which are also supposed to have been burrowers. The smooth exterior would have diminished friction and prevented sediment particles from adhering to and fastening between the sclerites. The presence of a wide and vaulted rhachis shows that there was plenty of space for appendage and other muscles between the dorsal exoskeleton and the appendage bases. These muscles would have provided the appendages with particular power, no doubt essential for burrowing trilobites. In other cases, however, a smooth exterior and a wide rhachis presumably indicating strong appendages, might signify an extraordinary swimming power. The actively swimming trilobites apparently differed from the burrowers in having a more slender and lighter exoskeleton and, in some instances, enlarged eyes or reduced enrollment capability. Olenids, remopleuridids and cyclopygids are thought to have a morphology characteristic of swimming trilobites.

Olenids and agnostids are supposed to have been pelagic in the Scandinavian Late Cambrian sea because faunistic and sedimentologic evidence of benthic life is almost entirely lacking. The olenid appendages, known from *Triarthrus*, were directed laterally and seem to have been well adapted to a swimming life. The agnostid morphology is alien to pelagic arthropods of today and it is possible that the agnostids lived associated with drifting seaweed. The reticulated exoskeleton of many agnostids reveals the presence of exceptionally large intestinal diverticula. This character is found in extant arthropods which feed by ingesting fluids and provides evidence that the agnostids differed from other trilobites in their choice of food.

The generally accepted idea that trilobites lacked jaws and fed from mud must be abandoned as a general description. Enditic jaws have been identified

and various kinds of evidence indicate that some trilobites hunted their prey in the sediment or in the water, whereas others may have fed on fluid food and still others may have been filter-feeders. Most trilobites probably were benthic crawlers, but many burrowed in soft sediment and others were nekto-benthic, pelagic, or epipelagic. The large number of undifferentiated appendages made them slow swimmers and enrollment was an important method of protection.

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Explanations of plates

Specimens covered with ammonium chloride, if not otherwise stated. Many specimens are plastic casts of natural moulds; this is then stated for each plate separately. LM in the collection number means that the specimen is preserved at the Palaeontological Institute in Lund, RM that it is preserved at the Naturhistoriska Riksmuseet, Stockholm. The family is mentioned within brackets in cases where the genus is not a type genus.

Plate 1. Paper models illustrating the sclerite mobility in various trilobites, including enrollment. Fig. 1. *Olenellus thompsoni* (Hall). The long vertical projection of the pleurae proves that the animal could not roll up. Fig. 2. *Kjerulfia lata* Kiær (Daguinaspidae) with imperfect enrollment. The thorax could roll up on itself but the cephalon was left unprotected ventrally. Figs. 3—4. *Centroleura phoenix* Öpik (Paradoxidae), exhibiting cylindrical enrollment. The genal spines help protect the body laterally. Fig. 5. *Holmia kjerulfi* (Linnarsson), with imperfect(?) enrollment. Fig. 6. *Fallotaspis typica* Hupé (Daguinaspidae), with cylindrical enrollment. Fig. 7. *Peltura scarabaeoides* (Wahlenberg) (Olenidae), with sphaeroidal enrollment. Fig. 8. *Ctenopyge spectabilis* Brøgger (Olenidae), with cylindrical enrollment which may not have been complete. Fig. 9. *Gigantopygus bondoni* Hupé, without enrolling capacity, as shown by the long sloping pleurae.

Plate 2. The following figures are based on plastic casts: 3—5, 7, 12—13, 15. Figs. 1—2. *Phacops* sp., surface view and X-ray picture (No. WS 713 made by Prof. W. Stürmer, Erlangen) of specimen from the Devonian Hunsrück Shale of the Rheinische Schiefergebirge, in the collections of Captain Günther Brassel, Flensburg. Three pairs of cephalic walking legs are visible. $\times 1.7$. Fig. 3. *Olenellus carinatus* Poulsen, from the Lower Cambrian of north-east Greenland. Note the absence of a horizontal hinge-line. Figured by Poulsen (1958, Pl. 2:4), preserved in the Mineralogisk Museum, Copenhagen, as No. 10685. $\times 3.4$. Fig. 4. *Olenellus* sp. indet., from the Lower Cambrian of north-west Greenland. Pleura in anterior view showing even curvature and lack of hinge-line. Note the marginal connective device at the base of the pleural spine. Figured by Poulsen (1927, Pl. 15:4), preserved in the Mineralogisk Museum, Copenhagen, No. 2239. $\times 6$. Fig. 5. *Holmia kjerulfi* (Linnarsson). Lower Cambrian, Tømten, Ringsaker, Norway. Dorsal furrow process approximately in correct position between first and second thoracic tergites. LM LO 4455 t. $\times 5$. Fig. 6. *Holmia* sp., Lower Cambrian, Bukówka, Holy Cross Mtn, Poland. Anterior portion of partly enrolled specimen. Collections of Dr. Hoffmann, Institute of Geology, Warsaw. $\times 1.6$. Fig. 7. *Schmidtellus mickwitzii torelli* (Moberg) (Holmiidae), from the Lower Cambrian of Björkelunda, Scania, Sweden. Dorsal furrow process well developed. LM LO 4465 t. $\times 4.6$. Fig. 8. *Kjerulfia* cf. *lata* Kiær (Daguinaspidiidae), Lower Cambrian, Ocieseki, Holy Cross Mtn, Poland. Strongly flexed part of thorax. Collections of Dr. S. Orłowski, Institute of Geology, Warsaw. $\times 1.7$. Figs. 9—10. *Hydrocephalus carens* Barrande (Paradoxididae). Middle Cambrian, Pod hrůškou, Tejšovic, Bohemia. Incipient anterior flange extending beyond the fulcrum (at the bend of the uppermost pleura in Fig. 10) and ending with flap-like marginal connective device. A bulge at the posterior margin marks the position where the flap was accommodated. LM LO 4540 t. $\times 2.5$ and $\times 1.0$. Fig. 11. *Hydrocephalus sjöegreni* (Linnarsson) (Paradoxididae). Middle Cambrian, Borgholm, Öland, Sweden. Flattened dorsal furrow process and, distal to the fulcrum, a weakly developed marginal connective device at the base of the pleural spine. LM LO 4541 t. $\times 1.0$. Figs. 12—13. *Asaphus* (*Neoasaphus*) *ludibundus* Törnquist. Middle Ordovician, collected as a boulder close to Vicklau and Atlingbo, Gotland. Pleural spines and anterolateral corner of pygidium on the left side of the animal in ventral view. Panderian protuberance and opening visible. RM Ar. 19471. $\times 4.8$, and $\times 2.1$, respectively. Fig. 14. *Olenus* sp. Upper Cambrian, probably Scania, Sweden. Ventral view of two fragmentary thoracic sclerites. Marginal connective device strongly developed at the base of the encased pleural spine. Fulcrum approximately in the middle of the pleurae, which are seen in ventral view. LM LO 4542 t. $\times 9$. Fig. 15. *Peltura scarabaeoides* (Wahlenberg) (Olenidae). Upper Cambrian, local boulder collected at Gislövshammar, Scania, Sweden by Mrs Agnes Rodhe, Lund. The

articulating half-rings, seen in ventral view in this flattened specimen, are well developed and indicate that there was a considerable amount of flexibility between the sclerites, presumably allowing enrollment. LM LO 4543 t. $\times 3.4$. Fig. 16. *Leptoplastus* sp. (Olenidae). Upper Cambrian of Andrarum, Scania, Sweden. Left lateral view of three thoracic sclerites exhibiting a marked flexure and still considerable overlap between rhachis rings and articulating half-rings, indicating even greater bending capacity. LM LO 4544 t. $\times 18$.

Plate 3. The following figures are based on plastic casts: 3—7, 12—13. Ammonium chloride not used for Figs. 8—10, 15. Figs. 1—2. *Peltura scarabaeoides* (Wahlenberg) (Olenidae). Upper Cambrian, probably Scania, Sweden. Articulating half-rings and short horizontal hinge-line well visible. Note the wide arched rhachis with considerable space for musculature. LM LO 4545 t. $\times 4.7$ and $\times 6.7$, respectively. Figs. 3—5. *Remopleurides* sp. Upper Ordovician, Skultorp, Västergötland, Sweden. Exterior and interior casts of one specimen, showing the strongly developed hollow "fulcral" condyles and corresponding sockets in dorsal furrow joint position because of the secondary loss of the horizontal hinge-line. The pleura is markedly reduced and consists only of a pleural spine. In Fig. 5 the ventral spine side exposes a shelf that functioned as a limiting device in enrolling. LM LO 4536 t, LO 4537 t. $\times 3.0$, $\times 3.0$ and $\times 6.6$. Fig. 6. *Remopleurides* sp. Same horizon and locality. Enrolled specimen with cephalic border partly visible outside the pleural spines. LM LO 4538 t. $\times 3.2$. Fig. 7. "*Illaeus*" *angelini* Holm. Upper Ordovician, Skultorp, Västergötland, Sweden. Ventral view showing ring process and socket joints, doublure under rhachis and long hinge-line. LM LO 4546 t. $\times 4.2$. Fig. 8. *Illaeus incisus* Jaanusson. Lower Ordovician, Husbyfjöl (=Västana), Östergötland, Sweden. Enrolled specimen with pygidium partly removed to show the terraced cephalic doublure, on which the pygidial margin rested. Compare Fig. 9. RM Ar. 46655. $\times 1.2$. Fig. 9. *Illaeus sarsi* Jaanusson. Lower Ordovician, Västana, Östergötland, Sweden. Enrolled specimen closely comparable with *I. incisus* in Fig. 8 but with pygidium undamaged. RM Ar. 17624. $\times 1.2$. Fig. 10. *Phacops* sp. Devonian, northern Africa. Enrolled specimen with pygidial margin displaced from vincular furrow, visible along cephalic margin. Belongs to Dr. O. Ryberg, Malmö. $\times 2$. Fig. 11. *Dalmanites vulgaris* Salter. Middle Silurian, Alvans, Gotland. Ventral view of part of two thoracic sclerites showing horizontal hinge-line, poorly developed articulation in dorsal furrow and articulating half-ring. Muscle apodemes extend to the level of the hinge-line, showing that the attached muscles had nothing to do with the enrollment. LM LO 4547 t. $\times 6$. Fig. 12. *Sphaerocoryphe dentata* Angelin (Cheiruridae, Deiphoninae). Upper Ordovician, Skultorp, Västergötland, Sweden. Marginal connective devices in fulcral position (fulcral joint) at the ends of the pleural flanges. Compare Fig.

13. LM LO 4535 t. $\times 3.0$. Fig. 13. *Skelipyx* cf. *can-crura* (Salter) (Cheiruridae, Eccoptochilinae). Upper Ordovician, Skultorp, Västergötland, Sweden. Ventral view showing sharp delimitation of encased pleural spines. Marginal connective devices at the spine bases are distal to the poorly defined fulcrum and did not function as pivot joints. Compare Fig. 12. LM LO 4534 t. $\times 3.0$. Figs. 14—15. *Atractopyge adornata* (Törnquist) (Encrinuridae). Enrolled specimen showing unique arrangement of the posteriorly directed pleural spines, which are strongly compressed from the sides and arranged in a transverse series rather than in a longitudinal series. The spine tips rest on the cephalic margin. LM LO 576 t. $\times 2.1$ and $\times 2.1$.

Plate 4. The following figures are based on plastic casts: 4—5, 12—17. Fig. 1. *Encrinurus punctatus* (Wahlenberg). Silurian, Gotland, locality unknown. Enrolled specimen. On the left side a few pleural tips are in correct position in the cephalic vincular furrow, while the other tips and the pygidial margin (except in the rear) have been forced out of position, revealing the vincular furrow. LM LO 4548 t. $\times 4$. Fig. 2. *Amphilichas* sp. (Lichidae). Upper Ordovician, Kallholn, Dalarna, Sweden. Posterior view of cephalon, showing short but distinct hinge-line, ended at the fulcrum. Compare Figs. 3—5. RM Ar. 47551. $\times 4.8$. Fig. 3. *Amphilichas lineatus* (Angelin) (Lichidae). Upper Ordovician, Östbjörka, Dalarna, Sweden. Posterior view of cephalon showing absence of horizontal hinge-line. RM Ar. 11455. $\times 2.5$. Figs. 4—5. *Platylichas laxatus* (M'Coy) (Lichidae). Upper Ordovician, Skultorp, Västergötland, Sweden. Interior and exterior views of one specimen. Fairly long hinge-lines and encased pleural spines without panderian organs are well visible. LM LO 4549 t. $\times 1.5$ and $\times 1.5$. Figs. 6—7. "*Cyphasps*" *elegantula* (Angelin) (Aulacopleuridae, Otariioninae). Middle Silurian, Djauvik, Eksta, Gotland. Specimens revealing the spiral enrollment. In Fig. 7 the pleural spines and the entire pygidium are concealed under the cephalic margin. In Fig. 6 this margin is broken away to show the position of the pygidium. RM Ar. 47531 and 47532. $\times 7$. Fig. 8. *Ellipsocephalus polytomus* Angelin. Middle Cambrian, Borgholm, Öland. Right halves of four thoracic segments. Posterior margin of posterior (second) preserved pleura is raised over the natural mould where the anterior margin of the next posterior pleura has fallen out. The pleurae are therefore imbricated along the hinge-lines. LM LO 4550 t. $\times 7$. Fig. 9. *Ellipsocephalus* (*Ellipsostrenua*) *gripi* Kautsky. Lower Cambrian, Aistjack, Lappland, Sweden. Spirally enrolled specimen with pygidium and pleural spine tips concealed under cephalic margin. Figured by Kautsky (1945, Pl. 15:6, 7). RM Ar. 9030. $\times 3$. Fig. 10. *Flexicalymene meeki* (Foerste) (Calymenidae). Edenian Stage, Ordovician, Stone Lick Creek, near Newtonville, Ohio. Unrolled spiral enrollment, in which only part of the pygidium is hidden beneath the cephalic margin. LM LO 4551 t. $\times 2.5$. Fig. 11. *Diacalymene* sp. (Calymenidae). Upper Ordovician, Alle-

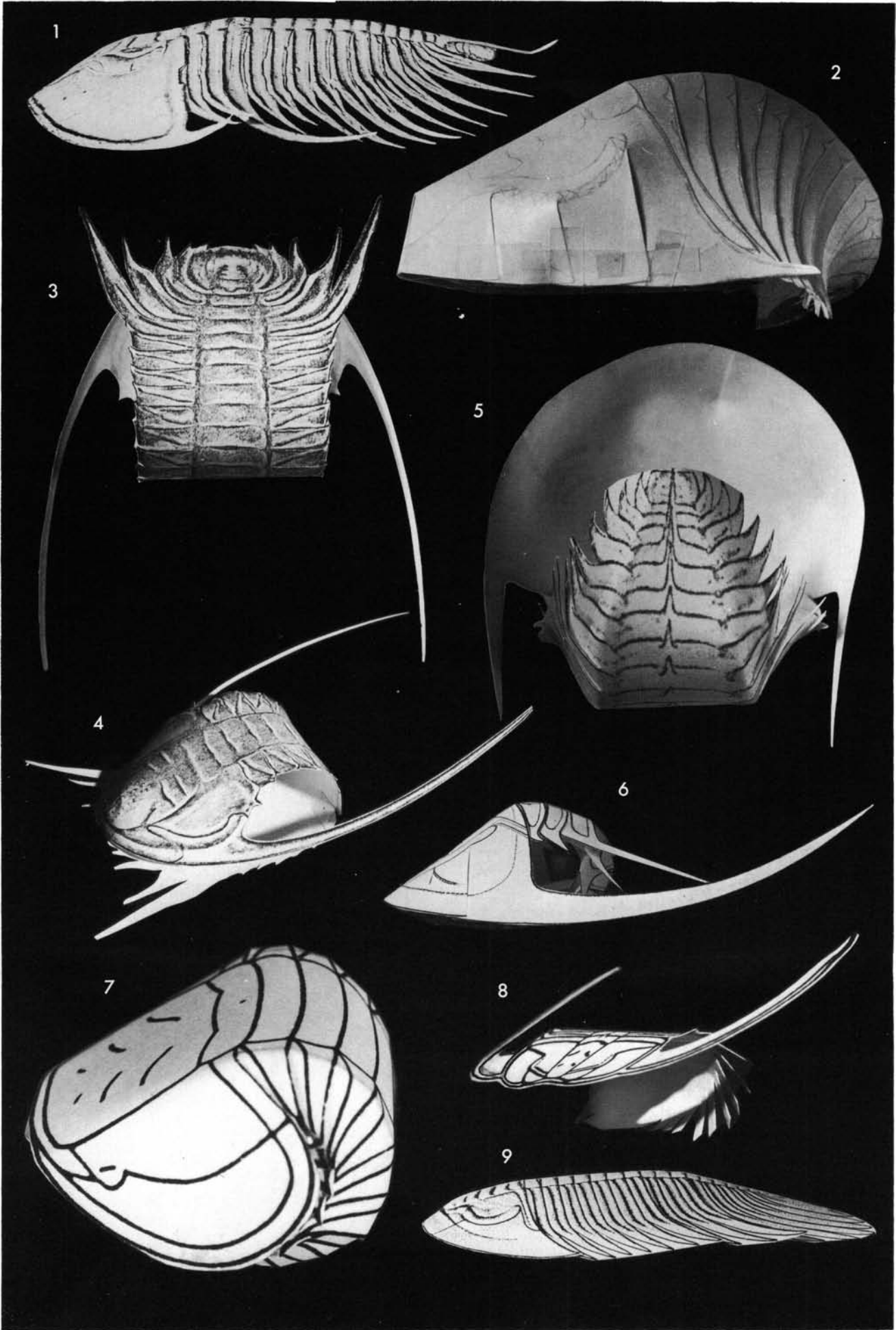
berg, Västergötland, Sweden. Ventral view of pleurae of right side. Anterolateral corner of pygidium to the right. The limiting mechanism with a panderian protuberance is seen in function close to the pygidium where the thorax is maximally flexed. The pleural spines are only partially encased ventrally by sclerotized exoskeleton. The non-sclerotized embayment is termed a panderian notch. LM LO 4552 t. $\times 3$. Figs. 12—16. *Tretaspis* sp. (Trinucleidae). Upper Ordovician, Skultorp, Västergötland, Sweden. Figs. 12—14 shows various aspects of two enrolled specimens. The margin of the pygidium is markedly flexed down and invisible in the enrolled individual. The pygidium fits as a lid in a box or basket. Figs. 15—16 shows the dorsal exoskeleton in ventral view. Ring joints and dorsal furrow joints are developed in the dorsal furrow. The strongly developed apodemes in the rhachis have their tips level with the long hinge-lines, showing that the attached muscles had no influence on the enrollment (cf. Pl. 3:11). LM LO 4553 t, LO 4554 t, and LO 4555 t. $\times 2.5$, $\times 5$, $\times 7$, $\times 3$, and $\times 10$. Fig. 17. *Lonchodomas portlocki* (Barrande) (Raphiophoridae). Upper Ordovician, Skultorp, Västergötland, Sweden. Ventral view, showing long hinge-lines, well developed ring joints and geniculated pygidium. LM LO 4556 t. $\times 3$.

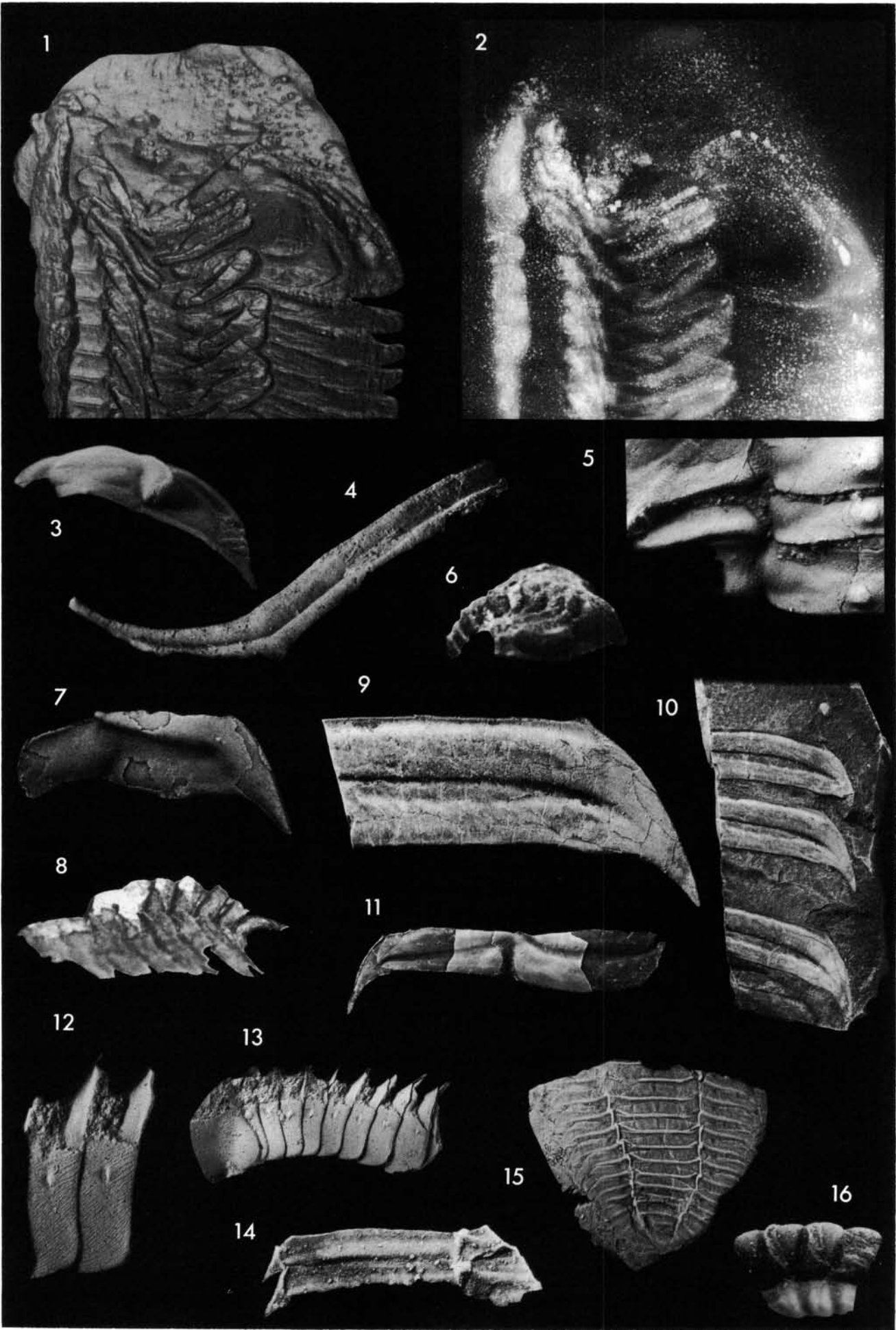
Plate 5. Ammonium chloride not used for Figs. 1, 3—8, 11. Fig. 1. undeterminable trinucleid (Trinucleidae). Ordovician, Koängen boring core, 12.90—12.93 m, Lund, Sweden. Courtesy of Mr. Ragnar Nilsson, Lund. Pygidium with geniculated border. LM LO 4557 t. $\times 2.5$. Fig. 2. *Ampyx nasutus* Dalman (Raphiophoridae). Lower Ordovician, Östergötland, Sweden, locality unknown. Enrolled specimen with geniculated border concealed under cephalic margin (basket and lid enrollment). Compare Pl. 4:17, and Pl. 5:1. RM Ar. 8881. $\times 3$. Fig. 3. *Agnostus pisiformis* (Wahlenberg). Upper Cambrian, boring core Bernstorp II, map sheet Örebro SO, Närke, Sweden. Enrolled isopygous meraspid larva in posterior view, showing that enrollment (or flapping together) was possible even before the thoracic tergites were separated from the protopygidium. The cephalon is up. Courtesy of Dr. Lars Karis, Swedish Geological Survey. Approximately $\times 80$. Fig. 4. *Alopecosa* (*Tarentula*) sp. Recent, determined by Dr. Sven Almquist, Malmö. Shed moult showing marginal splitting similar in position to the marginal or submarginal ecdysial suture of olenellids. Figs. 5—6. *Illiaenus sarsi* Jaanusson. Lower Ordovician, Åketorp, Råpplinge, Öland, Sweden. Individual in supposed life position in poorly bedded limestone, in which no burrows are preserved. Bedding slightly visible in Fig. 6. LM LO 4558 t. $\times 1.5$. Figs. 7—8. *Eccaparadoxides pinus* (Holm)? (Paradoxididae). Paper models of meraspid larvae showing the protective effectiveness of the spines in the enrolled individual. Based on figures in Moore (1959, Fig. 93). Fig. 9. *Cruziana dispar* Linnarsson. Lower Cambrian, Trolmen, Kinnekulle, Sweden. Rusophyciform trilobite burrow and "worm" burrow

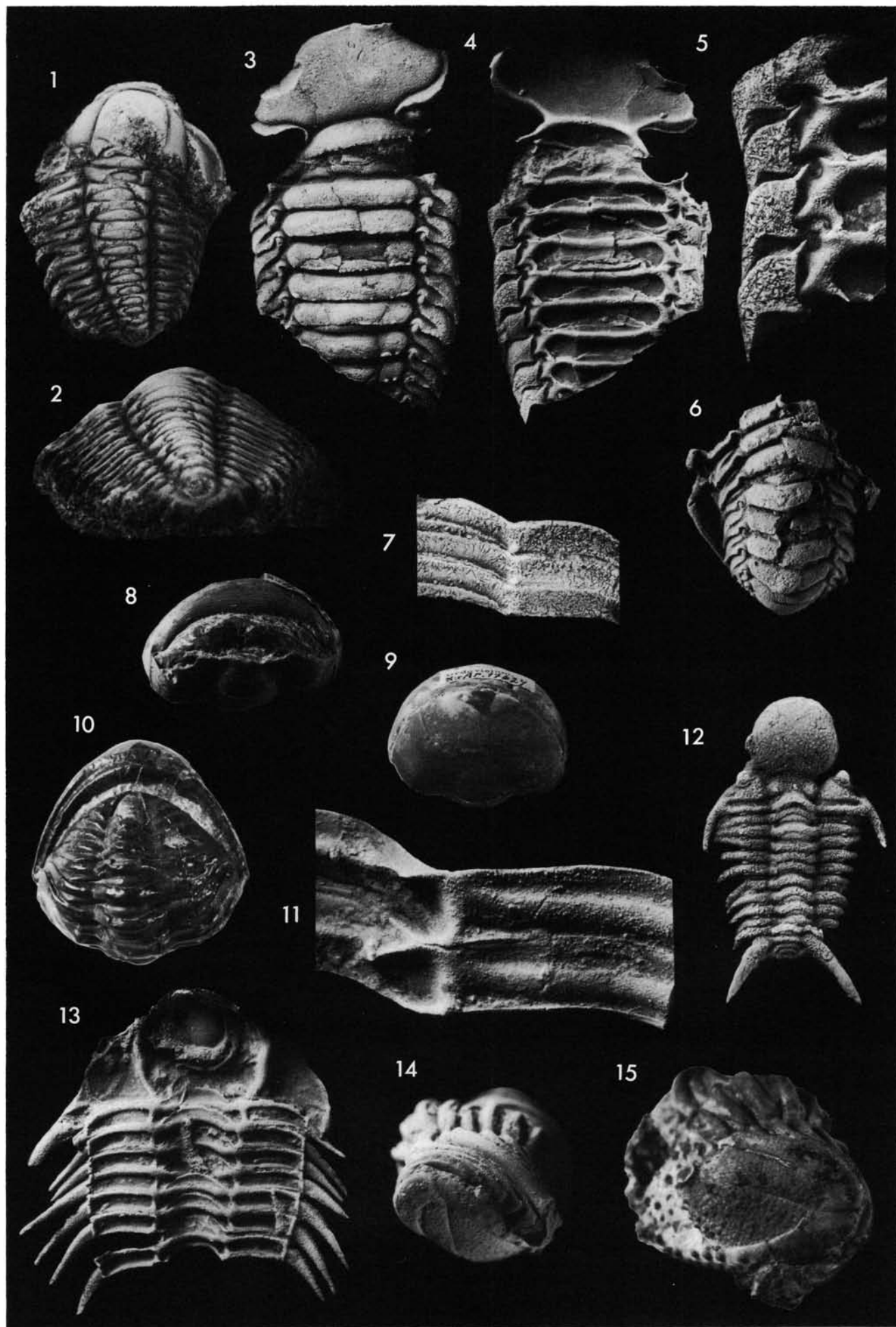
terminated at the trilobite burrow, indicating that the "worm" was caught by the trilobite. LM LO 4559 t. Scale in cm. Fig. 10. *Cruziana dispar* Linnarsson. Lower Cambrian, Lugnås, Västergötland, Sweden. A burrow similar to that in Fig. 9, with a "worm" burrow terminated beneath the trilobite burrow. Around the termination of the small burrow there are irregular scratches made by the trilobite feet, obviously a record of a successful hunting. LM LO 4560 t. $\times 1.0$. Fig. 11. Trilobite trackway. Lower Silurian, Malmøya, Oslo Fiord, Norway. The animal moved towards the left

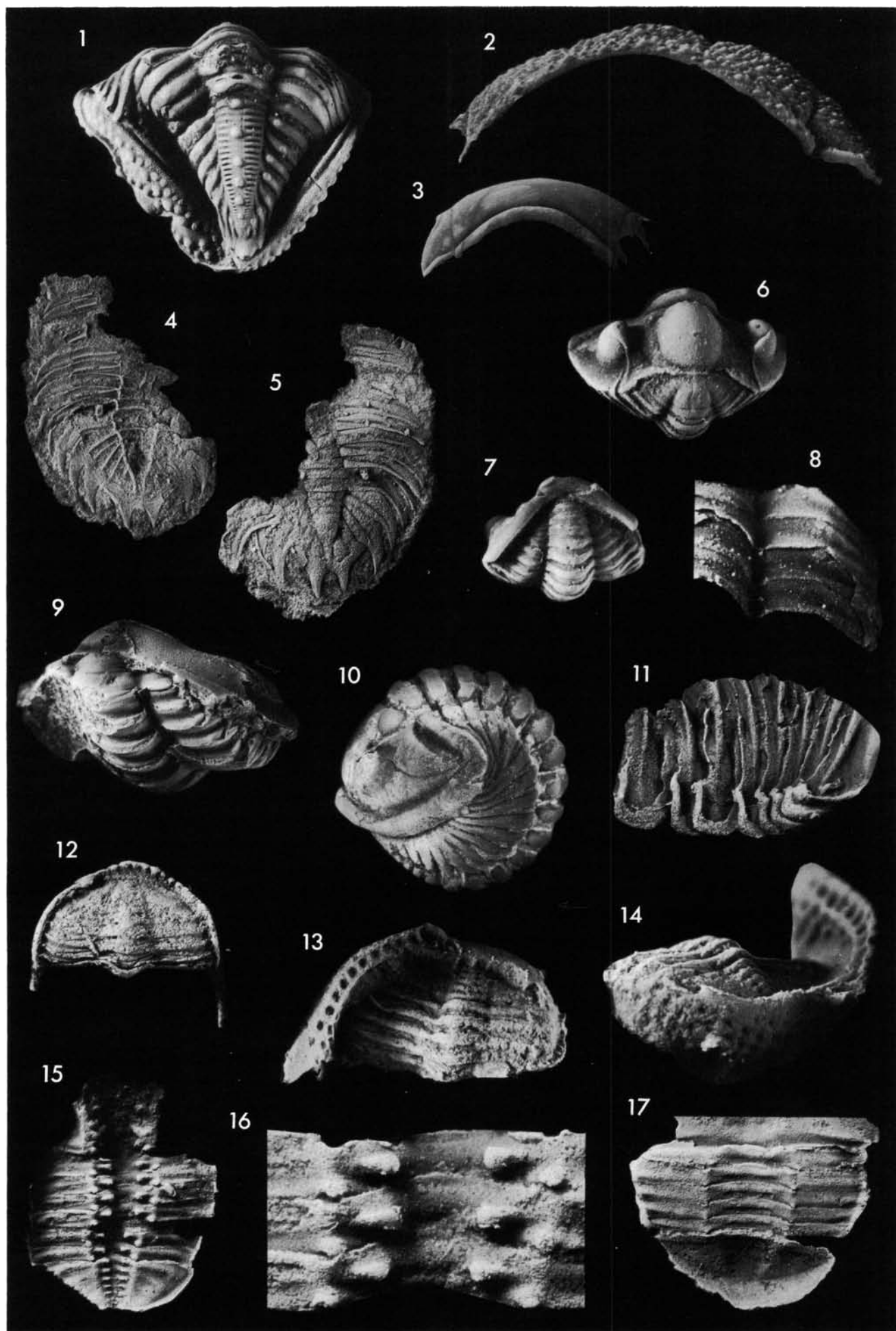
margin. On each side about 14 feet were used, the posterior ones fairly close together, the anterior ones coarser and further apart, causing V-shaped sets of tracks. A water current came in from the left. Photograph in the field. Scale in cm. Figs. 12—14. *Cruziana dispar* Linnarsson. Lower Cambrian, Västergötland, Sweden, locality unknown. Specimen showing the fasciculated character. Fig. 12, ventral view, Figs. 13—14 anterior views, different exposures. LM LO 4267 t. $\times 0.35$, $\times 0.45$ and $\times 0.6$, respectively.

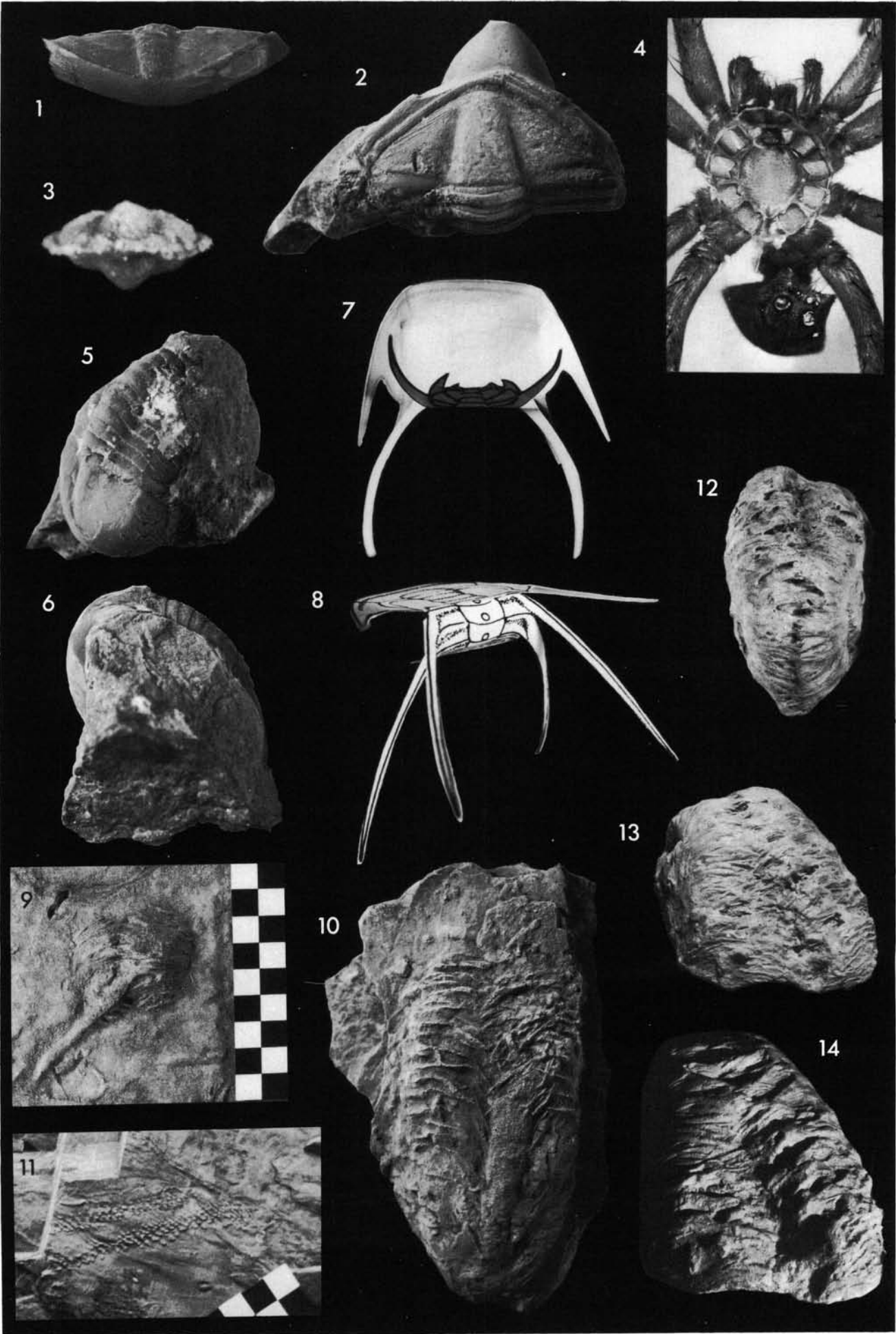
Plates











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The manuscript must be typewritten (carbon copy not acceptable) on one side of standardized paper, double spaced, and with an ample left margin. The text must be clear and concise, and written preferably in English; German or French manuscripts may be submitted. Manuscripts should be arranged in the following order: (1) Informative but brief title. Avoid titles with interrogative form, abbreviations, formulae, and brackets. (2) Author's name; one or more of his forenames unabbreviated. (3) A *short* abstract, always in English, not exceeding 12 lines (910 letters and spaces), and starting with a repetition of 2 and 1, with a translation in parentheses of non-English titles. (4) The author's professional address and a dating of the manuscript. (5) The main text. Use three or fewer grades of headings. Indicate in the left hand margin the approximate position of figures and tables. The words "Fig." ("Figs."), "Pl." ("Pls."), and "Table" (unabbreviated) are to be written with capital initials in the text. In the main text, Fossils and Strata does not use small capitals, bold-face, or letter-spacing. Instead of footnotes, insert paragraphs which can be composed in smaller type or use parentheses. (6) References shall conform to the examples given below. Abbreviations used should be consistent; necessary editorial changes will adhere to the usage in *International List of Periodical Title Word Abbreviations* (UNISIST/ICSU AB 1970). (7) Captions of illustrations, if any. Add an English caption below captions in other languages. *Figure captions and tables must be submitted on separate sheets.* (8) Tables, if any, with captions, numbered with arabic numerals. When possible, try to simplify table material so that it can be run in with the text. (9) Explanations of plates, if any.

ILLUSTRATIONS

Figures in the text should be reducible to a maximum size of 17.1×25.3 cm or less. It is recommended that figures be constructed *either* for the entire width of the type area (17.1 cm) *or* for the column width (8.1 cm). Line drawings (maps, sections, etc.) may occasionally be allowed to extend into the inner margin of the page by an additional 2 cm. On all figures should be the author's name and the figure number. Do not attach captions to the figure. Photographs are to be clear, sharply contrasted, and printed on white paper with glossy finish. Photographs of fossils, however, should be made without very pronounced light areas or very heavy shadows; the shadows are to fall consistently towards the lower right corner of the figure. Figures may be composed of several quadrangular units separated by 1 mm broad spaces. The items in composite figures should be similar to each other in tone. If the natural background is to be deleted, blackening is preferred.

Plates should be prepared for an area of 17.1×25.3 cm. The items of composite figures should be designated A, B, C, etc. (*not* a, b, c, etc.). The items in composite plates should be designated 1, 2, 3, etc. (*not* italics). All figures, plates, and tables are to be referred to by arabic numerals.

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FOSSILS AND STRATA

- No. 1. Hans L. Jessen: Schultergürtel und Pectoralflosse bei Actinopterygiern [Shoulder girdle and pectoral fin in actinopterygians]. Pp. 1—101, Pls. 1—25. Oslo, 5th May, 1972. Price 98,— Norwegian Crowns (U.S. \$20.00 1972).
- No. 2. Jan Bergström: Organization, life, and systematics of trilobites. Pp. 1—69, Pls. 1—5. Oslo, 27th April, 1973. Price 45,— Norwegian Crowns (U.S. \$9.00 1973).

