LOWER PALAEOZOIC TRILOBITA: THE CHEIRURIDAE; A PRELIMINARY ACCOUNT OF THE LLANDOVERIAN TRILOBITE FAUNA OF THE TYPE AREA.

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ABSTRACT

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The classification of the trilobite family Cheiruridae has been revised. The work has included visiting the institutions having the major palaeontological collections in this country, and much material has been borrowed for study and photography in Newcastle. The British species of Cheirurids described before about 1950 have been redescribed and figured. The nomenclature of the family at the specific, generic and subfamilial levels has been clarified. The subfamilies considered to belong to the Cheiruridae are as follows; Cheirurinae, Cyrtometopinae, Pilekiinae, Sphaerexochinae, Deiphoninae, Areinae and Acanthoparyphinae. The subfamily Hammatocneminae is excluded from the family and probably requires the erection of a new monotypic family. The genus Onycopyge is also excluded and considered to form a new monotypic subfamily of the Encrinuridae. With reference to all available world literature on the family, as complete as possible a list of Cheirurid species has been built up and a phylogeny of the genera is proposed. The distribution of these genera throughout the time range of the family (Upper Cambrian to Middle Devonian) is dealt with; the Upper Cambrian and Tremadocian genera (Pilekiinae) being widespread, the Ordovician genera being provincial in distribution in common with the pattern shown by many other trilobite families at that

time, and the Silurian and Devonian Cheirurids having world-wide distribution.

A very short preliminary account of the Llandoverian trilobites of the type area is included at the end of the thesis. The preliminary determinations of the trilobites, which are uncommon in these rocks, indicate about 12 genera to be present in the collections made by the author and in that made by Prof. O. T. Jones which is housed at the Sedgwick Museum, Cambridge University.

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INTRODUCTION

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1. Aims and scope of the thesis:

The aim of the thesis has been to reconsider the trilobite family Cheiruridae. At the suggestion of Dr. J. Shirley a revision was attempted since the family had last been considered as a whole by Öpik (1937), although Prantl and Přibyl (1947) had made a thorough study of the Bohemian members of the family.

The Museums in Britain having the major collections of trilobites, were visited and their Cheirurid specimens indexed for my own use. These museums are:

British Museum (Natural History),
Museum of the Institute of Geological Sciences,
Sedgwick Museum (Cambridge University),
Birmingham University Museum,
Oxford University Museum,
Royal Scottish Museum (Edinburgh),
Hunterian Museum (Glasgow University).

Specimens have been studied both at the museums and much material has been borrowed for study and photography at Newcastle. Most British type and figured material has been redescribed; species described in the last ten years or so have not been re-examined. A search for certain poorly known species has been made in some areas (e.g. the Malverns and the Lake District).

Except for small amounts of material of the foreign members of the family housed in the museums named above, the consideration of these has been by consulting as much literature as possible. Correspondence, and exchange of photographs and plaster casts of specimens, with workers on the family abroad, in North America, Australia and Germany has added to the amount of information gathered together in this work. An index of all Cheirurid genera and species has been built up (see Appendix 1a) and it is on this information together with the study of British Cheiruridae that the phylogeny of the family has been based.

Along with previous and recent workers on the Cheirurids it was realised that of the evolutionary changes within the family, the biggest changes are in the pygidium. This is especially true of the Cheirurinae although members of other subfamilies also show changes in the cephalon and thorax. By noting carefully the position in space and time of the occurrence of the species considered a phylogeny of the family has been constructed which is described in Chapter III. This phylogeny is the basis for the classification here accepted (text figure 2).

Study of all available literature on the family has resulted in a restriction on the use of some of the genera. For instance, the generic name Cheirurus has for many years been used for any species with a Cheirurid morphology. In fact, the genus Cheirurus was for Reed (1896) almost as broad a concept as the whole family is now, and since then it has generally been so broadly used to embrace what is considered here to constitute most of the subfamily Cheirurinae. Cheirurus as restricted here comprises a set of species of Wenlockian age, though some Lower Ludlovian species may also belong here.

2. Techniques:

As most of the material studied has been from museums, little mechanical preparation has been necessary or desirable. Some specimens have been improved by the removal of small quantities of matrix from furrows, and from around pygidial and other spines to give a more accurate picture of the extent of these. A few specimens have been prepared out by the use of Vibro-tool and mounted needle.

External moulds, where it was possible, were casted in a latex compound such as 'Rubbalin' or Dunlop latex 'A. 1121'. The latter compound was found to have advantages such as being quicker drying, having less shrinkage, and being cheaper. An initial two coats of latex 'A. 1121' mixed with Indian ink were applied to the mould (giving a matt black surface to the finished cast) and the cast then completed by a layer (or layers, depending on the convexity of the specimen) of latex mixed with ¼ its own weight of kaolin. This kaolin mixture gives a quicker drying and more rigid backing to the cast, and is also less liable to shrinkage.

Certain fragmentary specimens which could not be fixed together with Durofix because the adjacent broken surfaces were too small, were kept in position together by making a bed of 'Vinagel', which is pliable at room temperature until heated to 250°C for 30 minutes when it sets (for example see Plate 12, figure 1).

Various photographic set-ups have been employed. Initially a Zeiss ¼ plate camera was used (with Ilford R20 photographic plates); the Leica Aristophot equipment in this department has also been used (with both ¼ plates and film), until the presently used technique was tried. Most of the photographs in the plates in this work have been obtained by the use of an Asahi Pentax camera, with extending bellows and 50 mm. and 90 mm. lenses, on Adox KB 14 film. This film (with its advantages of fine grain and thin emulsion) was developed in Adox developer for 10 minutes at 20°C, and the prints obtained on Ilfobrom Grade 4 photographic paper.

All specimens were illuminated by two lamps placed in the north-west and south-east positions where possible, and were coated with ammonium chloride from a hot tube, although the less convenient method of coating by cold sublimation was tried. Unless otherwise stated in the plate descriptions the photographs are of the shell of the specimen oriented with the posterior edge of the occipital ring vertical ('Dorsal view'). 'Palpebral view' is a view of the cephalon with the palpebral lobes placed as near the horizontal plane as possible.

The following abbreviations have been used in the plate descriptions to identify specimens from the various collections:

BM (British Museum (Natural History));

BU (Birmingham University Museum);

GSM (Museum of the Institute of Geological Sciences);

HM (Hunterian Museum, Glasgow University);

MU (Manchester University Museum);

NU L (Geology Department, Newcastle University (Lane Collection));

NU S (Geology Department, Newcastle University (Shergold Collection));

NU T (Geology Department, Newcastle University (Teaching Collection));

OUM (University Museum, Oxford);

RSM (Royal Scottish Museum, Edinburgh);

SM (Sedgwick Museum, Cambridge University).

CHAPTER I

CHAPTER I

i) HISTORY OF CLASSIFICATION OF CHEIRURIDAE:

Hawle and Corda (1847) (text Figure 1) erected the subdivision 'Chirurides' comprising a group of trilobites they considered stood near their 'Lichades' on the one hand and 'Pelturids' on the other. They thought that the form of the facial suture differentiated the 'Chirurides' sufficiently from these other groups, but added that the construction of the pygidium (they placed much emphasis on the development of pygidial spines ('fringes')) was also different. Within the 'Chirurides' they recognised two tribes (Sippen) of genera, the genera in each group closely related by the structure of their cephala. The first, for which the term 'Chirurides' was also used was diagnosed as follows:- "Glabella flat, arched, laterally lobed" and included along with Beyrich's Cheirurus (which Hawle and Corda always spelled Chirurus) three new genera Placoparia, Eccoptochile and Actinopeltis. The second tribe, termed Trochurides was diagnosed "Glabella spherically swollen" and included two genera Trochurus and Sphaerexochus. In the text preceeding the tabulation of their classification Hawle and Corda say that for Trochurus " ...... we have retained Beyrich's older name, since Barrande's chosen name Staurocephalus has already been used." In fact they seem to have been mistaken about the true identity and use of the name Trochurus since they gave to what is really that genus the name Corydocephalus.

Text figure 1.

Diagram of the major classifications of the Cheiruridae

HAWLE AND CORDA 1847	BARRANDE 1852	SALTER 1864	SCHMIDT 1881	REED 1896b	RAYMOND 1913b	BARTON 1916	ÖPIK 1937	PRANTL AND PRIBYL 1947
CHIRURIDES	XIII FAMILLE	CHEIRURIDAE	CHEIRURIDAE	CHEIRURUS	CHEIRURIDAE	CHEIRURIDAE	CHEIRURIDAE	CHEIRURIDAE
CHIRURIDES: Chirurus Placoparia Eccoptochile Actinopeltis TROCHURIDES: Trochurus Sphaerexochus	Cheirurus Placoparia Sphaerexochus Staurocephalus Deiphon	C. (Cheirurus) C. (Crotalocephalus) C. (Eccoptochile) C. (Actinopeltis) Sphaerexochus Amphion Placoparia Typhloniscus Staurocephalus Deiphon ?Encrinurus ?Cybele ?Cromus ?Zethus	CHEIRURUS: I: C. (Cheirurus) C. (Cyrtometopus) C. (Sphaerocoryphe) II: C. (Nieszkowskia) C. (Pseudosphaerexochus) Sphaerexochus	C. (Anacheirurus) C. (Eccoptochile) C. (Cyrtometopus) C. (Hemisphaerocoryphe) C. (Sphaerocoryphe) C. (Nieszkowskia) C. (Pseudosphaerexochus) GROUP I: C. (Cheirurus) pars. GROUP II: C. (Cheirurus) pars. C. (Crotalocephalus)	CHEIRURINAE: Cheirurus Ceraurus Crotalocephalus Sphaerexochus Pseudosphaerexochus Nieszkowskia PLIOMERINAE: Pliomera Pliomerops Placoparia DEIPHONINAE: Deiphon Staurocephalus Sphaerocoryphe	GROUP I: Eccoptochile Cyrtometopus Anacheirurus Nieszkowskia Pseudosphaerexochus Sphaerocoryphe Hemisphaerocoryphe Actinopeltis Sphaerexochus Areia Placoparia Typhloniscus Prosopiscus Kawina Pilekia GROUP 2: Cheirurus Crotalocephalus Ceraurinus Ceraurus Lehua	CHEIRURINAE: Cheirurus Crotalocephalus Ceraurus Lehua Ceraurinus Krattaspis Pompeckia CYRTOMETOPINAE: Cyrtometopus Eccoptochile Pseudosphaerexochus Actinopeltis Nieszkowskia Hemisphaerocoryphe Pilekia Youngia Anacheirurus Kawina Parapilekia Seisonia Reraspis ?Protopliomerops DEIPHONINAE: Deiphon Onycopyge Sphaerocoryphe SPHAEREXOCHINAE: Sphaerexochus	CHEIRURINAE: C. (Cheirurus) C. (Crotalocephalus) C. (Pseudocheirurus) Ceraurus Lehua C. (Ceraurinus) C. (Osekaspis) Krattaspis Pompeckia CYRTOMETOPINAE: Cyrtometopus E. (Eccoptochile) E. (Eccoptochiloides) P. (Pseudosphaerexochus) P. (Pateraspis) Actinopeltis Nieszkowskia Pilekia Youngia Anacheirurus Kawina Parapilekia Seisonia Reraspis ?Protopliomerops DEIPHONINAE: Deiphon Onycopyge Sphaerocoryphe ?Hemisphaerocoryphe SPHAEREXOCHINAE: Sphaerexochus AREIINAE: Areia

Text figure 1

Although in his work of 1852 Barrande did not profess to classify trilobites, he discussed the Bohemian species within families (which he did not name but only numbered) and in these families grouped species together. His 'Family 8' corresponded to Hawle and Corda's 'Chirurides', and in this family Barrande named five genera represented in Bohemia, grouped as follows: Cheirurus and Placoparia: Sphaerexochus and Staurocephalus: Deiphon. His view on the systematic value of a genus was very broad and he had no hesitation in including Hawle and Corda's genera Actinopeltis and Eccoptochile as well as Green's Ceraurus within Cheirurus. Although he discusses in turn each point by which Hawle and Corda differentiated their Actinopeltis and Eccoptochile from Cheirurus Barrande included Ceraurus pleurexanthemus - the only species of that genus described to that date - without discussion.

Of Actinopeltis which was separated by the number of thoracic segments (which was stated by Hawle and Corda to be 10), and the form of these segments and that of the glabella, Barrande claims to have better material and says that these specimens actually have the eleven thoracic segments characteristic of Cheirurus. Furthermore, although he admits that the glabella of Actinopeltis is more swollen than in other 'congeneric species' he sees a passage towards such a glabellar form indicated by the species C. gibbus (now Crotalocephalina) and especially C. clavifrons (now Cyrtometopus). The form of the thoracic segment Barrande said was in perfect agreement with that of other species of Cheirurus having a form somewhere between the extreme types.

Eccoptochile, separated by Hawle and Corda by differences in the hypostoma, the thoracic pleurae, the number of thoracic segments and the pygidium is also discussed. The hypostoma, Barrande said, had the same elements as *C. gibbus* and *C. insignis* and these elements were disposed in a similar manner having only variations which he considered of specific rank. The pleurae, he considered, were constructed within the genus with a form at the opposite limit to that typified by *C. gibbus*. With his broad concept of a genus, Barrande thought that although *Eccoptochile* had 12 thoracic segments as opposed to the 11 typical of most of the species of *Cheirurus*, it was not a generic distinction and said that eleven other of his genera had a similar or much greater difference amongst their species. As for the pygidium with the same number of axial rings and three pleurae developed on each lateral lobe, he said that it was much like that in the group of species like *C. insignis* and *C. gibbus*. In conclusion, Barrande stated that the fact that the morphology of forms varied from one extreme to another was the reason he kept them all within the same genus. By citing examples of species within *Cheirurus* (in his sense) which are very similar in some characters and widely different in others, Barrande showed that he grouped into a genus all species showing any of a plexus of interrelated morphological characters.

Within his concept of the genus *Cheirurus*, Barrande set up a classification which, because it was based primarily on thoracic characters, resembles the present day divisions of the family Cheiruridae into subfamilies. Secondarily, it is based on cephalic characters and these divisions show relations to more recently accepted genera and subgenera.

Cheirurus was first divided into two sections, the first with weakly impressed pleural furrows parallel to the edges of the pleurae (corresponding to the modern concept of Cyrtometopinae), the second with deep oblique pleural furrows (corresponding to the Cheirurinae). Within his first section there was a tripartite division into those species having 10, 11 or 12 thoracic segments. The group with 12 segments contained the species *claviger* and *sedgwicki* (now belonging to *Eccoptochile* and *Placoparina* respectively), that with 11 only *globosus* (now *Actinopeltis*) and that with 10 *tumescens* and *scuticauda* (now *Eccoptochiloides*).

The second section, all members having 11 segments in the thorax was divided upon glabellar characters into two, depending upon whether the lateral glabellar furrows met or did not meet on the sagittal line. Thus the group where they do not, included species now referred to the genera *Cheirurus* s.s., *Pseudocheirurus*, *Cerauroides* and *Ceraurus*, and that with united lateral glabellar furrows species now placed in *Crotalocephalus* and *Crotalocephalina*. His species *quenstedti* (= *squarrosum* Zenker 1833) he placed in a position intermediate between these last two groups and today belongs to a separate genus. His final group was a provisional one consisting of species which apparently Barrande did not know sufficiently well to include in his classification.

Lastly Barrande made some interesting observations about the incidence in time of the characters he had discussed. He noted, for instance, that in his species, certain characters are found in the 'Lower Silurian' (Ordovician) which are not found in the 'Upper Silurian' (Silurian). In summary, Barrande said the Ordovician was characterised by species with pleural furrows parallel to the edges of the pleurae, 10 to 12 segments in the thorax and in the cephalon globular glabellae and the presence of anterior borders and anterior border furrows. Restricted to the Silurian proper he said were forms with oblique pleural furrows, 11 segments only in the thorax but lacking anterior borders and anterior border furrows mesially. These generalisations of Barrande are true with the exception that species with oblique pleural furrows and eleven segments in the thorax are found in Ordovician rocks. Barrande must have been in ignorance of the thoraces of these species.

Like Hawle and Corda, Barrande accepted Beyrich's genus Sphaerexochus as independant within his 'Family 8'. Within the family also he placed his own Deiphon as a separate genus although it was only known at that time by incomplete specimens.

Cheiruridae - the family name - was first employed by Salter (1864). Within it he recognised a group of genera, Cheirurus (with its subgenera Crotalocephalus, Eccoptochile and Actinopeltis), Sphaerexochus, Amphion, Placoparia, Typhloniscus, Staurocephalus and Deiphon all of which he definately included, and another group Encrinurus, Cybele, Cromus and Zethus of which he had little material and remarked that they ".... have so many differences of habit that I am doubtful if they should not form a distinct family". Sphaerexochus he thought probably ought to be added as a subgenus of Cheirurus, but he kept it separate for convenience. For the other genera he definately included, Amphion and Placoparia are synonyms, Typhloniscus is a genus of uncertain systematic position, and within Staurocephalus Salter included species now referred to that genus and to Sphaerocoryphe. As apparently did Barrande, he regarded the form of the pygidium as having little classificatory value.

In 1872 Barrande made no major change to his earlier classification of the family, which now he called 'Family 15'. He widened his concept of the genus Cheirurus further by describing under that name species now included in several different genera. In addition he erected Areia for the two blind Bohemian species fritschi and bohemica, and included Volborth's genus Crotalurus. Although this genus was later found to be a synonym of Cromus (Angelin) this latter genus was not included in his 'Family 15', but included with Encrinurus and Amphion elsewhere, (here disagreeing with Salter's opinion of Amphion being cheirurid). To Sphaerexochus Barrande attributed species now included in Nieszkowskia, Pompeckia, Hemisphaerocoryphe and Pseudosphaerexochus. Barrande stated that he did not intend to discuss at that time whether all these species belonged to Sphaerexochus. Although he mentioned Angelin (1854) he did not make reference to Sphaerocoryphe and possibly therefore did not consider this genus of Angelin distinct from Sphaerexochus. Deiphon, for the first time described completely, was retained as a separate genus.

Schmidt (1881) agreeing with Salter's earlier opinion about Amphion, replaces this genus within the Cheiruridae 'at least as a supplement' and adds that his new genus Diaphanometopus, now forming a monotypic subfamily within the Pliomeridae, belonged near to it. He also agreed with Salter about the importance of the course of the facial suture as a systematic character and excludes the opisthoparian Crotalurus which earlier Barrande had included here.

Making it clear that his classification is based upon his own and some Swedish specimens and therefore may only apply to them, he sets out his ideas as follows. Disagreeing with Angelin he includes Cyrtometopus and Sphaerocoryphe as subgenera of Cheirurus since he believed that there were "numerous transitions" which connected all the species making generic separation impossible. Also within Cheirurus, Schmidt erected the new subgenera Pseudosphaerexochus and Nieszkowskia. He divided the whole genus Cheirurus into two sections, each section containing two groups. The first section he characterised as follows: 11 segments in the thorax, each pleura with a constriction between inner and outer portions and with a narrow articulating band along anterior and posterior borders which ended at the constriction as a hooked ridge. The two groups within this section were separated by Schmidt on the possession of either an oblique or longitudinal furrow on the inner part of the pleurae, the first group characterised by the subgenus Cheirurus, the second by Cyrtometopus and also containing Sphaerocoryphe. Schmidt's "Section II' included subgenera with the following characters: twelve thoracic segments with no constriction so that they lie together for most of their length, with a longitudinal line of punctae (in the case of group 1, characterised by Nieszkowskia) or almost obsolete punctae or none at all (group II, characterised by Pseudosphaerexochus). Eccoptochile, which Schmidt did not know from specimens, he placed provisionally in section two, but not definitely in either group of that section. Actinopeltis he considered a poorly defined group and he preferred to disperse amongst the other subgenera of Cheirurus any species formerly referred to it. Sphaerexochus was considered a separate genus.

In 1896 Reed concerned himself mostly with notes on the evolution of Cheirurus s. l. but adds to the classification of the genus which he accepted in Schmidt's sense the subgenera Anacheirurus and Hemisphaerocoryphe, not accepting Actinopeltis but regarding it, like Schmidt, as an ill-defined group within Cheirurus. The subgenera Cheirurus and Crotalocephalus Reed split into two groups. Group I, "with Cyrtometopian pygidium" was composed wholly of species of Cheirurus (Cheirurus) in which the anterior pair of pygidial spines" is noticeably larger than the others. Group II contained all other species of Cheirurus s.s. and those of the subgenus Crotalocephalus. Reed added that the genus Youngia (Lindstrom 1885) was of doubtful relationships.

Beecher (1897) did not add to the classification of the family but simply listed the genera and subgenera (not distinguishing between these two taxa) he considered belonged to the Cheiruridae. Here were still included _Amphion_ and _Diaphanometopus_ whereas _Placoparia_ and _Areia_ were placed in the Encrinuridae.

In 1898 following his paper on _Cheirurus_, Reed considered the other genera of the Cheiruridae, especially those four which at that time had a doubtful position in the family. _Placoparia_ was regarded by Reed as an aberrant member of the family although "no line of ancestry or affinity connected it with other known genera", and much the same conclusion was reached after a discussion of _Amphion_. _Diaphanometopus_, Reed thought, was allied to _Amphion_ but want of material did not enable him to comment further on its affinities. _Ariea_,like _Placoparia_ excluded from the Cheiruridae by Beecher, was also included in the Cheiruridae by Reed because of its " ...... resemblance ..... to the early species and subgenera of _Cheirurus_". _Staurocephalus_ was excluded from this family and considered as a side branch from early Encrinurid stock.

In the second edition of Zittels 'Text-Book of Paleontology' (1913) Raymond divided the Cheiruridae into three subfamilies as follows:-

A. Cheirurinae containing _Cheirurus_, _Ceraurus_, _Crotalocephalus_, _Sphaerexochus_, _Pseudosphaerexochus_ and _Nieszkowskia_.

B. Pliomerinae containing _Pliomera_, _Pliomerops_ and _Placoparia_.

C. Deiphoninae containing _Deiphon_, _Staurocephalus_ and _Sphaerocoryphe_.

Raymond did not state whether or not he considered all these as genera or subgenera, and did not mention any others within the family since the work is a textbook. However, the work was important in that the Deiphoninae were here first recognised.

Barton 1916 proposed a revision of the Cheirurinae (in Raymond's sense). It followed for the most part Schmidt's and Reed's earlier classifications except that all taxa previously known as subgenera were raised to generic rank, and the sub-family was divided into two groups which were not further subdivided. In addition a two-fold 'artificial key' was given for the recognition of the genera based on the features firstly of the cephalon, and secondly on those of the thorax and pygidium.

Barton's second group (Cheirurinae with constricted pleurae and diagonal pleural furrows) corresponds to the Cheirurinae as accepted today and contained the genera Cheirurus, Crotalocephalus, Ceraurinus, Ceraurus and his new genus Lehua. His first group (Cheirurinae with pleural furrows horizontal, thoracic segments 10-12, rarely 9 in number) was larger and contained the seven subgenera of Reed's group I, raised to generic rank, namely Eccoptochile, Cyrtometopus, Anacheirurus, Nieszkowskia, Pseudosphaerexochus, Sphaerocoryphe and Hemisphaerocoryphe, and in addition Actinopeltis, Sphaerexochus, Areia and Placoparia. Two poorly known genera- Typhloniscus and Prosopiscus, and two new genera - Kawina and Pilekia were also considered to belong here.

Warburg (1925) in a short note on the family Cheiruridae mentioned Raymond's subdivision into the Cheirurinae, Pliomerinae and Deiphoninae.

She agreed with Barton (1916) about the reinstatement of Sphaerocoryphe in the Cheirurinae and further stated that Deiphon, a closely allied form, could not be considered to belong to a separate subfamily. Staurocephalus, the final member of Raymond's Deiphoninae was here considered to belong doubtfully to the Cheiruridae as it "does not seem to have any close affinities with any of the Cheirurids" (page 339). Of the Pliomerinae of Raymond, Warburg thought it "questionable whether it ought not be raised to the rank of family" (page 339). The result of these statements is that Warburg considered that major subdivisions of the Cheiruridae could not be recognised.

Opik 1937, considered the Cheiruridae to be composed of four subfamilies, two of which he erected. The Cheirurinae were defined as having diagonally furrowed pleurae and an eyeline which when seen is at a distance from the anterior section of the facial suture and runs down into the axial furrow. Here Öpik definitely included Cheirurus, Crotalocephalus, Ceraurus, Lehua and Ceraurinus. His new genus Krattaspis was placed here although the thorax was unknown, and Pompeckia was also provisionally included.

The Crytometopinae, a new subfamily, were separated by having pleural furrows or lines of punctae where are parallel to the edges of the segment. The false eyelines run along the facial suture and join the palpebral lobes to the anterior and lateral borders. He included Cyrtometopus, Eccoptochile, Actinopeltis, Nieskowskia, Hemisphaerocoryphe, Pilekia, Youngia, Anacheirurus, Kawina, Parapilekia, Seisonia and a new genus *Reraspis*; *Protopliomerops* was uncertainly included since it was not well known.

Although he accepted Raymond's Deiphoninae and included *Deiphon*, *Onycopyge* and *Sphaerocoryphe*, Öpik was less sure of it being distinct from the Cyrtometopinae. *Sphaerocoryphe* he thought greatly resembled *Cyrtometopus*, and *Hemisphaerocoryphe* which he considered Cyrtometopian he said fitted the definition of the Deiphoninae. This last genus is now included in the Deiphoninae, with some doubt.

Agreeing with Barton and Warburg, Öpik did not think *Staurocephalus* to be a cheirurid.

The fourth subfamily, Sphaerexochinae, he set up to embrace the single genus *Sphaerexochus*, because of its smooth pleurae. This genus and those of the Deiphoninae Opik considered to be derived from the Cyrtometopinae.

Areia, considered definitely a cheirurid, was not placed in a subfamily, but was thought to be connected to the Cyrtometopinae since it has a line of punctae on the thoracic pleurae.

The work of Prantl and Přibyl 1947 was prompted by their dissatisfaction with the systematic position of some of the Bohemian Cheiruridae. For the most part these had been placed within the family by authors who had not seen the Bohemian material but only Barrande's description and illustrations. Restudy of the type material allowed a new systematic arrangement of these forms which had been included within *Cheirurus* by Barrande.

The four subfamilies into which Öpik had divided the Cheiruridae were accepted by Prantl and Přibyl and a fifth added - the monotypic Areiinae. The Cheirurinae and Cyrtometopinae were accepted entirely in Öpik's sense and with his diagnoses. Within the former subfamily Prantl and Přibyl considered Crotalocephalus a subgenus of Cheirurus, and added two new subgenera to Öpik's list - Cheirurus (Pseudocheirurus) and Ceraurinus (Osekaspis). Two new subgenera were also added to the Cyrtometopinae - Pseudosphaerexochus (Pateraspis) and Eccoptochile (Eccoptochiloides). The delimitation of the Deiphoninae from the Cyrtometophinae was considered by Prantl and Přibyl to be much less certain. Although they accepted the subfamily they emphasised it had not the same significance as the Cyrtometopinae of which it was a late subdivision. Deiphon, Onycopyge and Sphaerocoryphe, argued by Whittard (1934) to be closely allied, were considered to belong here, and also possibly Hemisphaerocoryphe which Prantl and Přibyl thought could equally well be a Cyrtometopinid. They also accepted Öpik's Sphaerexochinae, containing only Sphaerexochus, but differed from that author in maintaining that it did not have such close relations to the Cyrtometopinae as he had considered it to have. For this point of view they point to the structure of the pleurae which are quite different from those of the Cyrtometopinids.

The Areiinae were diagnosed as Cheiruridae with pleurae of Cyrtometopinid type, small pygidium of only four "lobes", without eyes or facial sutures and with the anterior margin of the cephalon shifted forwards in steps in front of the glabella.

In 1951, Evitt set up the subfamily Heliomerinae to receive Heliomera (Raymond) and his new genus Heliomeroides which was separated from the former by a single character of the glabella (the inner ends of the lateral furrows are connected by a furrow which runs exsagittally in Heliomeroides). Since then, doubt has been expressed as to the distinction of these genera, Whittington (1965, pages 416-417) preferring to call them subgenera within Heliomera, and Tripp (1967, page 67) referring all the species to the undivided genus of that name. Whittington (1965, page 411) has also disputed the validity of the subfamily and included the subgenera Heliomera and Heliomeroides within the Sphaerexochinae.

The classification of the Cheiruridae proposed by Hupé in 'Traite de Paléontologie' in 1953 was basically in agreement with that of Öpik (1937). The work of Prantl and Přibyl (1947) was apparently not known to Hupe for he stated the Areiinae to be his own new subfamily, and although he separated Staurocephalus into a new monotypic subfamily, he still included this in the Cheiruridae contrary to the arguements of the Czech authors. Apart from this, in following Öpik, Hupé's classification was in the sub-families and their constituent genera much like that of Prantl and Přibyl who had also been in agreement with Öpik.

Within the Cyrtometopinae, Hupé proposed three groups of genera separable on the configuration of the glabella. These were -

a) glabella little inflated,

b) glabella very inflated but not contracted posteriorly and

c) glabella contracted posteriorly.

The division c) contained Sphaerocoryphe and Hemisphaerocoryphe about the position of which Öpik and Prantl and Přibyl had been unsure, but tended to place them in the Deiphoninae. Within the latter subfamily Hupé only mentions Deiphon.

The Acanthoparyphinae was erected by Whittington and Evitt (1953) to include genera with ovate glabellae having their maximum width across the basal lobes, eyes placed far forward, branches of facial suture at an acute angle to each other, thorax of cyrtometopinid type, and pygidium with two pairs of spines, the anterior pair often more strongly developed. Whittington and Evitt included Acanthoparypha, Nieszkowskia, and Holia.

Sdzuy (1955) noticed that the general similarity of the genera Pilekia (and Parapilekia which he considered a synonym), Anacheirurus and Tesselacauda, and for them he erected a new family - the Pilekiidae. This family he diagnosed as follows:

Cheiruracea with glabella parallel sided or narrowing forward, bearing unspecialised lateral furrows. Eyes placed moderately far forward and with true eye lines. Thoracic pleurae with furrows parallel to the edges cutting pleurae into two almost equally wide (sag.) parts. Pygidium with at least three axial rings and four pairs of spines. In addition to the genera named above Skzuy thought Metapilekia and Metapliomerops probably belonged to this family.

Henningsmoen (in Moore 1959) proposed a classification of the Cheiruridae which followed the work of Öpik and Prantl and Přibyl. The Cheirurinae, Cyrtometopinae, Acanthoparyphinae, Sphaerexochinae, Deiphoninae and Areiinae were accepted as in previous works, the Heliomerinae only questionably accepted as a distinct subfamily, and *Youngia* considered a genus of doubtful position in the family. Harrington in the same work considered the pilekiids to be a subfamily, and with the translated name Pilekiinae, placed this group in the Pliomeridae. Within the Pilekiinae, *Parapilekia* was considered a genus distinct from *Pilekia*, and *Anacheirurus*, *Metapilekia* and *Metapliomerops* were included: *Tesselacauda* along with *Emsurina* and *Seisonia* were placed here with some doubt.

Whittington (1961, 1966) has expressed opinions as to the position of the pilekiids. In 1961 (page 913) in dealing with the Pliomeridae he stated that the pilekiids were different from the other members of that family, and concluded that the pilekiids should be considered either a separate family, or be included in the Cheiruridae as a subfamily. In 1966 (page 705) in dealing with the Ordovician trilobites, Whittington makes it clear that he there considered the pilekiids as belonging to the Cheiruridae.

ii) ABSTRACT OF PRESENT CLASSIFICATION:

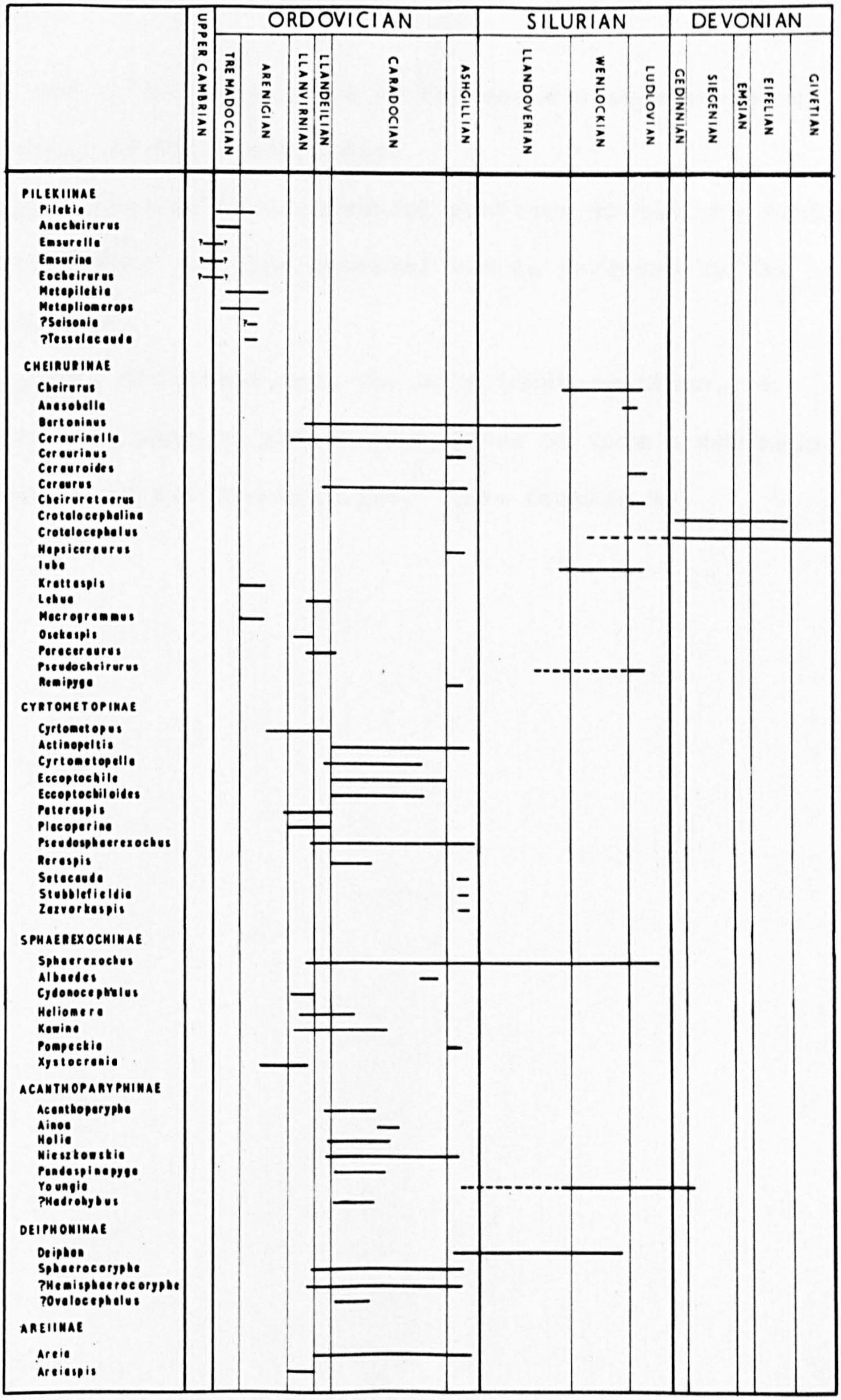
The classification of the present author is, like most workers since, based on that of Öpik, 1937. The Cheirurinae, Cyrtometopinae and Sphaerexochinae are accepted as in that work with small modifications (see Chapters 3 and 4). Diagnoses of the subfamilies will be found in Chapter 4. The Deiphoninae are accepted as a subfamily of equal status to the others (not as a group of genera derived from the Cyrtometopinae (Öpik, 1937)), chiefly on the highly specialised modifications of cephalon and pygidium which they show (see Chapter 3). The Areiinae are accepted as in Prantl and Přibyl, 1947, and the Acanthoparyphinae as in Whittington and Evitt, 1953. The Pilekiinae are considered to belong to the Cheiruridae since morphologically, especially in the medially placed transverse thoracic pleural furrows and the fewer pygidial segments, they resemble the later subfamilies of the family (and of which they are considered to be the ancestors) and are less closely related to the Pliomeridae. (See Chapter 3).

For the reasons given throughout Chapter 3, there are no subgenera in the present classification for the Cheiruridae, all subgenera of previous workers having been raised to generic status or considered to be synonyms of other genera.

In agreement with Whittington (1965) and Tripp (1967), the genus Heliomera (synonym Heliomeroides) is referred to the Sphae-

Text figure 2.

Classification of Cheiruridae adopted here, with ranges of the genera



Text figure 2

rexochinae and is not considered to represent a separate monotypic subfamily of the Cheiruridae.

Youngia, previously of doubtful position within the family is redescribed from the type material and is referred to the Acanthoparyphinae.

Onycopyge, described from the only known specimen, is rejected from the family, and is considered to form a new monotypic subfamily of the Encrinuridae. (See Chapter 4).

CHAPTER II

CHAPTER II

DISTRIBUTION OF THE GENERA OF THE CHEIRURIDAE

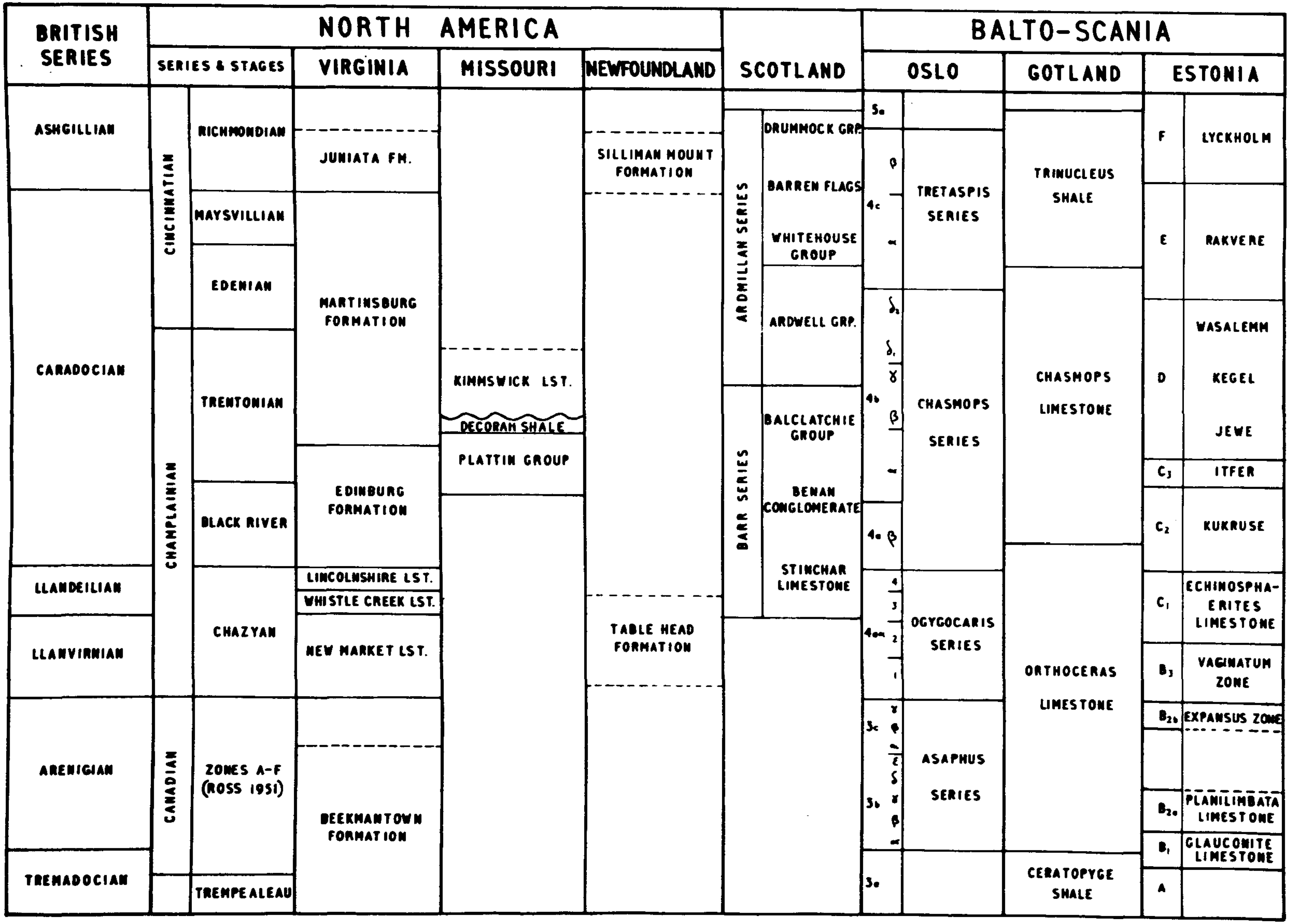
The earliest members of the family Cheiruridae - those genera which comprise the subfamily Pilekiinae - are found widely distributed mainly in rocks of Tremadocian age in many parts of the world. *Pilekia* (and *Parapilekia* considered by Sdzuy to be a synonym of the former genus) occurs in western and eastern North America, Scandinavia, the Frankenwald, Bohemia, Morocco and Korea. *Metapilekia* occurs in Korea and Argentina, whilst other Pilekiid genera are more localised in distribution, for instance *Metapliomerops* in Vermont, *Anacheirurus* in North Wales and *Emsurina* and *Eocheirurus* from Siberia. Thus, if we consider the six Tremadocian trilobite faunas as diagrammatised by Whittington (1966, textfigure 1.), *Pilekia* (with *Parapilekia*) occurs in five, *Metapilekia* in three, whilst the other genera of the subfamily, which are less well known, are restricted to one only.

Already in Tremadocian times, therefore, some of the early members of the Cheiruridae are widespread in distribution, others more restricted. The wide distribution of *Pilekia* indicates that there was a fair amount of mixing between faunas in these times. On the other hand any generalised statement as to the genera with restricted distribution, and therefore to faunal provinces at this time is on less sure ground because of the incomplete state of knowledge of Tremadocian trilobite faunas as a whole, and particularly those of Asia and Australasia.

Text figure 3.

Correlation chart for the northern province in Ordovician times

North America from Dunbar, 1954; Scotland from Walton, 1965; Balto-Scania from Moore, 1967.



Text figure 3

Knowledge of the trilobites which existed from Arenigian times onwards is more complete, and study of these trilobites has revealed that two main areas of distribution may be recognised. These two areas are separated by a line which runs approximately through Central America, east-north-eastwards through Ireland and approximately between England and Scotland, continuing eastwards south of Sweden, Estonia and the Urals. As with Tremadocian faunas knowledge of Asian and Australasian trilobites is too scanty to permit consideration of generalised statements regarding provincial distribution. As can be seen from the course of this line the British Isles are in an area of particular interest when considering Ordovician trilobite faunas.

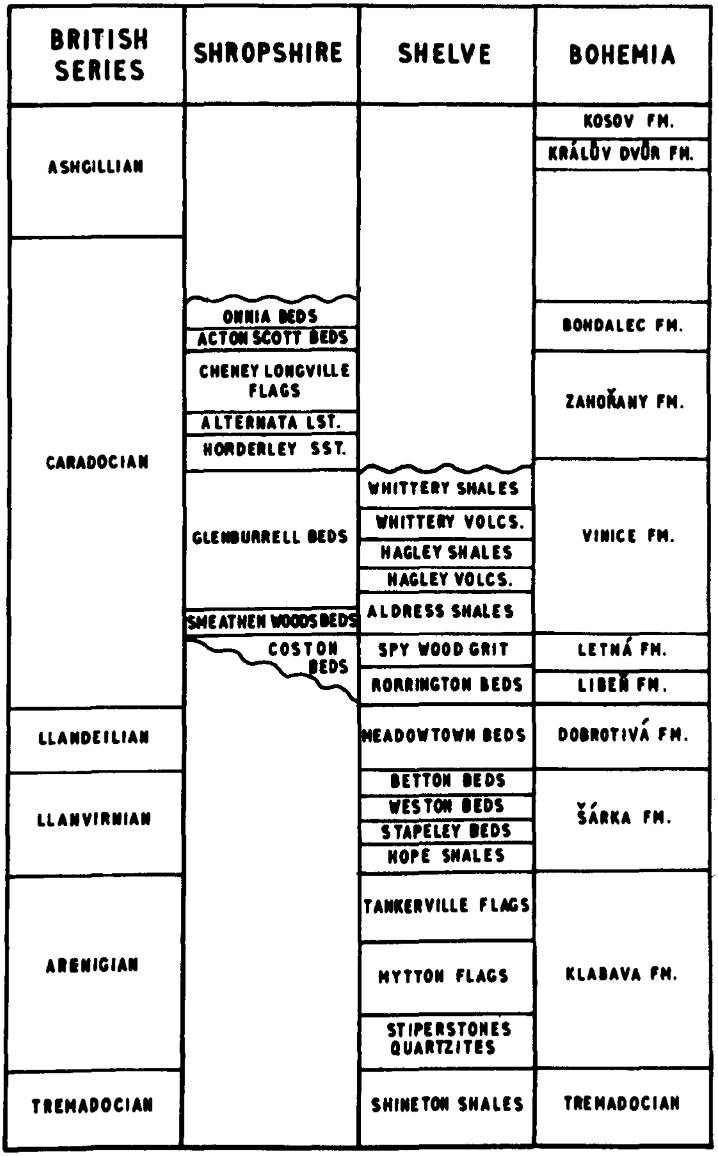
The two provinces of distribution were never completely isolated from one another. Whilst certain families of trilobites during Arenigian to Llandeilian times are restricted to either northern or southern provinces (e.g. Remopleurididae, Bathyuridae and Scutellids to the northern, and Trinucleids, Cyclopygidae and Calymenidae to the southern), other families, the Cheiruridae included, have representatives in both provinces. This isolation of the two areas was more marked earlier in the Ordovician than later, and this can be seen both by a study of trilobites at the family level as well as by considering the genera within the Cheiruridae.

Tabulation of the ranges of all cheirurid genera (text figure 2) shows that after the reign of the Pilekiinae in Tremadocian times a great diversification of genera occurred in Arenigian to Llandeilian times, so that by late Llandeilian times some thirty cheirurid genera are known. (For Ordovician correlations used in this discussion see text figures 3 and 4).

Text figure 4.

Correlation chart for the southern province in Ordovician times

Adapted from Dean, 1967.



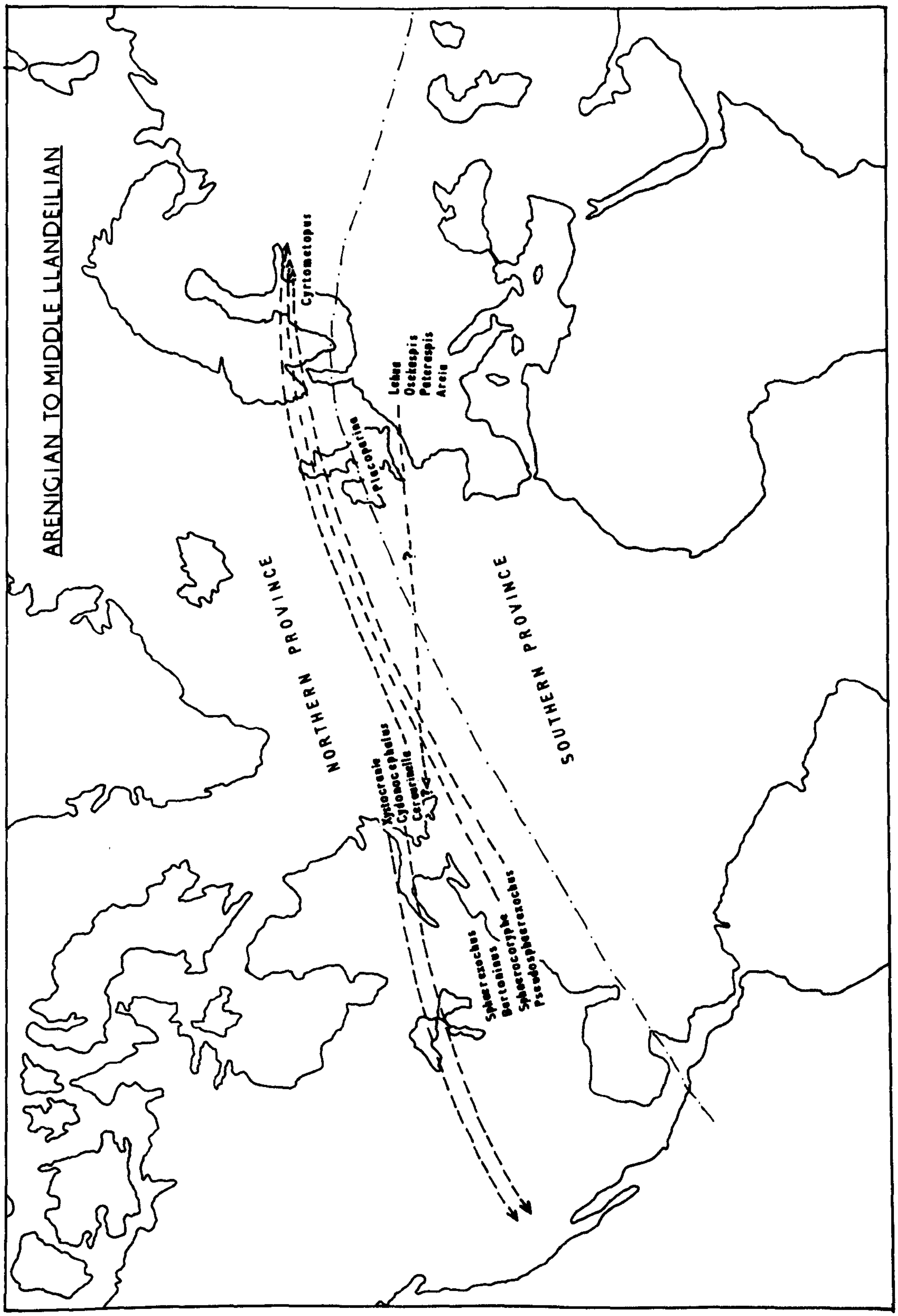
Text figure 4

In rocks of lower Arenigian age two genera which are known only from their cranidia are found - _Macrogrammus_ from the Shelve country and Argentina and _Krattaspis_ from Estonia. Because of the incomplete knowledge of these genera they are difficult to place with any certainty. _Krattaspis_, with a glabella which expands forwards is in this respect more specialised than the genera placed with certainty in the Pilekiinae which have glabellae parallel sided or narrowing forwards, and both _Krattaspis_ and _Macrogrammus_ have their eyes much more posteriorly placed than members of that subfamily. These two genera are possibly therefore the earliest members of the Cheirurinae, already one present in each of the two provinces which became clear from these times onwards.

Although some of the genera of the Cheiruridae are restricted in distribution in the northern province in Arenigian to Llandeilian times, other forms occurring in the same rocks are more widespread, (text figure 5). Hence, four genera of the Sphaerexochinae - _Kawina_, _Heliomera_, _Cydonocephalus_ and _Xystocrania_ (also known from older rocks in the Pogonip Group of western Utah) - found in the Table Head Formation of western Newfoundland and which are at first restricted to the North American continent and its islands, occur side by side with _Ceraurinella polydorus_ which even at specific level is very similar to _Ceraurinella ingricus_ from rocks of a similar age in Estonia. _Cyrtometopus_, again in rocks of this age, is restricted to the Balto-Scanian area. These distributions are probably to be explained by the ecological preferences of these genera, since the North American Sphaerexochinae mentioned are highly

Text figure 5.

Diagram illustrating the geographical extent of chosen genera during Arenigian to Middle Llandeilian times. The arrows do not necessarily imply directions of migration.



Text figure 5

specialised forms possibly demanding a special ecological niche. _Ceraurinella_, on the other hand, a much less specialised genus, possibly had tolerance to a greater variety of conditions.

The genus _Lehua_ presents us with an example of a form which occurs in the same rocks of the Table Head Formation of western Newfoundland and also in the southern province - in Bohemia. Although the cephala of the different species of _Lehua_ from these two provinces differ only in detail, the pygidium of the Newfoundland species apparently has only two axial rings and pairs of spines as compared with the three of the Bohemian type species. It is not impossible, however, that the two forms are the result of parallel evolution in which it could be expected that the less specialised cephala are similar but the pygidia, which in the Cheiruridae change more rapidly with time than the cephala, do not change in the number of segments present in the axis, within a single genus. This difference in the pygidia could reflect that the common stock from which these two forms were derived was widely dispersed in early or pre-Llanvirnian times and that these two forms had evolved separately. Until the pygidium of the Newfoundland form is definately associated with the cephalon this is no more than a suggestion.

Remaining in the northern province, _Sphaerocoryphe_ and _Pseudosphaerexochus_ present in the Chazyan are also found in Estonia in deposits of similar age. Also in the Chazyan, _Sphaerexochus_ and

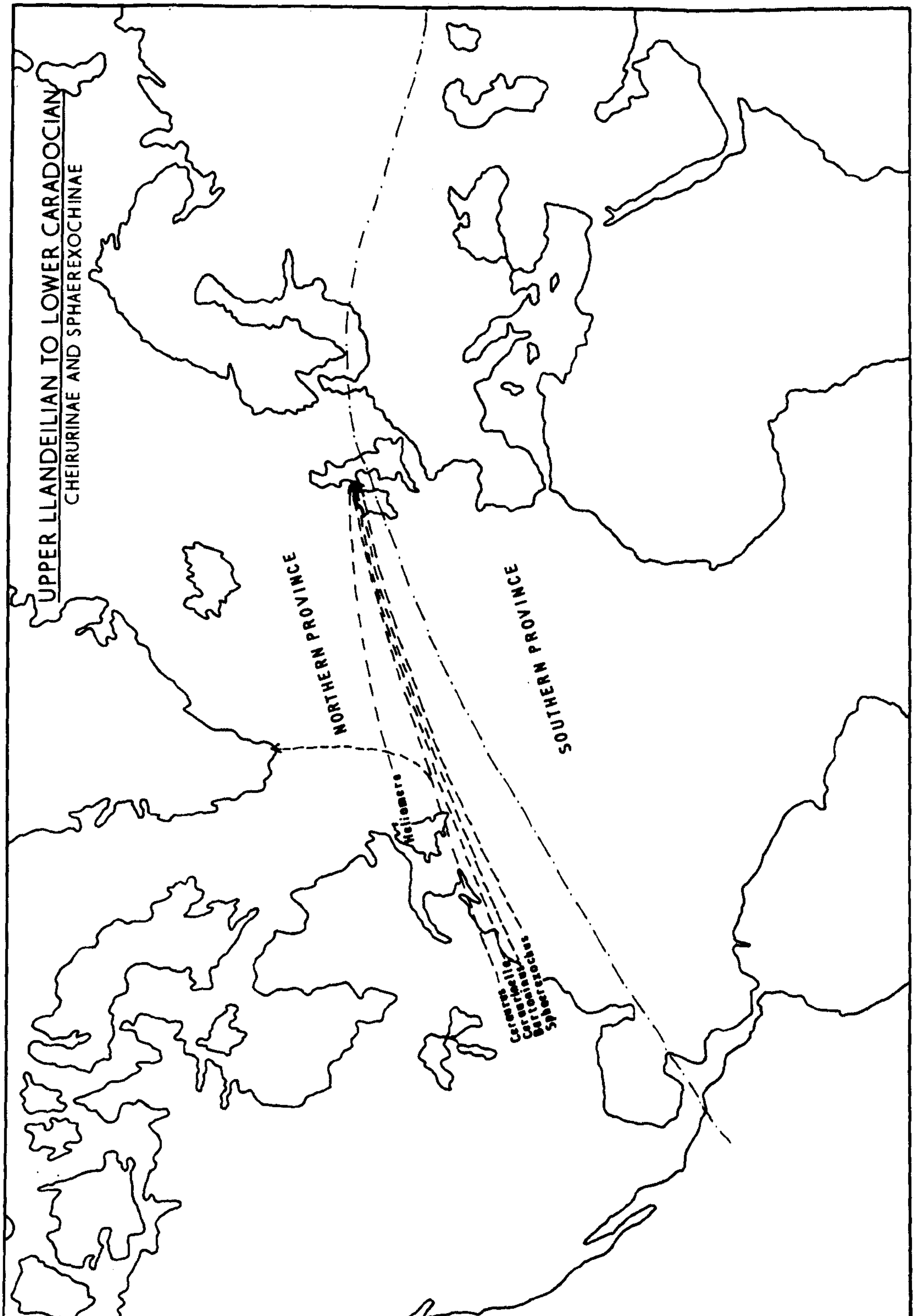
Bartoninus are, in Llanvirnian times, restricted to North America though they have a greater distribution later. Hemisphaerocoryphe and Paraceraurus present in the upper Llanvirnian of Estonia are restricted to the Balto-Scanian area throughout their ranges, the former into the Ashgillian, the latter into Lower Caradocian times.

In the Llanvirnian of the Southern province, in addition to Lehua discussed above, five other cheirurid genera are present. These genera are all restricted in their distribution and are known to have relatively few species and short ranges in time. Placoparina, probably restricted to the Shelve area is a monotypic genus which ranges from the highest beds of the Lower Llanvirnian to near the top of the Llandeilian. In Bohemia Osekaspis, also monotypic, is restricted to the Llanvirnian (Sarka Formation), whilst Pateraspis is known only from the type species in that same formation and a new undescribed species from the Dobrotiva Formation of Llandeilian age (Havlicek and Vanek, 1966). Areiaspis, also restricted to Bohemia, is known from the Llanvirnian, while Areia appears in the Llandeilian.

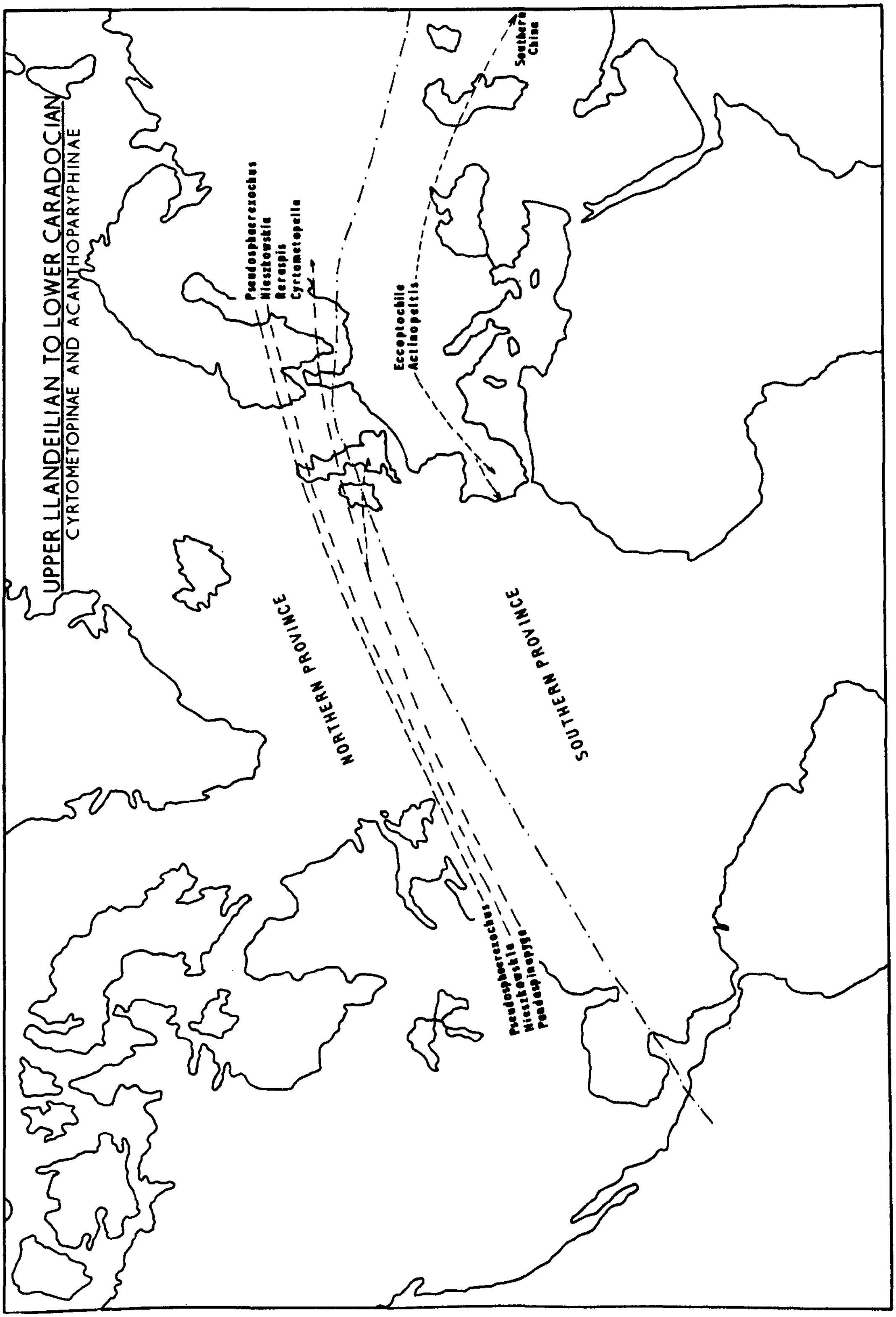
The uppermost Llandeilian and lowest Caradocian saw a second burst of evolution producing some dozen new genera, and several older genera apparently died out. In the northern province (see text figures 6a and b) in Balto-Scania Paraceraurus and Cyrtometopus are no longer found but Reraspis and Cyrtometopella appear and are restricted to that area. In eastern North America Ceraurus appears in the Valcour Chazy at about this time, and all but one of the genera of the Acanthoparyphinae

Text figures 6a & b.

Diagram illustrating the geographical extent of chosen genera during Upper Llandeilian to Lower Caradocian times. Arrows do not necessarily imply directions of migration.



Text figure 6a



Text figure 6b

(*Holia*, *Hadrohybus*, *Pandaspinapyga* and *Acanthoparypha*) also appear and are at first restricted to this area. *Nieszkowskia* appears here and in Estonia in rocks of roughly similar age.

In the southern province by this time *Placoparina* from the Shelve country, and *Osekaspis*, *Pateraspis* and *Lehua* from Bohemia have all died out. Replacing these Bohemian forms are *Eccoptochile* and *Actinopeltis* whilst no new forms appear in Britain.

During Caradocian times very little differentiation of the various cheirurid stocks took place so that genera present at, or shortly after, the beginning of this time continued into the Ashgillian or died out completely. Only *Ovalocephalus* a poorly known member of the Deiphoninae, which is monotypic and confined to the lower Caradocian of northern Kazakhstan, and *Ainoa* the remaining genus referred to the Acanthoparyphinae from the late middle Ordovician of Estonia arise as new forms. Early in the Caradocian, however, it is evident that considerable migration has occurred. *Bartoninus* and *Ceraurus* which first appeared in eastern North America are found in the Lower Caradocian of the Girvan District of Scotland, where also is found the specialised *Heliomera* recorded earlier only from north-eastern North America and western Newfoundland*. In rocks a little younger than these *Acanthoparypha* is found in Scandinavia, and *Pandaspinapyga* a closely related genus which like *Acanthoparypha* is first present in eastern North America, is found in Shropshire and Estonia.

**Kawina*, formerly only known in rocks from the latter area is found in the Middle Ordovician of north-east U.S.S.R.

The position of the Welsh Borderland up to this time in relation to the two major geographical provinces is uncertain when the genera of the Cheiruridae are considered. In the lower Arenigian the presence of Macrogrammus in this region and in Argentina indicates that at that time the small area was part of the southern province. Placoparina from Llanvirnian and Llandeilian rocks, which is restricted to this area gives no clue as to which province it was affiliated. Geographically, the area is close to the boundary between north and south provinces, and the fact that Placoparina seems to be related to Reraspis (which occurs only in Estonia) and also to Eccoptochile (which occurs only in the southern province) indicates that this part of Britain at this time had an intermediate position with regard to the two provinces. Thus, Pandaspinapyga at that time existed in areas close to the boundary between the two major provinces, and is recorded from the adjacent margins of each. At approximately the same time, however, Bartoninus, Heliomera and Ceraurus lived in the Girvan area of Scotland but are not recorded from the Welsh Borderland less than 200 miles away. This again is possibly to be explained by the ecology of the times and the varying conditions under which the various genera could exist.

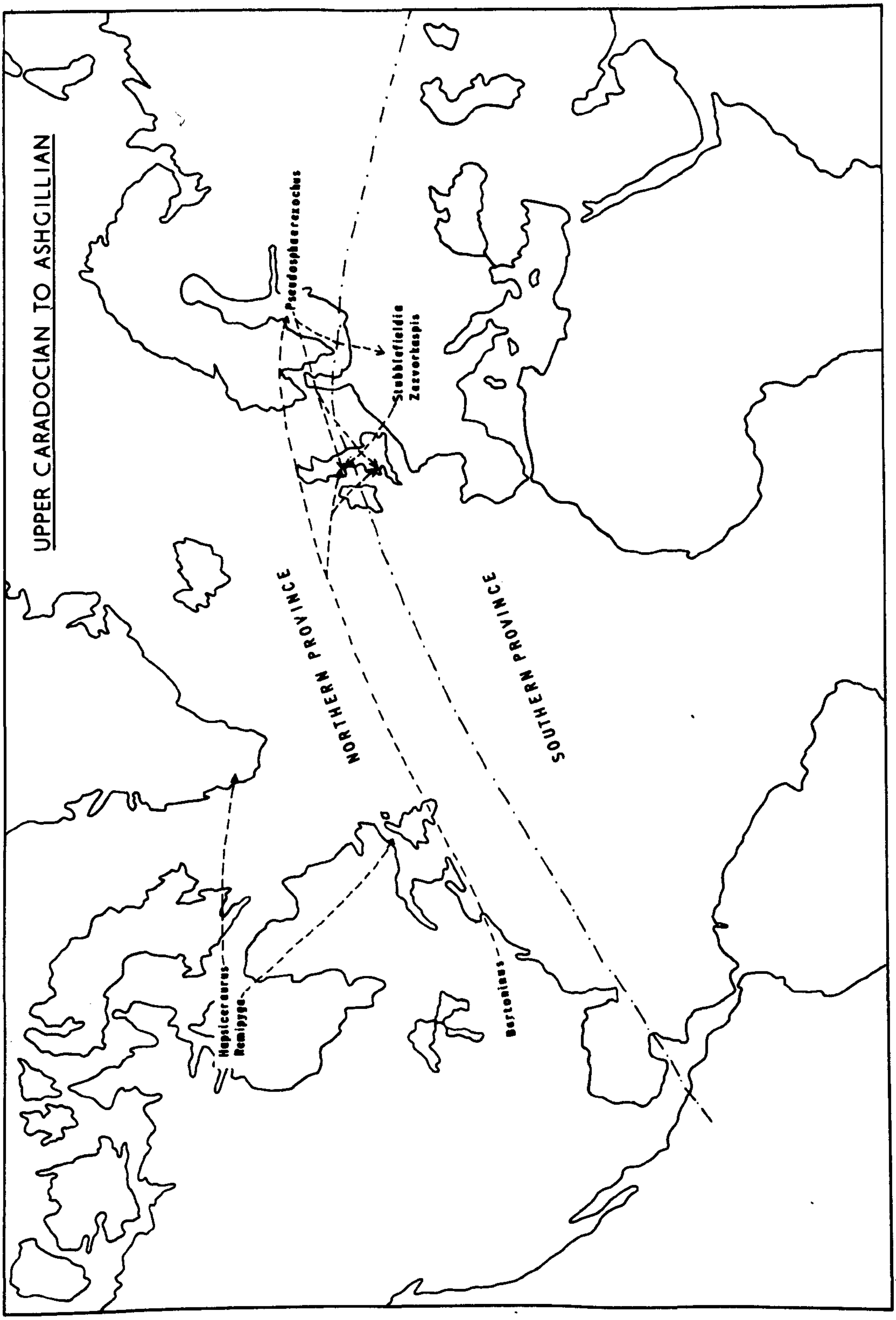
During these Caradocian times Pseudosphaerexochus becomes a common cheirurid genus especially in the Balto-Scanian area, although it also occurs in Britain and Greenland. It is not recorded in rocks younger than the Chazy in eastern North America. Bartoninus which arose in eastern North America also predominates at this time in Britain and Balto Scania. Sphaerocoryphe is present through Caradocian times in eastern North America, Britain and Balto-Scania, and Hemisphaerocoryphe is restricted to the latter area both genera dying out in the Asgillian. Ceraurus and Ceraurinella which appear first in the Llandeilian of North America, after being present in the lower Caradocian of the Girvan area are restricted to Greenland and eastern North America. Nieszkowskia which is widespread in the northern province in upper Llandeilian times is now restricted to Balto-Scania, and Sphaerexochus which first appeared at that time in Virginia early in Caradocian times, is found in the Girvan and Shelve areas and a little later also in Quebec.

In the southern province in Caradocian times there were many fewer cheirurid genera than in the northern province. Areia was still restricted to Bohemia whilst Eccoptochile and Actinopeltis also mainly restricted to that area are represented also by one species each in Spain and Portugal respectively.

The latest Caradocian and Ashgillian times (text figure 7) were a period of great change in the Cheiruridae. Migration between northern and southern provinces seems to have been somewhat easier during these times, and in addition there was some evolution of new but short ranging forms accompanied by the largest scale extinction of the genera of the Cheiruridae to take place in the history of the family.

Text figure 7.

Diagram illustrating the geographical extent of chosen genera in Upper Caradocian to Ashgillian times. Arrows do not necessarily imply direction of migration.



Text figure 7

Of the new genera in the northern province Hapsiceraurus and Remipyga which appear early in the Ashgillian of Arctic Canada and Greenland are mainly restricted to that area although Remipyga appears to be present in north-eastern U.S.S.R. These two genera do not survive into Upper Ashgillian times. Pompeckia, found only in Scandinavia, has a similar range. In the southern province the monotypic Zazvorkaspis is restricted to Bohemia, and Stubblefieldia is also predominantly a Bohemian form although it is present in the Ashgillian of the Girvan region of Scotland. These two genera are all restricted to the Upper Ashgillian.

Of the genera which ranged through the Caradocian into the Ashgillian, Nieszkowskia always restricted to the northern province and predominantly a European form is last recorded in the Richmondian of Canada. Ceraurinella, formerly restricted to North America is found in Ashgillian times in Northern England and Poland, but dies out before the end of the Ordovician as does Ceraurus, still restricted to North America and Greenland.

Although there is still some provincial distribution of the trilobites in Ashgillian times, it is evident from the faunas that what were formerly the northern and southern provinces, now contained more and more elements common to both. The cheirurids of the Ashgillian rocks of Britain tend to be similar in all the different areas. Very similar species of Bartoninus are found in South Wales, Northern England, Eastern Ireland and the Girvan area of Scotland, and similar forms are found in Scandinavia. _Pseudosphaerexochus_ is also found commonly in all the areas of Ashgillian rocks in Britain.

In the southern province _Areia_ has continued through the Caradocian in Bohemia but is last represented by a species in Sweden. In China a species which most resembles _Bartoninus_ is found. _Pseudosphaerexochus_, up to this time found only in the northern province, is represented in Bohemia, and is last reported from a species in Poland. _Eccoptochile_ and _Actinopeltis_ always restricted to the southern province die out at the end of the Caradocian, and towards the end of the Ashgillian respectively.

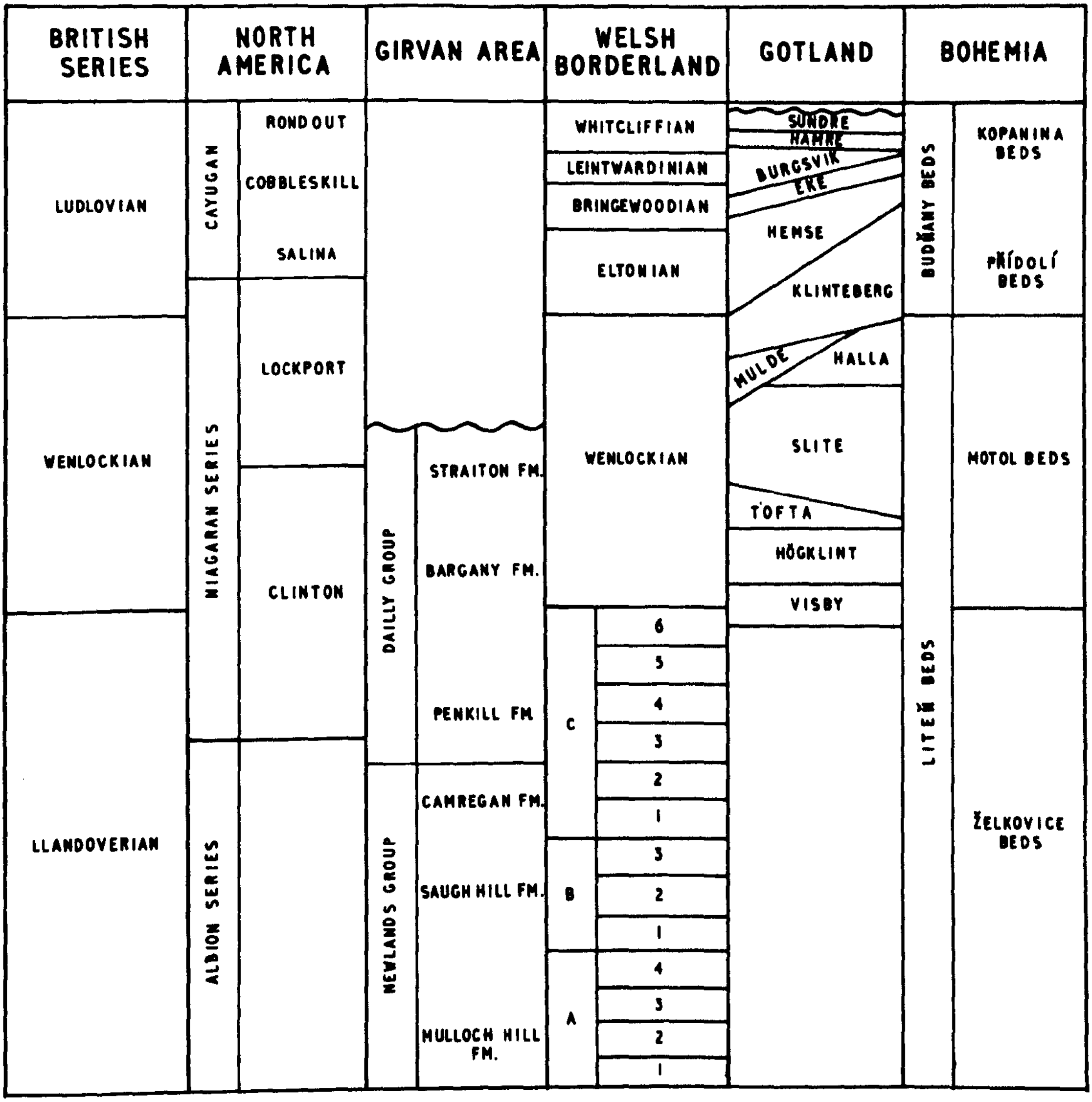
The result of all this migration and extinction in Ashgillian times is that only three genera of the Cheiruridae are found in rocks of both Ordovician and Silurian age. _Sphaerexochus_, always widespread in the northern province from early Caradocian times onwards, becomes most common in Bohemia, Britain and Balto-Scania in Silurian times although it is represented in North America as well. _Deiphon_ first appeared in the _Leptaena_ Limestone of Scandinavia and survived into Silurian times when it is found in all four regions which _Sphaerexochus_ is present in. The third genus to last into the Silurian is _Bartoninus_. This genus had a great explosion of species in Ashgillian times and lasted into the Upper Llandoverian, but at that time is apparently restricted to Britain, where it is found in South Wales, the Shelve country and the Girvan district.

Throughout Silurian times there was a renewed differentiation of the cheirurid stock apparently stemming from the genus Bartoninus. (Correlation chart for the Silurian is text figure 8). In the Middle Llandoverian of the Girvan area Pseudocheirurus occurs rarely although this genus is only next recorded and better known from the Ludlovian of Bohemia. Iuba appears in the Upper Llandoverian of Shropshire, spreads to Bohemia in Wenlockian times and lasted into the Ludlovian of both areas. Also in the Upper Llandoverian, this time in Estonia, 'Cheirurus' estonicus is present and may be the forerunner of Cheirurus s.s. which itself is present in the Wenlockian deposits of Britain, Gotland, western and eastern North America and Kazakhstan. What may be Cheirurus s.s. is present in the Ludlovian of the north of England. Crotalocephalus articulatus is present in the Wenlockian of Elbersreuth. Cheiruretaerus is found in the Wenlockian of Bohemia and the Lower Ludlovian of the Welsh Borders and Kazakhstan, and at a similar horizon Anasobella is found in the Henryhouse Formation of Oklahoma. Cerauroides again of Lower Ludlovian age is found only in Bohemia and Oberfranken. Of the Cheirurinae, only Crotalocephalus and Crotalocephalina are present in the Devonian. The latter genus ranges from Gedinnian to Eifelian and is found in the Harz Mountains, Bohemia, Gotland, Kazakhstan, the Kuznetsk basin and Australia. The Devonian species of Crotalocephalus which range into the Givetian are found in Bohemia, Kazakhstan, Siberia, Kuznetsk, the Harz, Poland, Wisconsin in North America, south western Britain and Japan.

Text figure 8.

Correlation chart for the major areas of Silurian rocks containing Cheiruridae.

Girvan Area from Walton, 1967; Welsh Borderland - Llandoverian from Jones, 1925, Ludlovian from Shergold and Shirley, 1968; Gotland from Martinsson, 1967; Bohemia modified from Prantl and Přibyl, 1954.



Text figure 8

Deiphon and *Sphaerexochus* which are also present in the Ordovician are found over a wide area in Silurian times. *Deiphon* did not last into Ludlovian rocks whereas *Sphaerexochus* did and both are found in North America, Britain, Balto-Scania and Bohemia; the latter genus is also recorded in India and Australasia.

The species '*Crotalocephalus*' *silverdalensis*, '*C.*' *sculptus* and '*C.*' *ednesdalensis* which probably require generic separation from *Crotalocephalus* s.s. and which are from Australia, may indicate that this area had some separation from the area of the earth's surface which now includes most of Europe, Asia and America. Within this small area evolution proceeded along some lines different from those in the other areas. The presence of *Sphaerexochus* and *Crotalocephalina* in the same general area, however, would suggest that the forms peculiar to Australia developed in a special ecological environment, or that there were times when this small area became more closely linked with the other, larger, portion of the Devonian sea.

Youngia, known only by its cephalon, is found in the Middle and Upper Llandoverian of Girvan and the north of England, the Wenlockian of Gotland, the Ludlovian of Turkestan and the Lower Devonian of Estonia.

CHAPTER III

CHAPTER III

PHYLOGENY OF THE CHEIRURIDAE

In studying the Cheiruridae it becomes clear that all the members of the other subfamilies evolved from the unspecialised Pilekiinae. It is therefore necessary to give a summary of the morphological features which characterise the members of that subfamily.

The Pilekiinae are proparian trilobites. The glabella is parallel sided or decreases in transverse width forwards, is never highly convex and has 3-4 pairs of lateral furrows which reach one third or less way across glabella. The eyes are placed far forward and have true eye ridges which run towards the anterior lobe of the glabella meeting the axial furrow just anterior to the fossulae. Each cheek region is subequal in area or larger than that of the glabella and these cheeks are pitted inside the border furrows. Anterior, lateral and posterior border and border furrows of the cephalon are distinct and genal spines are prominant. Little or nothing is known of the pilekiid rostral plate and hypostoma. The thorax is composed of 11 or 12 segments, each segment composed of an arched axial ring and pleural portions which end in spines and which bear grooves parallel to and equidistant from the edges of the pleurae. The pygidium has 2-4 (more usually 4) rings and a terminal piece in the axis, and 2-4 (again more usually 4) furrowed pleurae ending usually in free spines.

Primitive features shown by the Pilekiinae therefore are the four pairs of lateral glabellar furrows, the anterior position of the eyes and strongly marked eye ridges, and the presence of an anterior border in the cephalon. In the thorax and pygidium the least specialised feature is the lack of differentiation of the form of the pleurae and pleural spines in the pygidium from those of the thorax.

Within the Pilekiinae there is specialisation, showing itself mainly in the pygidium. In the Cheiruridae as a whole it is the pygidium which changed most rapidly with time. Although there is some question whether the two genera which show specialisation belong to the Pilekiinae, they demonstrate that some specialisation of the cheirurid or closely related stock was taking place. *Seisonia*, from the Lower Ordovician of South Korea, shows a reduction of the segments constituting the pygidium to two; *Tesselacauda*, another Lower Ordovician form from Western North America, has a pygidium with entire margin although six pairs of pleurae are present - this large number indicating that it may not be a cheirurid. The pygidium referred by Harrington to his genus *Metapilekia* shows a reduction of the pleurae and free spines to three pairs, and the terminal piece of the axis, in cheirurids usually triangular, in this specimen is reduced in size and narrow, elongated sagittally. Although Sdzuy (1955, page 43) doubts that this pygidium belongs to the unspecialised cephalon upon which *Metapilekia* was erected, it is undoubtedly a cheirurid and therefore shows specialisation in the stock during Lower Ordovician times. Also within the Pilekiinae, *Anacheirurus* shows the beginnings of a specialisation which is to become important in the subfamily Cheirurinae. The pleural groove in *Anacheirurus* is no longer parallel to the edge of the thoracic segments but runs slightly obliquely abaxially backwards.

It will be convenient to discuss the evolution of the different subfamilies separately and first the Cheirurinae will be dealt with.

Krattaspis and *Macrogrammus* occur in rocks of Lower Arenigian age, the former in Estonia and the latter from the Shelve area and Argentina. Because these genera are known only from cranidia they are difficult to assign with certainty to a particular subfamily. However, *Krattaspis* has a glabella which expands markedly forwards and both this genus and *Macrogrammus* have their eyes placed somewhat farther backwards than in genera referred with certainty to the Pilekiinae. Because of these specialisations they are regarded here as the earliest members of the Cheirurinae. Because the thoraces and pygidia of these genera are unknown they will not be discussed further.

In the Cheirurinae the evolution proceeded along definite lines although at different rates in different stocks. Also within their history there appear to have been two separate periods of evolution. The first of these evolutionary periods commenced in the Lower

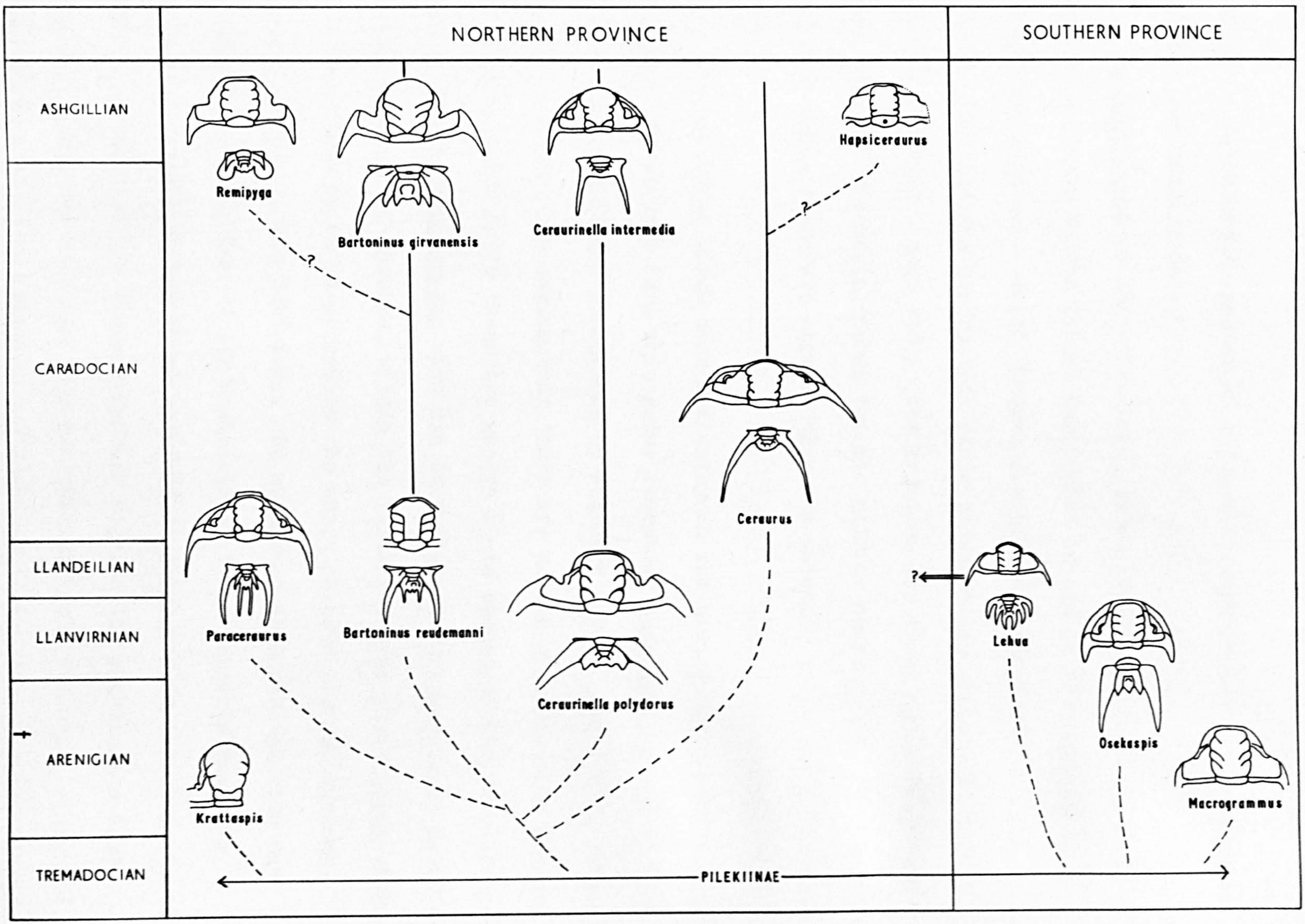
Ordovician and lasted into Llandoverian times and the second lasted from Llandoverian into the Middle Devonian.

The characters which are common to the genera of the Cheirurinae are as follows. As in all Cheiruridae with eyes, the Cheirurinae are proparian. The glabella is sometimes still, as in the Pilekiinae, parallel sided but more often expands forwards, in which case the anterior border and anterior border furrow are usually incorporated in the frontal lobe medially. The glabella always has three pairs of lateral furrows which although they specialise in different ways, the basal pair usually curve backwards to meet the occipital furrow thereby isolating the basal glabellar lobes. The eye is more posteriorly placed in the Cheirurinae than in the Pilekiinae except in some of the genera associated with the second period of evolution where it becomes anteriorly placed once again. Where known, the rostral plate is always short (sag.) and wide (tr.), and the hypostoma has a convex median body which decreases in width (tr.) backwards with distinct short maculae. In the thorax the number of segments in all but one genus in which the number is known is 11 (10 in Anasobella), and the pleural furrows have become specialised from the condition in the Pilekiinae, being shortened and obliquely directed so that the outer part of the pleurae which are free spines are unfurrowed. This increase in obliquity of the pleural furrow must be associated with the modified articulation of the segments in the Cheirurinae. In the Pilekiinae, the articulation is by a simple ridge on the edge of one pleura fitting against a furrow in the edge of the next posterior, these ridges and furrows being present along most of the length of the pleurae. In the Cheirurinae, the pleurae are only in contact for about half their length (tr.) the articulatory apparatus having decreased in length and modified from the simple furrow and ridge into a hooklike facet which fits against a similar facet on the adjacent segment. Presumably the pleural furrows were partly for the insertion of the muscles which activated the articulation between the pleurae, and a short diagonal furrow would give a greater length for muscle insertion that a furrow extending the same distance along the pleura but parallel to its edges. The pygidia of the Cheirurinae, with one possible exception have three rings and a terminal piece in the axis, and three pairs of spines (the posterior two pairs of which are often much reduced in size), with or without a terminal spine or projecting terminal piece.

The earliest member of the Cheirurinae in which the pygidium is known is _Osekaspis_ from the Dobrotiva Beds (Llanvirnian) of Czechoslovakia, see text figure 9. Although the cephalon of this genus is little specialised from the pilekiid type- the main difference being the more posterior position of the eye - the pygidium is very specialised; showing what is a common feature of the pygidium of members of the subfamily, the reduction of the posterior two pairs of spines. In _Osekaspis_ the mid pair of pygidial spines are much shorter than the long stout anterior pair, and the posterior pair have completely disappeared, the terminal piece of the axis enlarging to give a stout median spine. Already then in the early Ordovician this stock of the Cheirurinae has specialised considerably and reached

Text figure 9.

Diagram of the phylogeny of the Cheirurinae (Ordovician genera)



Text-figure 9

a stage of development reached by different stocks within the subfamily at different times later.

Paraceraurus, on the other hand, which is present in rocks from Upper Llanvirnian to the lowest Caradocian in age in Estonia, has a specialised cephalon. In it the eyes are placed posteriorly and far from the glabella and the rostral plate is partially visible in dorsal view (Mannil 1958 , page 170). The pygidium has three axial rings and three pairs of spines (although the mid pair is shorter than the posterior pair both these pairs are shorter than the anterior pair) and a terminal spine.

Another genus which occurred early in the history of the Cheirurinae is Lehua. In general form this genus resembles Anacheirurus and in fact the two were considered synonymous by Whittard (1966, page 285). Whilst Whittard was right in saying that there are points of similarity between the species referred to these two genera it is necessary and more convenient to retain Anacheirurus with its long pleural furrows almost parallel to the edges of the pleurae, within the Pilekiiae, and place Lehua within the Cheirurinae since it possesses the short oblique pleural furrows characteristic of this subfamily. As mentioned when dealing with the provincial distribution of the Cheiruridae, it is possible that the Bohemian and Newfoundland forms referred to Lehua may be the products of parallel evolution. In forms from both regions the cephala are very similar but the Newfoundland form has possibly only two axial rings and pairs of spines in the pygidium, as compared to the three of the Bohemian form. The definite association of a pygidium with the cephalon of the Newfoundland form will clarify the situation.

In Llanvirnian times, Ceraurinella (represented by the species C. ingricus from Estland and C. polydorus from Newfoundland) appeared. C. polydorus of which the pygidium is known has greatly enlarged anterior pygidial spines, the posterior two pairs being reduced in size. Of these two posterior pairs the mid pair are larger and are still connected to the mid axial ring, the posterior pair being somewhat separated from the posterior axial ring. Ceraurinella survived into Ashgillian times. During this period of time the evolutionary processes common to the Cheirurinae proceeded. In the lowest Caradocian, the pygidium of the type species (C. typa.) shows that although three pairs of spines remain, in relation to the earlier species the posterior two pairs of spines are very small and have no pleural connection to the posterior two axial rings. The youngest member of the genus is C. intermedia from the Staurocephalus clavifrons - zone of the Ashgillian of Poland. This species shows the end of this particular evolutionary line for the posterior two pairs of pygidial spines are lacking, there being an entire margin between the anterior or pair of spines which themselves are still large.

The cephalon of the species of this genus also show changes with time. In the Llanvirnian species the anterior border and preglabellar furrow of the cephalon are present and complete across the front of the short (sag.) frontal lobe, and the lateral glabellar furrows are short and hooked. In the type species from the Edinburgh Limestone of Virginia, the anterior border and preglabellar furrow are still complete, the frontal lobe is longer (sag.) in relation to the glabella and the lateral glabellar furrows are still short but straight. In the large forms of the Polish Upper Ashgillian species, the anterior border is medially included in the frontal lobe, which is relatively even longer still than in earlier species, and the lateral glabellar furrows have lengthened a little. In the young holaspids of this species the anterior border and preglabellar furrow are complete across the front of the frontal lobe.

Ceraurus, unlike Ceraurinella and Bartoninus (see later) shows a good deal less variation in morphology of the various species in its range from Chazyan (Llandeilian) to Ashgillian. The early species already have a highly specialised cephalon and pygidium which altogether varied little in the range of the genus. The cephalon of Ceraurus is characterised by a fairly convex (tr. and sag.) glabella which expands a little forwards and occupies about $\frac{1}{4}$ width of the cephalon at the odcipital ring, with short lateral glabellar furrows the anterior and posterior of the three pairs wider than the mid pair, giving the impression in the glabella that the 2L and 3L lobes are closer together and a little remote from 1L and the frontal lobe. This feature is more developed in some species than in others (eg. C. pleurexanthemus where it is well developed), and is also seen in some species of Ceraurinella. The eyes in Ceraurus are placed forwards on the genae (opposite 3L) and are wide apart; the genal angles bear widely divergent spines. The glabella characteristically has perforated coarse and fine tubercles. The pygidium of the genus has the anterior pair of spines long and divergent, and between these an entire posterior margin which is curved, convex backwards. In some species this margin is lobate or even bears small stout spines, but this lobation or spinosity can very even within a species and does not bear a simple phylogenetic relationship to time. Thus Ceraurus pleurexanthemus montyensis Evitt 1953 (see Pl. 8, figs. 11-14) exhibits individuals with a posterior margin with one pair, two pairs or two pairs and a median lobation, whilst Ceraurus pleurexanthemus (see Evitt 1953, Pl. 8. figs. 5-7) from a similar horizon has one weak pair of lobes or none at all. C. ruidus from the Edinburgh Limestone Formation of Virginia, one of the earliest species of the genus, has a posterior pygidial margin without lobes, as does C. tuberosus from the Ashgillian of Greenland, one of the last. Within this time range of the genus, in the cephalon the only significant change is that the later species tend to have a glabella which expands a little more forwards.

In the Ashgillian of Baffin Island and Greenland occur Hapsiceraurus and Remipyga. The cephalon of Remipyga is not unlike that of some species of Bartoninus and it is not impossible that the pygidium, with two large anterior paddle shaped spines and an entire rounded posterior margin with lobes corresponding to the mid and posterior segments (as in Ceraurus) is derived from that genus.

Hapsiceraurus of which the pygidium is not definately known has a cephalon with, in the glabella, short lateral furrows, the 3S and 1S wider than the mid pair as in Ceraurus. The pygidium which possibly belongs to Hapsiceraurus has a pair of very long anterior spines which on their course diverge strongly and then curve round so that their points approach each other. The rounded posterior margin has short, blunt protuberances. If this pygidium does belong to Hapsiceraurus it would be additional evidence of the relationship of this genus to Ceraurus.

Bartoninus, amongst the longest ranging members of the Cheiruridae, is possibly first represented in the Chazyan of New York State, and lasts into Upper Llandoverian times. During this time the members of the genus show similar evolutionary trends to Ceraurinella, the pygidium modifying less quickly, but the cephalon varying more quickly in time than in that genus.

Bartoninus ruedemanni is the earliest species referred to this genus. It has a pygidium with three pairs of spines graduated in size, the largest - which are very long - anteriorly placed, and these three pairs of spines connected by pleural ridges to the three axial rings, as is always the case in species of Bartoninus. The cephalon of this species is specialised somewhat in the same manner as that of Paraceraurus with posteriorly placed widely separated eyes, and in addition a tendency for the inner ends of the lateral glabellar furrows to be connected by a furrow which runs exsagittally.

The type species of Bartoninus, B. dispersus from the lower part of the Caradocian of the Girvan District of Scotland, apart from the three pairs of gradational spines in the pygidium, in the cephalon shows a convex glabella which expands very little forwards, an upward arching preglabellar furrow which separates only weakly the anterior border from the frontal lobe, and fairly short, straight lateral glabellar furrows. Within _Bartoninus_ this, the type species, represents a stage between two extreme forms, one more highly specialised than the other. The less specialised type is well represented by _B_. _gelasinosus_ from the Caradocian of Tyrone, Ireland. This species has a parallel sided glabella with short lateral furrows, a short (sag.) frontal lobe, well developed preglabellar furrow and anterior border, and the width of the glabella is less than $\frac{1}{3}$ width (tr.) of the whole cephalon. The pygidial spines are gradational in size, the mid pair being about midway in size between the other two pairs. In the case of species like _B_. _girvanensis_, however, an Ashgillian form, the anterior pair of pygidial spines are much longer than the other two pairs, although the three pairs are still gradational in size. Species such as _B_. _girvanensis_ also have glabellae which expand markedly forwards, have long lateral glabellar furrows, have long (sag.) frontal lobes into which mesially is incorporated the anterior border, the preglabellar furrow having died out laterally.

There is no evidence to suggest that the more specialised forms are on a separate line of evolution from the less specialised. There is no reason why the more specialised species could not evolve at different times from the less specialised stock by branching evolution, or indeed that zigzag evolution took place. In addition, no useful purpose would be served by separating the two types into different genera or subgenera and if this was done the difficulty of placing species like B. dispersus (the type species) and therefore deciding what exactly constituted the genus Bartoninus would be difficult (B. dispersus from the lowest Caradocian like B. glaber from the Ashgillian has a weakly distinguished, upward arching preglabellar furrow and anterior border).

Bartoninus is also found in Silurian rocks of Britain, as high as Middle Upper Llandoverian of the Lake District (B. skelgillensis). This species and B. elongatus show the limit of specialisation reached by Bartoninus. In the cephalon of these species the glabella expands moderately forwards, have a moderately long (sag.) frontal lobe, curved lateral glabellar furrows and no preglabellar furrow mesially in large specimens, though it is present in small individuals. In the pygidium the anterior pair of spines are very long and the mid and posterior pairs very short although they still retain the pleural ridges which connect them to the mid and posterior pleural rings.

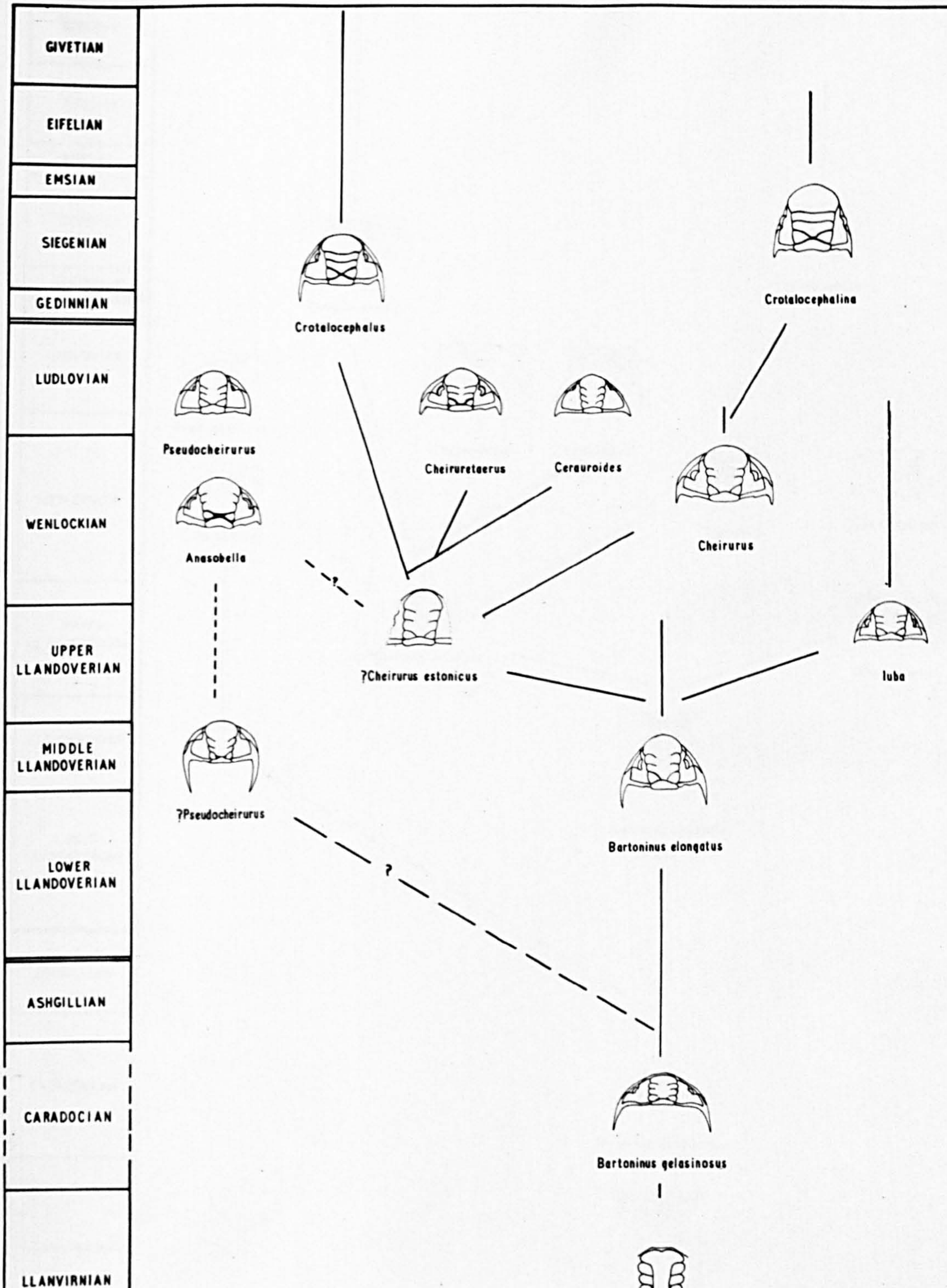
Bartoninus, whose range ended in the Upper Llandoverian progressed along the same evolutionary lines as Ceraurinella, for example. In that latter genus however, the posterior two pairs of pygidial spines became remote from the axial portions of the pygidium. This was not the case in Bartoninus, where these were retained as distinct but small spines with distinct pleural ridges throughout the range of the genus.

During Llandoverian and later times there was a second period of evolution within the Cheirurinae (see text figures 10a - b). The Upper Llandoverian rocks of Shropshire (Purple Shales) contain the first representative of _Iuba_, a genus apparently evolved from _Bartoninus_. In _Iuba_, the long anterior pygidial spines of _Bartoninus_ have become reduced in length to reach about as far back as the other two pairs of spines. These two posterior pairs of spines are relatively a little longer than in the youngest species of _Bartoninus_. They have, however, become separated from the axial rings, i.e. no pleural ridges are present. This is what also occurred in the stock of _Ceraurinella_. The cephalon of _Iuba_ is not very different from that of _Bartoninus_, the lateral glabellar furrows being relatively a little shorter than in the later species of that genus. Species here referred to _Iuba_ have been recorded from the Purple Shales of Shropshire, the Wenlockian of the Dudley District, the Ludlovian of Shropshire, and the Ludlovian (Kopanina Beds) of Central Bohemia.

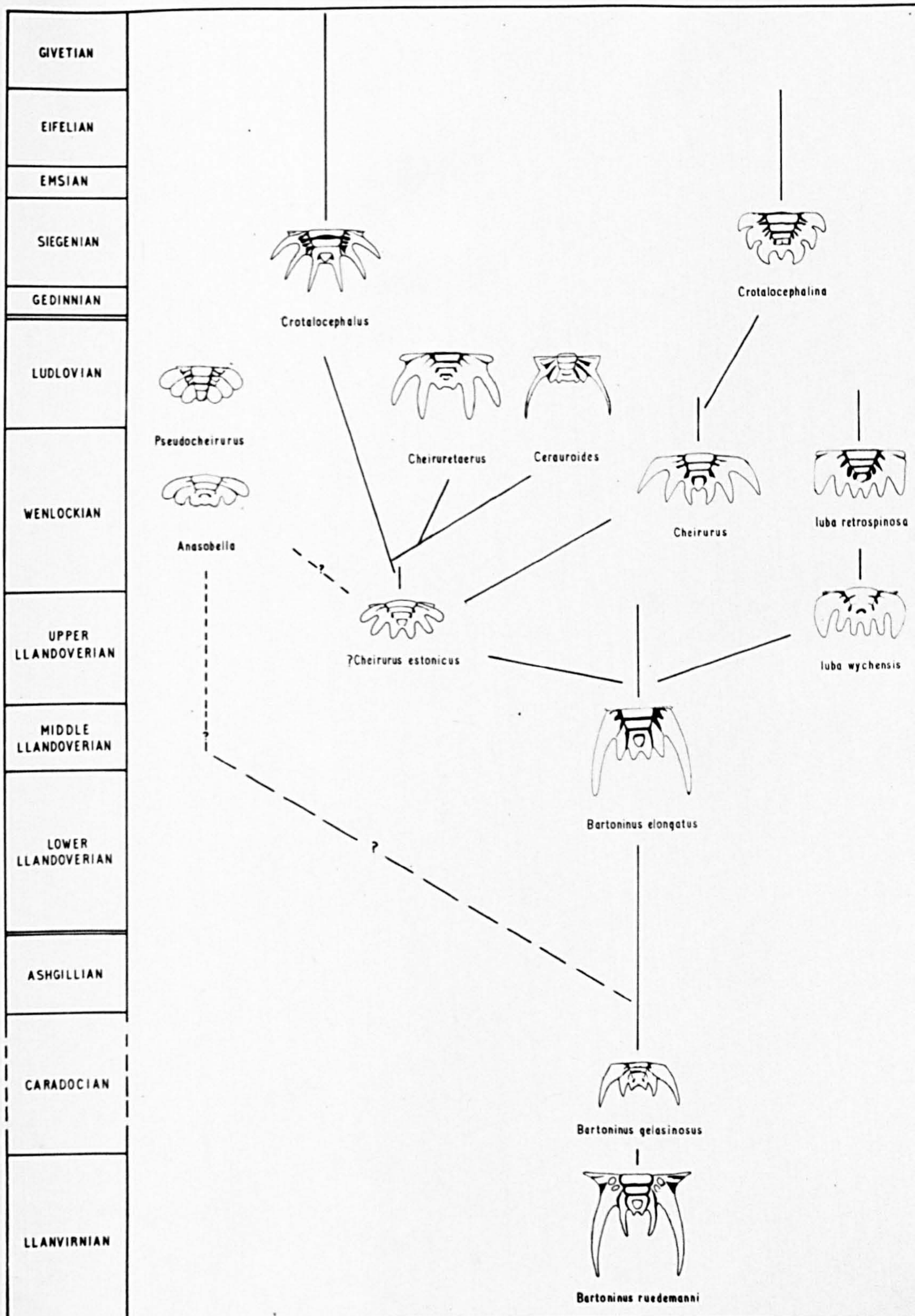
The _Iuba_ type of pygidium could be developed from the _Bartoninus_ type, by the three pairs of spines becoming subequal in length. All other Silurian and Devonian genera of the Cheirurinae have a common feature of the pygidium, this being that the pygidial spines have a radial arrangement, at least in their proximal parts. This too could be produced from the _Bartoninus_ stock (which because of the appearance in time of these other, new, types of Cheirurinae seems to be the only possible ancestor) by the loss of the great thickening at the proximal end of the anterior pygidial spine. This would produce a spine proximally transverse in dir-

Text figures 10a & b.

Diagrams illustrating the phylogeny of the Silurian Cheirurinae



Text figure 10a



Text figure 10b

ection, and a redevelopment of the mid and posterior spines from the condition in the youngest species of Bartoninus would give a radial spine arrangement. This is certainly what seems to have occurred in the cheirurid stock, and as such represents a regression in evolution as compared to the progressive shortening of the spines during Ordovician and early Silurian times. This regressive evolutionary step occurred in late Llandoverian times, when there were bursts of evolution in other groups (e.g. the Brachiopoda) coupled with a widespread transgression of the late Llandoverian sea. From then on, some of the evolutionary processes which were effective in the Ordovician come into play again. During the Silurian and Devonian three main evolutionary lines within the Cheirurinae may be recognised.

'Cheirurus' estonicus from the Upper Llandoverian of Estonia is the earliest Silurian species with a radial arrangement of the pygidial spines. It is included with some doubt within Cheirurus since it differs from all later species of the genus in not possessing a terminal mucronation in the pygidium. This is an interesting fact since Silurian species of Bartoninus do not have this mucronation and we may have in 'C.' estonicus a species morphologically, if not phylogenetically, close to the branching off of the later genera of the Cheirurinae. From the illustrations of 'C.' estonicus, this species also seems to possess a complete preglabellar furrow and anterior border which would also indicate, apart from the regression in the pygidium, a regression in the cephalon of the species. (Study of better material 'C.' estonicus would probably result in its generic separation from _Cheirurus_ s.s.). All later genera of the Cheirurinae have the anterior border included in the frontal lobe mesially. With the type of pygidium like '_C._' _estonicus_ as an ancestor, two lines of evolution seem to have arisen from it, and a third line probably independently from _Bartoninus_.

The first of the lines of evolution just mentioned gave rise to the genera _Cheirurus_ and _Crotalocephalina_. _Cheirurus_ first appeared in rocks of Wenlockian age, in which it is widespread. The difficulties of detailed correlation from continent to continent make it impossible to determine the earliest and latest species of this genus. The cephalon of _Cheirurus_ is very similar to that of some Ordovician Cheirurinae e.g. _Bartoninus_. The pygidium is characterised by three pairs of subequal spines (although there is a tendency in some species for the anterior to be largest and the other pairs gradational in size) and a terminal mucronation or spine of differing development. The genus probably lasted into Ludlovian times - _C._ _infensus_ is probably of this age, and the Ludlovian _C._ _postremus_ from the Lake District is most probably a true _Cheirurus_ although the pygidium is not known.

It seems probable that _Crotalocephalina_ a genus restricted to the Devonian (ranging from Gedinnian to Eifelian) is related to _Cheirurus_. The basic morphological pattern of the two genera is alike, but the Devonian genus has become much more specialised. In _Crotalocephalina_ the axial region of the animal developed at the expense of the pleural portions which became narrow and modified. In the cephalon, the glabella became gibbous, the 3S and 2S lateral glabellar furrows became continuous across, and the genae became reduced, the eyes migrating anteriorly. The thoracic segments have a convex (tr.) axial ring, and short pleural regions with broad short spines. The three pairs of pygidial spines are hooklike and the terminal mucronation is well developed. Crotalocephalina is the most highly specialised of the Cheirurinae. Some of the specialisations in this genus are also seen in the other two stocks of the subfamily yet to be described found in post Llandoverian times, notably the lengthening of the glabellar furrows so that they connect across the glabella, and the anterior migration of the eyes. Within Crotalocephalina Prantl (1947) noticed and described regressive mutation of the specialised lateral glabellar furrows. This regression takes the form of a re-shortening of the 2S or 2S and 3S furrows, along with the development of medial or sub-medial furrows connecting these lateral furrows. In addition the 2S and 3S furrows may become assymetrically placed on the glabella. Such features are apparently not uncommon amongst the most highly specialised of a stock "as the first intimation of the complete dying out of the whole genus or phylum" (p. 4).

The species 'Crotalocephalus' sculptus and 'Crotalocephalus' silverdalensis are morphologically between Cheirurus and Crotalocephalina. Their glabellae have lateral furrows running almost or completely across but the whole of the exoskeleton does not show the reduction of pleural portions. It is probable that further study of these Australian species (the available illustrations are poor) will require the erection of a new genus for their reception.

The second line of evolution arising from near '*Cheirurus*' *estonicus* produced the genera *Crotalocephalus*, *Cheiruretaerus* and *Cerauroides*.

The type species of *Crotalocephalus*, *C. articulatus* which ranges through Wenlockian and the lower part of the Ludlovian (Lütke 1964), is known only from its cranidium. This cranidium is highly specialised with eyes placed very far forwards and in the glabella not only lateral furrows 3S and 2S continuous across but 1S, as well as isolating the basal lobes, bifurcating to meet across the glabella. Lütke (1964) separated this species (and with doubt also *C. cordai* of which the cephalon is unknown) into a group within the genus. All other species at present referred to *Crotalocephalus* have eyes placed forward, in the glabellar the lateral furrows 3S and 2S are continuous across and the glabella itself occupies about $\frac{1}{3}$ transverse width of cephalon at the occipital ring. In the pygidium there are three pairs of long spines, about equal in length and (at least proximally) radially disposed. No terminal mucronation is present. All these species are Devonian in age as compared to the Silurian type species, the range of the genus thus understood being from Wenlockian to the Givetian. If the pygidium of *C. articulatus* is discovered it may be different from that of all Devonian species now referred to the genus, and a new genus would have to be erected to receive these Devonian forms.

In this second line of specialisation there is a repeat of one of the trends common in the Ordovician members of the subfamily - the reduction of the posterior pairs of pygidial spines. *Ceraurodes* has a long anterior pair of pygidial spines (radial proximally) and mid and posterior pairs very short; Cheiruretaerus on the other hand has anterior and mid pairs of spines long, and a much reduced posterior pair. Both of these genera have eyes placed forward and a glabella about $\frac{1}{3}$ width of the cephalon at the occipital ring, and in these respects resemble Crotalocephalus. Both genera differ from Crotalocephalus, however, in the form of their lateral glabellar furrows. In Cheiruretaerus with the single posterior reduced pair of pygidial spines the lateral glabellar furrows almost unite across the glabella, and in Cerauroides with the single long pair of pygidial spines these furrows reach only $\frac{1}{3}$ way across. Both Cerauroides and Cheiruretaerus are short ranging forms found in rocks of Wenlockian to Lower Ludlovian age.

The third line of specialisation within the post-Llandoverian Cheirurinae gave rise to the genera Pseudocheirurus and Anasobella. Previous to this work Pseudocheirurus was only recorded from the middle Lower Ludlovian of Bohemia, but herein are described two specimens from the Upper Llandoverian of the Girvan District, Ayreshire, which although no pygidium is known probably belong to that genus. The type species of Pseudocheirurus has lateral glabellar furrows 3S and 2S which reach more than $\frac{1}{3}$ way across the glabella but which are directed very strongly obliquely backwards adaxially. The pygidium is distinctive in not being spinose but rather lobate, with three pairs of lobes and a terminal lobe formed of the terminal piece of the axis, the seven lobes subequal in size. The eyes are placed opposite lateral glabellar lobe 3L. The true relations of this genus are not clear. In having a protruding terminal piece it would seem to be more closely related to the Cheirurus-Crotalocephalina stock than to the Cerauroides-Crotalocephalus-Cheiruretaerus. The question hinges on the Upper Llandoverian forms here described. If the pygidia of these forms turned out to be of the Pseudocheirurus type, it would seem to indicate that this line separated from the Bartoninus stock independantly during the late Llandoverian burst of evolution. If however, the pygidia of the Girvan species prove to be different from Pseudocheirurus, depending on the form of these it may be possible to say that the true Pseudocheirurus was developed from the Girvan form, or again that the genus arose independently from the Cheirurus stock in late Wenlockian or early Ludlovian times. The fact that Pseudocheirurus has not been recorded from rocks of Wenlockian age supports this last suggestion.

Anasobella is recorded to date only from the Henryhouse Formation (Upper Wenlockian to Lower Ludlovian) of Oklahoma. The pygidium of this genus is very similar to that of Pseudocheirurus, but the glabella is of much more 'normal' type for the subfamily with short lateral glabellar furrows 3S and 2S, and the eye more posteriorly placed. In addition Anasobella has only 10 thoracic segments all other Cheirurinae having 11. Until Anasobella becomes better documented in space and time its relation to Pseudocheirurus and to the other Cheirurinae remains obscure.

During their history therefore, the Cheirurinae underwent two major periods of evolutionary change. Derived from the Pilekiinae in Lower Ordovician times, they reflected evolutionary change especially in the pygidium, but also in the cephalon and to a lesser extent the thorax.

In the cephalon the main change was the expansion of the glabella forwards, with the mesial inclusion of the anterior border and the preglabellar furrow within the frontal lobe. There was also a tendency for the eye to move backwards and outwards from the pilekiid condition. In the pygidium, the axial rings and pleural spines were reduced from four in the Pilekiinae to three in the Cheirurinae and then a reduction of length of mid and posterior spines occurred in different stocks but at different rates. The main change in the thorax was the development of the short oblique pleural furrow in the Cheirurinae from the long transverse furrow as found in the Pilekiinae. In the genera of the second period of evolution, which are thought to have arisen from Bartoninus, the pygidial spines are radially disposed rather than backwardly directed as they are in the first period of evolution. In this second period of evolution there are three main stocks which can be followed by the development of the pygidia. Cheirurus and Crotalocephalina show three pairs of subequal pygidial spines and a terminal mucronation, the latter genus having reduced pleural portions and lateral glabellar furrows 3S and 2S continuous across; Crotalocephalus has three pairs of long subequal pygidial spines and no terminal mucronation (this genus also has continuous lateral glabellar furrows 3S and 2S) and to this same stock belong Cheiruretaerus and Cerauroides which have reduced posterior pair, and posterior two pairs of pygidial spines respectively; Pseudocheirurus and Anasobella have pygidia with three pairs of lobate spines and a terminal lobe. In these three stocks there is an additional tendency for the eye to migrate forwards once again. Degeneration of the cheirurid stock is seen in the highly specialised Crotalocephalina where the lateral glabellar furrows become variable in length and symmetry, and even longitudinal glabellar furrows placed sagittally or exsagittally are developed.

Throughout the history of the subfamily there is very little variation in the thorax (eleven segments are present in all but Anasobella). This is also true of the hypostoma which only differs in proportions during the long range of the subfamily. The rostral plate where known is always short (sag.) and wide (tr.), and subquadrate in shape.

The Cyrtometopinae, which ranged from the Arenigian to Upper Ashgillian, display a good deal more variation in form of cephalon, thorax and pygidium than do members of the previous subfamily. To some extent the evolutionary trends of the Cheirurinae are paralleled in this subfamily but others are seen. As compared with the Cheirurinae forms which could be considered both further removed and nearer the little specialised Pilekiinae are present in the Cyrtometopinae.

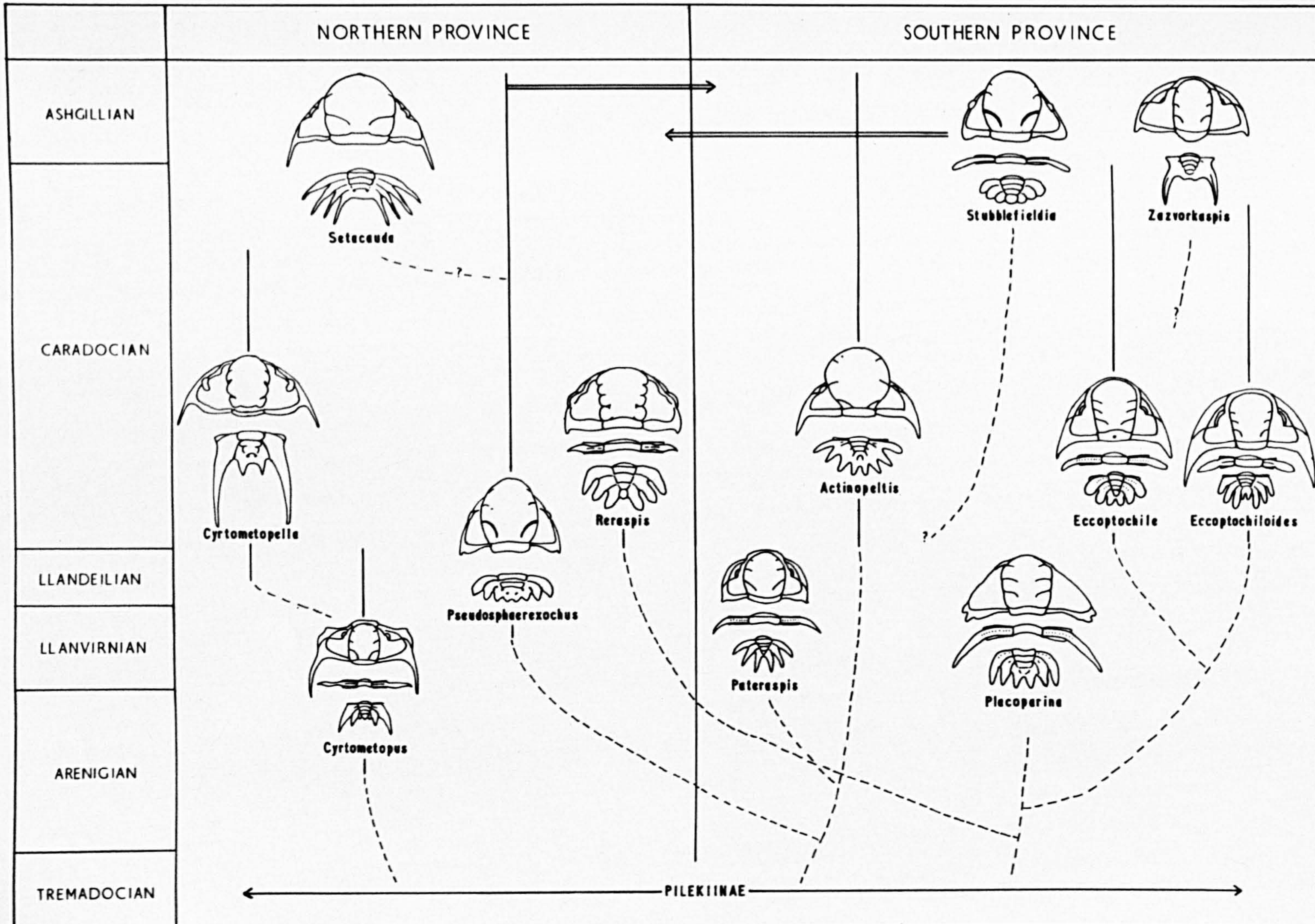
The general characters of this subfamily are as follows; glabella varying in form from parallel sided with low convexity to highly inflated, lateral glabellar furrow short. Eye placed fairly far forward in forms with less convex glabella with a false eye ridge following the course of the anterior section of the facial suture (β to γ). Thorax of 10 - 12 segments ending in free spines, with a pleural furrow or line of pits of varying extent parallel to the edges of the pleurae, or with these furrows or pits effaced. Pygidium with three to four axial rings and pairs of spines, these spines narrow and tapering to lobate in form.

The type genus, Cyrtometopus, is the earliest known in the subfamily (see text figure 11). It is recorded from the Upper Planilimbata Limestone of Sweden (Arenigian) and survived into the Llandeilian rocks of the same region. It belongs to the first of three evolutionary lines which appear to be present in the Cyrtometopinae. In these Lower Ordovician times Cyrtometopus was already quite highly specialised. Its glabella is convex and subovate in form, the eyes are far forward and the false eye ridge is present. The rostral plate is partially dorsal (this has also been seen in Paraceraurus). In the thorax the pleural furrows are well marked and are parallel to the edges of the segments, these segments ending in free spines. The pygidium has three pairs of spines of which the posterior two pairs are reduced so that a gradation in size of the spines is produced rather like that in some species of Bartoninus; unlike Bartoninus the terminal piece of the axis is extended into a spine.

The only other genus considered to belong to this first line of evolution within the Cyrtometopinae is Cyrtometopella, which ranged from Upper Llandeilian into Caradocian times. The cephalon in this genus is not unlike that in Cyrtometopus, but the glabella is more inflated and the lateral glabellar furrows are shorter, and 1S almost reaches the occipital furrow nearly isolating a knob-like basal lobe.

Text figure 11.

Diagram of the phylogeny of the Cyrtometopinae



Text figure 11

The pygidium is characteristic having, like Cyrtometopus, an anterior pair of spines which are long and stout, but between these a much shorter and slimmer pair of spines connected by pleural furrows to the mid axial ring, the posterior pair of spines having disappeared. This reduction and loss of the posterior pairs of pygidial spines in these two genera is an example of parallel evolution, between the Cheirurinae and the Cyrtometopinae.

The genera Placoparina, Eccoptochile, Eccoptochiloides and Reraspis represent the second evolutionary line within the Cyrtometopinae. These genera, unlike the other members of the subfamily, have less specialised cephala and because of this these have resemblances to some of the Cheirurinae.

Placoparina which is recorded from the Llanvirnian and Llandeilian of Wales and the Shelve area of Shropshire is an unspecialised trilobite with a parallel sided glabella of low convexity having three pairs of short lateral glabellar furrows; the eyes are placed very far forward but the posterior section of the facial suture cuts the lateral margin close to the genal angle, giving long narrow free cheeks; the thoracic segments have a line of pits on the pleurae parallel to its edges, and the pygidium has three pairs of lobate spines. It is not claimed for the genera named above that belong to the same area of the subfamily as Placoparina, that they evolved from this genus. Rather it is thought that some of the genetic changes which the Cheirurinae were undergoing were occurring in this part of the Cyrtometopinae at about the same time, and produced a group of related genera, some of which have similarities to some of the Cheirurinae.

The cephalon of Reraspis shows features, similar ones to which are seen in Ceraurus. The glabella of Reraspis has very short lateral furrows and the lateral lobes are also short, and inflated. The eyes are also placed as in Ceraurus - wide apart, opposite about half way back along the glabella - and quite unlike any other genus within the Cyrtometopinae. Here the similarity to Ceraurus ends, for the cephalon is relatively much longer (sag.) than in that genus and does not have the prominent divergent genal spines of Ceraurus. The thorax is typically Cyrtometopian with pleural furrows parallel to the edges of the segments; the pygidium is distinctive, having three pairs of short subequal spines which are parallel and point at about 45° to the transverse direction. Reraspis ranged only through the lower part of the Caradocian and so far as is known is restricted to Estland.

Eccoptochile and Eccoptochiloides which are restricted to the southern trilobite province ranged throughout Caradocian time. These genera also show some features, especially in the cephalon, which the Cheirurinae were developing at the same time, although the members of that subfamily developed them to a greater extent. Both Eccoptochile and Eccoptochiloides have glabellae which expand forwards to an expanded frontal lobe. In neither, however, is the anterior border or preglabellar furrow incorporated in this frontal lobe, but they are always distinct features. Of the lateral glabellar furrows, 3S and 2S are of the form found in the Cheirurinae, but the 1S furrow does not reach the occipital furrow. The genae occupy a similar proportion of the cephalon as in _Bartoninus_ or _Cheirurus_ for example, but the eyes are a little more anteriorly placed. The thoracic pleurae in _Eccoptochiloides_ bear a furrow parallel to the edges of the segment although it is shorter than in other genera, and the pygidium has four pairs of spines of which the posterior pair are much reduced in size. In _Eccoptochile_, the pleurae of the thorax bear a line of pits and the pygidium has three pairs of spines which are quite short, rounded distally and radially disposed. This last feature is only found in Silurian and Devonian Cheirurinae.

Whether _Eccoptochile_ can be said to be more highly evolved than _Eccoptochiloides_ is doubtful. In its cephalon and pygidium the former has progressed further along the same lines as the Cheirurinae than the latter, but _Eccoptochiloides_ with a reduced pleural furrow in the thoracic segments has gone part of the way towards which the Cheirurinae developed from the Pilekiinae. In addition _Eccoptochiloides_ has only 10 thoracic segments, a further specialisation, whereas _Eccoptochile_ with 12 is like the Pilekiinae. It is thought here that these different characters of the thorax, in addition to those of the cephalon and pygidium are sufficient to promote _Eccoptochiloides_ to generic status.

It is less certain whether the third group of genera within the Cyrtometopinae represent a evolutionary line. Rather they seem to represent an evolutionary trend within the subfamily. The genera concerned here are Pseudosphaerexochus, Pateraspis and Actinopeltis, and Setacauda and are similar in possessing a glabella which is large and inflated, the genae being relatively small. Although they cannot be regarded as an evolutionary line, i.e. a progression of forms one leading to the other, neither are these genera the products of different lines of evolution for they were present contemporaneous with or earlier than the other genera of the Cyrtometopinae.

The type species of Pseudosphaerexochus, P. hemicranium is characterised by an inflated elongate glabella with lateral glabellar furrows 3S and 2S weakly impressed and 1S with a subcircular course almost circumscribing the basal lobe; the genae are convex with a small eye placed opposite 2L, and the genal angle is rounded. The pygidium has four axial segments which terminate in four pairs of evenly spaced lobate spines. Within Pseudosphaerexochus there is also a group of species which differ from the type mainly in the pygidial segments terminating in four pairs of long spines rather than lobate ones. Both groups have a line of weakly impressed pits parallel to the edges of the pleurae, though these pits are generally only to be seen on the internal mould. As it has not been possible during this work to examine the type Estonian and Swedish material of the two groups within Pseudosphaerexochus they are retained within the single genus.

Pseudosphaerexochus is mainly a genus of the northern province (see Chapter on provincial distribution), which ranged from Upper Llanvirnian to Upper Ashgillian. Only in Ashgillian times is it reported from the southern province where it is last recorded from Poland. So far as is known, no species of this genus is present in the Silurian.

Setacauda, (see Chapter IV), from the Ashgillian of northern England and Ireland, is another form with highly inflated glabella. It seems to be more highly specialised than Pseudosphaerexochus even, in some of its cephalic characters, e.g. the sigmoidal course of the 1S furrow, and the subcircular-subquadrate outline of the glabella in dorsal view. These characters are like some to be found in the Sphaerexochinae in Middle Ordovician times. The affinities of Setacauda are not certain, but the general form is Cyrtanetopian (there are four pairs of pygidial spines and the anterior pleural ridge of the pygidium has a line of pits which may indicate a Cyrtometopian thorax) and it is included within this subfamily. It is not impossible that it evolved from Pseudosphaerexochus by the migration of the pygidial spines and further development of the glabella. The fact that the hypostomas of that genus and Setacauda are very similar may also indicate this origin.

Pateraspis, however, is restricted to the southern province (Bohemia) and is present in Llanvirnian and Llandeilian rocks. Morpholcgically it is much like Pseudosphaerexochus especially in the cephalon, which, isolated from the rest of the animal, is difficult to differentiate from that genus. The thorax and pygidium differ, however, Pateraspis having one less segment (11 only) and the pygidium having three pairs of tapering spines. These features of thorax and pygidium of Pateraspis indicate it to be more highly specialised than Pseudosphaerexochus, and in addition, it is more highly specialised earlier in time. Pateraspis has hitherto been regarded as a subgenus of Pseudosphaerexochus; when it is realised that the similarities are due to parallel evolution in different areas rather than to direct relation it is here considered that Pateraspis has generic status.

Actinopeltis is another genus confined to the southern province in which it occurs mainly in Bohemia but is also reported from Portugal and Southern China. It is present in rocks of lowest Caradocian to Upper Ashgillian in age. Kielan (1959) studied the genus in Bohemia where she had access to Barrande's types (four of the five Bohemian species were erected by Barrande) and constructed an evolutionary series within the genus. The genus is characterised by an inflated glabella, the inflation being mainly anterior to 1L, dominating over somewhat reduced genae, having three pairs of lateral glabellar furrows, posterior pair reaching the occipital furrow; the genal angle is generally spinose. The pygidium has four axial rings and four pairs of tapering spines. The changes which took place in the evolution of the genus were generally towards a "more compact body" (Keilan 1959, p. 50). A. completa, the earliest representative, has a barrel shaped glabella (maximum convexity across 2S) and a very long, stout genal spine in the cephalon, and in the pygidium four pairs of curved and tapering spines. By gradual inflation of the glabella and a reduction of the spinose portions of the body we reach the Ashgillian _A_. _insocialis_ which has a very convex glabella (maximum convexity across 3S) and a rounded genal angle, while the pygidium has short rounded spines. However, apart from this trend within the genus, there was possibly another line of evolution. This line is not well documented and is represented only by two unnamed species designated _A_. sp. A and _A_. sp. B. by Keilan. These species are known only from isolated pygidia which show a tendancy to increasing spinosity as the four pairs of spines are long and narrow. Their reference to _Actinopeltis_ will remain doubtful until more complete specimens are found.

Stubblefieldia and _Zagvorkaspis_ are two short ranging genera restricted to Ashgillian rocks. Both have been referred to the Cyrtometopinae but their relations to other genera within the sub-family remain obscure.

Stubblefieldia was classed as 'Cyrtometopinae incertae sedis' by Prantl and Pribyl when they erected the genus (1947, p. 32). Its cephalon is similar to those of the Cyrtometopinae with inflated glabella, and its pygidium not unlike _Eccoptochile_ with an additional terminal lobate spine. The thoracic segments, however, differ from other Cheiruridae since the pleurae have no furrow or line of pits but have a "narrow, horizontal, distinct, elevated pleural ridge which gradually widens in the direction towards the outer margin and ends in a blunt nodular expansion". (Prantl and Pribyl 1947, p. 33). Because of these pleural ridges the position of Stubblefieldia is uncertain, and will remain so until further study reveals their origin. The overall resemblance of Stubblefieldia to other Cyrtometopinids indicates that its relations lie in this subfamily. The pleural ridge could have a similar function to a pleural furrow and may be a development of it.

Zazvorkaspis has been recently described from the Ashgillian of Bohemia. It has been assigned to the Cyrtometopinae in the absence of knowledge of the thorax. However, the cephalon is typically Cyrtometopinid in form with a very convex glabella and eyes placed forward. Its authors (Pribyl and Vanek, 1964b, p. 163) have denied that this genus has any close phylogenetic affinities with Actinopeltis, Pseudosphaerexochus, Cyrtometopella or Stubblefieldia, but think rather that it may have a closer link with Eccoptochiloides. Zazvorkaspis is similar to the latter genus in the form of the glabella and lateral glabellar furrows, and the position of the eye. The pygidia of the two genera are quite different; Zazvorkaspis having a large anterior pair of spines with between a posterior border with two lobate spines. As Pribyl and Vanek stated, Zazvorkaspis could be a late aberrant member of the Eccoptochile-Eccoptochiloides stock but until the genus is better known, and especially until the thorax is discovered, it is impossible to place it with any certainty.

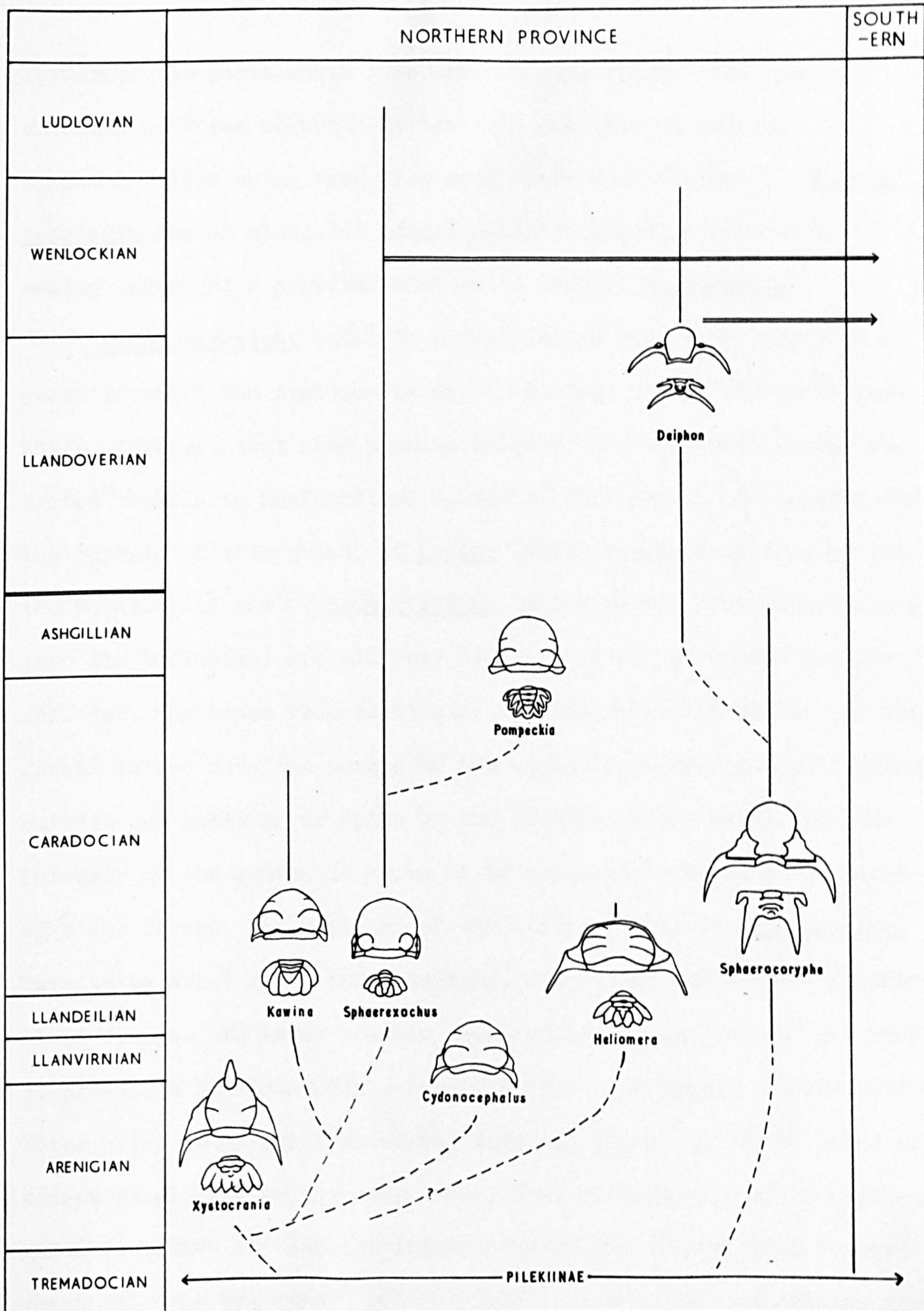
The Sphaerexochinae (text figure 12) constitute a group of highly specialised Cheirurid genera. They differentiated early from the Pilekiid stock, all the genera except one being present by Llanvirnian times. They are confined to the Ordovician except Sphaerexochus which survived into the Ludlovian.

The subfamily is characterised by genera with greatly swollen glabellae and very reduced genae. Lateral glabellar furrows 3S and 2S are generally weakly impressed or absent, but the basal furrow 1S is usually distinct and deep at least near the axial furrow, sometimes curving back to isolate a prominant basal glabellar lobe. The eye is small and placed close to the axial furrow. The rostral plate is wide (tr.) and short sagittally, and the hypostoma with a swollen median body is also wider (tr.) than long (sag.). The thoracic segments have a wide, arched (tr.) axial ring, the pleurae bearing neither furrows or pits. The pygidium has three axial rings and three pairs of spines which may be either free distally, or completely fused to give an entire, lobate margin.

Xystocrania which ranged from Arenigian to Llanvirnian is the earliest named genus of the Sphaerexochinae. Whittington (1965, pp. 411-2) stated, however, that '*Kawina*' *sexapugia* (Ross, 1951) may be generically different from the other Sphaerexochinae, in which case this would be the earliest genus. Xystocrania has an inflated glabella which is widest transversly across the basal lobes and which bears medially and anteriorly a long spine which is directed upwards and

Text figure 12.

Diagram of the phylogeny of the Sphaerexochinae and Deiphoninae



Text figure 12

forwards, the genal angle also bears a long spine. The pygidium consists of three segments in the axis and pleural regions, the pygidial spines being free from each other and divergent. '*Kawina*' *sexapugia* has an elongated (sag.) inflated glabella without a median spine and a pygidium similar to that of *Xystocrania*.

Cydonocephalus, which is restricted to the Llanvirnian, is a genus of which the pygidium is not definitely known. It seems probable, however, that some pygidia found in the same beds as the described cephala in Newfoundland belong to this genus. In general form the cephala of this genus, of *Kawina* (which ranged from Llanvirnian into the Caradocian) and of *Sphaerexochus* (which ranged from later Llanvirnian into the Ludlovian) are all very similar. Their glabellae are greatly inflated, the genae reduced in size and the posterior section of the facial suture cuts the margin of the cephalon posterolaterally although outside any swelling or spine on the lateral border which from the ontogeny of the genera is known to be equivalent to the genal angle of other forms. The pygidium of the early species of *Sphaerexochus* have three axial rings and a terminal piece, and three pairs of short blunt spines. In later species these spines become reduced and rounded to produce a pygidium with a lobate margin. In *Kawina* the pygidium has three axial rings and a prominant terminal piece, and three pairs of spines which have no, or very short, free portions producing a margin which is entire or slightly indented where the interpleural furrows reach it. The pygidium which possibly belongs to *Cydonocephalus* resembles that of _Kawina_, but with a smaller terminal piece in the axis and the spines being without free portions and longer. The thoracic segments of _Kawina_ and _Cydonocephalus_ are also similar (Whittington 1963, p. 98) and apparently different from _Sphaerexochus_ in which the segments articulate by the simple device of a boss of shell on the anterior edge of the segment abutting against a groove in the posterior margin of the segment in front. Although _Sphaerexochus_ appears later in time than _Cydonocephalus_ or _Kawina_ it seems probable that with its less specialised pygidium with small free spines still present, and the different form of the thoracic pleurae that this genus is further from the other two which are obviously closely related. It also seems possible that both these brances could have derived separately from the early stock of the Sphaerexochinae near _Xystocrania_.

Heliomera, another genus ranging from Llanvirnian into the Caradocian, is a somewhat aberrant member of the _Sphaerexochinae_. Although Evitt (1951, p. 588) thought this genus was distinct from all other Cheiruridae, and erected a subfamily to receive it, it was pointed out by Whittington (1965, p. 411) that the characters listed by Evitt agree with those of the Sphaerexochinae with the exception of the radial arrangement of the glabellar furrows. As has also been stated by Whittington (1965, p. 417) and Tripp (1967, p. 67) the character upon which _Heliomeroides_ - thought by Evitt to be a separate genus - was distinguished from _Heliomera_ (the presence in

Heliomeroides of an exsagittally directed furrow in the glabella connecting the radial glabellar furrows) is of variable development in different species, variable during the growth of the individual and also variable possibly on the internal and external moulds of the same individual. For this reason the present author is in agreement with Tripp (1967, p. 67) in regarding Heliomeroides as a synonym of Heliomera.

Apart from the maximum development of genera of the Sphaerexochinae in Middle Ordovician times, and the long ranging Sphaerexochus, only Pompeckia referred to this subfamily remains. This genus is present only in Ashgillian rocks of Sweden. Its cephalon much resembles Sphaerexochus with a subcircular inflated glabella and weak anterior two pairs, and strong basal pair of lateral glabellar furrows; these latter do not reach the occipital furrow as in Sphaerexochus however. The pygidium has in the axis three rings and a terminal piece, and three pairs of pleural and a terminal spine all of which bear a pair of intramarginal furrows, parallel and close to the edge of the spine. These intramarginal furrows are also present in the free spines of the thoracic pleurae. They are unlike any feature found in the Sphaerexochinae as is the inner part of the pleural portion of the segment which bears an oblique furrow which originates at the axial furrow a little way anterior to the posterior margin of the segment and runs obliquely forwards towards the fulcrum on the anterior margin. This furrow was thought by Warburg (1925, p. 369) not to be the oblique or parallel intrapleural furrow of the other subfamilies of the Cheiruridae but the exsagittal furrow which in the Cheirurinae separates the inner furrowed part of the pleurae from the other unfurrowed part. However, if this were the case it might be expected that if such a furrow which is linked with the articulatory musculature had migrated as Warburg thought there would be some migration of the articulatory facets of the segment. This in fact has not occurred, the articulation being accomplished as in _Sphaerexochus_. The problem of the origin of this furrow in _Pompeckia_, and of the true relations of the genus remain. The similarity of this genus and _Sphaerexochus_ is strong, particularly in the cephalon and pygidium, but its precise origin remains in doubt.

The subfamily Acanthoparyphinae was erected by Whittington and Evitt (1953, pp. 70-71) to include cheirurid genera with, amongst other characters, ovate glabellae with maximum width across the basal lobes; eyes relatively far inward and opposite lateral glabellar lobes 2L or 1L; two branches of the facial suture at an acute angle to one another, sometimes with a sutural ridge (false eye ridge); thoracic pleurae with a transverse row of pits; pygidium with two pairs of spines. An additional feature of most of the genera in this subfamily is that the exoskeleton is covered with large tubercles and short spines.

Acanthoparypha, _Pandaspinapyga_, _Holia_, _Nieskowskia_ and _Hadrohybus_ all appeared in the period Upper Llandeilian to lowest Caradocian. It is equally possible that they were derived from the Pilekiinae direct, or branched early from the Cyrtometopinae to which they are evidently closely related. With either ancestry, the Acanthoparyphinae have specialised along lines seen in other Cheirurids - inflation of the glabella, backward migration of the eyes (though in this case they have also migrated inwards), reduction of the transverse pleural furrow to a line of pits, and the reduction in the pygidium to two pleural spines, of which the posterior in some cases themselves become reduced in size.

The relationships between the genera within the subfamily are also not certain. This can partly be accounted for by the sudden appearance in uppermost Llandeilian times of most of the genera, already well differentiated from one another. Finds of specimens referable to this subfamily in rocks of Arenigian and/or Llanvirnian age would help clarify both the relationship of the Acanthoparyphinae to the other subfamilies of the Cheiruridae, and also the relations of the genera to each other.

Nieszkowskia, with a characteristically oval glabella has a spine placed on this posteromedially. _Hadrohybus_ also has a glabellar spine but this genus is incompletely known. _Holia_ has an occipital spine and two pairs of fixigenal spines, and in the pygidium long curved anterior spines and very short posterior ones and a modified axial region. _Acanthoparypha_ and _Pandaspinapyga_ have no prominent glabellar spines, except at the genal angles, their pygidia having two pairs of subequal spines, the axial region of _Acanthoparypha_ being modified to one ring and a terminal piece, while the other genus has three rings and a terminal piece; this difference in the axial region of the pygidium seems to have been the main feature of difference used for the separation of *Pandaspinspyga* as a genus distinct from *Acanthoparypha*, and not having seen material of these two the present author is not certain that the two are distinct genera.

Ainoa, from the mid Caradocian of Estonia, is only known from the cranidium. The glabella resembles that of *Nieskowskia* in shape but does not have a glabellar spine like that genus. Instead, *Ainoa* possesses a very stout, long occipital spine which rises steeply from the occipital ring and obliterates the occipital furrow mesially. The placing of this genus awaits the discovery of other parts of the exoskeleton but the occipital spine and position of the eye indicate it to be related to the Acanthoparyphinae.

Youngia, which has hitherto been regarded as a genus of uncertain affinities within the Cheiruridae, is here considered to belong to the Acanthoparyphinae. Although the genus is only known from the cranidium the glabella with maximum width (tr.) across the basal lobes, the eye very close to the axial furrow and opposite 2L, and the two sections of the facial suture lying at an acute angle to one another all point to its Acanthoparyphinid relationships. Like other genera in the subfamily *Youngia* bears a long slender occipital spine. The earliest species definitely referred to this genus is the type species *Y. trispinosus* from the Upper Llandoverian of the Girvan District of Ayrshire. This occurrence is considerably later in time than the other genera of the Acanthoparyphinae so far recorded. This is possibly due to the Llandoverian trilobite faunas being, on the whole, poorly known. '*Sphaerexochus*' *canadensis* from the Ashgillian of Anticosti Island may from the single poor illustration available be a species of *Youngia*.

The status of the Deiphoninae has been questioned by previous workers on the Cheiruridae. It was accepted as a distinct subfamily by Prantl and Pribyl (1947) but on the understanding that it did not have the same significance as the Cyrtometopinae of which 'it represents really only its evolutionary younger subdivision'. Here the Deiphoninae are regarded as a distinct subfamily containing *Deiphon* and *Sphaerocoryphe*, and probably also *Hemisphaerocoryphe* and *Ovalocephalus*. The characteristic features of the subfamily are as follows; glabella greatly inflated in front of the basal lobes which themselves are very small, genae very small and sometimes reduced to spinose extensions; thoracic segments of Cyrtometopian type or modified from this; pygidium with two pairs of spines of which the anterior are formed probably by a neotonous inclusion of the posterior segment of the thorax.

Sphaerocoryphe (see text fiture 12), one of only two genera definitely referred to this subfamily since it is only in these two genera that the thorax and pygidium is known, was present in rocks of the same age as most of the genera of the Cyrtometopinae. Although *Deiphon* is a somewhat extreme modification which occurs later, the occurrence in time of *Sphaereocoryphe* invalidates the statement that this subfamily is only a younger subdivision of the Cyrtometopinae. Rather, by the late Llanvirnian Sphaerocoryphe had evolved as a specialised form, which with Deiphon certainly, and possibly with Hemisphaerocoryphe and Ovalocephalus, retained their distinction from the other Cheiruridae. Sphaerocoryphe appeared in the Upper Llanvirnian and ranged through to the Middle Ashgillian. It has the characteristically swollen glabella anterior to the small conical basal lobes, and small genae bearing long genal spines. Both free and fixed cheeks bear a pair of small spines. The thorax of this genus is composed of nine segments of Cyrtometopinid type, with a line of pits extending as far along the pleurae as the articulatory apparatus - a simple ridge and furrow - extends. The pygidium has four rings and a terminal piece in the axis, and the anterior spines are exactly of the form of the thoracic pleural spines. The number of axial rings and the form of the anterior spines of the pygidium which are exactly like the thoracic spines is the only evidence that this portion is a neotonously included thoracic segment. No ontogeny of a species has been described, but the morphology indicates that this is the only reasonable explanation. Behind these spines lie a pair of stout, long spines, between which the posterior margin is entire and rounded, convex backwards.

Deiphon, appeared in the Leptaena Limestone of Sweden, very close to the time Sphaerocoryphe apparently died out. It is a very specialised form. The basal lobes of the glabella are very small, being reduced to small nodules in the deep composite occipital-basal glabellar furrow. The glabella anterior to this furrow is spherical in form and the genae are reduced to spinose projections. The thorax, again of nine segments, is also very specialised. The pleurae are completely free from one another, any articulation possible being at the articulating half rings in the axis. These pleurae bear a short median furrow adaxially. The pygidium of Deiphon also resembles that of Sphaerocoryphe in having an anterior segment of the form of the thoracic segments, and a pair of long spines behind these anterior ones which in this case are curved first outwards and subsequently inwards. The axial part of the pygidium bears a semicircular depression in which are indicated three rings and a terminal piece, the vestiges of a highly modified axis.

Hemisphaerocoryphe was in existance at about the same time as Sphaerocoryphe. It is only known from the cranidium which has small nodular basal glabellar lobes in front of which the glabella is swollen. The genae are small with genal spines. As the generic name suggests this genus is of the general form of Sphaerocoryphe but is less modified. The characters of the thorax and pygidium will be all important in placing Hemisphaerocoryphe with certainty within either this subfamily or the Cyrtometopinae, to which it may belong.

Ovalocephalus is another incompletely known genus referred by its author to the Deiphoninae. It occurs in Lower Caradocian rocks of Northern Kazackhstan and is known only from poorly preserved cranidia. It has a pestle-shaped glabella with a pair of nodular basal lobes separated by a deep furrow from the main swollen part of the glabella, which bears near this deep furrow a short second pair of lateral glabellar furrows. The genae appear to be quite large (from available poor illustrations). Some features of this genus, i.e. the pestle-shaped glabella with more than one pair of lateral glabellar furrows, resemble those of Hammatocnemis (see below). Again, more complete material of Ovalocephalus is required to be able to place the genus with certainty.

Areia and what is considered in the lastest work (Pribyl and Vanek, 1964b) to be its subgenus Areiaspis are the sole members of the subfamily Areiinae. Areia ranges from Llandeilian to Ashgillian and Areiaspis is present only in the Llanvirnian. Neither form has eyes, and they are also similar in having the glabella only one quarter to one fifth the width (tr.) of the cephalon at the occipital ring. In addition, in both, the anterior border is stepped forwards in front of the frontal lobe of the glabella. Here the resemblance ceases.

Areia has a glabella which decreases in transverse width forwards, three pairs of short lateral glabellar furrows which reach the axial furrow, and a raised ridge placed sagittally upon, and about $\frac{1}{4}$ widthof, the glabella, extending from the frontal lobe to near the occipital furrow. The genal angles bear short spines. The thorax is composed of nine segments which have a broad axis, the pleurae bearing a furrow parallel to the edges of the segment in which are 6-8 distinct pits. The pygidium has an axis with two rings and two pairs of slender spines of equal size, which are furrowed.

Areiaspis has a parallel sided glabella with three pairs of lateral glabellar furrows all of which are remote from the axial furrow abaxially, and the posterior of which are directed more obliquely back than either the other two, or those of Areia. On the genae adjacent to 3L there are remnant eye ridges and the genal angles bear spines which are relatively longer than in Areia. The thorax of Areiaspis is composed of eleven segments which have no pleural furrows but a line of 7 or 8 pits. The pygidium has three rings in the axis and three pairs of unfurrowed spines, the posterior pair reduced in size as compared to the others.

Areiaspis which occurs earlier, is less specialised in having eleven thoracic and three pygidial segments and the remnant eye ridges. Areia with only nine thoracic and two pygidial segments is more specialised in these respects, but is less specialised than Areiaspis in having a glabella which narrows (tr.) forwards, furrowed pleurae, and lateral glabella furrows which originate in the axial furrow. Within this plexus of developing characters it seems doubtful therefore whether Areiaspis was the direct ancestor of Areia as was thought by Pribyl and Vanek (1946b, p. 165). In addition when the morphological differences are taken into account it seems better to consider these two forms as generically distinct.

Hammatocnemis was included by Keilan (1960, p. 140) in a new monotypic subfamily of the Cheiruridae. This genus, found in the Ashgillian of Poland and Southern China is characterised by a glabella with nodular basal lobes placed in a combined occipital-basal lateral glabella furrow, in front of which the glabella exp ands markedly forwards to the rounded frontal lobe, and bears laterally an additional three pairs of short lateral glabellar furrows. The genae enclose most of the glabella and bear large eyes; the genal angles bear small spines which are placed posterolaterally. The facial suture is proparian. The number of thoracic segments is unknown. In these segments the axis occupies about $\frac{1}{4}$ width of the whole and the pleurae bear on their inner part two convex nodes placed in transverse line, the adaxial one a little larger than the other. The outer part of the pleurae (about $\frac{1}{2}$ the whole transverse width) is formed of a stout free spine which curves backwards and downwards. The pygidium is small with three axial rings and three blunt spines which are in contact for nearly the whole of their length; posteriorly there is an entire margin formed by a wide (tr.) terminal piece of the pygidium.

Keilan argues that this genus is unlike the Pterygometopid and Dalmanitid stocks which have moderately convex cephala, well developed lateral glabellar lobes and relatively large pygidia (p. 48). On the other hand, she says that Hammatocnemis has some similarities to the cheirurid line especially 'the differentiation of the cephalic (sic. should read thoracic) pleurae of the new genus into inner and outer portions, with two strongly convex triagonal areas on the inner one .... There is no diagonal furrow dividing the inner part of the pleurae as in the cheirurids, but the presence ... .. of two strongly convex nodules .... seems to be the same type of structure. The type of pygidium characteristic of the new genus does not occur in any cheirurid subfamily.'

No cheirurid except some of the Tremadocian Pilekiinae have four pairs of lateral glabellar furrows and in these cases the glabella is not inflated. Large eyes are not generally found in cheirurids. The thorax although it may represent 'the same type of structure' as in cheirurids does not necessarily have any close affinity with them. Admittedly the ventral cephalic sutures are unknown and may help to place this genus, but it seems more likely that a new family will have tobe erected to receive this unusual form.

Onycopyge, from the Silurian of New South Wales, is a genus formerly referred to the Cheiruridae. In this work it is excluded from the family. (See discussion of the genus in the systematic palaeontology).

CHAPTER IV

CHAPTER IV

SYSTEMATIC PALAEONTOLOGY

Introduction:

The morphological terms used in these descriptions are essentially those listed in 'Treatise on Invertebrate Paleontology', volume O. In addition the lateral glabellar lobes and furrows (indicated by the letters L and S respectively) are numbered from the posterior of the glabella. The facial suture is described by the help of the Greek Letters β , γ and ϵ which respectively are where the suture cuts the anterior margin of the cephalon, and the points where it meets the palpebral lobe anteriorly and posteriorly. 'Interring furrow' is used to describe the furrows between the axial rings of the pygidium.

Family CHEIRURIDAE Hawle and Corda, 1847

(*nom*. *transl*. Salter, 1864 (ex Chirurides Hawle and Corda, 1847)) Note. Henningsmoen (in Moore 1959) considered the authorship of the family was to be attributed to Salter (1864), and stated that Chirurides, Hawle and Corda 1847 was pending supression by ICZN. So far as is known no supression has ever appeared. Hawle and Corda used their term Chirurides in the same sense as Salter used the latinized term Cheiruridae, and it is here considered that the authorship of the family lies with Hawle and Corda and dates from 1847 as provided for in Article 11e iii of ICZN. Chiruridae Angelin, 1845 and Cerauridae Miller, 1889 need supression.

Subfamily CHEIRURINAE Hawle and Corda, 1847

(*nom*. *transl*. Raymond, 1913 (ex Chirurides Hawle and Corda, 1847)) Note. Henningsmoen (in Moore 1959) also considered the authorship of this subfamily was due to Salter (1864), (*nom*. *transl*. Raymond, 1913). However within their family Chirurides, Hawle and Corda recognised a subdivision to which they gave the same name as the family, and this subdivision is considered here to be the first designation of the subfamily.

Type genus. Cheirurus Beyrich, 1845.

Diagnosis:

Glabella parallel sided and convex to expanding forwards and very convex in which case the anterior border and border furrow are included in the frontal lobe mesially, occupying $\frac{1}{3}$ - $\frac{1}{4}$ transverse width of cephalon at occipital ring, with three pairs of lateral furrows. Basal lateral furrows deepest and most distinct, reaching occipital furrow, isolating a subtriangular to subquadrate basal lobe. Anterior two pairs of lateral furrows reaching a very short distance to completely across glabella. Genae subtriangular in shape, inside lateral border furrows coarsely pitted, each subequal in size to the glabella. Eyes placed most often opposite 2L, in some genera as far forwards as opposite 3S; eye ridge when present running from palpebral lobe to axial furrow adjacent to frontal lobe of glabella. Facial suture proparian. Rostral plate very narrow (sag.) and wide (tr.). Hypostoma with convex median body which narrows backwards and is rounded anteriorly and posteriorly, with oblique maculae; anterior wings long, lateral and posterior borders and border furrows distinct. Thorax of 10 - 11 segments; axial ring convex (tr.), pleurae composed of an inner articulated and outer free portion, inner portion with a deep, short, oblique furrow running from near axial furrow at anterior edge of segment, outwards and backwards, separating two subtriangular bosses of shell. Abaxial to this a wide shallow furrow runs exsagittally, and outside this there is a further swelling of the shell before the segment narrows to a free spine, these spines becoming increasingly curved back in the posterior segments of the thorax. Articulation of segment lies adjacent to the exsagittal shallow furrow and is composed of a hooked facet which abuts against a similar one on the next segment. Pygidium with three rings and terminal piece in the axis, and three pairs of free spines (of which the posterior two pairs can be variously reduced in size), which are sometimes lobate, with or without a terminal spine or lobe.

Genus *Bartoninus* Tripp, 1962

Type species (by original designation) *Bartoninus dispersus* Tripp, 1962, Stinchar Limestone, Minuntion, Girvan District, Ayrshire.
Diagnosis (slightly modified from Tripp, 1962, p. 16). Glabella parallel sided or expanding anteriorly with or without preglabellar furrow and anterior border. Basal lateral glabellar lobes about one-third width of the glabella. Exoskeleton non-tuberculate; inner areas of fixed and free cheeks pitted. Posterior margin of hypostoma transverse without lateral denticles. Pygidium with first pair of spines broad based and moderately long, third pair short, second pair intermediate in size; with or without terminal mucronation.

Bartoninus elongatus (Reed, 1931)

Plate 8, figs. 1-9

Plate 9, figs. 1-13

Plate 17, figs. 3-4

Plate 19, figs. 3, 6-7

1878 Cheirurus bimucronatus, Nicholson and Ethridge, p. 100.

1879 Cheirurus bimucronatus, Nicholson and Ethridge, p. 202, Pl.XIV, fig. 9.

1906 Cheirurus bimucronatus, Reed (pars), pp. 139-140, Pl. XIX, fig. 15.

1931 Cheirurus elongatus Reed, p. 103, Pl. IV, figs. 5-7, Pl. V, fig. 4.

1934 Cheirurus conjunctus Reed, pp. 55-56, Pl. IV, fig. 1.

Lectotype (here designated). HM A1074, external mould of pygidium. Figured Reed 1931, Pl. IV, fig. 7. Saugh Hill Group, Newlands, Girvan, Ayrshire. Paralectotypes. HM A1072, cranidia; HM A1075, hypostoma. All from the same horizon and locality as the lectotype.

Diagnosis:

A species of Bartoninus with glabella expanding forwards, and the preglabellar furrow interrupted by the frontal lobe mesially although in small holaspids this furrow is continuous across. Pygidium with three pairs of pleural spines, the anterior pair long and broad based, posterior two pairs much shorter reaching about equally far back, mid pair of stouter construction; terminal spine not present.

Range and distribution:

Saugh Hill Group, Newlands, Girvan, Ayr~~s~~shire; Newlands Sandstone, Newlands, Girvan, Ayr~~s~~shire; SN 74202818, South bank of River Sefin, 5 miles south of Llandovery, Carmarthenshire.

Description (based on internal moulds):

Cephalon subtriangular in outline, moderately convex (tr. and sag.). Glabellar less than $\frac{1}{3}$-width cephalon at occipital ring, expanding forwards. Frontal lobe forming widest part of glabella where it is half as wide again (tr.) as the occipital ring, convex, rounded anteriorly and anterolaterally, where it overhangs the axial furrow, posterolaterally (where 3S meets the axial furrow) angular. 3L & 2L subparallel sided, 3L a little wider (exs.) and almost parallel sided, 2L widening a little adaxially, nearly plane (exs.), and convex (tr.). 1L circumscribed, subtriangular, a little inflated, adaxial corners angular, a little over $\frac{1}{3}$ width of glabella (tr.). 3S a little over $\frac{1}{3}$ width of glabella, curved, moreso abaxially, where it is also at its deepest, 2S a little over $\frac{1}{3}$ transverse width of glabella, subparallel to but less curved than 3S, but of the same width and depth. 1S abaxially very deep, forming apodeme, straight, running a little obliquely back for $\frac{1}{4}$-way across glabella, suddenly shallowing and turning more obliquely back to meet the occipital two fifths way across glabella. Frontal lobe and mesial portion of glabella with many large tubercles, which are rare on other parts of the glabella. Occipital furrow wider than 1S, deep and distinct at apodeme laterally, arching forwards and shallowing mesially. Occipital ring widening mesially, abaxially half as wide as 3L, bearing small circular tubercles each surrounded by a small circular depression. These tubercles are also common on the lateral glabellar lobes (i.e. where the large tubercles are rare or not present) and also common on the adaxial part of the posterior border and on the fixed cheek adjacent to 1L. Axial furrow very deep from occipital ring to widest part of frontal lobe, overhung slightly by the glabella and cheeks. Preglabellar furrow dies out on mesial $\frac{1}{3}$ of frontal lobe.

Genae triangular, convex, sloping away from glabella. Posterior border convex, narrow adaxially, still narrower $\frac{1}{3}$ way to genal angle at articulation with first thoracic segment, widening increasingly to the genal angle which bears a spine. Lateral border wide, convex. Posterior border furrow wide and deep, distinct adaxially, a little arched forward where the posterior border narrows, widening and becoming less deep and distinct at the genal angle. Lateral border furrow narrowing and becoming more distinct anteriorly. Inside border furrows the cheeks are coarsely pitted. Free cheek subtriangular with a well developed border and border furrow inside which it is pitted like the fixed cheek. Eye surface cresentic with many small lenses, supported on a smooth, slightly concave ocular platform. Anterior border laterally narrow, dying out mesially.

Eye placed opposite 2S, $\frac{1}{3}$-way from axial furrow to lateral margin. Proparian, from β to γ facial suture weakly sigmoidally curved first round the lateral part of the frontal lobe, and then to the palpebral lobe, from ϵ suture running obliquely forwards at first then arching backwards gently until half-way across the lateral border, where it turns sharply obliquely back to cut the lateral margin opposite mid 1L.

Rostral plate unknown. Hypostoma with large convex median body, sub semicircular in front and semicircular behind where it is narrower with converging lateral margins, about twice as long (sag.) as wide (tr.). Posterior lobe of median body about $\frac{1}{4}$ sagittal length of the whole, and separated by distinct elongate oblique maculae which deepen and become more distinct abaxially. Anterior border narrow laterally, dying out mesially; anterior wings wide, angular. Posterolateral border narrower than anterior wings, narrowing backwards: posterior border narrowing mesially. Posterolateral border furrow wide and distinct, becoming less so backwards: posterior border furrow shallow and less distinct. Posterior margin straight, transverse. Median body coarsely and sparsely granulated.

Number of thoracic segments unknown. Pleurae of divided internal and spinose external type. Posterior margin of axial ring almost straight and transverse abaxial $\frac{1}{4}$ of ring widening towards axial furrow with a deep apodeme adjacent anteriorly; medial half of axial ring slightly arched forward with a less deep furrow separating the articulating half ring. Bosses on the internal portion of the pleurae subtriangular; axial, oblique dividing furrow and the furrow which bounds the bosses abaxially all distinct. Pleural spine almost plane dorsally, slightly arched forward then curving back. Ratio of transverse widths of axial ring to internal portion of pleurae (measured from the axial furrow to the abaxial part of the articulatory process) to the external portion of pleurae about 2:1:1.7. In the posterior segment, the pleural spines are wider, shorter and more hooklike.

Pygidium with axis tapering back composed of three rings and terminal piece. Axial furrow visible adjacent to the anterior two axial rings where it is distinct; posterior ring confluent with the pleural portions which bear two pairs of distinct furrows which reach the margin at the spaces between the pygidial spines, on the external mould the axial furrow is not seen adjacent to the mid axial ring. Three pairs of pygidial spines; anterior pair longest, of stout construction adaxially, where a deep short oblique furrow separates two bosses, this spine curving a little backwards and outwards, terminally running exsagittally; mid pair short and stoutly constructed, posterior pair a little shorter and slimmer than the mid pair, these two posterior pairs pointing backwards. Anterolaterally the pygidium has well developed spinelike extensions which bear the articulatory apparatus.

Discussion:

External moulds of this trilobite show that the wide and deep furrows of the internal moulds are narrower but still very distinct.

The glabella is everywhere, but especially on the frontal lobe and mesial portions coarsely tuberculated, these tubercles smaller and more frequent on the anterior of the frontal lobe, and the cheek regions inside the posterior and lateral border furrows pitted, the pits everywhere smaller than the glabella tubercles and increasing a little in size but getting fewer in number from the axial furrow to the genal angle. The cephalic border near the genal angle bears fine granulations on the inner portions, and larger less regular granulations on the external part of the border.

The smaller specimens, the cephalic ratios of which vary less than in large forms, (see below), have certain differences from these. In the cephalon, the lateral glabellar furrows are relatively shorter than in large specimens, and the basal lobes are not as wide. But in one important respect the smaller forms do vary from the larger ones. In the smallest specimens (cephala about .18" wide) the preglabellar furrow can be seen to be continuous across the front of the glabellar, although it is less distinct mesially. The smallest hypostomes also have a weak complete anterior border furrow. These furrows are reduced in the larger specimens so that the largest cephalon (1.3" wide posteriorly) has the mesial $\frac{1}{3}$ of the anterior of the frontal lobe without a furrow.

The species '*Cheirurus conjunctus*' Reed, 1934, is considered a wider form of *Bartoninus elongatus*. No specific differences could be found between cephala of the two types, and pygidia of two types are not present. The specific name therefore is unfortunately unsuitable for some of the members of the species. The lectotype has a cephalic ratio (transverse width to sagittal length) of about 1.6:1, whereas in some members of the species this ratio is about 2.2:1. Such variations in proportions have also been recorded by Tripp in *Bartoninus craigensis* (see Tripp, 1954 p. 19).

Other material. HM A772, 1045, 2983, 2987, 3721, 3826, 5710, 5714; BM In23400, 23412-23421, 42987, 43711, 43714, 43717-43721, 43728.

Bartoninus aff. *elongatus*

Plate 17, figs. 5-6

Material:

A single cranidium, GSM OTJ612.

Horizon and Locality:

Lower Llandoverian, Priory Mill Railway Cutting, Haverfordwest, Pembrokeshire.

Remarks:

This specimen is similar to *B. elongatus* but differs in detail. The anterior border of this specimen is incomplete mesially, but it is vertical laterally, continuing the convexity of the frontal lobe. In *B. elongatus* the anterior border is wider and not verticle. In addition in *B.* aff. *elongatus* there is a wider deeper separation between the basal lateral glabellar lobes, and the posterior border of the cephalon is narrower (exs.) adjacent to the occipital ring. It would be expected that the find of a pygidium of this species from this locality would settle the status of this specimen.

Bartoninus skelgillensis sp. nov.

Plate 10, figs. 1-9

Plate 19, figs. 4-5

1888 Cheirurus bimucronatus var. acanthodes, Marr and Nicholson, pars., p. 673.

Material:

Holotype. NU LS2/27, internal mould of pygidium.

Horizon and locality:

Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland.

Diagnosis:

A species of Bartoninus with frontal lobe markedly wider than the rest of the glabella, and the preglabella furrow interrupted mesially by the frontal lobe. Pygidium with three pairs of pleural spines, anterior pair very long and slender, mid pair short and stout, posterior pair very short; terminal mucronation or spine not present.

Description (based on internal moulds):

Cephalon semicircular in outline. Glabella a little less than $\frac{1}{3}$ transverse width of cephalon at occipital ring, expanding evenly forwards from occipital ring to 3L, frontal lobe markedly wider than this general expansion and about half as wide again (tr.) as the occipital ring. Frontal lobe rounded anteriorly and anterolaterally, occupying a little more than $\frac{1}{3}$ sagittal length of glabella, convex (tr. and sag.). 3L decreasing in width (exs.) a little adaxially, 2L increasing a little in width in this direction, both reaching about two fifths way across glabella, a little inflated and convex (tr.). 1L triangular, circumscribed, about $\frac{1}{3}$ width glabella at that point. 3S and 2S wide and deep, subparallel, approaching a little adaxially, both curved and running obliquely back adaxially. 1L less curved, deeper abaxially forming apodeme, narrower and more oblique. Occipital furrow deep and narrow exsagitally forming apodeme, mesially curving forward, widening and shallowing meeting 1S furrows in wide depressed area. Occipital ring convex (tr. and sag.), widening mesially. Axial furrow wide and very deep from adjacent to occipital ring to a deep fossula placed just anterior to 3S, continuing round the anterolateral part of the frontal lobe as a preglabellar furrow which dies out over about the mesial third.

Genae triangular, convex, sloping away from glabella. Posterior border narrow from adjacent to occipital ring to the articulation with the first thoracic segment about one third the distance from axial furrow to genal angle, abaxial to this widening a little. Posterior border furrow deep and distinct widening a little towards genal angle which bears a spine of unknown length. Lateral border wide, lateral border furrow wide and shallow. Genae inside border furrows coarsely pitted.

Eye placed opposite 2S or a little anterior to this; palpebral lobe with distinct palpebral furrow adaxially. Proparian, facial suture from β to γ gently curving convex outwards, from ϵ arching first gently forwards then backwards until less than half way across lateral border where it turns sharply obliquely back and cuts lateral margin opposite 1L.

Rostral plate unknown.

Hypostoma with convex median body, elliptical in front and semicircular behind where it is narrower. Posterior lobe of median body about $\frac{1}{4}$ sagittal length of whole separated off by distinct oblique maculae which are curved convex outwards and backwards. Lateral border furrow adjacent to posterior part of anterior lobe of median body deep and distinct, posterior border furrow wider and less distinct, anterior border furrow dying out over medial part of hypostoma. Anterior wings, lateral and posterior borders wide and convex.

Thorax of an unknown number of segments of the form typical of the genus.

Pygidium with three axial rings, axial furrow distinct adjacent to the anterior two. Three pairs of spines, anterior with broad furrowed pleural portion but free part long and slender; mid pair very short and stout, posterior pair very short indeed both these pairs having unfurrowed pleural portions adjacent. Terminal mucronation or spine of the pygidium not present.

The character of the surface of the internal and external surfaces of the exoskeleton is unknown.

Discussion:

The holotype, a small fragmentary pygidium, is unfortunately the only pygidium of this species known. It differs however, from the related B. elongatus mainly in the slender construction of the anterior spine, the mid pleural rib which here is narrower and the interpleural furrow between the mid and anterior pleural portions which dies out abaxially although it is distinct in B. elongatus . The cephala, as might be expected, differ little between the two species but in B. skelgillensis the lateral glabellar furrows are relatively longer, and the facial suture from β to γ does not have a sigmoidal curve. Other material (all from the horizon and locality of the holotype) NU LS2/8-26.

Bartoninus acanthodes (Marr and Nicholson, 1888)

Plate 17, figs. 1-2

1888 Cheirurus bimucronatus var. acanthodes Marr and Nicholson, pars. pp. 670 and 722, Pl. XVI, figs. 7-8.

Material:

Lectotype (here designated) SM A40330, internal mould of pygidium.

Horizon & Locality:

Zone of Phacops glaber, Skelgill, near Ambleside, Westmorland. Paralectotype. SM A40325, internal mould of cephalon. Same horizon and locality.

Discussion:

This species was considered a variety of Cheirurus bimucronatus by Marr and Nicholson although they noticed the long anterior pygidial spines. It appears to differ from the closely related B. skelgillensis in the more anterior position of the eye (it is difficult to tell with certainty from the types exactly how far forward the eye is as the rock has been distorted), the shorter less curved lateral glabellar furrows, and by the posession in the pygidium of a small terminal mucronation between the posterior pair of pygidial spines. The species is not described here as it is thought that more topotype material is necessary to give an accurate account of the morphology.

Bartoninus sholeshookensis sp. nov.

Plate 11, figs. 1-5

Plate 17, figs. 7-8

1846 *Cheirurus bimucronatus*, Salter, pars. Pl. VII, figs. 4-6.

1864 *Cheirurus bimucronatus*, Salter, pars. Pl. 5, fig. 1.

Material:

Holotype. BM I16399a and b. Internal and external moulds of pygidium.

Horizon & Locality:

Sholeshook Limestone, farmyard east of Prendergast Place, Haverfordwest, Pembrokeshire.

Diagnosis:

A species of *Bartoninus* with lateral glabellar furrows 3S and 2S almost straight and parallel and basal glabellar lobe triangular in outline, and in the pygidium the axial furrow well marked lateral to the axis, the terminal piece not separated from the posterior portion of the pygidium behind, and a well marked terminal mucronation between the posterior pair of pygidial spines.

Description:

Glabella less than $\frac{1}{3}$ width of cephalon at occipital ring, expanding forwards increasingly more rapidly from posterior to anterior, to the frontal lobe, where the maximum width of the glabella is reached being half as wide again as the occipital ring (tr.). Frontal lobe convex (tr. and sag.), less than half the length (sag.) of the whole glabella. 3L parallel sided (exs.), 2L increasing in width adaxially, both lobes convex (tr. and exs.). 1L a little inflated, triangular, circumscribed, about $\frac{1}{3}$ width of glabella at that point. 3S and 2S parallel deep and wide (still wider in internal mould) almost straight and running adaxially backwards to reach about two fifths way across glabella. 1S initially more oblique than 2S, here narrow and deep forming an apodeme, less than $\frac{1}{3}$ way across glabella turning to run more obliquely backward, shallowing and widening and meeting occipital furrow. Occipital ring widening mesially, convex (tr. and sag.). Occipital furrow narrow and deep abaxially forming apodeme, mesially wider and shallower. Axial furrow wide and deep from adjacent to the occipital furrow to the fossula placed just anterior to 3S, and continuing anteriorly as a shallowing preglabellar furrow which is absent over the medial $\frac{1}{3}$ of the frontal lobe.

Genae convex, triangular in shape. Posterior border convex and narrower than the adjacent part of the occipital furrow adaxially, narrowing very slightly to the articulation with the first thoracic segment, abaxial to this widening and less convex. Posterior border furrow narrow and deep adaxially, widening and shallowing towards genal angle which bears a stout fairly long spine. Palpebral lobe prominent extending from mid 2L to mid 3L. Proparian, from β to γ facial suture divergent from the axial furrow, from ϵ suture running slightly forward to the lateral border across which it cuts sharply backwards. Genae inside border furrows coarsly pitted.

Number of thoracic segments unknown, in form typical of the members of the subfamily.

Pygidium with three pairs of spines. Axis composed of three rings and a terminal piece. Axial rings convex (tr. and sag.), anterior widest bearing on its posterior margin an cylosed portion of the obsolete articulating half ring; mid axial ring also with an indistinct boss being an indication of a half ring. Interring furrows narrower exsagittally. Axial furrow well indicated adjacent to the axis. Terminal piece posteriorly not delimited from the posterior part of the pygidium. Anterior of three pairs of spines apparently stoutest and longest, bearing an oblique furrow adaxially. Mid and posterior spines with adjacent unfurrowed pleural portions which are convex and separated by a distinct furrow running exsagittally, both these pairs of spines shorter than the anterior pair, posterior piar shortest of all slightly hooked between the spines of this pair a well developed terminal mucronation being present.

<u>Discussion</u>:

This species is one of the large species of <u>Bartoninus</u> found in rocks of Ashgillian age in Britain. It is distinguishable from the others by the strightness of the lateral glabellar furrows, and especially by the form of the posterior two pairs of pygidial spines which are well developed, the posterior pair being hooked, and between these there being a well developed terminal spine. The free cheek, rostral plate and hypostoma are unknown.

The details of Salters figured specimens are as follows: Salter 1846, Pl. VII, fig. 4. GSM 24530 (here Pl. 11, fig. 4.), fig. 5. GSM 24572 (here Pl. 17, fig. 8.), fig. 6. GSM 24528. 1864, Pl. 5, fig. 1. is GSM 24530. GSM 24572 here referred to B. sholehookensis is from the Robeston Wathan Limestone, Robeston Wathan, Pembrokeshire. A pygidium also referred to this species is from near Llanddowror, Carmarthenshire.

Other material. Cranidia; BM I16400, MU L11655.

Bartoninus girvanensis sp. nov.

Plate 12, figs. 1-4.

Plate 13, figs. 1-5.

Plate 18, figs. 5-6.

1906 *Cheirurus bimucronatus*, Reed, pars. pp. 139-140.

1914 *Cheirurus keislevensis*, Reed, pp. 45-46. non Pl. VIII, fig. 1.

1931 *Cheirurus keislevensis*, Reed, pp. 21-22.

Holotype:

BM In 23407/1 internal and external moulds of pygidium.

Locality:

Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayr~~e~~shire.

Diagnosis:

A species of *Bartoninus* which attains a large size, characterised by the long curved lateral glabellar furrows, and in the pygidium by the long, very broad based rapidly tapering anterior spines, the short hooked mid pair of spines, and the very short posterior spines between which there is a convex backwards short posterior margin of the pygidium.

Description: (based on internal moulds)

Glabella just less than $\frac{1}{3}$ width of cephalon at occipital ring, expanding forwards to a maximum width across frontal lobe, where it is approximately half as wide again. Frontal lobe convex (tr. and sag.), approaching half the length (sag.) of whole cephalon. 3L decreasing a little in width (exs.) adaxially, 2L decreasing in width (exs.) in the opposite direction, both lobes convex (tr. and exs.). 1L a little inflated, subtriangular, circumscribed, just more than $\frac{1}{3}$ width of glabella at that point. 3S and 2S subparallel, deep and wide, slightly curved and running adaxially backwards to reach two fifths way across glabella. 1S initially more oblique than 2S, here narrow and deep forming apodeme, less than $\frac{1}{3}$ way across glabella turning more obliquely back, shallowing and widening, and meeting occipital furrow. Occipital ring exsagittally about half the width (exs.) of abaxial part of 3L, widening mesially, convex (sag. and tr.). Occipital furrow narrow and deep abaxially forming apodeme, mesially wider and shallower. Axial furrow wide and deep from adjacent to the occiptial ring to the fossula placed just anterior to 3S, and continuing anteriorly as a shallowing preglabellar furrow which is absent over the mesial $\frac{1}{3}$ of the frontal lobe.

Genae convex, triangular in shape, poorly preserved in the specimens to hand. Posterior border convex and half as wide as the adjacent part of the occipital ring (exs.), of near constant width as far as the articulation with the first thoracic segment which is placed just less than half way from the axial furrow to the inner margin of the genal spine, the posterior border abaxial to this constantly widening and becoming less convex. Posterior border furrow narrow and deep throughout its course. Lateral border wide and convex, lateral border furrow narrow but a little less distinct than the posterior border furrow. Genal angle bears a broad based spine of unknown length. Position of the eye uncertain, probably opposite 2S, Facial suture proparian, β to γ not seen in relation to axial furrow from ε arching first forwards then backwards to less than half way across lateral border, then turning sharply obliquely backwards to cut the lateral margin opposite the posterior part of 1L. Free cheek with wide border, conves dorsally, continued ventrally as equally wide convex doublure. Lateral border furrow of similar character to that on the fixed cheek. β to γ of facial suture curves from anterolaterally to the widest part of the glabellar, its relation to axial furrow not seen. Visual surface crescentic in dorsal view, convex from doraal to ventral margin and from anterior to posterior margin, bearing regularly arranged facets 1150 in number (approx.) in the specimen figured (Pl. 18, fig. 6.). Surface of genae and borders finely granulated, doublure more finely granulated; inside border furrows genae coarsely pitted.

Rostral plate poorly indicated, but appears to be very narrow (sag. and exs.) and wide (tr.).

Hypostoma with very convex median body rounded in front and behind, with maximum transverse width ($\frac{1}{4}$ way from anterior) about twice as great as the width $\frac{1}{4}$ way from the posterior. Maculae wide and shallow, commencing at lateral border furrow about $\frac{1}{3}$ way from the posterior of the median body, and running very obliquely backwards never reaching $\frac{1}{4}$ way across. Lateral border furrows deep and distinct, converging posteriorly, and curving round the posterior lobe of the median body as a posterior border furrow with an arcuate course and here less deep and distinct than the lateral border furrows. Anterior border furrow much shallower and narrower than other border furrows, not curving smoothly round the anterior of the anterior lobe but having mesially a slight rounded angulation in its outline, here very shallow and narrow. Lateral and posterior border wide and convex, widest just posterior to the anterior wings and posterolateral angles of hypostoma, where its outline in subangular. Anterolateral border adjacent to anterior wings as wide as widest part of lateral border. Anterior wings curving up dorsally, not well seen in specimens to hand.

Number of thoracic segments unknown, in form typical of the members of the Cheirurinae with the proportions of axis to inner furrowed part of pleurae to outer unfurrowed part about 2:1:2, on a segment towards the posterior part of the thorax. Articulation of the segments also typical of the members of the subfamily with facets placed adjacent to the adaxial part of outer unfurrowed portion of pleurae. Doublure of thorax under spinose part of pleurae reaching adaxially as far inwards as the abaxial end of articulatory facets.

Pygidium with three pairs of spines. Axis composed of three rings and terminal piece. Axial rings convex (tr. and sag.), anterior most so, this ring also widest (tr.) bearing on its posterior margin an ancylosed portion of the obsolete articulating half ring. Mid axial ring also with a very small boss being part of an obsolete articulating half ring. Interring furrows deeper and narrower exsagittally. Axial furrow indicated adjacent to anterior axial ring, but less distin ct posteriorly. Terminal piece posteriorly hardly delimited from the posterior portion of the pygidium.

Anterior of three pairs of spines longest, from adjacent to anterior axial ring obliquely furrowed pleural portion widens in a direction 45° to the transverse, being widest at a line drawn from the margin between anterior and mid spine to the rounded anterolateral corner of the pygidium , convex in this line, posterior to this narrowing rapidly, and produced into a long narrow spine. Mid and posterior spines with unfurrowed convex pleural portions separated by deep distinct furrows running nearer exsagittal direction, both these pairs of spines very much shorter and relatively stouter than the anterior pair, posterior pair smallest of all, and the two spines of this pair separated from each other by the short posterior margin of the pygidium which is a little convex backwards. Anterior edge of anterior pleural portion bears a process which widens abaxially and is separated from the pleural portion by a furrow. The process bears the facet which articulates with the posterior thoracic segment.

Doublure of pygidium extending ventrally to a line drawn from junction of abaxial part of articulatory process and anterior border of pygidium to a point under the axis approximately at the furrow between the third ring and the terminal piece. Near the inner edge of the doublure there is a raised area, strip-like in form and widening adaxially. This doublure is everywhere granulated, the granulations small on the part underneath the broad base of the anterior pygidial spine, becoming larger and more sparse on the portion immediately adjacent to the strip-like raised border, on this border again fine and closely packed.

Discussion:

This species is another of those large species of Bartoninus which occur in the British Asgillian. Like the others it seems to be restricted to a particular area. From the fragments available it seems that this species must have attained a length of at least 170mm. sagittally, assuming it to have had the eleven thoracic segments characteristic of the subfamily.

Other material. BM In 23407/2-4, 23408/1-9, 23409/1a & b. 23424a & b. All from the horizon and locality of the holotype.

Bartoninus keisleyensis (Reed, 1896)

Plate 14, figs. 1-8

Plate 15, figs. 1-3

1896 *Cheirurus keisleyensis* Reed, p. 417, Pl. XX, figs. 7-9.

non 1913 *Cheirurus keisleyensis*, Reed, pp. 45-46.

non 1931 *Cheirurus keisleyensis*, Reed, pp. 21-22.

Lectotype:

SM A11847, internal mould of fragmentary pygidium. Keisley Limestone, Keisley, Westmorland.

Diagnosis:

A species of *Bartoninus* which attained a large size, characterised in the cephalon by a glabella which is almost plane (sag.) posterior to the frontal lobe, and which has long, narrow, parallel lateral furrows 2S and 3S, and by the anterior section of the facial suture which from the anterior margin curves round to opposite to widest part of the frontal lobe, posterior to this being almost straight and directed obliquely outwards abaxially; the pygidium has a long, broad based anterior spine, a tapering, slightly hooked mid spine, and a very short posterior spine on each side; between the posterior pair of spines there is no terminal mucronation or posterior margin to the pygidium.

Description:

Glabella (external mould) convex (tr.) posterior to frontal lobe almost plane (sag.), expanding forwards to frontal lobe where it is half as wide (tr.) again as the occipital ring. Frontal lobe semicircular just less than half the length of the glabella excluding the occipital ring, highly convex (tr. and sag.), rounded anteriorly and anterolaterally. 3L parallel sided, a little wider (exs.) abaxially than 2L, this latter widening adaxially. 1L subtriangular, inflated, about $\frac{1}{3}$ width of glabella at that point, circumscribed. 3S and 2S, parallel, gently curved, sloping a little obliquely backwards adaxially, narrow and distinct, reaching two fifths way across glabella. 1S initially parallel to 2S but wider and deeper, forming apodeme $\frac{1}{3}$ way across glabella turning back and shallowing to meet occipital furrow. Occipital ring narrow (exs.) abaxially, widening mesially, convex (tr. and sag.). Occipital furrow wide and distinct especially abaxially at apodeme, mesially curving forward. Axial furrow narrow and deep with a deep fossula placed just anterior to 3S, preglabellar furrow shallower and dying out $\frac{1}{4}$ way across frontal lobe.

Genae fragmentary. Posterior border convex (tr. and exs.), adaxially narrower than the adjacent occipital ring, widening a little adaxially over the portion seen. Posterior border furrow narrower and as distinct as the occipital furrow. Eye placed opposite the posterior of 3L. Of the facial suture only β to γ seen, originating just abaxial to where the preglabellar furrow dies out curving round to opposite widest part of frontal lobe and then running in an almost straight line obliquely backwards abaxially to δ . Genae inside posterior border furrow coarsely spaced granules, which on the internal mould are less distinct.

Hypostoma with large convex median body. Posterior lobe delimited by weak maculae and occupying about one fifth the sagittal length of the whole. Anterior border furrow narrow, lateral and posterior border furrows wider, the latter indistinct mesially. Anterior border not present mesially, laterally present and continuous with anterior wings. Lateral border wide immediately behind anterior wings, then narrowing backwards and becoming wide again posterolaterally. Posterior border narrower mesially than laterally. Surface of hypostoma everywhere finely granulose.

Thorax composed of an unknown number of segments of the type characteristic of the genus.

Pygidium with axis composed of three rings and a subtriangular terminal piece. Anterior axial ring wider (sag. and exs.) than the others. Sides of the axial rings converge backwards so that the posterior transverse width of a ring is less than the anterior width of the ring behind. Posterior transverse width of third ring about equal to the maximum width of the terminal piece. Furrows between anterior and mid, and mid and posterior rings curve backward mesially, the former most so. Furrow between terminal piece and posterior ring curves forward so that this ring is narrower sagittally than exsagittally. All rings markedly convex (tr. and sag.), terminal piece slightly inflated. Axial furrow adjacent to axial rings narrow and indistinct, adjacent to terminal piece wide, deeper and distinct, the terminal piece posteriorly confluent with the small posterior part of the pygidium. Anterior pair of spines only partially preserved, but they are the largest, the pleural portion adjacent broad and crossed by deep, oblique, straight furrows. Mid spines shorter, curving backwards and a little upwards, running near to the exsagittal direction, those spine and pleural parts unfurrowed, separated from anterior and posterior pleural portions by furrows which are deep, wide and distinct adaxially, but reach the margin at the rounded angles between the spines as less distinct features. The anterior of these two furrows is curved, adaxially parallel to the oblique furrow of the anterior pleural portion, abaxially running close to the exsagittal direction; the posterior is straight and runs exsagittally. Posterior spines very short and broad based, mid spines longer than these. Pleural portions of posterior spines very narrow, running between mid pleural portion and terminal piece, convex (tr.), almost exsagittally directed but approaching a little posteriorly.

Discussion:

Reed erected this species on 'two fragmentary pygidia' which are figured here (Pl. 14, figs. 7 & 8). The cephalon he figured is not typical of the species in that it has been flattened dorsoventrally, and in addition it is an internal mould which has been weathered to some extent, which is uncommon for Keisley Limestone material.

B. keisleyensis most closely resembles B. girvanensis sp. nov. From that species, however, it differs in the cephalon by the straight course of the portion of the anterior section of the facial suture between palpebral lobe and the widest part of the frontal lobe, and the less curved, less oblique lateral glabellar furrows, and in the pygidium by the longer mid pleural spine, and the shorter pair of posterior spines between which there is no posterior margin to the pygidium as there is in B. girvanensis.

Like B. girvanensis and B. sholeshookensis, B. keisleyensis attained a large adult size. Judging from the fragments available, and again supposing that the species had eleven thoracic segments, this species must have attained a length of about 160mm.

Other material. SM A11842, 11846, 11848-58.

<u>Bartoninus</u> cf. <u>keisleyensis</u>.

Plate 16, fig. 6.

Plate 19, figs. 1-2.

1864 <u>Cheirurus</u> <u>bimucronatus</u>, Salter, pars, Pl. 5, figs. 2 and 12.

<u>Material</u>:

GSM 35369, (cephalon figured by Salter, 1864, Pl. 5, fig. 2); and GSM 35383, (pygidium figured by Salter, 1864, Pl. 5, fig. 12). RSM 1870 12 891A, (hypostoma). All external moulds from the Chair of Kildare Limestone, Kildare, Ireland.

<u>Remarks</u>:

From the little material available it seems that the species from the Chair of Kildare Limestone is probably conspecific with the Keisley Limestone species. Until more material from the former locality is available it is considered better not to make a final decision.

Bartoninus cf. glaber (Angelin, 1854)

Plate 15, figs. 4-7

Material:

RSM 1870 12 891C, (cranidium), Chair of Kildare Limestone, Ireland; SM A11859, (cranidium), Keisley Limestone, Keisley, Westmorland.

Description:

Cephalon more than a semicircle in outline, ratio of width (tr.) to length (sag.) less than 2 : 1, gently convex (tr. and exs.).

Glabella expanding a little forwards, $\frac{1}{3}$ width of glabella at occipital ring. Frontal lobe elliptical in shape in front, as long (sag.) as 3L and 2L, convex (tr. and sag.), forming widest part of glabella, 3L and 2L gently convex (tr. and exs.); 3L parallel sided, slightly wider (abaxially) than 2L which increases in width adaxially. Basal lobes subtriangular, circumscribed, inflated, less than $\frac{1}{3}$ width glabella (tr.) at that point. 3S and 2S parallel, same width and depth reaching $\frac{1}{3}$ way across glabella, almost straight and transverse. 1S abaxially straight, as wide and deep as 2S, less than $\frac{1}{3}$ way across glabella shallowing, widening and turning to run exsagittally, meeting the occipital furrow which here is curved forward. Occipital ring convex (tr. and sag.), widening mesially. Axial furrow wide and distinct from adjacent to occipital ring to 3L, narrower and shallower around the lateral curvature of the frontal lobe, continuing across the front of glabella as a shallow, narrow preglabellar furrow which arches upwards mesially.

Genae convex, sloping away from glabella. Posterior border furrow distinct, but less distinct than the lateral glabellar furrows, running obliquely forwards abaxially to the genal angle where it is widest and least distinct, and joins the wider shallow lateral border furrow. Posterior border narrow, convex, widening abaxially, widest at genal angle where it joins lateral border which narrows anteriorly. Genal angle bears a spine which is about as long as sagittal length of 3L and 2L.

Eye placed opposite posterior of 3L, $\frac{1}{3}$ way from glabella to lateral margin. Palpebral lobe, extending from anterior of 3L to anterior of 2L, rises from cheek steeply in front, vertically behind, with adaxially, a sigmoidally curved palpebral furrow. Facial suture proparian, β to γ curving round the widest part of the frontal lobe, where it also approaches nearest to preglabellar furrow, from ε , suture runs obliquely forward to reach as far forward as 2S at inner margin of lateral border furrow, curving back across this furrow and inner $\frac{1}{3}$ of lateral border, then turning sharply back to cut lateral margin opposite mid 1L.

Fixed cheek inside border furrows with large shallow pits. Surface of shell and internal mould everywhere very finely ganulated.

Discussion:

This species which apparently occurs in both Keisley and the Chair of Kildare Limestones differs from other British species of

Bartoninus from these localities in the relatively short (sag.) frontal lobe of the glabella, the relatively short almost straight and transverse lateral glabellar furrows, and especially in the presence of the preglabellar furrow mesially. It appears to be closest to *Bartoninus glaber* (Warburg, 1925 Pl. IX, figs. 12-13), from the *Leptaena* Limestone of Scandinavia.

<u>Bartoninus</u> <u>gelasinosus</u> (Portlock, 1843).

Plate 16, figs. 1-4

1843 <u>Amphion</u> <u>gelasinosus</u> Portlock, pars. pp. 289-290, Pl. III, fig. 4a. non. fig. 4b.

1843 <u>Arges</u> <u>planospinosus</u> Portlock, Pl. V, figs. 9a & b.

1845 <u>Cheirurus</u> <u>gelasinosus</u>, Beyrich, p. 19.

1853 <u>Cheirurus</u> <u>gelasinosus</u>, Salter, pars. p. 11.

1864 <u>Cheirurus</u> <u>gelasinosus</u>, Salter, pars. pp. 71-72, Pl. 5, figs. 7-8, non. fig. 6.

non 1906 <u>Cheirurus</u> <u>gelasinosus</u>, Reed, pp. 140-141, pl. XVIII, figs. 5-6.

1952 <u>Ceraurinus</u> <u>gelasinosus</u>, Reed, pp. 120-121.

<u>Lectotype</u>:

GSM 35373 (cranidium), 'Caradoc', Tyrone, Ireland. Original of Portlock 1843, Pl. III, fig. 4a.

<u>Diagnosis</u>:

A species of <u>Bartoninus</u> characterised in the cephalon by a glabella subquadrate in outline with short (sag.) frontal lobe, lateral furrow 3S curved and 2S straight and near transverse; preglabellar furrow and anterior border distinct, the latter angular laterally where the anterior section of the facial suture cuts it. The pygidium is characterised by three pairs of spines, the anterior pair longest and stoutest, the posterior pair shortest, and the mid pair intermediate in size between these two; axis of pygidium with three rings and a small terminal piece, the anterior axial ring laterally lobate.

Description: (of internal moulds)

Cephalon elliptical in outline, about four times as wide (tr.) as long (sag.) partially due to the turning down of the frontal lobe of the glabella and the anterior border, convex (tr. and sag.).

Glabella subquadrate in outline, parallel sided, forming about $\frac{1}{4}$ transverse width of cephalon at the occipital ring. Frontal lobe rounded anteriorly and anterolaterally, gently convex (tr. and sag.). 3L and 2L gently convex (tr. and sag.), 3L increasing in width from axial furrow adaxially then decreasing a little, 2L subparallel sided, the glabella across these lobes a little wider than across the frontal lobe. Basal lobes almost circumscribed, triangular in outline, less than $\frac{1}{3}$ width glabella at this point. 3S and 2S of about the same length, reaching just more than $\frac{1}{3}$ way across glabella, 3S curved and directed obliquely back adaxially, 2S almost straight and transverse, both wide and deep. 1S abaxially straight, running a little obliquely backwards adaxially for about $\frac{1}{3}$ width of glabella, here as wide and deep as 2S, from here connected to occipital furrow by an indistinct depression. Occipital ring most convex and narrowest exsagittally, a little wider and less convex sagittally, Axial furrow wide and distinct with a deep fossula just anterior to 3S. Anterior and adaxial to this fossula the preglabellar furrow is narrower and less distinct than the axial furrow. Anterior border wide laterally where it is angular in outline where the anterior section of the facial suture cuts it.

Genae wide (tr.) convex and triangular. Posterior border very narrow and convex, posterior border furrow very narrow and distinct, both widening a little adaxial to the articulation with the first thoracic segment placed about half way from axial ring to inner margin of genal spine. Lateral border wide, lateral border furrow wide and shallow. Eye placed opposite 2S about half way from axial furrow to lateral margin. Facial suture proparian, β to γ running in a broad curve, from ϵ the suture arching forwards then back to about half way across the lateral border, then turning sharply back and cutting lateral margin opposite 1L. Free cheek not preserved, triangular in outline. Fixed cheek within border furrows coarsley pitted.

Axis of pygidium tapering backwards, composed of three rings and a small terminal piece. Articulating half ring convex (tr. and sag.), wider sagittaly than exsagittally, separated from anterior axial ring by a furrow which is wide and deep over the mesial $\frac{2}{3}$ of the axis, narrows and becomes very deep exsagittally. Anterior axial ring trilobate, composed of two large lateral, round, flat topped bosses, and a smaller mesial one, this ring distinctly delimited from the pleural region by the axial furrow which is wide deep and distinct around the outer edge of the lateral bosses. Structure of axis posterior to anterior axial ring very modified. Mid axial ring convex (tr. and sag.) with a faint indication of a trilobate structure, confluent with mid pleural ridge with no indicati n of the pleural furrow. Posterior axial ring and terminal piece convex (tr. and sag.), furrows between mid and posterior axial ring wide and indistinct, shallower sagittally, and between posterior axial ring and terminal piece wide and indistinct. Pleural portions strongly divided into three ridges by two furrows which originate adjacent to the two anterior interring furrows of the axis, are deeper and narrower adaxially, and reach margin of pygidium between spines as wider less distinct features, both curved, the anterior running nearer the transverse, the posterior nearer the exsagittal direction. Anterior pleural ridge subdivided by a short fairly distinct furrow which runs from the axial furrow a short way abaxially. Mid and posterior pleural ridges convex (exs.), widening and becoming flat at the origin of the free spines. Three pairs of spines, anterior largest, most curved and directed furthest from the exsagittal direction, posterior pair very short and directed only slightly from the exsagittal direction, mid pair intermediate in size and direction.

Discussion:

The single cranidium (Pl. 16, figs. 1-2) and two pygidia (Pl. 16, figs. 3-4) all internal moulds, are the only specimens of this species known to the author. The precise horizon and locality from which they came is not known, but from the general level of organisation within the Bartoninus plexus, it seems most likely that the species is from the lower part of the Caradocian. This would indicate it to be a primitive species of the genus, and the primitive characters exhibited include the parallel sided glabella the frontal lobe of which does not form the widest part, the well developed anterior border and the relatively low inequality of the sizes of the pygidial spines, when compared to the Ashgillian species such as _B_. _girvanensis_.

Bartoninus craigensis (Tripp, 1954)

Plate 18, figs, 1, 3-4.

1864 *Cheirurus gelasinosus*, Salter, pars. Pl. 5, fig. 6.

1952 *Ceraurinus* cf. *icarus*, Reed, pars. p. 121.

1954 *Ceraurinus craigensis*, Tripp, pp. 675-677, Pl. III, figs. 33-46.

1962 *Bartoninus craigensis*, Tripp, p. 17.

An adequate description is to be found in Tripp, 1954.

Remarks:

Figured here (Pl. 18, fig. 1) is GSM 35380 the original of Salter 1964, Pl. 5, fig. 6.

Bartoninus susceptus, (Reed, 1931)

Plate 18, figs. 2, 7-8

1906 Cheirurus gelasinosus, Reed, P. 140, Pl. XVIII, figs. 5-6.

1931 Cheirurus (Ceraurinus) susceptus Reed, p. 22.

Lectotype:

BM In23425, fragmentary distorted cranidium, internal mould.

Horizon and Locality:

Stinchar Limestone, Craighead, Girvan, Ayrshire.

Description:

Glabella subparallel sided, gently convex (tr. and sag.), rounded anteriorly and anterolaterally, with three pairs of lateral furrows. Frontal lobe rounded in front, sagittally less than $\frac{1}{3}$ the length of the glabella, gently convex (tr. and sag.). 3L parallel sided, 2L increasing in width (exs.) adaxially, both about $\frac{1}{3}$ or a little more width (tr.) of the glabella. 1L subtriangular in outline, a little inflated, circumscribed. 3S and 2S parallel, curved, quite wide and distinct, running a little adaxially backwards, reaching a little more than $\frac{1}{3}$ way across the glabella at that point. 1S initially stright, narrower and running more obliquely back than 2S until about

$\frac{1}{3}$ way across glabella where it turns to run almost exsagittally, shallowing and widening, and reaching occipital furrow as an indistinct feature. Occipital furrow narrower adjacent to 1L than mesially. Occipital ring sagittally as wide (exs.) as 2L, narrowing a little abaxially, convex (tr.) almost plane (sag. and exs.). Axial furrow wide and deep (where seen), with, anterior to 3S, a fossula adjacent to the widest part of the frontal lobe. Axial furrow continuing in front of glabella as narrower, less distinct preglabellar furrow.

Genae only seen from poorly preserved fragment of anterior of fixed cheek. Eye apparently opposite 2S, portion of fixed cheek adjacent to and anterior to eye very narrow.

Portion of thorax referred to this species (BM In23426), shows parts of five segments which are disarticulated and much distorted. Axis about $\frac{1}{4}$ width of whole segment. Pleurae with inner part obliquely furrowed and outer part unfurrowed and spinose.

<u>Relationships</u>:

This species differs from <u>B</u>. <u>craigensis</u> (Tripp 1954) in that the lateral glabellar furrows are more curved and a little longer, the portion of the fixed cheek anterior to the eye is narrower, and the anterior border is also much narrower. From <u>B</u>. <u>dispersus</u> Tripp 1967, this species differs in having less convex glabella with longer more curved lateral furrows, and in addition the eye seems to be placed a little further forward.

Bartoninus williamsii (M'Coy, 1849)

Plate 13, fig. 6.

1849 Ceraurus Williamsii M'Coy, p. 408

1851 Ceraurus Williamsii M'Coy, p. 155, Pl. 1F, figs. 13, 13a & b.

1854 Ceraurus Williamsii M'Coy, p. 146.

1864 Cheirurus Williamson Salter, pars. p. 67, Pl. 5, fig. 4.

1873 Cheirurus bimucronatus, Salter, pars. p. 77.

1891 Cheirurus bimucronatus, Woods, pars. p. 141.

Lectotype:

SM A10309, a poorly preserved internal mould of a complete specimen, the unique specimen; Lower Llandoverian, Golen Goed, Myddfai, near Llandovery, Carmarthenshire.

Diagnosis:

A species of Bartoninus of which the characters are not absolutely clear but in which the anterior pygidial spines are long and stout, and the posterior two pairs are subequal in length, narrow and quite long.

Description:

Glabella subparallel sided, frontal lobe slightly wider (tr.) than width of glabella across 3L. Frontal lobe about $\frac{1}{3}$ length (sag.) of glabella, 3L parallel sided, 2L increasing in width a little adaxially, 1L subtriangular, circumscribed, inflated, more than $\frac{1}{3}$ width of glabella at that point. 3S and 2S parallel, curved, running obliquely back adaxially, probably more than $\frac{1}{3}$ width of the glabella. 1S straight abaxially, more oblique than 2S, shallowing and curving to run nearer exsagittal direction about $\frac{1}{3}$ way across glabella. Occipital ring wider sagittally than exsagittally, occipital furrow abaxially narrower and deeper than sagittally where it curves forward. Axial furrow wide and deep, preglabellar furrow apparently complete across front of frontal lobe, where it is wide and shallow.

Genae triangular, badly damaged. Posterior border widens abaxially to wide lateral border, this border narrower but parallel sided on free cheek, anterior border very narrow. Eye opposite 3L; facial suture proparian, anterior section running straight forwards from γ initially, posterior section arching gently backwards from ε to just inside lateral border, there turning very obliquely back across external part of lateral border.

Thorax of 11 segments typical of the genus.

Pygidium badly damaged, but with three pairs of spines, anterior pair by much the stoutest and longest, posterior two pairs of about the same length, mid pair stouter and reaching least far back, posterior pair curved and close together, about as long as exsagittal width of 2L of glabella.

Discussion:

Because of the poor state of preservation of this specimen, it is thought better to retain the specific name '*williamsii*' only for it.

Bartoninus sp.

Plate 16, fig. 5

1843 *Amphion gelasinosus*, Portlock, pars. Pl. III, fig. 4b.

1853 *Cheirurus gelasinosus*, Salter, pars. p. 11.

1864 *Cheirurus gelasinosus*, Salter, pars. pp. 71-72.

1952 *Ceraurinus* cf. *icarus*, Reed, pars. p. 121.

Material:

GSM 35376 and 35378, two portions of the same cranidium with anterior border and genal spines missing. Caradoc, Tyrone.

Description: (Internal mould).

Cephalon elliptical in outline, a little more than twice as wide (tr.) as long (sag.), gently convex (tr. and sag.).

Glabella subquadrate in outline, parallel sided, forming about $\frac{1}{4}$ width of the cephalon at the posterior margin. Frontal lobe subquadrate, rounded anteriorly and anterolaterally, gently convex (tr. and sag.). 3L and 2L gently convex (tr.) almost plane (exs.), parallel sided, of the same width (exs.), the glabella across these lobes a little wider than across frontal lobe. Basal lobes almost circumscribed, subquadrate in outline, just less than $\frac{1}{3}$ width of glabella at this point. 3S and 2S of the same length, reaching less than $\frac{1}{3}$ way across glabella, parallel, wide and deep, slightly curved backwards adaxially. 1S abaxially straight, running a little obliquely backwards adaxially for less than $\frac{1}{3}$ width of glabella, here as narrow and deeper than at apodeme 2S, then shallowing and widening to form a rounded depression having a very indistinct extension just reaching the occipital furrow. Occipital ring most convex and narrowest exsagittally, wider and less convex sagittally where it forms the highest point of the glabella. Axial furrow wide and distinct with a deep fossula anterior to 3S. Anterior to this fossula preglabellar furrow is narrower and less distinct than the axial furrow, anterior border and preglabellar furrow missing mesially.

Genae convex, triangular. Eye not preserved but placed opposite anterior of 2L $\frac{1}{3}$ way from glabella to lateral margin. Facial suture proparian, from β (not seen) to γ curving back convex outwards, from ε running obliquely forward reaching opposite posterior of 3L at the lateral border furrow, then turning back to cut the lateral margin opposite 1S. Posterior border furrow deep, distinct adaxially, becoming a little less distinct towards the lateral margin, curving gently forwards. Lateral border furrow shallower, wider and less distinct than this. Posterior border narrowest and most convex adaxially, much less distinct, less convex and wide at the genal angle. Lateral border gently convex (tr.). Free cheek not preserved, triangular in outline. Fixed cheek within border furrows finely granulose and coarsely pitted.

Discussion:

This specimen is the original of Portlock 1843, Pl. III, fig. 4b. As noticed by Reed, 1952, p. 121, it does not appear to be conspecific with the lectotype of *Bartoninus gelasinosus* as was thought by Portlock and Salter. Although the anterior border is missing, the differences in the course and length of the lateral glabellar furrows, and the position of the eye seem to be sufficiently great to not include it in Portlock's species. In the absence of a find of a pygidium of *Remipyga* type in Ireland or any part of the British Isles, it is thought best not to refer the specimen to *Remipyga* cf. *icarus*.

Genus *Cheirurus* Beyrich, 1845

Type species (by subsequent designation, Barton 1916, p. 129) *Cheirurus insignis* from the Motel Beds (Wenlockian) of Bohemia. non *C. exsul* subsequent designation of Reed 1896, because this species was not originally included within the genus by Beyrich (ICZN Art. 67h.)

Diagnosis:

Glabella expanding forwards, convex; furrows 3S and 2S almost straight parallel, and short; basal glabellar lobe subtriangular and isolated. Eyes opposite 2S. Rostral plate very short (sag.) and wide (tr.). Hypostoma with large convex median body tapering backwards, posterior lobe about one sixth length (sag.) of whole; anterior wings about half way from anterior margin. Thorax of eleven segments. Pygidium with three pairs of radially disposed spines and a terminal mucronation.

Cheirurus centralis (Salter, 1853)

Plate 1, figs. 1-6

Plate 2, figs. 2-3

Plate 3, figs. 3-5

Plate 20 figs. 6-7

1848 Cheirurus speciosus, Salter, p. 345, Pl. 7, fig. 7. non figures 4-6.

1853 Cheirurus bimucronatus var. β centralis, Salter, p. 1, Pl. 2, fig 16, figs. 8-9. non figures 1-7, 10-15.

1864 Cheirurus bimucronatus var. β centralis, Salter, p. 64, Pl. 6, figs. 9, 11a & b, 14, 18. non figures 10, 12-13, 15-17.

Lectotype (here designated):

GSM 36099, internal mould of pygidium. Wenlock Shale, Nelson's Tower Wood, Llandeilo, Carmarthenshire.

Diagnosis:

A species of Cheirurus with glabella expanding most rapidly forwards at frontal lobe, lateral furrows 3S and 2S subparallel and short. Eyes placed opposite 2S. Hypostoma with large convex median body having short (sag.) posterior lobe, anterior wings placed almost half way back. Thorax of eleven segments. Pygidium with three pairs of spines subequal in size but anterior pair longest stoutest and most curved, posterior pair least so with a distinct terminal mucronation between; the spines are radially disposed.

Description: (except the pygidium, based on external moulds).

Cephalic ratio width (tr.) to length (sag.) 3:2. Glabella large, dominating the cephalon, slightly less t han $\frac{1}{3}$ width of the cephalon at the occipital ring, inflated (tr. and sag.), increasing in transverse width forwards in front of basal lobes to maximum width across frontal lobe which extends in front of the general cephalic outline and is strongly convex (tr.) and sloping increasingly steeply down in front, about half the length of glabella excluding occipital ring (sag.). Transverse convexity of glabella across 3L and 2L a little greater than across frontal lobe, less convex across 1L. 3L parallel sided, 2L increasing slightly in width adaxially. Basal lobes triangular, about $\frac{1}{3}$ width of glabella at this point, glabella a little wider across here than across 2L. 3S and 2S near parallel and only a little curved reaching $\frac{1}{4}$ way across glabella, fairly wide and deep, running slightly obliquely back adaxially. 1S initially slightly more oblique, wider and deeper than 3S and 2S, then $\frac{1}{3}$ way across glabella becoming very oblique, very wide and shallower to meet the wide shallow occipital furrow in a medial depressed area which separates the inner angles, of 1L. Highest point of glabella, excluding the occipital ring, lies on the medial line opposite 1S. Medially the glabella adjacent to the adaxial portion of 1L has a well rounded feature (convex backwards) caused by a break in slope on the backward sloping surface of the glabella. Occipital ring more convex (tr.) than 1L, convex (sag. and exs.), widening (exs.) adaxially, ratio of sagittal to exsagittal width 3:2, bearing a median tubercle. Occipital furrow arching forward medially, narrower and deeper abaxially. Axial furrow narrow, fairly deep and distinct; preglabella furrow dying out mesially.

Genae sub-triangular, sloping away from the glabella, convex (tr. and exs.). Posterior border furrow wide, deep and distinct. Posterior border convex (exs.) most so $\frac{1}{3}$ way from occipital ring to lateral margin at articulation with first thoracic segment. Lateral border wide and convex. Lateral border furrow shallower than the posterior border furrow. Genal angles bear spines which reach at least as far back as the 2nd axial ring.

Eye placed approximately $\frac{1}{2}$ way from glabella to lateral margin; cresentic in plan, eye surface sloping steeply. Extent of eye from 3S almost 1S. Palpebral lobe a small feature compared to the size of the eye. Facial suture proparian, β to γ from opposite greatest width of frontal lobe curving a little across anterior part of lateral border and border furrow then running almost exsagittally to the palpebral lobe; from ε suture running slightly obliquely forward, arching to run slightly obliquely backwards just internal to the lateral border furrow, this course maintained until half way across the lateral margin where it turns suddenly backwards to cut the margin opposite mid 1L. Free cheek small and triangular. Cheeks inside border furrows coarsly pitted, glabella coarsely but sparsely tuberculate, the whole finely granulated.

Rostral plate very narrow (sag.) placed almost vertically.

Hypostoma with large inflated median body, wide semi-circular in front, and narrower subquadrate behind with almost straight converging sides: maximum height reached a little way anterior of half the length. Posterior lobe very small and weakly differentiated from the anterior by shallow depressed maculae. Well marked border surrounds the body, widest and with a shallow border furrow behind. Anterior wings rounded placed almost half way back. Posterolateral and posterior margin subquadrate, the latter somewhat curved concave backwards. Hypostoma reaches from anterior margin of cephalon as far back as 1L.

Thorax of 11 segments of the form typical of the genus. Axial rings strongly convex (tr.) and convex (sag.) maximum height attained towards the back of the ring, with a pair of tubercles each just exsagittally placed. Inner portions of pleurae with a furrow which runs obliquely backwards, separating two triangular equally pronounced inflated bosses of shell. Abaxially to these a broad shallow indistinct furrow runs exsagittally, this followed by a decrease in width of the pleura and an increase in convexity adjacent to the articulary processes. The external part is cutlass shaped and turned down, increasing so in the posterior pleurae. The shell of the thorax is finely granulated.

Pygidium spinose, excluding the spines triangular, with three axial rings and terminal piece all convex (tr. and sag.) decreasing in width posteriorly. Axial furrow indicated adjacent to two anterior rings by a weak discontinuous furrow, and adjacent to the posterior two portions of the axis by pairs of fairly well marked pits. Adjacent to first ring a furrow runs obliquely backwards and outwards and separates two triangular inflated portions of the shell. Three pairs of spines, anterior pair stoutest running almost transversely at first then curving backwards and reaching least far back. Posterior pair narrowest, running almost exsagittally and reaching furthest back. Middle pair are intermediate in size. Between the posterior pair a distinct terminal mucronation is present, a continuation of the slightly inflated terminal piece of the axis. The surface of the pygidium is finely granulated.

Discussion:

This species and *Iuba retrospinosa* gen. et sp. nov. are the ones to which the name '*Cheirurus bimucronatus*' has most often been given.

The species *Paradoxides bimucronatus* was first recognised by Murchison (1839), who figured (pl. 14, figs. 8 & 9) a pygidium and its counterpart and a portion of a thorax showing five segments. The horizon and locality of the fragments was given as 'Wenlock Limestone of the Malvern Hills' and the collector named as Mr. B. Bright, so that the specimens were probably found ' ..... in the quarries upon the estate of his (Mr. B. Bright's) father at Brand Lodge' (page 414).

Beyrich (1845) placed the species in his new genus *Cheirurus*.

In the text of the fourth and fifth editions of 'Siluria' (Murchison 1867 and 1872), Cheirurus bimucronatus was stated as being common in the Caradoc, and present in the Llandovery of the respective type areas, although in neither case was it listed with the faunas. However, in an appendixed comprehensive faunal list, the species was shown as occurring in the 'Caradoc','Llandovery' and 'Wenlock' rocks. In plate XIX of these editions, C. bimucronatus was refigured as in Murchison (1839) but without the counterpart of the pygidium, the horizon and locality given as it was originally. In addition, the same figure was shown in plate III, fig. 5, and the species stated to be 'common in the Caradoc or Bala Limestone'. The figuring of this particular pygidium as from the Caradoc appears to have been a mistake since when it was first figured in 1839 no mention of the species was made from the 'Lower Silurian'. At that time Murchison stated that he could find no species of trilobite occurring in both 'Lower' and 'Upper' Silurian. The Caradoc form of 'C. bimucronatus' was probably that now placed in Ceraurinella intermedia (Kielan 1955), see Whittington (1965, p. 35).

Salter (1853) distinguished two varieties of C. bimucronatus on the absence or presence of a central mucronation between the posterior of the three pairs of pygidial spines. These varieties he called var. α bimucronatus (= I. retrospinosa) and var. β centralis respectively. Study of the figures and descriptions reveals that none of the pygidia mentioned by Salter were identical to the original figure of C. bimucronatus, and although this species is quoted in the synonymy of var. α bimucronatus the pygidium was not refigured.

Since 1853 most British Cheirurus like forms have been placed in one of Salters varieties, with the result that the name C.bimucronatus has been used indiscriminately for species occurring in rocks of Caradocian to Ludlovian age, as a glance at the synonymies of the species within the Cheirurinae described in this work will show.

Range and Distribution:

Cheirurus centralis is from the following horizons and localities: 'Woolhope Shale', Malvern (BU Ketley 264 and 268); 'Woolhope Beds', Malvern (GSM 36067); Wenlock Limestone, Malvern (BM 58596 and 44228); Wenlock Shale, Malvern (GSM 36096 and 36097, BM In 37675); Wenlock Shale, Dudley (SM A28582, BM 59012); Wenlock Limestone, Dudley (BM 17956 and 17958, GSM 49819).

Cheirurus longifrons sp. nov.

Plate 2, fig. 1.

Plate 3, fig. 2.

Plate 4, figs. 5-6

Cheirurus bimucronatus var. *pyrifrons* Huxley and Etheridge MS.

Holotype:

GSM 36283, external mould of complete individual, Wenlock Limestone, Malvern, Worcestershire.

Diagnosis:

A species of *Cheirurus* with a wide (tr.) and long (sag.) frontal lobe of the glabella which has curved furrows 3S and 2S. Eyes placed opposite anterior of 2L. Thorax of eleven segments with a markedly tapering axis. Pygidium with three pairs of spines of subequal length and similar stoutness of construction, between posterior pair a terminal mucronation is present.

Discussion:

This species is broadly similar to *C. centralis* but the points of difference are as follows. In the glabella as the name indicates the frontal lobe is relatively larger in its transverse and sagittal dimensions than in *C. centralis* and the 3S and 2S furrows are a little longer and more curved in form. On the cheek regions the eyes are placed slightly further back, and the proparian facial suture from β to γ is curved, and from ϵ runs not arching first forwards then back to half way across the lateral margin, but in a slightly curved line running a little obliquely forwards. In the thorax the axis tapers markedly posteriorly so that it occupies $\frac{1}{3}$ of the transverse width in the anterior thoracic segment, but only $\frac{1}{4}$ or less of this width in the posterior. In the pygidium, the three pairs of spines are all quite stoutly constructed and long, the distance between the tips of the anterior and mid spines being nearly twice as great as that between the mid and posterior.

Other material:

GSM 36097, Wenlock Shale, Wych, Malvern, Worcestershire; GSM 36103, Wenlock Limestone, Malvern, Worcestershire.

Cheirurus latiaxis sp. nov.

Plate 2, fig. 4.

Holotype:

BM I13649, external mould of complete individual, Wenlock Shale, Malvern, Worcestershire.

Diagnosis:

A species of *Cheirurus* with, in the glabella, the basal lateral lobes subtriangular in shape and a little more than $\frac{1}{3}$ width of the glabella at that point, and on the cheek the eye opposite 2S. In the thorax the axis is wide, comprising more than $\frac{1}{3}$ the transverse width in the anterior segment and a little less than this proportion in the posterior segment, the axis having narrowed very gradually in this distance. In the pygidium the three pairs of spines are short, and between the posterior pair the terminal mucronation is only poorly developed.

Discussion:

This species is similar to the previous two in its general morphology. The cephalon is very much like that of *C. longifrons* with a large frontal lobe to the glabella, and in the course of the facial suture. The basal lobes of the glabella, however, are relatively wider in this species under consideration, and tend to be bilaterally symmetrical about a transverse line which is not the case in any of the other species of Cheirurus discussed here. The thorax of this species has a wide axis as the chosen specific name implies. Of the three pairs of pygidial spines the anterior pair are broad based and taper rapidly to their end. The posterior two pairs are slimmer in construction but are still short, the posterior pair exsagittally directed and the mid pair pointing outwards at a small angle to this direction. The terminal mucronation is represented by no more than a convex backwards swelling of the posterior margin of the pygidium.

Cheirurus inusitatus sp. nov.

Plate 3, figs. 6-7

Holotype:

GSM 36094, external mould of complete individual, Wenlock Shale, Wych, Malvern, Worcestershire.

Diagnosis:

A species of *Cheirurus* with a glabella subpentagonal in outline, expanding rapidly and evenly forward to a wide convex frontal lobe. Anterior section of facial suture running parallel to the anterolateral curvature of the frontal lobe, cutting the margin in front of the widest part of the glabella. Pygidium with three pairs of stout spines, gradational in size, anterior pair largest, distally all more or less posteriorly directed. Terminal mucronation weakly developed.

Description:

Cephalic ratio width (tr.) to length (sag.) about 2:1. Glabella large, convex (tr. and exs.), somewhat pentagonal in shape, $\frac{1}{3}$ or slightly more width of the cephalon behind, increasing in width forwards to a maximum at the frontal lobe where it is half as wide again as behind. Frontal lobe about $\frac{1}{3}$ length (sag.) of glabella. Transverse convexity of glabella excluding occipital ring increases from across 1L to the frontal lobe. 3L parallel sided, 2L increasing markedly in width adaxially. 1L triangular, a little over $\frac{1}{3}$ width glabella at this point, circumscribed. 3S and 2S parallel, equally long, shallow, slightly curved, transverse, each reaching $\frac{1}{3}$ way across glabella. 1S wider and deeper, initially running obliquely back across glabella, medially becoming wider, forming a median depression between inner angles of 1L. Occipital ring most convex (tr. and sag.) part of glabella, narrow (exs.) becoming wider (sag.), ratio of these widths about 1:2. Occipital furrow arching forward medially meeting 1S where it is wide, abaxially narrower and deeper. Axial furrow fairly shallow and narrow.

Genae sub-triangular, sloping away from the glabella, convex (tr. and exs.). Posterior border furrow narrow, as wide as 2S and 3S, distinct, transverse. Posterior border narrow, widening suddenly half way from axial furrow to genal angle when it becomes twice as wide as adaxially; convex, most so where it is narrowest. Lateral border furrow on the free cheek distinct, on the fixed cheek wider and indistinct meeting the posterior border furrow at the genal angle where it is less distinct than adaxially. Lateral border twice as wide as widest part of posterior border, narrowing slightly forward. Genal angles produced into spines which reach at least as far back as the second axial ring o f the thorax.

Eye placed $\frac{1}{3}$ way from glabella to lateral margin, cresentic in plan, visual surface steep, extending from the anterior of 1L to posterior of 3L. Palpebral lobe slopes fairly steeply upwards from the palpebral area to the facial suture above the eye.

Facial suture proparian, anterior section from β to γ running parallel to the anterolateral curvature of the frontal lobe, then exsagittally to the palpebral lobe, from ϵ running slightly obliquely forward, reaching its most anterior position opposite $\frac{1}{4}$ way forward along the eye - immediately internal to the lateral border furrow, then curving back across the interior $\frac{1}{2}$ - $\frac{2}{3}$ of the lateral border reaching a position which is transversely slightly anterior to the posterior of the eye, when it turns sharply back (forming an angle of about 130°), cutting lateral margin opposite mid 1L or just posterior tothis.

Free cheek small and subtriangular in plan, the border almost as wide as the portion of the cheek inside the lateral border furrow. Cheeks inside border furrows pitted and coarsly granulated.

Hypostoma not seen.

Thorax of eleven segments of the form typical of the genus. Axial rings strongly convex (tr. and sag.), maximum height attained towards the back of the ring, with a pair of tubercles, one placed just either side of the sagittal line. Inner portions of the pleurae with an oblique furrow which runs back from the anterior of the segment for a short distance, separating two inflated subtriangular bosses of shell. Abaxial to these a shallow indistinct furrow runs exsagittally across the pleurae which at this point are narrower and more convex (exs.) than adaxially, adjacent to the articulatory processes of the segments. The external parts are cutlass shaped and deflexed. The shell of the thorax is finely granulose.

Pygidium spinose, excluding the spines triangular in shape, with three convex axial rings and a convex rudimentary terminal piece forming an axis which decreases in width posteriorly. Axial furrow indicated adjacent to the posterior of the anterior axial ring as an indistinct narrow furrow, and possibly also by shallow pits just posterior to and outside the mid and posterior axial rings. On the pleural portions a furrow runs out from the first axial ring slightly obliquely backwards for a short distance only, separating two slightly inflated portions of shell. Three pairs of spines, more or less backwardly directed, the anterior pair at a slight angle to the exsagittal direction, mid pair at an even smaller angle to this direction. Anterior pair of spines stoutest, reaching least far back; posterior pair narrowest, raching furthest back; mid pair intermediate in size and extent, free ends of the three pairs lying on a gently curved line. Between the posterior pair of spines a small terminal mucronation is present. Surface of pygidium with both fine closely spaced, and coarse sparse granulations.

Remarks:

This species may be distinguished from other members of the genus by the pantagonal outline of the glabella. In addition the pygidium is distinct in that the main part of the large anterior spine, and both the mid and posterior spines, are almost exsagittally directed.

Range and distribution:

C. inusitatus is recorded only from the Wenlock Shale; at the following localities: The Wych, Malvern (the holotype) and Dudley (BM It2247). For one specimen the locality is unknown (BM I2002).

Cheirurus cf. insignis Beyrich, 1845

Plate 3, fig. 1.

Material:

OUM C187, 729. Wenlock Shale, west side of Malvern Railway Tunnel (Spoil Heaps), Herefordshire.

Description:

Glabella convex (tr. and sag.), a little less than $\frac{1}{3}$ width cephalon at occipital ring, increasing evenly in width from here forward to 3L, frontal lobe markedly wider. Frontal lobe rounded anteriorly and anterolaterally, convex, half as wide again as occipital ring (tr.), sagittally as long as 3L and 2L. 3L parallel sided, 2L increasing in width adaxially. 1L circumscribed, triangular, wider than 2L (exs.), two fifths width of glabella (tr.) at that point, a little inflated. 3S and 2S parallel, shallow, $\frac{1}{3}$ width of glabella, transversely and very slightly curved. 1S runs obliquely back adaxially meeting occipital furrow near sagittal line of glabella, deeper and more distinct than 2S and 3S. Occipital ring slightly wider sagittally than exsagittally, forming highest point of glabella and bearing a medial tubercle. Occipital furrow curves forward medially. Axial furrow wide, deep and distinct, preglabellar furrow dying out over mexial $\frac{1}{3}$ of frontal lobe. Surface of glabella coarsely granulated.

Genae triangular, convex, sloping away from glabella. Posterior and lateral borders of almost constant width, former narrowing a little adjacent to articulation with first thoracic segment, genal angle bearing spine which is at least as long as 3L and 2L (exs.). Posterior border furrow deep and transverse, lateral border furrow deep and distinct, narrowing a little forwards. Palpebral lobe opposite 2L. Facial suture proparian from β to γ curving round frontal lobe of glabella anterolaterally, then running exsagittally to palpebral lobe, posterior section running from ϵ opposite anterior of 1L obliquely forwards to reach opposite mid 2L just adaxially to lateral border furrow, then turning to run almost transversely until $\frac{1}{2}$ way across lateral border there turning obliquely back to cut lateral margin opposite mid 1L. Genae everywhere finely granulated, inside border furrows coarsley pitted.

Thorax of 11 segments of the form typical of the genus, axis just less than $\frac{1}{3}$ transverse width of segments.

Pygidium, excluding spines, triangular in shape. Axis, comprising three rings and terminal piece, tapers backwards, Axial furrow, intrapleural and interpleural furrows distinct adjacent to anterior ring, axial furrow indicated adjacent to mid axial ring as a break in slope between ring and pleural ridge, pits placed laterally to posterior ring and terminal piece are remnants of axial and inter pleural furrows. Three pairs of curved spines, subeuqal in length, anterior pair stoutest and longest running a little abaxially backwards (forming an angle of about 120° with adjacent pleural ridge) reaching least far back. Mid pair at a very small angle to exsagittal direction, posterior pair running exsagittally, shortest, of slimmest construction, reaching furthest back. Between posterior pair of spines a well developed mucronation is present. Surface of shell of pygidium is now smooth, but may have been coarsely granulated since canals filled with black sediment which may have led to such tubercles can still be seen in the shell.

Discussion:

Although *C. insignis* has been recorded in areas as far from the occurrence of the type material in Bohemia as Australia and California the species has not been recorded from Britain. This is because of the use of *C. bimucronatus* as a collective term for many British Cheirurid trilobites. In addition it may proove that the specimens referred to *C. insignis* from those distant areas belong to distinct species.

Since Barrande's monumental work on the trilobites of Bohemia the name *C. insignis* has been used somewhat in the manner *C. bimucronatus* has been used in this country. This was partially due to Barrande including several species under the one name in his work, and especially *C. bicuspidatus* has been mixed up in the name *C. insignis*. Prantl and Vanek (1957, p. 269) have righted this situation and chosen a lectotype (Barrande 1852, Pl. 41, fig. 8) which unfortunately is only the pygidium. Of the British species of *Cheirurus* the two specimens here mentioned most clearly resemble the lectotype. They do differ, however, in the form of the pleural portion of the mid pygidial spine which is not transversely furrowed as it is in Barrande's figure, and in addition the terminal mucronation is less prominent *C*. cf. *insignis* will probably be specifically separable from the species to which it is compared when a figure of the rest of that species is published.

Cheirurus postremus sp. nov.

Plate 3, figs. 1-2, 7-8

Holotype:

SM A38677. Internal mould of cranidium. Upper Coniston Flags, Helm Knot, Dent, Yorkshire.

Diagnosis:

A species of *Cheirurus* with, in the glabella, a frontal lobe $1\frac{3}{4}$ times as wide (tr.) as the occipital ring and just less than half as long as the whole. Eye placed opposite 2S. From the anterior of the palpebral lobe a distinct eye ridge runs obliquely forwards towards the axial furrow which it indents opposite the 3S furrow of the glabella.

Description:

Glabella large, very convex (tr. and sag.), expanding forwards, frontal lobe markedly wider than 3L (tr.) and $1\frac{3}{4}$ times as wide as the occipital ring. Frontal lobe very convex (tr. and sag.), vertical and more than a semicircle in front, just less than $\frac{1}{2}$ as long as the whole glabella (sag.). 3L subparallel sided, 2L increasing in width adaxially, and abaxially narrower (exs.) than 3L, both convex (tr. and exs.). 1L subtriangular, more than $\frac{1}{3}$ width of the glabella at that point, inflated, circumscribed, 3S and 2S subparallel, gently curved, wide and deep, running obliquely back adaxially, 3S less than, 2S about equal to $\frac{1}{3}$ width of the glabella at their respective points. 1S abaxially narrow and deep at apodome, $\frac{1}{4}$ way across glabella suddenly widening and shallowing to meet occipital furrow which is arched strongly forward mesially, and forming a depression which is convex (tr.) between the inner angles of 1L. Occipital ring at least twice as wide sagittally as exsagittally. Axial furrow wide and deep from adjacent to occipital ring to the posterior of 3L, here deepening to a very deep fossula adjacent to 3S, shallowing again adjacent to the widest part of the frontal lobe, anterior to this the preglabellar furrow rapidly becoming indistinct and dying out $\frac{1}{4}$ way across frontal lobe.

Genae small, gently convex (tr. and exs.). Posterior border furrow wide and deep adaxially, near genal angle widening and meeting wide lateral border furrow. Posterior border damaged, fairly narrow. Lateral border wider very convex (tr.) with a steep long slope into the lateral border furrow near the genal angle. Genal spine present. Eye placed opposite 2S. Facial suture proparian, from β to γ curving round anterolateral part of frontal lobe to opposite widest part of this then running in a straight line exsagittally to the palpebral lobe; from ε the suture running near transversely in a slight curve to the lateral border furrow here turning very obliquely back and running across lateral border to cut lateral margin opposite mid 1L.

From anterior of palpebral lobe an eye ridge runs forward obliquely adaxially on a slightly sigmoidal course to form an overhanging boss in the abaxial margin of the axial furrow opposite 3S. Genae inside border furrows coarsely pitted.

Glabella where surface not damaged (frontal lobe) covered with many large tubercles which become smaller on the vertical anterior part, and absent anterolaterally. Lateral glabellar furrows finely granulated as are posterior border furrow and lateral border.

Discussion:

This species is the youngest referred to the genus *Cheirurus* in Britain. It is very like the Wenlockian Welsh Border forms in general morphology but differs in possessing an eye ridge. This re-appearance of a primitive character in the stock may be connected with the approaching extinction of *Cheirurus*. With such a feature making an appearance in the glabella of the species it is unfortunate that no pygidium has been found associated with the cephala, for these might show some differences from the true *Cheirurus* type. In the absence of a pygidium it is only sensible to refer the species to *Cheirurus*, which genus, the eye ridge apart, it greatly resembles.

The preservation of a coarse granulation on parts of the glabella of this species is interesting. All specimens from the Welsh Borderland seen by the author, have been attacked to varying degrees with acid during their preparation. It may have been that these Wenlockian species also possessed such a granulation.

<u>Other material</u>:

BM 42905, Upper Silurian, (?Kirkby Moor Flags), Benson Knot, Kendal, Westmorland.

Cheirurus sp.

Plate 21, fig. 5.

Material:

SM A40883, a unique pygidium; Wenlock Shale, Left Bank of River Severn, 300 yds. south-east of Buildwas Abbey, Shropshire.

Description:

Axis gently convex (tr.), tapering to a terminal piece which is ill defined and convex only anteriorly (tr.). Three gently convex axial rings decreasing in transverse width posteriorly, furrows separating rings are wide and shallow in the median half of their course deepening suddenly and narrowing, then shallowing a little and narrowing further, immediately adjacent to the axial furrow, so that these furrows have an abaxial constriction. Axial furrow very indistinct adjacent to the axial rings. Adjacent to and just posterior to the furrows between axial rings, deep pits are developed, these pits extending across pleural portions of pygidium marking the divisions between the segments. In the anterior segment the pit appears as a deeper transverse distinct furrow becoming shallow, and in the posterior two, as more or less indistinct furrows whose courses are exsagittal in the case of the posterior segment and at 45° to this direction in the case of the mid segment. Inner portion of pleuron of anterior segment bearing a short narrow oblique furrow; outer portion wider, a little inflated, the whole running more or less transversely except for a short, sharp spine which terminates the segment and points outwards and backwards at an angle of about 45° to the transverse direction, reaching as far back as the posterior of the third axial ring. Pleural portions of mid and posterior segments run out respectively at about 45° to, and in an exsagittal direction, short and slightly swollen each terminated by a short hooklike spine, more rounded in the latter case, pointing in an exsagittal direction and reaching increasingly further backwards. Between the posterior spines a small but prominent, triangular, sharp mucronation is present. Surface of shell bears fine granules and punctae.

Discussion:

Like the specimen described next this pygidium appears to be morphologically between the genera *Cheirurus* and *Crotalocephalina*. As compared to *Cheirurus* the spines are shorter and stouter, but not as hook-like as they are in *Crotalocephalina* proper. This specimen indicates like the next, that the reduction in the proportions of the pleural regions which lead to the evolution of *Crotalocephalina* was taking place in Wenlockian times. Because it is still close to *Cheirurus* in general organisation, it is referred to with doubt to that genus.

Genus Crotalocephalina Přibyl and Vaněk, 1964a

?Crotalocephalina sp.

Plate 4, figs. 3-4

Material:

NU S451. Internal mould of fragmentary cranidium; high Lower Eltonian, Millichope, Shropshire.

Description:

Glabella expanding rapidly forwards from occipital ring which is estimated to be $\frac{1}{3}$ transverse width of glabella at that point. Frontal lobe very convex (tr. and sag.) more than $\frac{1}{3}$ sagittal length of glabella. 3L parallel sided, 2L increasing in width (exs.) adaxially, both convex (tr. and exs.). 1L triangular, inflated. 3S and 2S furrows parallel, wide and deep especially abaxially, about $\frac{1}{3}$ width of cephalon. 1S very deep abaxially at apodeme, shallowing adaxially. Axial furrow very wide and deep, with a deep fossula just anterior to 3S, anterior to this shallowing and narrowing to form preglabellar furrow.

Genae convex, small. Posterior border narrow and convex exsagittally, widening a little abaxially to the articulation with the first thoracic segment. Posterior border furrow wide and deep, widening abaxially. Genal angle with short spine. Genae inside border furrow coarsely pitted.

Palpebral lobe large, extending from anterior of 3L to mid 2L, with wide and distinct palpebral furrow adaxially. Facial suture proparian, from β to γ curving round the widest part of the frontal lobe then running in a straight line exsagittally to the palpebral lobe; from ϵ arching forwards and then turning sharply back across the lateral border to cut the lateral margin opposite 1L.

Glabella coarsely granulated especially medially.

Discussion:

This unique cranidium is from the collection made by Shergold in Shropshire (J. H. Shergold, PhD. Thesis. 'The faunal stratigraphy of Ludlovian rocks outcropping between Much Wenlock and Craven Arms, Shropshire' Newcastle University 1966). The general proportions of the glabella to the genae and the size and position of the palpebral lobe are reminiscent of the genus to which it is referred with some doubt. The short lateral glabellar furrows, however, indicate that this specimen is on a line of evolution which was proceeding from the *Cheirurus* type of organisation towards the *Crotalocephalina*, and as such it cannot be satisfactorily placed in either genus. It is unfortunate that further material is not available. Until further material is found, the specimen is referred to *Crotalocephalina* to indicate that evolution of the cheirurid stock was taking place in Britain in Ludlovian times.

Genus *Iuba* gen. nov.

Type species:

Iuba retrospinosa sp. nov. Wenlockian, Dudley, Worcestershire.

Diagnosis:

Glabella expanding forwards, frontal lobe markedly wider (tr.) than glabella across 3L. anterior border included in frontal lobe mesially; basal glabellar lobes a little more than $\frac{1}{3}$ transverse width glabella. Palpebral lobe extending from almost 1S to mid 3L. Proparian, posterior section of facial suture running a little obliquely backwards from the posterior of the palpebral lobe. Thorax of eleven segments. Pygidium with three rings and small terminal piece in axis, and three pairs of spines all more or less exsagittally directed, and reaching about the same distance posteriorly.

Range and Distribution:

Upper Llandoverian, Shropshire; Wenlock Shale and Limestone, Dudley, Worcestershire; Wenlock Shale, Malvern, Worcestershire; Lower Eltonian, Upper Westhope, Shropshire; Kopanina Beds, Bohemia.

Iuba retrospinosa gen. et sp. nov.

Plate 5, figs. 1-8.

Plate 6, figs. 1-7.

Plate 7, figs. 6-7.

Text Figure 13

1853 Cheirurus bimucronatus var. α bimucronatus Salter p. 1, Pl. 2, figs. 1-6, 11-13.

1864 Cheirurus bimicronatus var. α bimucronatus Salter, p.64, Pl. 6, figs. 10, 15-17.

Holotype:

BU 413 (ex Holcroft 239), complete individual with shell preserved; Wenlock Limestone, Dudley, Worcestershire.

Diagnosis:

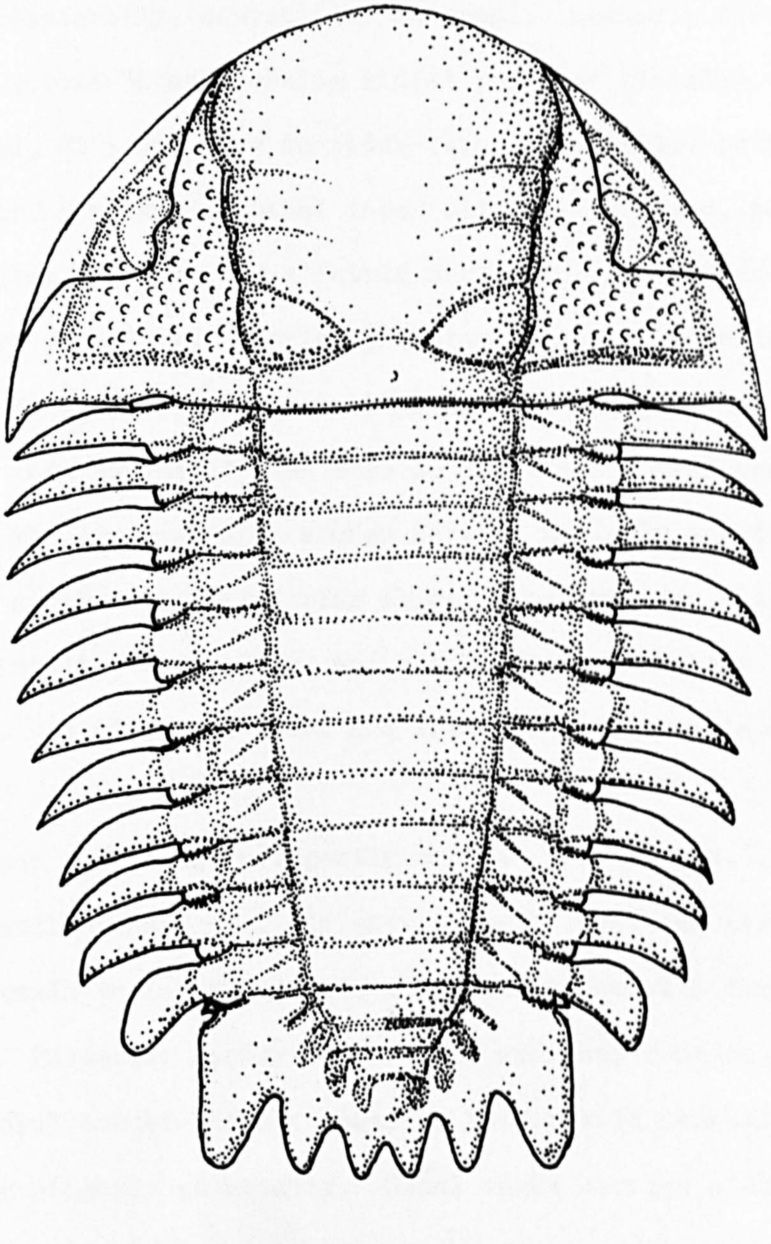
A species of Iuba with the six pygidial spines stoutly constructed and with equally broad spaces between. The spines taper evenly to a rounded tip.

Description:

Cephalic ratio of width (tr.) to length (sag.) 2:1. Glabella about $\frac{1}{3}$ width of cephalon behind, extending slightly in front of the general outline in front; behind frontal lobe, gently convex (tr.) and almost plane (sag.). Frontal lobe semi-circular, rounded anteriorly

Text figure 13.

Reconstruction of Iuba retrospinosa gen. et sp. nov. approximately X8



Text figure 13

and anterolaterally, convex (tr. and sag), markedly wider than glabella across 3L and forming widest point of glabella. 3L parallel sided, 2L increasing in width (exs.) adaxially, both slightly convex (tr. and exs.). Basal lobes slightly inflated, subtriangular, inner angles separated by a fairly narrow furrow. 3S and 2S shallow, quite wide, parallel, reaching $\frac{1}{3}$ distance across glabella. 1S wide and deep at apodome, directed slightly more obliquely back adaxially initially than 3S and 2S then more so for a short distance, joining the occipital furrow which arches forward medially and is as wide and deep as 1S. Occipital ring approaching twice as wide sagittally as exsagittally, convex (tr. and exs.), forming highest point of glabella. Axial furrow wider and more distinct than lateral glabellar furrows.

Genae subtriangular, gently convex (tr. and exs.). Posterior border gently convex (tr. and exs.), most convex and narrowest $\frac{1}{3}$ way from glabella to lateral margin at articulation with first thoracic segment. Posterior border furrow wide and deep continuing as a wider deep lateral border furrow. Lateral border with convex upper surface, narrowing slightly anteriorly. Genal angle carries a stout genal spine reaching as far back (at least) as the first axial ring of the thorax. Anterior section of facial suture from β to γ curving sigmoidally following shape of the anterior part of glabella, posterior section from ε running very slightly obliquely backwards in an almost straight line from the posterior of the palpebral lobe, to half way across lateral border when it turns sharply backwards, running very obliquely across outer half of the border to cut margin opposite mid 1L. Eye cresentic in plan, slightly nearer glabella than lateral margin, visual surface approaching vertical; palpebral lobe extending from mid 3L to 1S. Cheeks coarsely pitted inside lateral and posterior border furrows.

Hypostoma with large inflated median body semicircular in front, less than a semicircle behind, maximum height reached about $\frac{1}{4}$ way from anterior margin. Posterior lobe of median body about one fifth sagittal length of whole, separated from anterior lobe by maculae which narrow and deepen abaxially. Anterior margin of hypostoma with no border mesially. Anterior wings angled. Border of posterolateral and posterior margins wide, outline forming rounded angles, posterior margin straight and transverse. Surface coarsely granulated, coarsest and most sparsely on frontal lobe of median body, granules decreasing in size and increasing in number posteriorly; anterior wings and posterolateral and posterior borders less coarsely but more closely granulated.

Rostral plate not known.

Thorax of eleven segments of the form typical of the subfamily. Axis forming about $\frac{1}{3}$ of the transverse width, convex (tr. and sag.). Pleurae with inner obliquely furrowed portion and outer spinose portion, the spines narrow, tapering and transversely directed in the anterior segments, becoming a little broader and more curved backwards posteriorly, the pleural spine of the posterior segment broad and hook-like.

Pygidium with three rings and a terminal piece in the axis decreasing in transverse width and convexity backwards. Three pairs of spines, outline of pygidium including these spines rectangular. Anterior pair of spines stoutest and longest with its outer margin running in an exsagittal direction or at a small angle to this outwards posteriorly; pleural portion adjacent to these spines bear a short oblique furrow which originates at the axial furrow. Pleural portions posterior to this only bear indistinct interpleural furrows. Axial furrow weakly indicated adjacent to mid and posterior axial rings, adjacent to terminal piece small elongated depressions run exsagittally which are probably the remnants of this axial furrow. Mid and posterior pairs of spines of similar stoutness, mid pair a little longer than the posterior but shorter than the anterior pair so that all the spines reach to approximately the same distance back. Anterolaterally the pygidium bears a short process elongated transversely, which carries the articulatory apparatus which fits against that of the posterior thoracic segment. Doublure of pygidium about as wide as the anterior axial ring (sag.), running on a course from the anterolateral corner of the pygidium to a point approximately underneath the terminal piece of the axis. Just over half way along this course the doublure widens a little and then narrows sagittally.

Discussion:

Complete or almost complete specimens of this species are known having sagittal lengths of 13 mm. to 41 mm. Certain small changes are seen in the proportions of the individuals of these different sizes. In the smaller specimens the eye tends to be relatively longer and wider than in the larger, extending from 3S to 1S - in larger examples from mid 3L to 1S, and the genal spines (so far as can be seen) are also relatively larger in smaller individuals. There is also some variation in the relative lengths of the pygidial spines. In the smallest specimen the anterior pair of spines extend a little further back than the others, the posterior two pairs having the same posterior extent. In the larger specimens there is a tendancy for the posterior pair to extend, by a small amount, furthest back, with the anterior and mid pairs about equal. In all cases, however, the six free points lie almost on the same transverse line.

This genus is believed to have been derived from Bartoninus, by the main change of the shortening of the anterior pair of pygidial spines. It is interesting to note that small individuals of this species have these anterior pygidial spines reaching a little further back than the other two pairs. It is unfortunate that no ontogeny of a member of this genus is known for this might enable the author to be certain as to the evolution of this genus.

Iuba bicuspidata (Bouček 1933) from the Kopanina Beds (Ludlovian) of Central Bohemia differs from the type species in the following ways. In the cephalon the glabella is relatively longer, and the basal lobes are more rounded and are separated by a well marked depression. The hypostoma is narrower and is more rounded posterolaterally. In the pygidium, the three pairs of spines are of narrower construction and the anterolateral process bearing the articulatory apparatus is wider (exs.).

Range and Distribution:

Iuba retrospinosa is almost completely restricted to the Wenlock Shale and Limestone of the Dudley District. Only two rather poorly preserved specimens from the Wenlock Shale of Malvern are known (OUM C728 and 730).

Additional Material:

BU (Holcroft) 10, 81, 119, 240, 255, 296, 338, 370, 396, 575; BU (Ketley) 256; OUM C699, C701; BM 41954, It2245-6, It2248-52, It 2254, I1473, I1478, I4136, I7957; GSM 36089, 36093, 36095, 36278-81, 82877, 90019.

Iuba wychensis gen. et sp. nov.

Plate 7, figs. 4-5, ?3.

Holotype:

OUM C6543a & b, internal and external mould of pygidium; Wyche Beds, Upper Llandoverian (C6), Old Storridge Common Area (SO 74055167), Shropshire.

Diagnosis:

A species of *Iuba* only definately known from the pygidium, anterior pair of spines stoutly constructed with curved exterior margin; mid and posterior pairs of spines much narrower, shorter; mid pair directed outwards at a small angle to the exsagittal direction posteriorly.

Description:

Pygidium spinose, including spines subrectangular in shape. Axis composed of three rings decreasing in transverse width posteriorly, and a small terminal piece, all convex (tr. and sag.), separated by deep, wide furrows. Axial furrow indicated adjacent to anterior axial ring (strongly on internal mould, indistinctly on external mould), posterior to this indicated only as rounded deep pits adjacent to the interring furrows of the axis. Adjacent to anterior axial ring a very short oblique pleural furrow originates and runs abaxially separating two slightly raised elongate portions of the shell. Posterior to the anterior pleural ridge a furrow which originates in the axial pit adjacent to the anterior interring furrow of the axis runs posteriorly and outwards at about 40° to the transverse direction, becoming narrower and very shallow, and indistinct abaxially at the junction of the anterior and mid spines. Posterior to this, furrows on the pleural portions are most distinct. Three pairs of more or less exsagittally directed spines. Anterior pair stoutest, longest, and reaching by a small amount furthest back, curving a little dorsally, and in its course turning through about 90° from adjacent to the anterior axial ring to its final exsagittal course. Posterior two pairs of spines subequal in size, the mid pair a little wider and less convex dorsally, and reaching least far back by a small amount. Anterior edge of anterior spine where this runs transversely bears a distinct articulatory facet separated from the spine by a narrow, distinct furrow which runs close to the transverse direction.

Discussion:

The cephalon referred with doubt to this species is of the Iuba type, but as it comes from a slightly different locality from the holotype pygidium, it cannot be definitely associated with I. wychensis. This cephalon is of small size (about 3.4mm wide posteriorly) and a description of the charaters of such a small specimen might be misleading. However, like other species of the genus it has short lateral glabellar furrows on a glabella which expands forwards and occupies about $\frac{1}{3}$ or a little less of the transverse width of the cephalon posteriorly.

Iuba gen. nov. sp. A

Plate 7, figs. 1-2.

Material: NU S579/3, external mould of partial cranidium; high Lower Eltonian, Upper Westhope, Shropshire.

Discussion:

This specimen is also from Shergold's Shropshire collection. It belongs to *Iuba* without doubt, differing only in detail from *I. retrospinosa*. The main differences are the curved lateral glabellar furrows 3S and 2S (these are almost straight in the type species), and 1S curves forwards a little abaxially. The eye is slightly more posteriorly placed, the posterior part of the palpebral lobe being opposite the anterior angle of 1L. In his Ph. D. thesis, Shergold also figured a fragment of a pygidium from the same horizon and locality (NU S577/12). It showed the ventral surface of two pairs of spines which were short and exsagittally directed, and the posterior part of the doublure. This specimen has evidently been lost, but was obviously referrable to *Iuba*, and therefore probably belonged to *I.* sp. A.

Genus *Cheiruretaerus* gen. nov.

Type Species:

Cheiruretaerus *falcatus* sp. nov. 'Upper Silurian' (?Lower Ludlovian), Sedgley, Staffordshire.

Diagnosis:

Glabella expanding forwards, width across frontal lobe markedly greater than across 3L; frontal lobe more than $\frac{1}{3}$ sagittal length of glabella and extending in front of the general cephalic outline in front. Lateral glabellar furrows 3S and 2S distinct for two fifths way across glabella, their inner ends connected mesially by indistinct depressions. 1L lobes subtriangular, their inner angles separated by a backwardly facing tongue shaped portion of the mesial part of the glabella. Eye large, placed opposite 2S and close to the axial furrow. Thorax of eleven segments. Pygidium with three pairs of spines, anterior and mid pairs equally long, curved, posterior pair very short.

Range and Distribution:

Budňany Limestones, Bohemia; Wenlock Limistone, Malvern, Worcestershire; Upper Silurian, Turkestan.

<u>Cheiruretaerus</u> <u>falcatus</u> gen. et sp. nov.

Plate 20, figs. 1-5

Text figure 14

<u>Holotype</u>:

BU 420 (ex Holcroft 186), external mould of complete individual bent double; 'Upper Silurian' (?Lower Ludlovian), Sedgley, Staffordshire.

<u>Diagnosis</u>:

A species of <u>Cheiruretaerus</u> characterised by a large frontal lobe, large eyes, wide distinct posterior and wider lateral border and short genal spines in the cephalon, and by stoutly constructed anterior two pairs of pygidial spines, small but distinct posterior spines, and well developed anterolateral processes which bear the articulatory apparatus, in the pygidium.

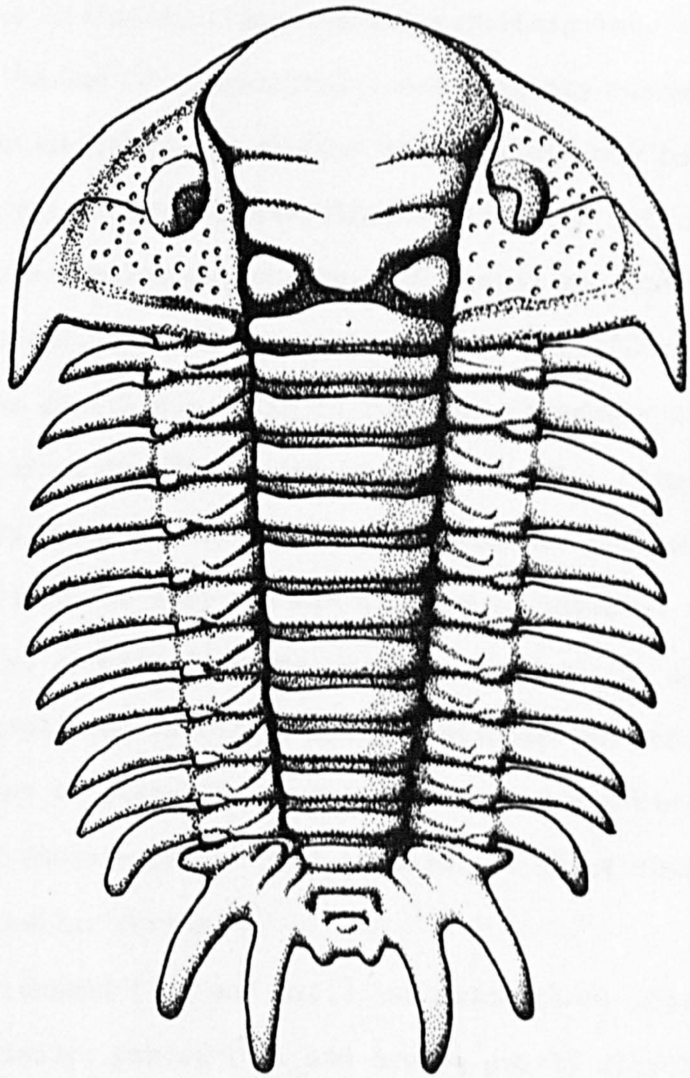
<u>Description</u>:

Cephalon semicircular, moderately convex. Glabella rounded in front, moderately convex (tr. and sag.), less than $\frac{1}{3}$ width of cephalon at occipital ring, expanding forwards, frontal lobe markedly wider than glabella across 3L. Frontal lobe rounded anteriorly and anterolaterally, moderately convex (tr. and sag.), protruding in front of general cephalic outline. 3L widening slightly abaxially, 2L widening

Text figure 14.

Reconstruction of *Cheiruretaerus* *falcatus* gen. et sp. nov.,

approximately X4.



Text figure 14

in the other direction. Basal lobes subtriangular, circumscribed, slightly inflated. 3S and 2S subparallel, both slightly curved and running a little back adaxially, of similar depth, width and length, reaching two fifths the way across the glabella, their inner ends joined across the glabella by a shallow depression. 1S deeper and more distinct abaxially at apodeme, running more obliquely back at first than 3S or 2S, $\frac{1}{3}$ way across glabella turning to run very obliquely back, meeting occipital furrow two fifths way across glabella. Inner angles of 1L separated by a backwardly facing tongue-shaped portion of the glabella. Occipital furrow as deep and distinct as 1S, abaxial one fifth running transversely, curving forwards over the rest of its course. Occipital ring moderately convex (tr. and sag.) with median tubercle, forming highest point of glabella. Axial furrow deep and distinct, continuing in front of fossula placed just anterior to 3S as shallower, less distinct preglabellar furrow.

Genae convex (tr. and exs.), subtriangular. Posterior border narrow abaxially, convex (tr. and exs.), gently sigmoidally curved, widening beyond articulation with first thoracic segment placed about $\frac{1}{3}$ distance to genal angle. Posterior border furrow as wide, deep and distinct as 1S adaxially, gently sigmoidally curved and running a little obliquely forwards, becoming wider and less distinct at the genal angle. Genal angle bears a pointed spine which reaches as far back as (at least) the second axial ring. Lateral border wider than posterior border, convex, narrowing slightly anteriorly. Lateral border furrow as wide and distinct as adjacent part of posterior border furrow at genal angle, anteriorly narrowing and becoming more distinct. Eyes large, extending from mid 2L to 3S, placed near axial furrow. Palpebral lobe forming highest point of cephalon, abaxially sloping very steeply to the axial furrow. Visual surface crescentic in plan, convex (exs. and dorsoventrally), sloping steeply to small, vertical visual platform, facial suture from β to γ originating where anterior part of glabella begins to protrude in front of general cephalic outline, curving round widest part of glabella where it comes very close to the axial furrow, from there running slightly abaxially; posterior section from ϵ running obliquely forwards to reach lateral border furrow opposite 2S, curving back across inner half of lateral border then turning sharply back to run very obliquely across the outer half, cutting margin opposite mid 1L. Surface of cheeks inside border furrows coarsely pitted, these pits larger and a little more widely spaced on the free cheeks.

Rostral plate short (sag.) and wide (tr.), a little wider than the occipital ring, convex and placed near the vertical.

Hypostoma unknown.

Thoracic segments eleven in number of the form typical of the subfamily. Axial rings very convex about two fifths transverse width of the segment, each bearing a pair of tubercles just exsagittally placed. Oblique furrow and bosses of shell on inner portion of pleurae very pronounced. Free pleural spines curved, increasingly so in the posterior segments.

Pygidium with axis formed of three rings and a terminal piece rapidly narrowing posteriorly. Axial furrow only seen as a weak groove adjacent to the posterior part of the two anterior axial rings and to the parallel sided third axial ring. Pleural portion of first segment with short oblique furrow, interpleural furrows less distinct than this. Three pairs of spines, anterior two pairs long and stoutly constructed, both curved the anterior a little more so. Posterior pair very short, rounded and distinct. Anterolaterally the pygidium bears a stout rounded process which carries the articulatory apparatus.

Discussion:

This species most resembles *C. squarrosus* (Zenker 1833) (= *C. quenstedti* Barrande 1846). From that species, *C. falcatus* differs in having a wider lateral cephalic border, a shorter genal spine, a posterior cephalic margin which is convex backwards, a more curved posterior section of the facial suture and a larger eye placed nearer the glabella; in the thorax a shorter internal part of the pleurae and a more curved external part; in the pygidium better developed anterolateral processes.

Additional material:

BU 417 (ex Holcroft 322), BU 418 (ex Holcroft 368), BU 419 (ex Hollier).

Cheiruretaerus gen. nov. sp. A.

Plate 21, figs. 3-4

Material:

BM I1479. Fragmentary cranidium of large specimen. Wenlock Limestone, Malvern, Worcestershire.

Description:

Glabella convex (tr. and exs.) expanding but little forward, rounded in front. Frontal lobe rounded anteriorly and anterolaterally, convex (tr. and exs.), a little longer (sag.) than 3L and 2L. 3L narrowing a little adaxially, convex (tr. and exs.). 2L widening slightly adaxially, convex (tr. and exs.). Basal lobe triangular, probably completely circumscribed, slightly inflated. 3S broad and deep, slightly curved, and running a little obliquely backwards across the glabella for just over two fifths of its width at this point. 2S similarly wide and deep, more curved, less oblique, reaching two fifths way across glabella. 1L as wide as 2S, straight, initially deeper, becoming shallower suddenly $\frac{1}{3}$ way across glabella, where it also becomes more oblique than 3S when initially it was less so. Axial furrow narrow and deep adjacent to 1L, widening anteriorly, becoming a shallow pre-glabellar furrow which dies out mesially. Surface of the glabella is finely punctate.

Genae known only from fixed cheek, slightly convex. Posterior border furrow wider than glabellar furrows, deep and parallel to 3S adaxially. Proparian, facial suture from β to γ running from anterior to widest part of frontal lobe in a curve, almost touching axial furrow at this widest part, from there running exsagittally; from ε running slightly obliquely forwards initially. Palpebral lobe extending from mid 2L to mid 3L, close to glabella with adaxially a palpebral furrow which is deepest posteriorly.

Discussion:

This specimen is from an individual 2 to 3 times larger than other Cheirurid species known from the Wenlock Limestone of Malvern. In the courses and lengths of the lateral glabellar furrows and the position and relative size of the eye it most resembles *Cheiruretaerus*, the available specimens of which are much smaller than this individual. It differs from *C. falcatus* in the course of the facial suture from β to γ , and 3S and 2S are more obliquely directed. With regard to these differences this specimen cannot be reffered to that species.

?*Cheiruretaerus* gen. nov. sp. B.

Plate 21, figs. 1-2

Material:

BM In48514, internal mould of partial cranidium; Wenlock Limestone, locality unknown.

Description:

Glabella narrow, subparallel sided; frontal lobe large, semicircular, convex (tr. and sag.), almost vertical in front. 3L and 2L inflated; 1L subtriangular, $\frac{1}{3}$ width glabella at that point, circumscribed, inflated, inner corners separated by a tongue like backward extension of the sagittal part of the glabella. Three pairs of lateral glabellar furrows, 3S and 2S almost parallel, markedly curved, 2S hooked backwards adaxially, both running obliquely back adaxially, wide and deep, for a little over 2/5ths way across, shallowing mesially and meeting as indistinct shallow depressions; 1S as wide and deep for $\frac{1}{3}$ way across glabella, then turning back to meet occipital furrow which arches forward mesially. Genae coarsely pitted.

Discussion:

This specimen differs from both *C. falcatus* and *C.* sp. A. in the following ways. It has a narrower, more parallel sided glabella, which is more convex, has a relatively larger frontal lobe and 2S is markedly hooked adaxially. In addition it differs from _C_. _falcatus_ in having wider, more distinct, slightly longer and more oblique lateral glabellar furrows 2S and 3S. It also differs from _C_. sp. A. in having a semicircular frontal lobe.

The specimen is referred to the genus _Cheiruretaerus_ with doubt since although it has long lateral glabellar furrows and the mesial tongue like portion of the glabella which separates the basal lobes, both features being characteristic of this genus, the glabella is parallel sided. A parallel sided glabella is not known in a described species of _Cheiruretaerus_.

Additional Material:

LM 4796.

Genus Pseudocheirurus Prantl and Přibyl, 1947.

Pseudocheirurus sp. A.

Plate 21, figs. 6-7.

Material:

BM In23423 a distorted cranidium; Upper Llandoverian, Camregan Group, Bargany Pond Burn, Girvan, Ayrshire.

Description:

Cephalon considerably distorted, glabella expands forward, frontal lobe markedly wider (tr.) than glabella across 3L. Frontal lobe $\frac{1}{2}$ sagittal length of glabella, convex (tr. and sag.). 3L and 2L parallel sided, 3L slightly wider (exs.). 1L abaxially wider than 3L, triangular, circumscribed, all three pairs of lateral lobes inflated. 3S curved, sloping obliquely backwards; 2S straighter, less oblique, 1S most oblique, curving back to occipital furrow. Occipital ring widening mesially. Axial furrow narrow and distinct, passing into narrow pre-glabellar furrow which dies out over mesial $\frac{1}{4}$ of frontal lobe.

Genae subtriangular in shape, free cheeks (missing) very small. Posterior border adaxially narrow and convex, just less than $\frac{1}{2}$ way to lateral margin becoming twice as wide and flat (exs.), and broadening a little further abaxially. Lateral border wider than this, flat. Genal spine present, broad based, its junction with posterior margin of cephalon a rounded acute angle. Posterior border furrow narrow, deep and distinct, widening a little abaxially, lateral border furrow shallow and wider, indistinct. Eye placed opposite 3L, $\frac{1}{3}$ distance from axial furrow to lateral margin. Facial suture proparian, from β to γ running on a course first convex approaching axial furrow at widest part of glabella, and then in a broad curve diverging from the axial furrow, posterior section from ε running in an almost straight line obliquely forward to just inside indistinct border furrow, curving back across this furrow and the inner part of the lateral border, from there turning sharply back to cut lateral margin opposite the anterior of 1L. Cheeks inside border furrows coarsely pitted. Fragments of shell preserved are finely granulated.

Additional material:

A poorly preserved portion of thorax from the same horizon and locality as the cranidium here described may belong to this species, BM In23421.

Discussion:

Although in the absence of a pygidium it is difficult to place this specimen, the features of the glabella and position of the eye indicate that it belongs to *Pseudocheirurus*. This genus has only previously been described from the Ludlovian rocks of Bohemia, (see Chapter III).

Pseudocheirurus sp. B.

Plate 21, figs. 12-13.

Material:

BM In23418, cranidium; Lower Tarranon, Penkill Group, Penwhapple Glen, Girvan, Ayrshire.

Description:

Cephalon excluding genal spine semicircular in outline, convex (tr. and sag.), ratio of width (tr.) to length (sag.) 2:1.

Glabella strongly convex (tr. and sag.) widening forward so that the greatest transverse width (across frontal lobe) is half as great again as width of occipital ring (est.). Frontal lobe half sagittal length of glabella (excluding occipital ring), semicircular in front where it approaches vertical, rounded laterally and anterolaterally, strongly convex (tr. and sag.). 3L and 2L of about same width (exs.), parallel sided, a little inflated. 1L subtriangular, circumscribed, inflated, about $\frac{1}{3}$ width of glabella at that point. 3S and 2S parallel, deep and wide, running very obliquely back adaxially, 2S a little longer so that it reaches at least two fifths way across glabella, 3S reaching about $\frac{1}{3}$ way across. 1S initially parallel to 2S, then $\frac{1}{3}$ way across glabella shallowing and turning to run in an almost exsagittal direction, reaching occipital furrow. Occipital region damaged. Axial furrow probably deep and distinct.

Genae subtriangular in shape, markedly convex. Fixed cheek very large. Posterior border narrow and convex, widening a little and curving forwards abaxially. Lateral border wide, gently convex dorsally. Genal angle bearing a spine which narrows rapidly at first, then tapers to a slender long spine the length of which is a little less than the sagittal length of the glabella excluding the occipital ring. The junction of spine and posterior margin is a rounded acute angle. Posterior border furrow narrow and distinct, lateral border furrow wider and less distinct. Eye placed opposite 3S, very near to axial furrow. Facial suture proparian, from β to δ following the outline of the frontal lobe, from ε running outwards and backwards in a curve until half way across lateral border (here opposite 2S) where it turns obliquely back and cuts the lateral margin approximately opposite 1S. Genae inside border furrows coarsely pitted.

Discussion:

As stated in the discussion of the last species, the absence of a pygidium makes the placing of this specimen also in *Pseudocheirurus* not certain. However, the position of the eye, and the oblique courses of the lateral glabellar furrows 3S and 2S are very much like the characters of the type species of that genus.

Genus Macrogrammus Whittard, 1966

?Macrogrammus sp.

Plate 21, figs. 8-11

Material:

Two glabellae, GSM 16193 and RSM 1889 91 32B, Balclatchie Group, Balclatchie, Girvan, Ayreshire.

Description:

Glabella subquadrate, widening a little forwards, gently convex (tr. and sag.). Frontal lobe small, rounded in front, convex. 3L and 2L subparallel sided, about equal width (exs.); 1L trapezoid, longer (exs.) than 2L and 3L only weakly delimited from mesial part of glabella. 3S narrow and distinct, originating in the axial furrow at the anterolateral corner of the glabella, running obliquely back adaxially for $\frac{1}{4}$ distance across glabella, there turning more obliquely back, shallowing and dying out $\frac{1}{3}$ way across, 2S initially less oblique than 3S for one fifth way across glabella, then turning to parallel the adaxial part of 3S, as narrow and distinct as this furrow, a little longer. 1S parallel to inner part of 2S for just less than $\frac{1}{3}$ way across glabella, there turning to run exsagittally and almost dying out to reach occipital furrow as weak indistinct furrow. Occipital ring mesially almost as wide as 2L (exs.), narrowing in abaxial quarter. Occipital furrow deep, narrow, and very distinct. Axial furrow narrow and distinct from adjacent to occipital ring to anterolateral corner of glabella, with a fossula adjacent to 3S, curving across front of frontal lobe as narrow distinct preglabellar furrow.

Posterior border adaxially half as wide (exs.) as occipital ring parallel sided adaxially. Posterior border furrow narrow and shallow. Palpebral lobe opposite 2S, small. Posterior section of facial suture from ϵ curves forward from palpebral lobe; anterior section running slightly obliquely outwards from γ . Anterior border narrow, widening exsagitally.

Surface of glabella everywhere covered with closely packed tubercles.

Discussion:

These specimens, probably of Lower to Middle Caradocian age, are considerably younger than the other known scant representatives of Macrogrammus. They differ from that genus in that the glabella widens a little forwards, and the eye is opposite 2S, and is apparently without the eye ridge characteristic of Macrogrammus. The features in common with the type species M. scylfense, are the courses and positions of the lateral glabellar furrows, the form of the anterior border and the character of the surface tuberculation. These features are unlike any other known Ordovician Cheirurid genus.

The differences from the type species of *Macrogrammus* are consistent with the normal evolutionary processes seen in the Cheirurinae modifying the unspecialised morphology of that Arenigian form. It seems that the more backwardly placed eye, and the slight expansion of the glabella forwards are specialised characters although some primitive ones are retained, such as the very short (sag.) frontal lobe. It is therefore probable that these specimens differ generically from *Macrogrammus*, but as these two specimens are the only ones known, and Macrogrammus itself is known only from two Shropshire specimens, and one from Argentina, it seems better to do no more than indicate the relationship thought to exist and refer them with doubt to that little known genus. More and better material is required of the Balclatchie form before a new genus could be erected.

Subfamily CYRTOMETOPINAE Öpik, 1937

Type Genus:

Cyrtometopus Angelin, 1854.

Diagnosis:

Glabella varying in form from subparallel sided with low convexity to subcircular and highly inflated, with generally short lateral furrows. Eyes placed further forward in forms with less convex glabellae, sometimes with a flase eye ridge which follows the course of the facial suture from β to γ. Forms with inflated glabellae have eyes placed further backwards and relatively small genae. Hypostoma with parallel sides, rounded anteriorly and more angular behind with convex median body similar in outline to whole hypostoma. Thorax of 10-12 segments. Pleurae with inner transverse articulated portion and outer free spine, this latter portion usually the shorter. Inner part of pleurae with transverse furrow or line of pits, or these furrows and pits effaced. Articulation between pleurae by a parallel sided ridge on one pleura fitting into a furrow on the segment behind. Pygidium with three to four axial rings and pairs of spines, these spines long and tapering to lobate, with or without a terminal spine.

Genus *Pseudosphaerexochus* Schmidt, 1881

Type Species: (By subsequent designation, Reed, 1896b)

Sphaerexochus hemicranium Kutorga, 1854 from the Llandeilian of Estonia.

Diagnosis:

Glabella inflated, oval in outline with three pairs of lateral furrows, the posterior pair most distinct and curving round to almost meet the occipital furrow, sometimes connected to this by an indistinct depression. Genae small, posterior section of facial suture running obliquely backwards. Hypostoma with subquadrate outline and convex median body which narrows (tr.) posteriorly. Thoracic pleurae with a line of pits parallel to the edges of the segment, these pits sometimes only visible on internal moulds. Pygidium with three rings and a small terminal piece in the axis, and four pairs of spines which may be short and blunt to long and tapering.

Pseudosphaerexochus girvanensis sp. nov.

Plate 24, figs 1-9

Plate 25, figs 1-8

1906 Cheirurus (Cyrtometopus) octolobatus, Reed, Pl. XVIII, figs. 8-11.

1914 Cheirurus octolobatus, Reed, p. 46.

?1935 Pseudosphaerexochus subquadratus, Reed, p. 56, Pl. IV, fig. 3.

?1935 Pseudosphaerexochus granulatus, Reed, p. 56, Pl. IV, fig. 2.

Holotype:

HM A846/3, external mould of cephalon and part of thorax, Starfish Bed No. 1, Ladyburn, Girvan, Ayrshire.

Diagnosis:

A species of Pseudosphaerexochus with a glabella oval in outline and lateral glabellar lobes 1L occupying about $\frac{1}{4}$ width of the glabella in dorsal view, and almost circumscribed by 1S which curves through less than 90°; 3S and 2S are wide and distinct. Eye placed close to the glabella opposite the anterior of 2L. Surface of internal and external moulds of glabella with fine closely spaced and coarser more widely spaced granulations. Pygidium with three rings and a very small terminal piece in the axis, and four pairs of spines which are all very short and stout, which decrease in length a little from anterior to posterior pairs, the posterior pair a little closer together than the others.

Description:

Glabella tumid, $\frac{1}{3}$ width cephalon at occipital ring, oval in outline, with three pairs of glabellar furrows. Frontal lobe short (sag.), vertical to overhanging, elliptical in front. 3L and 2L near vertical, convex (tr.), of about the same width. 1L oval, angular anterolaterally, almost circumscribed, inflated, just less than $\frac{1}{3}$ width (tr.) glabellar circumference. 3S and 2S short and curved, vertical, wide and fairly shallow, subparallel, their inner ends separated by a distance equal to or a little more than their combined lengths. 1S wider, deeper and more distinct abaxially, curving back and shallowing joined to occipital furrow by a wide shallow, very indistinct depression. Occipital furrow deep and wide. Occipital ring half as wide (exs.) as 2L, subparallel sided, curving a little forward abaxially, bearing a large medial tubercle. Axial furrow wide, very deep, and distinct, continuing in front of the glabella as a wide distinct preglabellar furrow which is overhung by the frontal lobe. In the axial furrow adjacent to 3S are fossulae and at this point the axial furrow is less distinct. Surface granulation of the glabella of two sizes - coarse tubercles most common on 1L and less common and smaller elsewhere, and fine granulations overall.

Genae triangular. Posterior border convex, narrow adjacent to the axial furrow, narrowing further first towards the genal angle, then widening and joining convex lateral border. Posterior border furrow narrow and distinct adaxially, widening and shallowing, and becoming less distinct at genal angle. Lateral border indistinct. Genal angle with very short slender spine. Anterior border plane dorsally. Free cheek with distinct border and border furrow both a little narrower than the part of the lateral border and border furrow on the fixed cheek. Eye placed opposite the anterior of 2L, visual surface rectangular, bearing many small hexagonal equidimensional lenses (400 were counted on an eye about 3.5mm long, occurring in rows of 11-15 high). Ocular platform quite wide and convex. Palpebral lobe narrow and steep, adaxial to which there is a distinct palpebral furrow which dies out anteriorly and posteriorly. Anterior section of facial suture from β to γ runs parallel to the axial furrow in a gentle curve. Posterior section runs from slightly obliquely backward from the posterior of the palpebral lobe until half way across the lateral border, then turning back to cut the lateral margin opposite mid 1L. Genae inside border furrows coarsely pitted, and finely granulate.

Hypostoma subquadrate in outline. Median body rounded in front and behind where it is narrower, convex, subtriangular, divided by elongate oblique maculae into anterior and posterior bodies, the ratio of their sagittal lengths 2:1. Anterior border furrow narrow, narrowing mesially, and abaxially passing into the long anterior wings; lateral border furrow deeper, more distinct and passing into shallower, less distinct posterior border furrow. Lateral border narrow and very convex, posterolaterally rising before posteriorly and mesially becoming less convex and curving dorsally. Medial body with scattered coarse tubercles especially anteriorly, the hypostome everywhere covered with small, distinct tubercles.

Thorax composed of 12 segments. Axial ring convex (tr.and sag.), about $\frac{1}{3}$ width of the whole segment. Pleurae unfurrowed and not pitted, convex (exs.) inner part transverse then curving back and down, here tapering to end as a free spine. Articulating ridge present on inner transverse part of pleurae, narrowing and disappearing where pleurae begin to curve back. Surface of thorax very finely pitted and granulated.

Pygidium short (sag.) and broad (tr.). Axis tapers rapidly back, composed of three rings and a rudimentary terminal piece. Pleural portions bear two pairs of distinct furrows which run out form the axis to the spaces between the free ends of the pleurae. Pygidial spines eight in number, very short, terminally rounded, their free ends lying on a curved line. Anterior two pairs of pygidial spines point posteriorly, at right angles to the transverse pleurae, Posterior pair of spines shortest with a small space between the other interspine spaces being larger ~~thick~~ and equal.

Discussion:

This species is most similar to P. octolobatus. From that species it differs in having wider lateral glabellar furrows 3S and 2S, 1S curves through less than 90°, lateral glabellar lobes 3L and 2L are equal in width (exs.), the eye is placed a little further back; the thoracic pleurae have no row of pits on the internal mould; the pygidium has a very small terminal piece to the axis, and the spines are of stouter construction and shorter.

Horizon and Localities:

Starfish Beds Nos. 1 and 2, Ladyburn, Girvan; Upper Drummock Group, South Threave Glen, Girvan.

Additional Material:

Cranidia. - HM A3580, 558, 540/1-3, 3657, 993, 1048, 1050, 3005, 5463, 5465; BM In 23448, 23449, 41352, 41366, 47163; RSM 1859 33 206. Pygidia. HM A2993, 846/2; BM In 43057, 43057/1.

Pseudosphaerexochus juvenis (Salter, 1848)

Plate 26, figs. 1-7

Lectotype:

GSM 24534, internal mould, Sholeshook Limestone, Haverfordwest. Pembrokeshire.

Remarks:

This species has recently been discussed by Whittington (1965, pp. 40-41). Because of the variation in the type material, and because only the cranadium has been figured it is impossible to compare this species with other species of Pseudosphaerexochus, or even to be sure that indeed it belongs to this genus. The lectotype has an ovate glabella and in some respects resembles the cranidium of Stubblefieldia (compare here Pl. 26, fig. 3 with Pl. 27, fig. 1). All material of this type from Sholeshook is given the name P. juvenis but in addition there seems to be a different species (genus?), represented by forms such as theone figured here (pl. 26, figs. 6-7). This specimen and one of the paralectotypes (here Pl. 26, fig. 4) have a glabella subcircular in outline and may therefore be different from the others. Until thoraces and pygidia are known from Sholeshook the name P. juvenis is retained for all this material. Sphaerexochus boops (Salter, 1864, Pl. 6, figs. 27-8) is possibly a weathered posterior portion of the glabella of a specimen of this species.

Pseudosphaerexochus consimilis sp. nov.

Plate 27, figs. 6-11

Holotype:

HM A1049. External mould of cranidium, Starfish Bed, Upper Drummock Group, Ladyburn, Girvan, Ayrshire.

Diagnosis:

A species of Pseudosphaerexochus in which the glabella is parallel sided between 1L and 3L, moderately convex (tr.) and strongly convex (sag.). Axial furrow and preglabellar furrow wide and deep, anterior border narrow (sag.) and ridge-like. Eye placed opposite 2L.

Description:

Glabella large, moderately convex (tr.) a strongly convex (sag.) less than $\frac{1}{3}$ width cephalon at the occipital ring, parallel sided between 1L and 3L, subquadrate in outline, with three pairs of lateral furrows. Frontal lobe elliptical in front, about $\frac{1}{3}$ sagittal length of whole glabella in palpebral view, vertical, convex (tr. and sag.). 3L and 2L steeply inclined, convex (tr. and exs.), parallel sided and of equal width. 1L oval in outline, inflated, about $\frac{1}{3}$ width of glabella 3S and 2S short, narrow and shallow, slightly curved and running obliquely back adaxially, parallel, the space between the inner ends of each pair equal to the combined length of the respective pair. 1S furrows wider, deeper, and much more distinct than 2S and 3S, abaxially subparallel to 2S, curving back and dying out suddenly without reaching the occipital furrow, to which they are connected by shallow indistinct depressions. Occipital furrow deep abaxially at apodeme, shallower and less distinct mesially. Occipital ring half as wide as 2L, convex (tr.), almost plane (sag. and exs.). Axial furrow wide and very deep, adjacent to 1L curving to convex abaxially, continuing in front of the glabella as a distinct pre-glabellar furrow which narrows mesially. Fossulae placed anterior to where 3S meet the axial furrow. Surface granulation of the glabella everywhere is of small closely packed tubercles.

Genae triangular. Posterior border convex, transverse, narrowing at first abaxially. Posterior border furrow narrow, deep and distinct widening towards the genal angle. Anterior border narrow (sag.) and ridge-like. Free cheek unknown. Fixed cheek inside border furrows coarsely and sparsely pitted. Palpebral lobe placed opposite 2L, extending from 2S to almost 1S.

Other parts of the trilobite unknown.

Discussion:

In the parallel sided nature of the glabella of this species it is unlike other known species of Pseudosphaerexochus. No thorax or pygidium has been found at the type locality which may be referred to this species, and because it is incompletely known it is referred to Pseudosphaerexochus which genus it most closely resembles.

<u>Additional material</u>:

BM In47165, from the same horizon and locality as the holotype.

Pseudosphaerexochus sp. A.

Plate 23, figs. 5 & 9

Material:

Two small cranidia SM A9583 & 4, external moulds from the Ashgillian Limestone Dyke, 2000' south of Horton in Ribblesdale Railway Station, Yorkshire.

Discussion:

These small specimens were referred to P. aff. conformis (Angelin), by King (1932, pp. 103-4). As they are so small it is impossible to have any certainty as to their true affinities. They could equally well belong to any of the Ashgillian species of Pseudosphaerexochus found in the north of England, or even to Setacauda cancrura (see below). In the absence of larger individuals or more complete material they are referred to Pseudosphaerexochus, to which they seem to have the closer affinities.

Pseudosphaerexochus sp. B.

Plate 26, figs. 8-10

Material:

HM A3638, a single glabella with fragments of the genae in place, preserved as an internal mould, from 7' above Starfish Bed No. 3, Ladyburn, Girvan, Ayrshire.

Discussion:

In comparison to other species of Pseudosphaerexochus found at Girvan, this specimen has a less inflated glabella, and is covered with coarse closely spaced granulations. In the absence of more, and more complete material it is recorded here as being distinct, but not dealt with further.

Genus Stubblefieldia Prantl and Přibyl, 1947.

Type species:

Cheirurus neglectus Barrande, 1872 from the Králův Dvůr Beds (Ashgillian) of Bohemia.

Diagnosis:

(Prantl and Přibyl page 32). Cyrtometopinae of 11 thoracic segments, with a cephalon reminiscent of the genus Cyrtometopus Angelin, 1854, whereas the shape of the (seven-lobate) pygidium is reminiscent of the genus Eccoptochile Hawle and Corda, 1847. By the shape of its pleurae it differs from all the representatives of the family Cheiruridae.

Stubblefieldia verrucosa sp. nov.

Plate 27, figs. 1-5

Holotype:

BM In47164, internal mould of pygidium from the Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire.

Diagnosis:

Glabella very convex (tr. and sag.), oval in form and almost twice as long (sag.) as wide (tr.) in palpebral view. Basal lateral glabellar furrows 1S very wide and deep, circumscribing oval basal lobes which are $\frac{1}{3}$ width of glabellar circumference at that point. Axis of pygidium with three rings, three pairs of lobate spines with a terminal lobate spine.

Description:

Glabella expanded, about twice as long (sag.) as wide (tr.) in palpebral view, less than $\frac{1}{3}$ width of cephalon at occipital ring, oval elongate in outline with three pairs of lateral furrows. Frontal lobe small, near vertical, rounded in front. 3L and 2L because of tumidity of glabella steeply inclined, not inflated independent of the glabellar convexity, 2L a little wider (exs.). 1L ovate, circumscribed, a little inflated, about $\frac{1}{3}$ width of glabella. 3S and 2S short, curved back adaxially, falling steeply to the axial furrow, abaxially fairly wide and distinct, their inner ends separated by a distance a little less than their combined length. 1S deeper and more distinct abaxially, curving back and shallowing, meeting occipital furrow as a wide shallow furrow. Occipital furrow deep, transverse. Occipital ring narrow, widening and curving forwards very slightly abaxially. Axial furrow deep and distinct, continuing anteriorly as a wide distinct preglabellar furrow which the frontal lobe overhangs. In the axial furrow a little forward of 3S are indistinct fossulae.

Genae triangular. Posterior border very narrow and convex adaxially, wide and plane at the genal angle which possibly bears a small spine. Posterior border furrow wide and distinct adaxially, abaxially curving forward and down becoming a little wider and less distinct. Eye placed opposite 2L. Palpebral lobe narrow running obliquely abaxially backward, and adaxial to which there is a wide palpebral furrow which anteriorly causes a slight indentation in the abaxial wall of the axial furrow opposite the posterior of 3L. Anterior section of facial suture runs from β in a curve then from opposite 3S parallel to the axial furrow to γ ; posterior section runs from ϵ slightly obliquely backwards at first, then transversely until half way across lateral border furrow where it turns sharply back through almost a right angle to cut the lateral margin very close to the genal angle.

Glabella covered with closely placed equidimensional tubercles, fixed cheek inside border furrows with shallow indistinct pits and tuberculation similar to the glabella.

Pygidium about three times wider (tr.) than long including terminal spine. Axis composed of three rings which are convex (tr.

and sag.), anterior two of similar width (tr. and sag.), posterior narrower in these directions. Anterior two interring furrows of axis wide and distinct, much deeper exsagitally than sagittally. Posterior interring furrow not present medially so that it is composed of two elongate (tr.) pits. Axial furrow wide and distinct adjacent to anterior two axial rings, adjacent to posterior axial ring very weakly delimited. Margin with three sets of paired spines associated with the three axial rings. Anterior pleural ridge runs transversely from the axial furrow for a short distance before curving through about 90^{o} to form the anterior spine which is longest and reaches by a small amount least far back. Mid pleural ridge runs transversely for a very short distance before turning through a similar angle to form the mid spine, which is shortest and reaches furthest back of the paired spines, runs exsagitally from the posterior axial ring. Terminal spine of pygidium similar to posterior pair and reaching a little further back than these.

Discussion:

The genus *Stubblefieldia* was erected mainly on the characters of the thorax. In the thorax of the type species the pleurae have a ridge running parallel to the edges of the segment, which is a feature unlike any other cheirurid. The position of the genus has been discussed elsewhere. This species has been assigned to *Stubblefieldia* in the absence of knowledge of the thorax, since the pygidium fits the diagnosis of that genus. The single terminal spine apart, the pygidium of this species greatly resembles that of *Pseudosphaerexochus girvanensis* (compare Plate 24, fig. 5 with Plate 27, fig. 5), of which at one time the author thought it may be a sexual dimorph. However, the pygidium here referred to _S. verrucosus_ fits best the diagnosis of that genus. In addition, this type of pygidium occurs rarely in these Girvan Ashgillian deposits as compared to _P. girvanensis_, as does the cranidium referred to _S. verrucosus_ which differs significantly from _P. girvanensis_ especially in the shape of the glabella, the size of the basal glabellar lobes, the fact that these are circumscribed, and in the surface granulation of the glabella and genae. The surface granulation of the genae of the cranidium is like that on the seven-lobate pygidium here described.

If _Stubblefieldia_ is regarded as being derived from _Pseudosphaerexochus_, that their pygidia are very similar can be accounted for. As suggested in another chapter a detailed description of the thorax of the type species is needed to discover the true nature of the pleural ridge and so that the relationship of these two, apparently related, genera can be found.

This is the first record of this genus outside Bohemia.

Additional material:

Cranidia. HM A846/1; BM In47168. Pygidium BM In47170.

Genus *Setacauda* gen. nov.

Type species:

Cheirurus cancrurus Salter, 1853 from the Chair of Kildare Limestone (Ashgillian), Kildare, Ireland.

Diagnosis:

Glabella subcircular in dorsal view, very convex, frontal lobe overhanging; basal lateral glabellar furrow slightly curved forward adjacent to axial furrow, then curved strongly back, not isolating basal lobes 1L. Eye placed opposite anterior of 2L. Hypostoma with parallel sides and a quadrate inflated median body. Pygidium with three rings in the axis, and four pairs of subequally sized spines, the posterior pair of which are separated by a posterior margin of the pygidium equal in width to the width (tr.) of the mid axial ring.

Discussion:

The shape and orientation of the glabella of *Setacauda* is unlike that found in *Pseudosphaerexochus*, having a subcircular dorsal aspect, and in lateral profile the sagittal line of the glabella is plane and horizontal between the basal lobes, but anteriorly curves through more than a right angle so that much of the glabella is vertical or overhanging. The sigmoidal course of the basal lateral glabellar furrows, and the degree of isolation of these from the occipital furrow are also characters different from those found in <u>Pseudosphaerexochus</u>. The pygidium has, like some species of <u>Pseudosphaerexochus</u>, four pairs of spines, but in that genus they are equally spaced around the pygidium, never having a wide posterior margin between the posterior pair.

The cephalic characters which distinguish <u>Setacauda</u> from <u>Pseudosphaerexochus</u> are similar to some of those which distinguish the Sphaerexochinae from other Cheirurids. In particular in sigmoidal course of the basal lateral glabellar furrow, and the subcircular shape of the glabella (because of its high sagittal convexity) are features found in <u>Kawina</u> and <u>Sphaerexochus</u> respectively. In other respects the genus is like members of the Cyrtometopinae to which subfamily it is assigned, even though the thorax is not known, because of its occurrence in time, and because it is unlikely that the three fused pygidial spines of the Sphaerexochinae could give rise to a pygidium such as belongs to <u>Setacauda</u>. In addition the short line of pits on the anterior pleural ridge of the pygidium indicate that the thorax may be Cyrtometopian in type.

Setacauda cancrura (Salter, 1853)

Plate 22, figs. 1-8

Plate 23, figs. 1-4,6-8.

Plate 25, fig. 9.

1846 Cheirurus gelasinosus, M'Coy(non Portlock), p. 44

1853 Cheirurus cancrurus Salter, p. 11.

1859 Cheirurus cancrurus Murchison, p. 538.

1864 Cheirurus (Cheirurus) cancrurus Salter, pp. 72-3, Pl. 5, fig. 15.

1891 Cheirurus clavifrons, Nicholson & Marr, p. 507.

1891 Sphaerexochus calvus, Nicholson and Marr, p. 507.

1896a Cheirurus (Pseudosphaerexochus) subquadratus, Reed, pp. 421-3. Pl. XX, figs, 10-11.

1896a Cheirurus (Pseudosphaerexochus) conformis var. Reed, p. 420-1.

Lectotype:

GSM 35367, fragmentary weathered internal mould of pygidium, Chair of Kildare Limestone, Kildare, Ireland.

Diagnosis:

As for genus.

Description:

Glabella tumid, over $\frac{1}{3}$ width of cephalon at occipital ring, subcircular in outline, in dorsal view, with three pairs of lateral glabellar furrows. Frontal lobe small, rounded in front, vertical posteriorly and overhanging in front. 3L and 2L same width (exs.) at axial furrow, steeply inclined, convex (tr. and exs.) due to the tumidity of the glabella, the sagittal line of glabella at 3L and 2L in lateral view forming a quadrant of a circle. 1L ovate, truncated at axial furrow, angular anterolaterally, not circumscribed, a little inflated. 3S and 2S a little less than $\frac{1}{3}$ circumference of glabella from axial furrow at one side to the other, approaching vertical, narrow and shallow, parallel to one another. 1S wider and deeper than 3S and 2S, straight and running obliquely back adaxially over a distance adjacent to axial furrow curved forwards then running almost straight for a short distance to about one fifth circumference of the glabella at that point, then curving strongly back, and dying out before reaching occipital furrow. Occipital furrow as wide as 1S and deep especially adjacent to 1L at apodeme where it curves convex backwards over $\frac{1}{3}$ its length (tr.), the medial third also curved convex backwards, but only very slightly, and transversely a little anterior to the abaxial portions adjacent to 1L. Occipital ring mesially $\frac{1}{2}$ as wide (sag.) as 1L at the axial furrow, abaxial parts a little narrower and slightly curved convex backwards similarly to the occipital furrow, occipital ring ending on same exsaggital line as the axial furrow adjacent to the posterolateral corner of 1L. Axial furrow adjacent to 3L and 2L wider and deeper than 1S, descending in a curve becoming near vertical; narrower and shallower adjacent to occipital ring, and adjacent to 3S widening and shallowing into a shallow fossula. Preglabellar furrow at first as wide and deep as axial furrow adjacent to 3L and 2L, mesially narrowing and overhung by glabella. Surface of glabella everywhere covered by equidistant near equidimensional tubercles, and in addition the surface appears to be minutely granulated.

Genae triangular. Posterior border $\frac{1}{2}$ as wide (exs.) as occipital ring at axial furrow (where it is adjacent to the middle of the occipital ring), widening a little, and running obliquely back abaxially. Posterior border furrow narrow and distinct adaxially, wider and less distinct at the genal angle which bears a short stout spine. Anterior border narrow and convex.

Eye placed opposite anterior of 2L, palpebral lobe rising steeply from the cheek. Anterior section of facial suture running from anterior of palpebral lobe in a curve convex adaxially, approaching most closely to glabella adjacent to the fossula in the axial furrow adjacent to 3S, cutting curved anterior margin at an obtuse angle. Posterior section from posterior of palpebral lobe running at first close to the transverse direction then obliquely backwards and out crossing lateral border furrow and finally running even more obliquely back across lateral border, cutting lateral margin a little way in front of genal spine. Genae everwhere with tuberculation similar to the glabella, and inside border furrows sparsely pitted.

Hypostoma with large parallel sided median body, gently curved anteriorly and semicircular behind, a little longer sagittally than transversely. Maculae weak separating a small posterior lobe about one sixth of the sagittal length of the whole median body. Anterior border furrow wide and distinct, lateral and posterior border furrows wider and even more distinct, especially posterolaterally. Lateral and posterior border wider than anterior border, all borders convex, posterior border curving up somewhat dorsally and angular mesially. Internal mould with a few large indistinct tubercles.

Sagittal length of pygidium about equal to transverse width of anterior axial ring. Axis tapering backwards composed of 3 rings which decrease in convexity (sag.) but increase a little in width (sag.) backwards, all convex transversely. Furrow between anterior and mid rings deepest and most distinct, within it mesially an elongate ridge tapering to both sides and about $\frac{1}{4}$ width of the axis at that point, representing an anchylosed portion of the articulating half ring; furrows of axis posterior to this less deep and distinct, mesially less distinct, posterior furrow narrow abaxially and not present mesially for $\frac{1}{3}$ width of the axis. Axial furrow represented adjacent to anterior axial ring as a weak, and adjacent to mid axial ring as an even weaker furrow, not present adjacent to posterior ring, and at junction with interring furrows seen as deep rounded depressions. Between posterior furrow of axis and posterior margin a gently convex (tr. and sag.) subrectangular area is present. Pleural regions simple, composed of distinct curved ridges between anterior two rings and anterior two pairs of spines, on the internal mould the anterior ridge with a centrally placed short line of pits neither reaching axial furrow nor free spine. Between the curved ridges lie distinct, wide, curved furrows adjacent to the two anterior interring furrows of the axis. On the pleural region behind the two anterior ridges lies a gently convex area with a weak depression running from the margin at the junction between the posterior two pairs of spines for a short distance adaxially. Spines subequal in length, equally spaced on either side, curved, convex dorsally, the anterior by a little stoutest in construction, posterior most slender . Anterior pair run at an angle of about 30° to the transverse direction, and the posterior pair at about 15° to the exsagittal direction. Between the posterior pair of spines the margin is somewhat angular, near the spines sloping obliquely back adaxially, with a transverse straight posterior margin, about half as wide (tr.) as the anterior axial ring.

Surface of axis and free spines bearing large irregularly placed tubercles, whole surface of pygidium very finely granulose.

Discussion:

Salter (1853, p. 11) set up the species C. cancrurus on the poor pygidium figured here (Pl. 23, fig. 6.), although he did not figure it himself at that time. In 1864, he figured the pygidium, and described it. The species has not been redescribed since that time. Reed (1896, pp. 421-423, Pl. XX, figs. 10-11) erected P. subquadratus on cranidia only, and he believed the species to lie close to P. hemicranium. It is only in this work that the pygidia and the cranidia have been associated. Better specimens of the pygidium are now available than were seen by Reed, from which it immediately becomes clear that the surface granulation and tuberculation characteristic of the cephala is also present on these. In addition, more circumstantial evidence for the cephala and pygidia belonging to the same species is that both are obviously cheirurid in character, and these are the only cheirurid remains from the Keisley and Chair of Kildare Limestones which were not definately associated with the other part of any particular animal. In view of these facts, it can hardly be doubted that the cephalon of '*P. subquadratus*' belongs to '*C*'. *cancrurus*, so that the former is a junior subjective synonym of the latter.

Additional material:

SM A11843-5, 11863, 11866-75; RSM 1870 12 1173A; GSM 35368, 35379.

Genus *Placoparina* Whittard, 1940.

Type species:

Cryphaeus sedgwicki M'Coy, 1849. Zone of *Glyptograptus teretiusculus* (Llandeilian), two miles north of Builth, Radnorshire.

Discussion:

In Chapter III on the phylogeny of the family it will be found that like Whittard (1958, p. 112) and unlike Prantl and Přibyl (1947, p. 25) the present author accepts *Placoparina* as a genus within the Cyrtometopinae.

Placoparina sedgwicki (M'Coy, 1849).

Plate 28, figs. 1-4.

A complete synonymy with diagnosis and description of this species will be found in Whittard 1958.

Genus *Eccoptochile* Hawle and Corda, 1847.

Type species:

Cheirurus claviger Beyrich, 1845. (By subsequent designation Barton, 1916).

Eccoptochile pectinatus Salter MS.

Plate 28, figs. 5-6

1940 *Eccoptochile pectinatus*, Whittard, p. 169.

Description:

The original specimen is a poorly preserved and damaged complete trilobite, oval in form but nearly as wide as long (sag.).

Cephalon and anterior part of the thorax are badly damaged so that it can only be seen that the specimen is of low convexity, the cephalon is elliptical in outline and bears a long, straight, narrow genal spine which runs outwards and backwards at an angle of about 40° to the transverse direction. The thorax is composed of ?10 segments, with an axis about one sixth the transverse width of the whole. The pleurae are parallel sided and transverse for the inner half of their course and here possibly have a median line of pits or furrow, while over their outer half they taper to backward curving slender spines which in the posterior segments run increasingly closer to the exsagittal direction. The pygidium is composed of three segments, with three pairs of spines, less curved and a little stouter in construction than those of the thorax.

Discussion:

As remarked by Whittard (1940, p. 169) the original specimen of Salter's manuscript name (GSM 35241-2) is too poorly preserved to attribute it with certainty to a genus. However, from the features to be seen it is possible to disagree with Reed's (1896, pp. 119-120) comment that it is closely allied to *Placoparina sedgwicki*, for as Whittard said the specimen has a long genal spine, and further examination of the specimen also shows that the pleural spines occupy a greater proportion of the length of the pleurae of the thorax than in that genus. In addition, '*E*.' *pectinatus* probably has fewer thoracic segments than the twelve of *Placoparina*. An isolated pygidium (GSM 69759, counterpart GSMb 3022-3) from the same horizon and locality as the more complete specimen would seem to belong to the same species.

It is probable that this specimen belongs to an undescribed genus which belongs to the Cyrtometopinae and has some relation to *Eccoptochile*. Until better material becomes available this new genus is not described and the name kept as a manuscript name.

Horizon and locality:

Llanvirnian, Cefn Gwynlle, Shelve, Shropshire.

Subfamily SPHAEREXOCHINAE Öpik, 1937.

Type genus:

Sphaerexochus Beyrich, 1845.

Diagnosis:

For a recent diagnosis see Whittington, 1965, p. 411.

Genus *Sphaerexochus* Beyrich, 1845.

Type species:

Sphaerexochus mirus Beyrich, 1845. Lower Wenlockian, Bohemia.

Diagnosis:

Glabella highly inflated, subcircular in outline. Three pairs of lateral glabellar furrows, anterior two pairs weakly impressed, basal pair wide and deep, curving round to meet occipital furrow. Axial furrow distinct. Genae small; proparian, posterior section of facial suture cutting posterolateral margin of cephalon. Hypostoma with convex median body which is a little wider than long (sag.). Rostral plate wide (tr.) and narrow (sag.). Thorax of 10 segments with wide, convex axial rings, and convex, rounded, unfurrowed pleurae. Pygidium with two rings and a terminal piece in the axis, and with three pairs of very short or lobate spines.

Sphaerexochus mirus Beyrich, 1845.

Plate 29, figs. 1-9.

Material:

Topotype material, BM It2456-2467; It5439; 23774; 42439.

Diagnosis:

Glabella inflated, wider than long (sag.). Occipital furrow very wide. Palpebral lobe opposite anterior of 1L. Pygidium with terminal piece of axis with indented sides (internal mould) indicating two segments.

Description:

Cephalon more than a semicircle in outline, highly inflated, ratio of width to length in dorsal view about 3 : 2. Glabella very large forming major part of glabella, almost hemispherical, wider (tr.) than long (sag.). Basal lobes circumscribed, subcircular, inflated independantly of glabella, because of convexity of glabella facing outwards and backwards, almost vertical. 1S wide and deep with a semicircular course from axial to occipital furrow. Medial part of glabella between basal lobes narrows slightly backwards and is wider than the diameter of a basal lobe. 3S and 2S indicated as indistinct narrow furrows, neither reaching axial furrow but stopping at point of widest lateral extent of glabella, before that small portion of glabella which curves down and under to form one wall of the axial furrow; the two furrows parallel, because of the convexity of the glabella nearly vertical, 2S reaching slightly further across glabella than the width of the basal lobe, 3S about $\frac{3}{4}$ this length.

Occipital ring narrow (sag. and exs.) about $\frac{1}{2}$ width of posterior margin of cephalon in dorsal view, very arched (tr.) so as to form almost a semicircle. Occipital furrow wide and deep medially, narrower and deeper adjacent to basal lobes. Axial furrow wide and distinct, continuing forwards to form wide and distinct preglabellar furrow which narrows and becomes more distinct sagittally. Surface of glabella finely granulated.

Genae small and vertical, poorly preserved in material to hand. Eye small placed opposite anterior 1L. Posterior border indistinct. Posterior part of cheek inflated, pyramidal.

Hypostoma trapezoid in outline, formed of a trapezoidal slightly inflated median body, surrounded by a furrow and border narrowest and most distinct in front, both wider laterally and greatly wider posteriorly. Anterior wings rounded. Surface covered by small, closely packed equally sized granules.

Pygidium subtriangular in outline, ratio of greatest transverse width to length 2 : 1. Axis composed of two rings, about $\frac{1}{2}$ width of pygidium in front, and a posterior inflated portion which narrows posteriorly. Axial rings narrow a little exsagittally, convex (tr. and sag.). Furrows between axial rings slightly wider and more distinct exsagittally than sagittally. Furrow between posterior ring and terminal piece of axis wider, deep and fairly indistinct, especially behind where it slopes up to the terminal piece. Terminal piece inflated, with indented sides rounded behind. Axial furrow indistinct, indicated as a break in slope between axial rings and pleural portions; adjacent to terminal piece there is an indistinct widening and deepening of this furrow, best seen on internal moulds. Pleural portions triangular in shape, formed of three segments. Anterior segment longest running from the axis almost transversely for a short distance before turning down and back to run at about 45° to this direction ending in a rounded lobe at the margin, where this ridge is a little wider than adaxially. Mid segment has a very short faintly indicated adaxial portion running at about 30° to the transverse direction, then curving down and back, and widening to end in a rounded projection wider than in the anterior segment. Posterior segment subtriangular in shape, exsagittally directed, lying between the mid pleural segment and the terminal piece of the axis, ending with the widest rounded projection. These ridges are only a little convex exsagittally. Pleural furrows narrow, widening a little abaxially, somewhat rectangular in section, indistinct (especially the posterior furrow) adjacent to axial furrow, and not recognisable as furrows near to the indentation in outline of pygidium between rounded lobes which terminate the pleural ridges. Surface of pygidium covered with equally sized, closely spaced small granules.

Sphaerexochus aff. mirus Beyrich, 1845

Plate 30, figs. 1-11

Plate 31, figs. 1-9

1853 Sphaerexochus mirus, Salter, Pl. 3, figs. 1-13.

1864 Sphaerexochus mirus, Salter, Pl. 6, figs. 1-6.

Horizon and localities:

Wenlockian Shale and Wenlock Limestone of the Dudley and Malvern areas.

Diagnosis:

In form very like type species, glabella more circular in outline, occipital ring wider (exs.). Axial rings of pygidium narrow (exs.) terminal piece subtriangular in shape.

Description:

Cephalon semicircular in outline, highly convex (tr. and sag.), posterior margin a little curved concave backwards, ratio of length (sag.), to width (tr.) about 1 : 2. In dorsal view the glabella occupies the great majority of the cephalon, wider than long, narrowing posteriorly rounded in front and much inflated. Basal lobes subcircular, slightly inflated independently of the glabella, completely circumscribed by 1S which is wide and deep and runs from the axial furrow obliquely forwards before curving back through a large angle to run exsagittally to the occipital furrow. Between the basal lobes the medial portion of the glabella adjacent to the occipital furrow 1S rectangular in shape, wider than the basal lobes. Other glabellar furrows weakly impressed. Occipital ring $\frac{1}{2}$ width cephalon, very arched (tr.). Occipital furrow wide and deep, most so where it is joined by the 1L. Axial furrow wide and deep, not visible anterolaterally to the glabella. Anterior section of facial suture seen (in lateral profile) to run parallel to the axial furrow; posterior section curved, running generally obliquely out and backwards cutting the margin of the very convex genal angle posterolaterally just in front of the genal angle indicated by a slight swelling. Cheek regions very convex, almost vertical, only the posterior portion of the fixed cheek visible in dorsal view, this part small, triangular. Anterior portion of fixed cheek narrow, parallel sided and overhung by glabella. Palpebral lobe small and very close to glabella, opposite anterior 1L. Free cheek small sub-trapezoidal in shape, in dorsal view overhung by fixed cheek. Posterior border furrow deep and wide, becoming wider towards genal angle where it meets the wide deep lateral border furrow. Posterior border convex (tr. and exs.). Lateral border convex, wide, just visible in dorsal view posteriorly, narrowing and dying out anteriorly, just posterior to where it is cut by the facial suture. Surface of cephalon finely granulated.

Thorax formed of ten segments, convex (tr. and sag.). Axis narrowing slightly and evenly posteriorly, convex (tr.), less so than the occipital ring, clearly separated from the pleural portions although there is hardly a distinct axial furrow. Pleurae as far as fulcra horizontal, convex (exs.), outside this narrowing, bending down and back, and ending as rounded spines. Fulcra seen as a slight elbow in the outline of the posterior margin of each pleura, which abuts against an indentation in the anterior margin of the next posterior.

Pygidium somewhat oval, ratio of greatest transverse width to sagittal length 5 : 2. External margin lobate. Axis of three rings, anterior two arched and convex (exs.), separated from the third by a wide shallow furrow. Measured sagittally third ring as long as first two combined, reaching to posterior margin of pygidium. Pleural portions with three segments indicated, anterior pair longest, horizontal to the fulcrum, then bending down and back to terminate in a rounded lobe at the margin. Middle pair lie almost completely behind, and outside the mid axial ring, and are subtriangular and rounded exteriorly. Third pair indicated lie alongside i.e. adaxial to, the second pair, subtriangular, shortest, least well defined, rounded exteriorly. These pleural segments demarkated by distinct narrow, deep grooves. Surface of shell of thorax and pygidium with medium to fairly large tubercles closely spaced.

Discussion:

S. aff. mirus is the British species which hitherto has always been referred to S.mirus. The British form is very much like the Bohemian type species, but differs on close examination in various points. These are as compared to _S. mirus_, the glabella is more circular in outline, the occipital ring is wider (exs.), lateral glabellar furrows 3S and 2S converge abaxially, and the portion of glabella between the basal lobe is rectangular in shape; the eye is a little more anteriorly placed. The furrows of the pygidial axis are wider and uniformly deep in their course across axis, and on the pleural portions of the pygidium the inter pleural furrows are at a larger angle to the transverse direction, and are also wider and deeper.

The British form has here not been named or fully discussed, as it and the Bohemian species are at present under consideration by Dr. Dean (British Museum) who kindly allowed the present author to see the topotype material of _S. mirus_ described above.

Sphaerexochus balclatchiensis Reed, 1914.

Plate 32, figs. 1-9

Plate 33, figs. 1-8

1914 Sphaerexochus mirus var. balclatchiensis Reed, p. 47, Pl. VIII, fig. 2.

Lectotype:

BM In23532a & b, pygidium, internal and external moulds.

Paralectotypes:

Cephala - BM In23533a & b, In23534, In23535a & b, In23536, In23537;

Thoracic segment In23538a-c; Pygidium In 23539a & b.

Horizon and locality:

Balclatchie Group, Balclatchie, Girvan, Ayrshire. Material preserved as distorted internal and external moulds in decalcified dark grey indurated mudstone.

Diagnosis:

Cephalon of the form typical of the genus. Pygidium with axis composed of three rings and a terminal piece, the posterior ring weakly demarkated from the terminal piece, and posterior to the anterior two rings ancylosed portions of articulating half rings are present sagittally.

Three pairs of spines, short but with free ends.

Description:

Cephalon semicircular in outline, dominated by greatly inflated glabella which was probably subcircular in outline, bearing three pairs of lateral glabellar furrows. On both internal and external moulds 3S and 2S indistinct except adjacent to the axial furrow where they are represented by notches in the glabella. 1S distinct, wide and deep, at first running from axial furrow slightly obliquely backwards, then curving round and shallowing just before reaching the occipital furrow which it meets about $\frac{1}{3}$ way across glabella, a little less than this in smaller specimens. Frontal lobe, 3L and 2L indistinctly delimited from the rounded mass of the glabella. 1L rounded in outline, circumscribed and very little inflated independantly of the glabellar convexity. Occipital ring about $\frac{2}{3}$ width (tr.) of widest part of glabella (which is approximately across 2L), convex (tr. and sag.), narrowing (exs.) abaxially, bearing a median tubercle. Occipital furrow adjacent to 1L deep and distinct, over medial $\frac{1}{3}$ of glabella shallower and wider.

Axial furrow deeply impressed, a little wider than abaxial part of occipital furrow, everywhere overhung by glabella. In axial furrow adjacent to 3S lies a fossula, furrow continuing round front of frontal lobe as distinct overhung preglabellar furrow.

Genae small, convex, lying in a plane approaching the vertical. Posterior border convex (exs.) most so where it is also narrowest adjacent to the occipital ring, towards genal angle less distinct. Posterior border furrow also narrower, deeper and more distinct adaxially. Eye small, placed opposite 2L. Facial suture proparian, anterior section from anterior of palpebral lobe in a gentle curve gradually approaching axial furrow and running round anterolateral corner of glabella; posterior section curving backwards and outwards from posterior of palpebral lobe, cutting rounded posterolateral margin of cheek in front of a slight swelling apparently on posterior margin of cephalon taken as genal angle.

Thorax of an unknown number of segments. Axial ring of single available segment about $\frac{1}{3}$ width (tr.) of whole, convex (tr. and sag.), a little narrower mesially than exsagittally, with a wide distinct furrow which curves forward and separates articulating half ring which is convex (tr. and sag.) and wider sagittally than exsagittally. Pleurae curved downwards, adjacent to axial furrow as wide as adjacent part of axial ring abaxially widening to about $\frac{1}{3}$ distance from axial furrow, from there tapering and ending as a spine. Widest part of pleurae bear articulartory apparatus, posteriorly a protrusion of the shell giving an elbow like outline to the posterior margin of the pleurae, this elbow abutting against a groove in the anterior edge.

Pygidium with three rings and a terminal piece in the axis, and three pairs of blunt spines. Axis tapering backwards with anterior ring of form of the thoracic axial rings, and mid ring which from the sagittal line widens then narrows again towards the axial furrow, anterior to anterior ring an articulating half ring and between anterior two rings a small transversely elongate anchylosed portion of a half ring about $\frac{1}{3}$ width of the axis at that point. Posterior axial ring separated from mid ring by a distinct furrow in which there is a second smaller less distinct anchylosed portion of half ring but indistinctly separated from terminal piece, this terminal piece triangular in shape, tapering backwards, narrow based with a narrow projection at apex running to posterior margin of pygidium between posterior pair of spines. Pleurae with three ridges anterior running near transverse direction, posterior nearer exsagittally, with distinct furrows between. Three pairs of spines, short and wide, about as long as transverse width of third axial ring, having bluntly rounded ends. Between spines are narrow spaces which in internal mould are wider and rounder proximally. Doublure extending at least under free spines of thorax, but its full extent not seen in pygidium.

Surface granulation only seen on outer parts of free spines of thorax, and on the doublure of the pygidium as distinct small tubercles.

Discussion:

Although this species agrees well with the diagnosis of the genus, as would be expected in an early member, it shows primitive features as compared to the type species which is of Wenlockian age. The cephalon is extremely like that of other species of *Sphaerexochus* but as compared to later species the distance between the basal lateral glabellar lobes is relatively less, and the eye is placed a little further forwards. As reference to Plate 33, figures 7-8 and Plate 30 figures 10-11 (*S.* aff. *mirus*) will show the form of the thoracic segments is hardly different to these two species which are widely separated in time. The pygidium shows primitive features, these being the presence of a third axial ring (in later species this ring and the terminal piece have become fused), the remnant articulating half rings anchylosed in axis, and the free spines which in later species become shorter and lobate in form.

Sphaerexochus eurys Tripp, 1962 from the 'confinis' Flags of the same area, which occurs earlier in time than the species here redescribed is morphologically more specialised in some respects. In S. eurys there is only a trace of one anchylosed half ring between the anterior and mid axial rings of the pygidium, and the spines are more lobate in form. The third axial ring, however, is much more clearly delimited in this species than in S. balclatchiensis, and this indicates that within this genus, as in others in the Cheiruridae, there is a plexus of developing characters.

Sphaerexochus calvus M'Coy, 1846

Plate 34, figs. 1-10.

1846 Sphaerexochus calvus M'Coy, p. 44, Pl. IV, fig. 10

1853 Sphaerexochus mirus, Salter, Pl. III, figs. 14-15.

1854 Sphaerexochus angustifrons, Angelin, Pl. XXXVIII, fig. 16a. non 17. (Pl. XXXVIII, fig. 16, Pl. XXII, fig. 8.)

1864 Sphaerexochus mirus, Salter, Pl. 6, figs. 26a-b.

1881 Sphaerexochus angustifrons, Schmidt, p. 189. Pl. IX, figs. 17a-b, Pl. XVI, fig. 38.

1896a Sphaerexochus latirugatus, Reed, p. 423, Pl. XX, fig. 12.

Material:

RSM 1870 12 1173B-F; 1870 12 893a.

Horizon and locality:

Chair of Kildare Limestone, Kildare.

Description:

Cephalon almost circular in outline in dorsal view, the near vertical very small cheeks hardly visible, highly convex. Glabella very tumid a little wider (tr.) than long. Basal lobes circumscribed, ovate, elongated on a line running approximately 45° to the transverse direction, a little inflated independently of the general glabellar convexity. 1S wide and deep, running from axial furrow slightly obliquely forward before curving back to run abaxially at a very small angle to the exsagittal direction, here widening and becoming less distinct. Quadrate tongue-shaped portion of glabella between basal lobes, in smaller specimens as wide, in large specimens wider than the greatest dimension of 1L. 2S and 3S on external mould as short, wide distinct furrows visible for one eig th to one tenth of the circumference of the glabella at that point, near vertical, running a little obliquely forwards. On internal mould these furrows much more distinct, visible for $\frac{1}{4}$ circumference of glabella. 3L a little wider (exs.) than 2L, both vertical and parallel sided. Occipital ring more than half width (tr.) of cephalon at that point, convex (tr. and sag.). Occipital furrow as wide (sag. and exs.) as occipital ring, a little wider, deeper and less distinct where it is joined by 1L. Axial furrow wide and deep, of the same width from adjacent to occipital ring to 3S where a fossula is present, anterior to this preglabellar furrow decreasing in width to sagittal line, everywhere these furrows overhung by glabella.

Genae very small and vertical. Free cheek not seen. Fixed cheek anterior to palpebral lobe narrow, between anterior section of facial suture and axial furrow; posterior to eye fixed cheek, a triangular area composed of a parallel sided posterior border, a wide distinct posterior border furrow, a furrow running from behind posterior of palpebral lobe along the posterior section of facial suture, and between these furrows and the axial furrow a very small triangular based pyramid of cheek, its apex near the junction of posterior border furrow and axial furrow.

Palpebral lobe opposite posterior of 2L. Anterior section of facial suture curves in a wide arc first away from axial furrow then approaching preglabellar furrow to cut anterior margin near sagittal line. Posterior section curves back in a small arc to cut the posterior lateral margin of cephalon.

Surface of shell everywhere except in the various furrows covered by small, closely packed granules. Furrows have minute granules.

Pygidium subtriangular in outline, ratio of greatest width (tr.) to length (excluding articulating half ring) 2:1. Posterior margin lobate. Axis tapering backwards, composed of two rings and a triangular terminal piece as long (sag.) as the two rings. Posterior of axial rings narrower (tr.) and wider (sag.) than anterior, both convex (tr. and sag.), separated from each other, and the posterior from the terminal piece by broad distinct furrows which narrow and deepen exsagittally. Articulating half ring intermediate in width (tr. and sag.). Pleural portions with ridges, the anterior most distinct, the posterior two pairs less distinct. Anterior pleural ridge longest, curved, running at a small angle to the transverse direction, second running at 45° to that direction, posterior running exsagittally, all three ending in rounded lobes at the margin. Axial furrow indicated adjacent to the two axial rings as a break in slope between ring and pleural ridge, adjacent to terminal piece as a wide indistinct furrow with a round pit $\frac{1}{3}$ way from anterior of this piece indicating the two segments which form the terminal piece. Surface of shell granulated like cephalon.

Discussion:

This Ashgillian species of which the type material has not been seen is morphologically more advanced than the two previously described within the genus. In *S. calvus* almost all trace of the anchylosed articulating half rings has disappeared, and the terminal piece of the axis is triangular; that it is formed of the third axial ring and the terminal piece is only betrayed by the pits placed laterally to it.

Albaedes shallochensis gen. nov. sp. (Reed, 1935).

Plate 33, figs. 9-10

1935 Sphaerexochus? shallochensis, Reed. Pl. 1, figs. 20, 20a.

Lectotype:

BM In36969, specimen preserved with shell showing eleven thoracic segments and the pygidium.

Horizon and locality:

Whitehouse Group, (Ashgillian). Whitehouse Bay, Girvan, Ayrshire.

Diagnosis: (of genus and species)

Cephalon unknown. Thorax of (at least) eleven segments, with convex axis, pleurae unfurrowed with inner transverse, articulated portion, and outer backwardly curving free spine. Pygidium with two rings and terminal piece in axis, and five spines.

Description:

Thorax composed of (at least) eleven segments. Axis about $\frac{1}{4}$ width (tr.) whole, tapering backwards. Axial rings arched (tr.), convex (sag. and exs.), separated from the similarly arched and convex articulating half rings by wide, deep furrows. Pleurae unfurrowed, inner half transverse and parallel sided, outer half curving backwards and downwards as a free spine. Articulation of pleurae by a furrow on the posterior edge which is wide and shallow adaxially, narrowing abaxially and dying out where the pleurae begin to curve back and down, this furrow abutting against the anterior edge of the next posterior pleura.

Pygidium with transversely convex axis which tapers rapidly backwards, having three rings, and a small terminal piece which is indistinctly separated from the posterior spine of the pygidium, but which is distinctly delimited from the posterior axial ring by deep triangular pits laterally. Axial rings convex (tr. and sag.), decreasing in transverse width but increasing in sagittal width a little posteriorly. Interring furrows much more deep adjacent to the axial furrow than mesially. Axial furrow indicated adjacent to the axial rings by shallow depressions. Anterior pleurae of pygidium much of the form of the thoracic pleurae, but wider (exs.) and with outer free part relatively longer and bearing distally a median furrow. Mid and posterior pleural parts adjacent to mid and posterior axial rings are short and flat and are terminated by a single wide (tr.) and blunt spine at each side which reaches less far back than the anterior spines, and slightly less far back than the posterior spine which lies between them.

Axis of thorax with indistinct tuberculation, and fine perforations not always coincident with these. Internal part of pleurae very finely granulated, the free spines with coarse sparser tubercles. Pygidium everywhere granulated, most sparsely so on inner pleural region and most so on the free spines and the mid part of the axis.

Discussion:

As mentioned by Reed (1935, p. 57) the position of this species in the absence of knowledge of its cephalon is uncertain. It is certainly cheirurid in character, and does not fit any previously described genus. The form of the thoracic segments is of Sphaerexochinid type, and the new genus is referred to that subfamily. Its relation to the other genera of that subfamily is now known, but with its longer free anterior pygidial spines and the single terminal spine it does not appear to be closely related to *Sphaerexochus* or *Pompeckia* the only other sphaerexochinid genera which were present in Ashgillian times. Rather it must have developed from the earlier sphaerexochinid genera (e.g. *Xystocrania* or '*Kawina*' *sexapugia*) which have three pairs of free spines. It is separated from those Middle Ordovician genera by a large gap in time and until the range of *Albaedes* is known to go back into Caradocian times, or intermediate forms are found, the question must remain in doubt.

Subfamily DEIPHONINAE, Raymond, 1913.

Type Genus:

Deiphon, Barrande, 1850.

Diagnosis:

Glabella in front of 1L subspherically swollen, 1L lobes nodular and placed in combined occipital-basal lateral glabellar furrow. Genae small, major part composed of backwardly curving spines which bear short secondary spines. Hypostoma subrectangular in outline with convex median body. Rostral plate not present. Thorax of nine segments. Pygidium with four rings in the axis, and two pairs of spines, anterior pair of the form of the thoracic spines and probably arising from the failure of the posterior segment to separate from the protopygidium during the ontogeny of the individual. Posterior pair of pygidial spines long, between which the posterior margin is entire.

Genus Deiphon, Barrande, 1850.

Type species:

Deiphon forbesi.

Diagnosis:

Glabella, in front of combined occipital-basal lateral furrow which contains the nodular basal lobes, subspherically swollen. Genae spinose, curving backwards, bearing secondary spines on anterior edge; free cheeks very small. Eye small, surrounded by convex rim. No rostral plate. Hypostoma subrectangular in outline with convex median body. Thorax of nine segments with spinose pleurae not in contact with one another. Pygidium with anterior pair of spines of the form of the thoracic pleural spines and posterior to these a pair of long, curved, sometimes stout spines; axis of pygidium much modified showing four rings, three rudimentary and in a medial depression.

Deiphon forbesi, Barrande, 1850.

Plate 36, figs. 4-6

Material:

SM A3307-9.

Horizon and Locality:

Lower Wenlockian, Listice, Bohemia.

Discussion:

Until further topotype or the type material is seen no description of this species is attempted. A description based on more material is to be found in Whittard 1934, pp. 506-510.

Deiphon barrandei, Whittard, 1934.

Plate 35, figs. 1-11.

Plate 36, figs. 1-3.

1854 Deiphon forbesi, Murchison, p. 235.

1865b Deiphon forbesi, Salter, p. 88, Pl. VII, figs. 1-12.

1865 Deiphon forbesi, Salter and Woodward, Pl. IV, fig. 54.

1934 Deiphon forbesi var. barrandei, Whittard, p. 513, Pl. 16, figs. 1-4.

Holotype:

OUM 1. Wenlock Shales, Malvern, Worcestershire.

Paratypes:

OUM 2; SM A3296; BM 38953.

Horizons and localities:

Wenlock Shales of Malvern and Dudley areas. Wenlock Limestone of Dudley, Worcestershire.

Description:

Glabella in front of 1S subspherical, unfurrowed, a little wider (tr.) than long (sag.), although in smaller individuals this part of the glabella tends to be circular in dorsal view. Basal lateral glabellar lobes small, poorly developed, appearing as swellings in the wide deep furrow between the tumid part of the glabella and the occipital ring, this furrow composed of the occipital furrow and 1S. Occipital ring very convex (tr. and sag.) about half as wide as the widest part of the glabella (tr.). Axial furrow indistinct adjacent to the occipital ring, wide and shallow adjacent to the occipital furrow, 1L and 1S at apodemes, narrower and more distinct where is ascends adjacent to the palpebral lobe, passing in front of the glabella as wide, shallow pre-glabellar furrow, which arches upwards a little mesially. Abaxial to the occipital ring there is an articulating facet which abuts against the first thoracic segment. Running slightly obliquely outwards anteriorly from this facet is the posterior part of the fixed cheek, which is slightly convex dorsally. This portion of the fixed cheek meets the major spinose portion of the cheek behind the eye. Spinose cheeks slender in young specimens (tending to stoutening and swellings in larger specimens), curved, oval in section, nearly twice as long as the widest part of the glabella, curving first outwards then backwards, bearing $\frac{1}{3}$ way from glabella a secondary spine which points somewhat backwards, downwards and obliquely outwards.

Eye placed on anterior margin of spinose cheek separated from the glabella by a space which is relatively narrower in larger specimens. Palpebral lobe convex dorsally, forming a rounded border from which the eye projects. With a similar border on the free cheek, the eye surface is surrounded. Eye surface elongated in a direction parallel to the axial furrow where it is twice as long as wide.

Anterior section of facial suture runs from the eye close to the axial and pre-glabellar furrows around the front of the glabella. Posterior section of facial suture starts near the secondary spine on the cheek and runs obliquely backwards to cut the eye rim $\frac{1}{2}$-$\frac{1}{3}$ way from its anterior end. Glabella coarsely granulated especially posteromedially, genae more finely granulated.

Hypostoma longer (tr.) than wide, subrectangular in outline but narrowing posteriorly. Median body ovate, inflated, tapering posteriorly. Anterior border and border furrow narrow, curving around anterior of median body. Lateral and posterior border furrows deeper, the adjacent borders wide and convex, especially posterolaterally. Median body granulated, borders finely granulated.

Thorax of nine segments with convex (tr. and sag.) axial rings, and unfurrowed pleurae not in contact with one another. These free spines are slender, the anterior ones shorter and directed forwards, the sixth directed near transversely and the posterior ones curving backwards.

Pygidium with a posterior pair of stout spines which run transversely proximally before tapering and curving through more than 90°, and an anterior pair of spines of the form of the t horacic pleurae. These anterior spines and the associated axial ring are thought to have been neotonously retained in the pygidium. Axis of pygidium posterior to anterior axial ring formed of three rings the posterior two placed within a shallow oval depression.

Discussion:

As compared to the type species, D. barrandei differs in the following respects; the swollen part of the glabella tends to be wider (tr.) and long, the genae are more stoutly constructed, the posterior pygidial spines are stouter and although they run transversely proximally in larger specimens, in smaller specimens they run obliquely outwards posteriorly (in D. forbesi the posterior pygidial spines of even small individuals are transverse proximally, contrast Plate 36, figures 1 and 6.).

Additional material:

SM A3291 - 3306, A3310-11; BM I2727-8, In28843-5, 44208/1-3, 44209, 44266, 58952; BU ex Holcroft 131, 490, 507, ex Ketley 299, 309, 298 (= BU 63-5); GSM 49816.

Deiphon circularis sp. nov.

Plate 36, figs. 7-9.

1932 Deiphon cf. forbesi, Whittard, p. 880.

1934 Deiphon forbesi cf. var. dikella, Whittard, P. 517, Pl. XVI, figs. 5-6.

Holotype:

OUM C14771, internal mould of glabella and left fixed cheek.

Horizon and locality:

Venusbank Formation, Upper Llandoverian, Joseys Wood. SJ 36560213, Shropshire.

Diagnosis:

A species of Deiphon with glabella almost circular in dorsal view, distinct basal glabellar lobes, narrow (sag.) occipital ring and furrow, and spinose genae which are slender and curve markedly forwards proxim ally.

Description:

Glabella in front of 1S spherical, unfurrowed, outline in dorsal view almost circular. Basal lateral glabellar lobes triangular, elongate (tr.), distinctly marked off anteriorly and posteriorly by 1S and occipital furrow which converge and meet at inner angle of 1L about one fifth way across glabella at that point. 1S wider than occipital furrow abaxially, after joining forming a distinct narrow furrow which arches upwards aagittally due to the convexity of the glabella. Occipital ring convex (tr. and sag.), narrow (sag. and exs.), about $\frac{3}{4}$ as wide as the widest part of the glabella (tr.). Axial furrow wide and indistinct adjacent to occipital ring and 1L this latter only weakly delimited from the inner posterior part of the fixed cheek, adjacent to occipital furrow, tha axial furrow pitlike and deep, adjacent to 1S and postero-lateral part of tumid portion of glabella very deep and wide, anteriorly rising first vertically and then steeply to just behind widest part of glabella adjacent to that part of the fixed cheek adaxial to the palpebral lobe where, at the widest part of the glabella, it arches upwards and then downwards anteriorly continuing around the front of the glabella as a narrower, distinct and overhung preglabellar furrow.

Genae small, comprising a long spine which originates as a ridge adjacent to 1L, and runs obliquely forward to where it becomes a spine, then curving backwards and narrowing, bearing a small secondary spine which points obliquely abaxially forwards and down from the anterior edge of the main spine close to where the posterior section of the facial suture (not preserved) must have cut the margin of the cephalon. Posterior to the ridge on the fixed cheek, the posterolateral margin of the cheek is quadrate adjacent to the occipital ring and here probably bears an articulatory facet. Anterior to the cheek ridge a shallow furrow separates it from the raised convex part of the cheek which bears the palpebral lobe, this latter not preserved. Free cheek very small.

Posterior part of swollen portion of glabella apparently coarsely granulated, cheek spines (as seen from the external mould of a part of the ventral surface) finely and closely granulated.

Discussion:

The cranidia described by Whittard as D. forbesi cf. var. dikella (GSM 53479-80) probably belong to this species. It differs from D. barrandei in the shape of the glabella in dorsal view, the better developed basal lateral lobes, the narrower (sag.) occipital furrow, and the relatively wider (tr.) occipital ring.

Genus *Sphaerocoryphe* Angelin, 1854.

Type species:

Sphaerocoryphe dentata Angelin, 1854.

Diagnosis:

Basal lateral glabellar lobes nodular and well developed, glabella in front of 1S subcircularly swollen. Genae small; thorax of nine segments, pleurae with short weakly impressed transverse furrow composed of inner transverse articulated portion and shorter, free, curved spinose outer portion. Pygidium with anterior segment of the form of the thoracic segment, behind which there is indication of three axial rings, and a single pair of stout nearly exsagittally directed straight spines.

Sphaerocoryphe thomsoni (Reed, 1906).

Plate 37, figs. 1-5.

1865 Staurocephalus unicus, Salter, pars. p. 86, Pl. VII, fig. 22. non figs. 23-4.

1878 Staurocephalus maclareni, Etheridge, p. 39.

1878 Staurocephalus unicus, Nicholson and Etheridge, pars. Pl. VIII, figs. 9, 12-16 (non figs. 10-11) and p. 120, figs. 6A-B.

1906 Cheirurus (Sphaerocoryphe) thomsoni, Reed, pp. 146-8, Pl. XVIII, fig. 17; Pl. XIX, figs. 1-7.

Material:

BM In23465-9.

Horizon and locality:

Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire.

Description:

Cephalon elliptical in outline, dominated by swollen anterior part of glabella, which is subspherical in shape and oval in outline, a little more than half its sagittal length extending in front of the general outline of the cheeks. Posterior part of glabella comprises a pair of nodular basal lobes, anterior to which a broad shallow furrow separates them from the inflated part of glabella. Occipital ring highly convex (tr.), narrow (sag.) , as wide (tr.) as glabella across 1L, these basal lobes more distinct and rounded behind than in front. Occipital furrow broad, arched forward between basal lobes where it is shallow, becoming deeper and vertical behind the basal lobes. Axial furrow runs more or less exsagittally from adjacent to occipital furrow to 1L, anterior to this running obliquely abaxially; where occipital furrow and 1S meet distinct apodemes are developed; adjacent to expanded part of glabella this furrow very much overhung, as is the shallower distinct preglabellar furrow.

Genae convex (tr. and exs.), excluding spines triangular in outline, bearing pedunculated eyes. Posterior border distinct and ridge-like. Posterior border furrow transverse, wide and deep. Lateral border wider than posterior, lateral border furrow as wide and deep as posterior border furrow but less distinct. At genal angle border becomes very wide due to the presence of a broad based genal spine which curves backwards and downwards and is about as long as the sagittal length of the inflated part of the glabella. Anterior to genal spine there are two other fixigenal spines which are short, point slightly forwards and down, the anterior one placed immediately posterior to where the posterior section of the facial suture cuts the lateral margin. Free cheek very small comprising little more than a portion of the lateral border and border furrow.

Eye raised on a peduncle opposite the posterior of the inflated part of glabella (in smaller specimens relatively a little posterior to this), mid way between glabella and lateral margin, approximately $\frac{1}{3}$ as wide as the cheek at that point. Visual surface semicircular in plan, beneath visual surface peduncle vertical, cylindrical, narrower than the upper part bearing the visual surface. Facets concave with only narrow ridges between. Anterior section of facial suture runs more or less exsagittally, posterior section curves forward a little from the transverse direction.

Thorax composed of nine segments. Axis narrow, about $\frac{1}{4}$ width of thorax, highly convex (tr.) narrowing a little posteriorly. Axial furrow distinct, deepening between the segments. Inner part of pleurae (about half the whole in the anterior segments, less than this in the posterior ones), horizontal, convex (exs.), abaxially raised into a convex swelling; adjacent to this the pleurae constricted. Outer part of pleurae bending backwards and downwards, flat cylindrical in section, ending in separated blunt spines which point increasingly back in the posterior segments.

Pygidium excluding spines subrectangular in shape. Axis decreasing in transverse width backwards, in front slightly over $\frac{1}{3}$ width excluding spines, 4 rings visible plus a very small terminal piece, the anterior largest, most convex and most distinct. Axial and interpleural furrows represented as elongate pits which slope backwards from just between the axial rings onto the adaxial part of the pleural portions. Margin bearing two pairs of spines, anterior pair shorter and more curved continuing the trend of the thoracic spines. Posterior pair of spines connected to second axial ring by a low ridge across pleural region, much longer than anterior pair, straight, projecting at an angle of about 15° to the exsagittal direction, longer than the sagittal length of the pygidium. Margin of pygidium between anterior and posterior spines straight running abaxially anteriorly at a small angle to the exsagittal direction; between posterior pair of spines margin curved to angular forming an angle of about 160°. Posterior two axial rings have extensions as small short ridges on the pleural regions. From the ends of these ridges the pleurae slope down in a curve to the posterior margin.

Sphaerocoryphe globiceps (Portlock, 1843)

Plate 37, fig. 6.

1843 *Ceraurus globiceps*, Portlock, p. 257, Pl. 1, figs 7a-c.

1846 *Staurocephalus globiceps*, Barrande, pp. 53, 66.

1854 *Staurocephalus globiceps*, Morris, p. 115.

1865a *Staurocephalus globiceps*, Salter, Pl. 5, fig. 6.

1865b *Staurocephalus globiceps*, Salter, p. 85, Pl. VII, fig. 21.

1877 *Staurocephalus globiceps*, Woodward, p. 59.

1878 *Staurocephalus globiceps*, Nicholson and Etheridge, p. 117.

1940 *Sphaerocoryphe globiceps*, Begg, p. 298.

Lectotype:

GSM 35462, poorly preserved and damaged internal mould of complete individual.

Horizon and locality:

Caradocian, Desertcraight, Tyrone.

Description:

Cephalon elliptical in outline, with large subspherical anterior part of glabella protruding forwards, at least $\frac{3}{4}$ of its sagittal length extending in front of the general outline of the cheeks. Posterior part of glabella comprises a pair of nodular basal lobes, anterior to which a broad shallow furrow separates them from the inflated anterior part of the glabella. Occipital region damaged, occipital ring convex (tr. and sag.), $\frac{1}{4}$ width glabella at posterior margin, occipital furrow narrower than that which separates basal lobes from anterior part of glabella. Axial furrow deep adjacent to occipital ring and furrow, and furrow anterior to basal lobes, shallow adjacent to basal lobes.

Genae convex (tr. and exs.), excluding spines triangular in outline, bearing the damaged remains of eye peduncles. Posterior border wide and convex (exs.), running close to the transverse direction. Posterior border furrow transverse narrower than posterior border. Lateral border wider than posterior border, narrowing anteriorly, lateral border furrow apparently more distinct than posterior border furrow. At genal angle border very wide, bearing a large slender tapering genal spine which reaches at least as far back as the 5th axial ring of the thorax. Anterior to the genal spine there is a remnant base of a spine situated just anterior to the basal lobes in a transverse line. Course of facial suture not seen. Free cheek apparently very small.

Eye peduncle placed just anterior to the furrow anterior to basal lobes.

Thorax composed of 9 segments. Axis narrow, about $\frac{1}{4}$ width of the whole. Axial furrow apparently distinct. Inner part of pleurae (about $\frac{1}{2}$ the whole) horizontal, parallel sided, outer part tapering to backward curving spine.

Pygidium badly damaged, with at least three rings in the axis, and a pair of long, broad based spines longer than the genal spines which diverge then curve adaxially, with a rounded posterior margin between. Anterior to large spines, lateral margin of pygidium possibly has another short pair of spines.

Discussion:

This specimen is poorly preserved but seems to differ from *S. thomsoni* in the character of the borders and border furrows of the glabella, the position of the eye peduncles and the greater proportion of the gibbous anterior portion of the glabella which protrudes in front of the general outline of the cheeks. *S. globiceps* is, however, similar to *S. thomsoni*. As mentioned by Begg (1940) this species is clearly a member of the genus *Sphaerocoryphe* from its overall morphology.

Subfamily ACANTHOPARYPHINAE Whittington and Evitt, 1953.

Type species:

Acanthoparypha Whittington and Evitt, 1953.

Diagnosis:

A diagnosis is given in Whittington and Evitt, 1953.

Genus <u>Youngia</u> Lindstrom, 1885.

<u>Type species</u>:

<u>Cheirurus</u> <u>trispinosus</u> Young, 1868.

<u>Diagnosis</u>:

Glabella inflated, widest across basal lateral lobes with three pairs of lateral furrows, basal pair deepest and most distinct. Genae small, bearing long spines at the angles as does the occipital ring. Eye placed opposite 2L very dose to axial furrow. Two branches of proparian facial suture meet at an acute angle at the eye. Glabella very coarsely, genae less coarsely granulated.

Youngia trispinosa (Young, 1868).

Plate 38, figs. 1-8.

Plate 39, figs. 1-7.

1868 Cheirurus trispinosus Young. pp. 169-171, Pl. I, figs. 4-5, 6a-b.

1876 Cheirurus trispinosus, Armstrong and Young, p. 15.

1878 Cheirurus trispinosus, Nicholson and Etheridge, p. 105, Pl. VII, figs. 10-17.

1885 Youngia trispinosa, Lindstrom, p. 49.

1898 Youngia trispinosa,Reed, p. 212.

1906 Cheirurus (Youngia) trispinosus, Reed, pp. 148-9, Pl. XIX, figs. 8-12.

Lectotype:

HM A52/1, internal mould of cranidium.

Horizon and locality:

Penkill Group, Penkill, Girvan, Ayrshire.

Diagnosis:

As for genus.

Description:

(Internal moulds). Glabella inflated, ovate in outline, widest (tr.) approximately across $\frac{1}{3}$ way from anterior of 1L; three pairs of lateral glabellar furrows. Frontal lobe short (sag.), rounded in front. 3L and 2L subparallel sided, 3L narrower (exs.) than 2L. 1L two fifths the width of the glabella (tr.), inflated, circumscribed. 3S and 2S weakly impressed, gently curved, and sloping adaxially backwards, reaching about $\frac{1}{4}$ way across glabella. 1S wide, deep and distinct, abaxially parallel to 2S where this persists, then curving back, widening and shallowing and reaching occipital furrow two fifths way across glabella. Internal moulds 1S dies out before reaching occipital furrow). Where 1S reaches occipital furrow this is indented on its anterior margin. Occipital furrow wide and deep, curving concave forwards around posterior of 1L, where it also curves downwards, medially transverse. Occipital ring convex (tr. and exs.) curving strongly down laterally where it also narrows, medially bearing a stout spine at least as long as the exsagittal length of 1L and 2L. Axial furrow narrow and deep adjacent to occipital region and genae, preglabellar furrow shallower and less distinct, arching upwards mesially.

Genae small, subtriangular. Posterior border narrow adjacent to the occipital ring, rapidly widening towards genal angle which bears a long spine which curves upwards then down from its broad base to its tapering free end. Posterior border furrow narrow and distinct. Lateral border furrow indistinct near genal angle. Eye small placed opposite 2L. Facial suture proparian, anterior branch parallel to axial furrow, posterior section running from palpebral lobe forwards so that the angle between two sections is acute.

Surface of glabella very coarse granulations which were possibly perforated, genae with smaller tubercles.

Axial ring of thoracic segment referred to this species convex (tr.) with subparallel edges. A line of small tubercles curves from the anterior corner of the ring, backwards to near the posterior margin mesially and then forward again. Portion of ring anterior to this at a lower level than the part behind and may be part of the articulatory apparatus.

Discussion:

As mentioned in Chapter III, this genus formerly given a doubtful position in the Cheiruridae is here referred to the Acanthoparyphinae. The features which associate *Youngia* with that subfamily are the convex glabella with maximum width posteriorly, the eyes placed opposite 2L and close to the axial furrow, the two sections of the facial suture at an acute angle to one another, the spinose genal angles and occipital ring, and the coarse tuberculation of the cranidium.

Youngia aff. trispinosa

Plate 40, figs. 6-7.

Material:

HM A1111, internal mould of small cranidium.

Horizon and locality:

Saugh Hill Group, Newlands, Girvan, Ayrshire.

Description:

Cephalon semicircular in outline, about twice as wide (tr.) as long (sag.).

Glabella tumid, occupying more than $\frac{1}{3}$ of the cephalon behind, oval in outline, with three pairs of lateral furrows. Frontal lobe small, because of the convexity of the glabella approaching vertical . 3L and 2L of equal width (exs.), very slightly convex independently of the convexity of the glabella; 1L occupying more than 2/5 of the transverse glabellar width, oval in shape, wider (exs.) than 3L and 2L, angular adaxially, inflated. 3S slightly curved, short, and indistinct especially where it meets the axial furrow; 2S deeper, more distinct, except abaxially reaching almost $\frac{1}{3}$ way across glabella. 1L very distinct deep and wide, parallel to 2S as far as 2S persists then curving back in a quadrant of a circ le, and shallowing, to almost reach the occipital furrow, to which it is connected by a shallow depression. Occipital furrow wide and deep, somewhat overhung by the basal lobes, the adaxial part of 1S appearing as a shallow U-shaped depression in the anterior side of the furrow. Occipital ring narrow, subparallel sided, curving forward mesially and abaxially. Axial furrow very deep, wide and distinct adjacent to the occipital ring, shallowing a little forward and produced into a distinct pre-glabellar furrow.

Genae subtriangular, small. Posterior border narrow adaxially, widening rapidly towards the genal angle which is produced into a stout spine. Posterior margin of cephalon runs obliquely backwards abaxially from the occipital ring. Lateral border wide and convex near the genal angle. Posterior border furrow transverse, narrow, deep and very distinct adaxially, wider and distinct at the genal angle. Lateral border furrow wide and distinct near the genal angle.

Eye placed opposite mid 2L, reaching from 2S to 3S. Anterior section of facial suture runs parallel to the axial furrow; posterior section runs a little obliquely forward abaxially to the inner part of the lateral border where it turns back sharply through an angle of about 130° to cut the lateral margin opposite mid 1L.

The whole exsoskeleton is covered with tubercles, mainly of large size, but with smaller ones between.

Discussion:

This specimen will not be named until it is more completely known or until more material of it is known. It differs from _Y. trispinosa_ in that 3L and 2L are of equal exsagittal width, the lateral border furrow is distinct near the genal angle, and the basal lateral glabellar lobes reach further across the glabella. How many of these differences are due to the small size of the specimen it cannot be said.

Youngia moroides (Marr and Nicholson, 1888).

Plate 40, figs. 4-5.

1888 *Cheirurus* (*Pseudosphaerexochus*) *moroides*, Marr and Nicholson, pp. 722-3, Pl. XVI, figs. 9, 10, 10a.

Material:

SM A40325-6. Three fragments of glabellae on two pieces of rock.

Horizon and Locality:

Zone of *Phacops glaber*, Middle Skelgill Beds, Skelgill, Near Ambleside, Westmorland.

Discussion:

From the fragments available it is not possible to improve upon the short description given by Marr and Nicholson. A search has been made for further material of this species, but as yet has prooved unsuccessful. From the fragments it appears that the species more closely resembles *Y.* aff. *trispinosa* than *Y. trispinosa* in the shape of the basal lobe of the glabella.

Family ENCRINURIDAE Angelin, 1854.

Subfamily ONYCOPYGINAE subfam. nov.

Type genus:

Onycopyge Woodward, 1880.

Diagnosis:

Frontal lobe of glabella subspherically swollen, lateral lobes 2L and 3L indicated only laterally in a deep wide (sag.) pre-occipital furrow. Basal lobes 1L very small. Genae composed of small triangular inner portion and a long spine, bearing pedunculated eyes. Rostral plate present. Hypostoma with convex elongated (sag.) median body. Thorax composed of nine segments with a narrow axis, pleurae with horizontal, parallel sided adaxial part which bears a transverse furrow placed close to the posterior edge, and an outer spinose part which is a little longer than the inner part. Pygidium with 7(?8) axial rings and pleural ridges, the anterior two of these developed into long curved spines, and in addition a pair of short spines placed posteriorly.

Genus *Onycopyge* Woodward, 1880.

Type species:

Onycopyge liversidgei Woodward, 1880, from the Silurian of New South Wales.

Diagnosis:

As for subfamily.

Onycopyge liversidgei Woodward, 1880.

Plate 40, figs. 1-3

1880 Onycopyge liversidgei, Woodward, pp. 97-99, fig.

1917 Onycopyge liversidgei, Etheridge and Mitchell, p. 506.

1934 Onycopyge liversidgei, Whittard, pp. 521-524, Pl. XVI, figs. 10-11.

Lectotype (here designated):

BM I107a & b.

Horizon and locality:

'Silurian', near Bombala, New South Wales, Australia.

Description:

Cephalon dominated by globular anterior part of the glabella, this part of the glabella subspherical, a little wider (tr.) than long (sag.) in dorsal view. Posterior to the swollen part of the glabella lies a broad (sag.) pre-occipital furrow which is transversely convex. Laterally this furrow displays two short knob-like lobes on each side, placed immediately above the axial furrow. Axial ring short (tr. and sag.), less than half as wide as the widest part of the glabella, and narrower (sag.) than the pre-occipital furrow. Axial furrow poorly displayed, best seen adjacent to the posterior part of the swollen portion of the glabella, here it is deep; just anterior to the occipital ring the axial furrow bears a deep pit (apodeme).

Genae small consisting of a small triangular inner portion and a long genal spine. Posterior border from adjacent to the occipital ring curving forward, first fairly wide and slightly convex, half way from axial furrow becoming narrow and very convex, and from there widening to the genal angle. Genal spine stoutly constructed, curving and tapering posteriorly, bearing just posterior to its origin on the anterior-ventral edge a stout secondary spine which points downwards and forwards. Posterior border furrow very wide and deep, especially near the genal angle, anterior to this continuing as a wide less distinct furrow which runs exsagittally past the palpebral lobe and dies out on the anterolateral border of the cheek. Cheeks inside border furrows poorly preserved but appear to be flat. Palpebral lobe conical or pedunculate, placed near anterior border of cheek, just posterior to the widest part of the glabella. Proparian, the facial suture not well seen; anterior section from palpebral lobe runs obliquely inwards and under the swollen part of the glabella; posterior section appears to run transversely outwards from the palpebral lobe curving round under the anterolateral border of the cheek. Dorsal part of free cheek very small, ventrally swollen into a boss-like protruberance.

Counterpart of cephalon shows some of the ventral structures. Swollen part of glabella produced far in front of anterior border. From the courses of the sutures it appears that a rostral plate is present forming at least part of the anterior border and is possibly transversely elongate. Hypostoma with large, rounded, widely separated anterior wings which insert in the axial furrow adjacent to the posterior part of the swollen portion of the glabella. Median body of the hypostoma elongate sagittally bearing indistinct maculae placed far back.

Surface of glabella and hypostoma coarsely tuberculate, occipital ring and pre-occipital furrow finely granulated.

Thorax composed of 9 segments. Axis narrowing only slightly backwards, about one sixth the transverse width of the thorax composed of strongly convex (tr.) and narrow (sag.) rings. Pleurae composed of a horizontal, parallel sided adaxial part which is separated from the outer slightly longer spinose part by a small elongate boss. Each horizontal portion of pleura bears a transverse furrow near its posterior margin which separates off the articulatory ridge, this ridge fitting over another narrow transverse extension on the anterior edge of the pleura behind.

Surface of thorax coarsely tuberculate.

Axis of pygidium composed of 7(?8) rings, and ending with a rounded terminal peice. Adjacent to the anterior two rings backwardly curving pleural ridges extend laterally, from the axis first narrowing and becoming very convex before widening abruptly at the margin of the pleural region and giving rise each to a spine which is therefore broad based but which initially rapidly tapers then curves backwards and downwards in the manner of the free spines of the thoracic pleurae. Posterior to each of these pleural ridges is a lunate depression, the posterior of which bears very narrow pleural ridges originating adjacent to the third and fourth axial rings and which run obliquely back abaxially. Less distinct similar ridges originate adjacent to the fifth, sixth (the longest) and seventh axial rings, and run across the posterior part of the pleural region which slopes upwards from the posterior of the two lunate depressions. Posteriorly the pygidium bears a pair of short broad spines. Surface of pygidium at least on dorsal surface of anterior pleural ridge and ventral surface of anterior spine coarsely tuberculate.

Discussion:

Since the time Woodward described this genus and compared it with *Deiphon* and *Staurocephalus* it has always been placed within the Cheiruridae. Because of its resemblance especially to the former genus it has been placed within the subfamily Deiphoninae. On re-examination of the original specimen from which the genus was described it appears that the resemblance to *Deiphon* is only superficial, and characters are present which have necessitated the removal of *Onycopyge* from the Cheiruridae. The systematic position of this genus depends upon the interpretation of the characters tobe seen on this somewhat poorly preserved specimen, but they are believed to be as follows.

In the cephalon the structure of the glabella and the pattern of the sutures is all important. The glabella was thought by Whittard (1934, p. 522) to be like that of *Deiphon*, i.e. with an occipital ring and pre-occipital furrow which contained the small basal lateral glabellar lobes, anterior to which the rest of the glabella is swollen. Close examination of the specimen reveals two small boss-like lobes situated laterally in the pre-occipital furrow rather than a single one. It is here thought that these lobes are the 2L and 3L lobes, the 1L lobes either being not present or being very small and not seen in the poor preservation of the specimen. This opinion is supported by the character of the rostral plate, hypostoma and the associated sutures. The rostral and hypostomal sutures bounding the rostral plate are placed underneath the posterior portion of the inflated part of the glabella, and the anterior wings of the hypostome are seen to reach the axial furrow at a position level approximately with the posterior of the inflated part of the glabella. This anterior wing, and the fossula with which it is associated are normally in the Cheirurina adjacent to 3S or anterior to this. This indicates the inflated part of the glabella of Onycopyge is composed of the frontal lobe only. In Deiphon (see Pl. 35, fig. 1) the inflated portion of the glabella is composed of everything anterior to 1L, and this only overhangs the anterior border and does not extend far in front of it. In addition the rostral plate and hypostoma of Deiphon are situated underneath the anterior part of the swollen glabella.

It is not absolutely clear whether the rostral plate lies on the ventral surface of the inflated portion of the glabella or whether it forms the dorsal, or ventral, or both surfaces of an anterior border which lies underneath the swollen frontal lobe. From the specimen, however, it appears that the former case is more likely.

The hypostoma of _Onycopyge_ also is not Cheirurid in character. Although Whittard stated (1934, p. 523) the hypostoma to be 'clearly of the _Deiphon_ type' he said in the next sentence that it had a median body which was 'pear-shaped'. In addition the hypostoma of _Onycopyge_ has widely separated anterior wings and this along with the shape of the median body are not Cheirurid characters.

The thoracic segments divided unequally by a transverse furrow are not Cheirurid in character. The thorax as a whole, however, has a superficial resemblance to that of _Sphaerocoryphe_ for example, but the pleurae of that genus have the typical medially placed transverse line of pits.

Finally, the pygidium of _Onycopyge_, with 7 or 8 axial rings, and a similar number of pleural ridges is quite unlike any Cheirurid.

The characters of the cephalon, thorax and pygidium are therefore Encrinurid in type. The genus cannot be included within any of the subfamilies within this family and it has therefore been necessary to erect a new subfamily for its reception. The form of the pygidium alone is thought enough to exclude it from the Staurocephalidae to which the characters of the cephalon have some similarities.

APPENDIX 1a.

Species listed alphabetically after the type species under genera.

Subfamily CHEIRURINAE, Hawle and Corda, 1847.

Cheirurus Beyrich, 1845.

C. insignis Beyrich, 1845. Liteň Beds (Wenlockian), Bohemia.

C. bifurcatus Barrande, 1852. Wenlockian, Bohemia.

C. centralis Salter, 1853. Wenlockian, Welsh Borders.

C. dilatatus Raymond, 1916. Waldron Shale (Wenlockian), Indiana.

C. gotlandicus Lindström, 1885. Wenlockian, Gotland.

C. infensus Campbell, 1967. Henryhouse Formation (U. Wenlockian - L. Ludlovian), Oklahoma.

C. inusitatus sp. nov. Wenlockian, Welsh Borders.

C. latiaxis sp. nov. Wenlockian, Malvern.

C. longiaxiatus Weber, 1951. Upper Silurian, Ura Tyube, Tadzhikskaya, U.S.S.R.

C. longifrons sp. nov. Wenlockian, Malvern.

C. niagarensis (Hall, 1867). Niagaran (Wenlockian), New York State.

C. obtusatus Hawle and Corda, 1847. Liteň Beds, (Wenlockian), Bohemia.

C. patens Raymond, 1916a. Niagaran (Wenlockian), Illinois.

C. postremus sp. nov. Ludlovian, Northern England.

C. strabo Weber, 1932. Wenlockian, Turkestan, U.S.S.R.

C. tarquinius Billings, 1869. West Point Formation (Wenlockian), Arctic Canada.

C. uratubensis Weber, 1932. Wenlockian, Ura Tyube, Tadzhikskaya, U.S.S.R.

C. estonicus Mannil, 1958. Upper Llandoverian, Estonia.

C. gerassimovi Yanishevski, 1918. Upper Silurian, Urals.

Anasobella Campbell, 1967.

A. aspera Campbell, 1967. Henryhouse Formation (Upper Wenlockian - Lower Ludlovian), Oklahoma.

Bartoninus Tripp, 1962.

B. dispersus Tripp, 1962. confinis Flags (Lower Caradocian), Girvan Area.

B. acanthodes (Marr and Nicholson, 1888). Skellgill Beds (Upper Llandoverian), Northern England.

B. clasoni (Tornquist, 1905). Leptaena Limestone (Ashgillian), Sweden.

B. craigensis (Tripp, 1954). Craighead mudstone (Lower Caradocian), Girvan Area.

B. elongatus (Reed, 1931). Middle to Upper Llandoverian, Girvan Area.

B. elongatus (Cooper, 1930). Middle Ordovician, Eastern North America.

B. gelasinosus (Portlock, 1843). Caradocian, Ireland.

B. girvanensis sp. nov. Drummock Group (Ashgillian), Girvan Area.

B. glaber (Angelin, 1854). Leptaena Limestone (Ashgillian), Sweden.

B. helgoeyensis (Nicholaisen, 1961). 4b (Middle Caradocian), Heligoland.

B. kassini (Chugaeva, 1958). Anderkenyn Beds (Ashgillian), Kazakhstan.

B. keisleyensis (Reed, 1896a). Keisley Limestone (Ashgillian), Northern England.

B. percensis (Cooper and Kindle, 1936). Upper Ordovician, Quebec.

B. punctatus (Angelin, 1854). Leptaena Limestone, (Ashgillian), Sweden.

B. ruedemanni (Raymond, 1916b). Chazyan (Llandeilian), New York State.

B. sexermis (Öpik, 1937). Upper Rakvere (Upper Caradocian), Estonia.

B. sholeshookensis sp. nov. Sholeshook Limestone (Ashgillian), South Wales.

B. skelgillensis sp. nov. Skelgill Beds (Upper Llandoverian), Northern England.

B. subulatus (Linnarsson, 1869). Trinucleus Shale (Ashgillian), Sweden.

B. susceptus (Reed, 1931). Stinchar Limestone (Lower Caradocian), Girvan Area.

B. tornquisti (Warburg, 1925). Leptaena Limestone (Ashgillian), Sweden.

B. williamsii (M'Coy, 1849). Lower Llandoverian, Carmarthenshire.

B. fortis (Barrande, 1872). Ashgillian, Bohemia.

B. mitis (Salter and Blanford, 1865). Ordovician, India.

B. perlongus (Brøgger, 1882). 4b (Middle Caradocian), Sweden.

B. scutiger (Eichwald, 1860).

B. xiushanensis (Sheng, 1964). Lower Upper Ordovician, south-eastern Szechwan.

Ceraurinella Cooper, 1953.

C. typa (Cooper, 1953). Edinburg Limestone (Lower Caradocian), Virginia.

C. angusta (Raymond, 1925). Benbolt Limestone (Lower Caradocian), Virginia.

C. buttsi Cooper, 1953. Effna Limestone (Lower Caradocian), Virginia.

C. chondra Whittington and Evitt, 1953. Lincolnshire Limestone (Upper Llandeilian) Virginia.

C. ingrica (Schmidt, 1881). B2b (Upper Arenigian), Estonia.

C. intermedia (Kielan, 1955). Upper Ashgillian, Western Europe.

C. latifrons (Warburg, 1925). Leptaena Limestone (Ashgillian), Sweden.

C. magnilobata Tripp, 1967. Upper Stinchar Limestone (Lower Caradocian), Girvan.

C. polydorus (Billings, 1865). Table Head Limestone (Llanvirnian), Newfoundland.

C. longispina (Angelin, 1854). Caradocian, Gotland.

C. ornatus (Dalman, 1828).

C. platycanthus (Bradley, 1930). Kimmswick Limestone (Lower Caradocian), Missouri.

C. scofieldi (Clarke, 1897). Ordovician, Minnesota.

C. tenuisculptus (Bradley, 1930). Kimmswick Limestone (Lower Caradocian), Missouri.

Ceraurinus Barton, 1913.

C. marginatus Barton, 1913. Richmondian (Ashgillian), Ontario.

Cerauroides Prantl and Přibyl, 1947

C. hawlei (Barrande, 1852). Budňany Beds (Ludlovian), Bohemia.

C. propinquus (Münster, 1840). Silurian, Elbersreuth.

Ceraurus Green, 1832

C. pleurexanthemus Green, 1832. Lower Middle Ordovician, eastern North America.

C. binodosus Cooper and Kindle, 1936. Middle Ordovician, Quebec.

C. bispinosus Raymond and Barton, 1913. Black River Limestone (Lower Caradocian), Quebec.

C. bituberculatus Troedsson, 1929. Richmondian (Ashgillian), northern Greenland.

C. breviceps Cooper, 1953. Effna Limestone (Lower Caradocian), Virginia.

C. convexus Cooper, 1953. Effna Limestone (Lower Caradocian), Virginia.

C. dentatus Raymond and Barton, 1913. Trentonian (Middle Caradocian), Ontario.

C. elginensis Slocum, 1913. Ashgillian, North America.

C. globulobatus Bradley, 1930. Kimmswick Limestone (Lower Caradocian), Missouri.

C. granulosus Raymond and Borton, 1913. Chazyan (Llandeilian), Valcour Island.

C. hermanni Walters, 1924. Platteville Limestone (Caradocian), Iowa.

C. hudsoni Raymond, 1905. Chazyan (Llandeilian), New York State.

C. infrequans Phleger, 1933. Caradocian, California.

C. mantranseris Sinclair, 1947. Trentonian (Caradocian), Quebec.

C. milleranus Miller and Gurley, 1893, Lorrainian (Caradocian), Cincinnati.

C. misneri Foerste, 1909.

C. parvilobatus Troedsson, 1929. Cape Calhoun Beds (Ashgillian), Northern Greenland.

C. plattinensis Foerste, 1920.

C. pleurexanthemus montyensis Evitt, 1953. Trentonian (Caradocian), Virginia.

C. proicens Tripp, 1967. Upper Stinchar Limestone (Lower Caradocian), Girvan.

C. ruidus Cooper, 1953. Edinburg Limestone (Lower Caradocian), Virginia.

C. sagagei Walters, 1924. Elgin Formation (Ashgillian), Iowa.

C. simmonsi Hussey, 1926.

C. *tenuicornis* Raymond, 1925. Athens Group (Lower Caradocian), Tennessee.

C. *trapezoidalis* (Esker, 1964). Bromide Formation (Lower Caradocian), Oklahoma.

C. *tuberosus* Troedsson, 1929. Cape Calhoun Beds (Ashgillian), Northern Greenland.

C. *whittingtoni* Evitt, 1953. Trentonian (Caradocian), Virginia.

C. sp. Ross, 1967. Pogonip Group (Arenigian), California.

Cheiruretaerus gen. nov.

C. *falcatus* sp. nov. Lower Ludlovian, Staffordshire.

C. *bimucronatus* (Murchison, 1839). Wenlockian, Malvern.

C. *grammatus* (Weber, 1951). Upper Silurian, Turkestan.

C. *squarrosus* (Zenker, 1833). Wenlockian, Bohemia.

C. *squarrosus orientalis* (Maksimova, 1960). Upper Silurian, Kazankhstan.

C. *praecursor* (Frech, 1888).

C. *speciosus* (Hisinger, 1837). Wenlockian, Sweden.

Crotalocephalina Přibyl and Vaněk, 1964a.

C. *gibba* (Beyrich, 1845). Middle Lower Devonian, Bohemia.

C. *brevispinosa* (Erben, 1952). Upper Lower Devonian, Giessen, Western Germany.

C. *chlupaci* (Přibyl and Vaněk, 1962). Lochkov Formation, Bohemia.

C. *cruciata* (Hawle and Corda, 1947). Lower Devonian, Bohemia.

C. *gaertneri* (Alberti, 1962). Lower Devonian, Western Germany.

C. *globifrons* (Hawle and Corda, 1847). Middle Lower Devonian, Bohemia.

C. hexaspina (Maksimova, 1960). Lower Devonian, Kazankhstan.

C. interrupta (Barrande, 1852). Middle Devonian, Bohemia.

C. packhami (Strusz, 1964). Lower Devonian, New South Wales.

C. yavorskiyi (Tschernysheva, 1951). Upper Lower Devonian, Kuznetsk.

Crotalocephalus Salter, 1853.

C. articulatus (Münster, 1840). Wenlockian to Lower Ludlovian, Elbersreuth.

C. affinis affinis (Hawle and Corda, 1847). Lower Devonian to Middle Devonian, Bohemia.

C. affinis neomyops Lütke, 1961. Upper Middle Devonian, Harz.

C. bitumulatus Weber, 1951. Upper Ludlovian, Turkestan.

C. cordai (Barrande, 1846). Lower Middle Devonian, Bohemia.

C. insulsus Lütke, 1961. Upper Lower Devonian, Harz.

C. japonicus Kobayashi and Igo, 1956. Lower Devonian, Japan.

C. myops myops (Roemer, 1850). Upper Ludlovian.

C. myops scissa Weber, 1951. Upper Silurian, Turkestan.

C. parvus Tschernysheva, 1951. Lower Middle Devonian, Kuznetsk.

C. pengellii (Whidborne, 1889). Upper Middle Devonian, Southern England.

C. sternbergi sternbergi (Boeck, 1827). Lower Devonian, Harz.

C. sternbergi interruptus (Kayser, 1878). Lower Devonian, Harz.

C. tardus Maksimova, 1955. Lower Devonian, Siberia.

C. transiens (Bouček, 1934). Upper Budňany (Upper Ludlovian), Bohemia.

C. lenoiri Bergeron, 1887. Lower Devonian, France.

C. welleri (Raymond, 1916b). Niagaran (Ludlovian), eastern North America.

?*C. pauper* (Barrande, 1852). Middle Lower Devonian, Bohemia.

?*C. ednesdalensis* (Mitchell,).

?*C. sculptus* (Etheridge and Mitchell, 1917). Lower Devonian, New South Wales.

?*C. silverdalensis* (Etheridge and Mitchell, 1917). Lower Devonian, New South Wales.

Hapsiceraurus Whittington, 1954.

H. hispidus Whittington, 1954. Ashgillian, Baffin Island.

H. horridus (Troedsson, 1929). Upper Caradocian, Northern Greenland.

Iuba gen. nov.

I. retrospinosa sp. nov. Wenlockian, Shropshire.

I. bicuspidatus (Bouček, 1933). Kopanina Beds (Lower Ludlovian), Bohemia.

I. wychensis sp. nov. Upper Llandoverian, Shropshire.

I. sp. A. sp. nov. Lower Ludlovian, Shropshire.

Krattaspis Öpik, 1937.

K. viridatus Öpik, 1937. Lower Arenigian, Estonia.

Lehua. Barton, 1916.

L. vincula (Barrande, 1872) Upper Llanvirn, Bohemia.

?*L. argus* Whittington, 1963. Lower Head (Upper Arenigian), Newfoundland.

?*L. inexpectatus* (Reed, 1906). , India.

Macrogrammus Whittard, 1966b.

M. scylfense Whittard, 1966b. Lower Arenigian, Shelve.

M. sp. (Harrington and Leanza, 1947). Arenigian, Argentina.

Osekaspis Prantl and Přibyl, 1947.

O. comes (Barrande, 1872). Llanvirnian, Bohemia.

Paraceraurus Mannil, 1958.

P. aculeatus (Eichwald, 1860). C2-3 (Lower Caradocian), Estonia.

P. exsul (Beyrich, 1846). C1a (Upper Llanvirnian), Estonia.

P. gladiator (Eichwald, 1857). C1b (Llandeilian), Estonia.

P. macropthalmus (Kutorga, 1854) C1a (Upper Llanvirnian), Estonia.

P. spinulosus (Nieszkowski, 1857). C1c (Llandeilian), Estonia.

P. wahli (Öpik, 1928). C2c (Lower Caradocian), Estonia.

?P. dubius (Pompeckj, 1890). Chonetes Limestone (Llandeilian), Lithuania.

Pseudocheirurus Prantl and Přibyl, 1947.

P. beyrichi (Barrande, 1846a). Budňany Formation (Ludlovian), Bohemia.

P. sp. A. sp. nov. Penkill Group (Upper Llandoverian), Girvan Area.

P. sp. B. sp. nov. Camregan Group (Upper Middle Llandoverian), Girvan.

Remipyga Whittington, 1954.

R. glabra Whittington, 1954. Sillimans Fossil Mount (Ashgillian), Newfoundland.

R. daedalus (Cox, 1933). Richmondian (Ashgillian), Baffin Island.

R. icarus icarus (Billings, 1860). Ashgillian, Anticosti Island.

R. icarus noduliferous (Roy, 1941). Sillimans Fossil Mount (Ashgillian)(Newfoundland).

R. meekanus (Miller, 1889). Ashgillian.

?*R. confluens* (Barton, 1913). Upper Trentonian (Middle Caradocian), Ontario.

?*R. jakovlevi* (Chugaeva, 1958). Anderkenyn Beds (Ashgillian), Kazankhstan.

?*R. nuperus* (Billings, 1866). Ashgillian, Anticosti Island.

?*R. pompilius* (Billings, 1865). Ashgillian, Anticosti Island.

?*R. trentonensis* (Barton, 1913). Lower Trentonian (Caradocian), Ontario.

Subfamily CYRTOMETOPINAE Öpik, 1937.

__Cyrtometopus__ Angelin, 1854.

__C.__ __clavifrons__ (Dalman, 1827). Upper Arenigian, Estonia.

__C.__ __affinis__ Angelin, 1854. Llanvirnian, Sweden.

__C.__ __diacanthus__ Angelin, 1854. Llandeilian, Sweden.

__C.__ __elatifrons__ Krause, 1894.

__C.__ __priscus__ Tjernvik, 1956. Upper Planilimbate Limestone (Arenigian), Sweden.

__C.__ __verrucosus__ Brøgger, 1882. Lower Ordovician, Sweden.

?__C.__ __pacificus__ Kobayashi, 1934b.

?__C.__ __primagena__ __primagena__ Angelin, 1854. Lower Ordovician, Sweden.

?__C.__ __primagena__ __lamanskii__ Schmidt, 1907. Lower Ordovician, Estonia.

__Actinopeltis__ Hawle and Corda, 1847.

__A.__ __globosa__ (Barrande, 1846). Zahořany Formation (Middle Caradocian), Bohemia.

__A.__ __barrandei__ Keilan, 1959. Králův Dvůr Formation (Ashgillian), Poland.

__A.__ __completa__ (Barrande, 1872). Zahořany Formation (Middle Caradocian), Bohemia.

__A.__ __gryphus__ (Barrande, 1872). Králův Dvůr Formation (Ashgillian), Bohemia.

__A.__ __insocialis__ (Barrande, 1852). Upper Králův Dvůr Formation (Ashgillian,) Bohemia.

__A.__ __wattisoni__ Curtis, 1961. Ordovician, Portugal.

__A.__ sp. a. Kielan, 1960. Upper Ashgillian, Poland.

__A.__ sp. b. Kielan, 1960. Upper Ashgillian, Poland.

Cyrtometopella Nikolaisen, 1961.

C. askerensis Nikolaisen, 1961. 4aB (Lower Caradocian), Norway.

C. rosenthali (Schmidt, 1881). Kukkers Formation (Lower Caradocian),

C. tumula Nikolaisen, 1961. Ampyx Limestone (Lower Caradocian), Norway.

?C. aries (Eichwald, 1843). C1 (Llandeilian), Estonia.

?C. sphaericus (Esmark, 1833). Middle Ordovician, Sweden.

?C. sulcata (Thorslund, 1940). Chasmops Series (Caradocian), Sweden.

Eccopotochile Hawle and Corda, 1847.

E. clavigera (Beyrich, 1845). Middle Ordovician, Bohemia.

E. quilleri Tromelin, 1875.

E. marianus (de Verneuil and Barrande, 1855). Middle Ordovician, France.

?E. scrobiculatus (Angelin, 1854). Middle Ordovician, Sweden.

Eccoptochiloides Prantl and Přibyl, 1947.

E. tumescens (Barrande, 1852). Caradocian, Bohemia.

E. scuticauda (Barrande, 1846). Caradocian, Bohemia.

Pateraspis Prantl and Přibyl, 1947.

P. pater (Barrande, 1872). Šárka Beds (Llandeilian), Bohemia.

Placoparina Whittard, 1940.

P. sedgwicki (M'Coy, 1849). Llandeilian, Shelve.

Pseudosphaerexochus Schmidt, 1881.

P. hemicranium (Kutorga, 1854). C1a-c (Landeilian), Estonia.

P. approximatus (Eichwald, 1860).

P. bulbosus Nicholaisen, 1965. 4b (Middle Caradocian), Norway.

P. chazyensis Raymond, 1905. Chazyan (Upper Llanvirnian), New York.

P. conformis (Angelin, 1854). Leptaena limestone, (Ashgillian), Sweden.

P. conformis major Warburg, 1925. Leptaena Limestone (Ashgillian), Sweden.

P. consimilis sp. nov. Upper Drummock Group (Ashgillian) Girvan Area.

P. densigranulatus Nikolaisen, 1965. 4bδ2 (Middle Caradocian) Norway.

P. elongatus Thorslund, 1940. Caradocian, Sweden.

P. girvanensis sp. nov. Upper Drummock Group (Ashgillian) Girvan Area.

P. juvenis (Salter, 1848). Sholeshook Limestone (Ashgillian), Pembrokeshire.

P. octacanthus (Angelin, 1854). Chasmops Limestone (Caradocian), Sweden.

P. octolobatus (M'Coy, 1849). Caradocian, Bala Area.

P. orvikui Mannil, 1958. C1c (Llandeilan), Estonia.

P. pahnschi Schmidt, 1881. D (Middle Caradocian), Estonia.

P. pectinifer (Barrande, 1872). Ashgillian, Bohemia.

P. platycranium (Kutorga, 1854). C1 (Llandeilian), Estonia.

P. ravni Olin, 1906. Ashgillian, Sweden.

P. roemeri Schmidt, 1881. F1 (Upper Ashgillian), Estonia.

P. tuberculatus Warburg, 1925. Leptaena Limestone (Ashgillian), Sweden.

P. tvaerensis Thorslund, 1940. Chasmops Limestone (Caradocian), Sweden.

P. wolkae Kielan, 1960. Upper Ashgillian, Poland.

P. sp. A. sp. nov. Ashgillian, Northern England.

P. sp. B. sp. nov. Drummock Group (Ashgillian), Girvan Area.

?*P. granulatus* (Angelin, 1854). Leptaena Limestone,(Ashgillian), Sweden.

?*P. praecursor* Regnell, 1941. Platilimbata Limestone (Lower Arenigian), Oland.

Reraspis Öpik, 1937.

R. plautini Öpik, 1937. Kukruse Beds (Lower Caradocian), Estonia.

R. kaljoi Mannil, 1958. Kukruse Beds (Lower Caradocian), Estonia.

Setacauda gen. nov.

S. cancrura (Salter, 1853). Ashgillian, Ireland and Northern England.

Stubblefieldia Prantl and Přibyl, 1947.

S. neglecta (Barrande, 1852). Králův Dvůr (Ashgillian), Bohemia.

S. verrucosa sp. nov. Drummock Group (Ashgillian), Girvan Area.

Zazvorkaspis Přibyl and Vaněk, 1964b.

Z. neutra (Barrande, 1872). Králův Dvůr (Ashgillian), Bohemia.

Subfamily PILEKIINAE Sdzuy, 1955.

Pilekia Barton, 1916.

P. apollo (Billings, 1864). Lower Ordovician, North America.

P. anxia Sdzuy, 1955. Tremadocian, Germany.

P. bohemica Kobayashi, 1934b. Tremadocian, Bohemia.

P. olesnaensis (Ruzicka, 1934). Tremadocian, Bohemia.

P. speciosa (Dalman, 1827). Lower Ordovician, Sweden.

?P. foveolatus (Angelin, 1854). Lower Ordovician, Sweden.

?P. trio Hintze, 1953. Arenigian, Utah.

Anacheirurus Reed, 1896b.

A. frederici (Salter, 1864). Tremadocian, Wales.

Emsurella Rozova, 1960.

E. humila Rozova, 1960. 'Upper Cambrian' (Tremadocian), Salair, U.S.S.R.

?E. laevigata Rozova, 1960. 'Upper Canbrian' (Tremadocian), Salair, U.S.S.R.

Emsurina Sivov, 1955.

E. sibirica Sivov, 1955. 'Upper Cambrian' (Tremadocian), Western Siberia.

E. fulita Rozova, 1960. 'Upper Cambrian' (Tremadocian), Salair, U.S.S.R.

E. minuta Rozova, 1960. 'Upper Cambrian' (Tremadocian), Salair, U.S.S.R.

Eocheirurus Rozova, 1960.

E. salairicus Rozova, 1960. 'Upper Cambrian' (Tremadocian), Salair, U.S.S.R.

E. probus Rozova, 1960. 'Upper Cambrian' (Tremadocian), Salair, U.S.S.R.

E. subtilis Rozova, 1960. 'Upper Cambrian' (Tremadocian), Salair, U.S.S.R.

Metapilekia Harrington, 1938.

M. bilirata Harrington, 1938. Lower Ordovician, Argentina.

Metapliomerops Kobayashi, 1934b.

M. extenuata (Raymond, 1924). Lower Ordovician, Vermont.

M. latidorsatus Raymond, 1937. Lower Ordovician, Vermont.

?Seisonia Kobayashi, 1934b.

S. sphericauda Kobayashi, 1934b. Lower Ordovician, Korea.

?Tesselacauda Ross, 1951.

T. depressa Ross, 1951. Lower Ordovician, Utah.

T. flabella Kobayashi, 1955. Lower Ordovician, British Columbia.

Subfamily SPHAEREXOCHINAE Öpik, 1937.

Sphaerexochus Beyrich, 1845.

S. mirus Beyrich, 1845. Wenlockian, Bohemia.

S. balclatchiensis Reed, 1914. Balclatchie Group (Middle Caradocian), Girvan Area.

S. beyrichi Lindström, 1885. Wenlockian, Gotland.

S. bilobatus Whittard, 1958. Whittery Shales, (Middle Caradocian), Shropshire.

S. bohemicus Barrande, 1872. Wenlockian, Bohemia.

S. bridgei Cooper and Kindle, 1936. Lower Ashgillian, Quebec.

S. calvus M'Coy, 1846. Ashgillian, Ireland, Northern England and Sweden.

S. desertus Billings, 1865. Middle Ordovician, Quebec.

S. discrepans Raymond, 1925. Upper Llandeilian, Virginia.

S. eurys Tripp, 1962. Confinis Flags (Lower Caradocian), Girvan Area.

S. filius Tripp, 1967. Stinchar Limestone. (Lower Caradocian), Girvan area.

S. hapsidotus Whittington and Evitt, 1953. Lincolnshire Limestone, (Upper Llandeilian) Virginia

S. hisingeri Warburg, 1925. Leptaena Limestone, (Ashgillian), Sweden.

S. idiotes Salter and Blanford, 1865. , Himalayas.

S. laciniatus Lindström, 1885. Wenlockian, Gotland.

S. latens Barrande, 1872. Upper Llandoverian, Bohemia.

S. laticeps Linnarsson, 1866. Ashgillian, Gotland.

S. latifrons Angelin, 1854. Upper Ordovician, Sweden.

S. parvus Billings, 1865. Caradocian, Quebec.

S. pulcher Whittington and Evitt, 1953. Edinburg Limestone, (Lower Caradocian), Virginia.

S. romingeri Hall, 1862. Wenlockian, Wisconsin.

S. scabridus Angelin, 1854. Upper Ordovician, Sweden.

S. tamyricus Balashova, 1960. 'Middle to Upper Ordovician, Tamyr'

S. tuberculatus Warburg, 1925. Leptaena Limestone (Ashgillian), Sweden.

?*S. brevimucronatus* (Münster, 1840). Wenlockian, Germany.

Albaedes gen. nov.

A. shallochensis (Reed, 1935). Whitehouse Group (Upper Caradocian), Girvan Area.

Cydonocephalus Whittington, 1963.

C. griphus Whittington, 1963. Lower Head (Middle Ordovician), Newfoundland.

C. mercurius (Billings, 1865), Lower Head (Middle Ordovician), Newfoundland.

C. prolificus (Billings, 1865). Lower Head (Middle Ordovician), Newfoundland.

C. prominulus Whittington, 1963. Lower Head (Middle Ordovician), Newfoundland.

C. scrobiculus Whittington, 1963. Lower Head (Middle Ordovician), Newfoundland.

C. torulus Whittington, 1963. Lower Head (Middle Ordovician), Newfoundland.

Heliomera Raymond, 1905.

H. sol (Billings, 1861). Table Head (Middle Ordovician), Newfoundland.

H. alacer (Whittington, 1963). Lower Head (Middle Ordovician), Newfoundland.

H. albata Whittington, 1963. Lower Head (Middle Ordovician) Newfoundland.

H. chipperfieldi Tripp, 1967. Stinchar Limestone (Lower Caradocian) Girvan Area.

H. raymondi Bradley, 1930. Kimmswick Limestone (Lower Caradocian), Missouri.

H. teres (Evitt, 1951). Lincolnshire Limestone (Upper Llandeilian), Virginia.

H. treta (Evitt, 1951), Athens Group (Lower Caradocian), Virginia.

Kawina Barton, 1916.

K. vulcanus (Billings, 1865). Lower Head (Middle Ordovician), Newfoundland.

K. approxima (Raymond, 1905). Chazyan (Middle Ordovician), New York State.

K. arnoldi Whittington, 1963. Lower Head (Middle Ordovician), Newfoundland.

K. billingsi (Raymond, 1905). Chazyan (Middle Ordovician), New York State.

K. divergens Reed, 1945. Lower Ordovician, Ireland.

K. limbata Whittington, 1963. Lower Head (Middle Ordovician), Newfoundland.

K. plana Chugaeva, 1964. Middle Ordovician, Northeastern U.S.S.R.

K. trentonensis (Clarke, 1897). Trentonian (Middle Caradocian), Minnesota.

Pompeckia Warburg, 1925.

P. wegelini (Angelin, 1854). Leptaena Limestone (Ashgillian), Sweden.

P. minor Warburg, 1925. Leptaena Limestone, (Ashgillian), Sweden.

<u>Xystocrania</u> Whittington, 1965.

<u>X</u>. <u>perforator</u> (Billings, 1865). Table Head (Middle Ordovician), Newfoundland.

<u>X</u>. <u>glaucus</u> (Billings, 1865). Table Head (Middle Ordovician), Newfoundland.

<u>X</u>. <u>unicornica</u> (Hintze, 1953). Arenigian, Utah.

Subfamily ACANTHOPARYPHINAE Whittington and Evitt, 1953.

Acanthoparypha Whittington and Evitt, 1953.

A. perforata Whittington and Evitt, 1953. Edinburg Limestone, (Lower Caradocian) Virginia.

A. chiropyga Whittington and Evitt, 1953. Lincolnshire Limestone, (Lower Caradocian) Virginia.

A. gibba (Angelin, 1854). Caradocian, Sweden.

A. gibba perconvexa (Nikitin, 1956). Lower Ordovician, N.E. Central Kazakhstan.

A. subcircularis (Bradley, 1930). Kimmswick Limestone (Lower Caradocian), Missouri.

A. tumida (Angelin, 1854). Middle Ordovician, Gotland.

A. tumida perconvexa (Ivshin, 1955). , N.E. Central Kazakhstan.

A. mutica (Schmidt, 1881). C1 (Lower Caradocian), Estonia.

?A. raripustulata (Weber, 1948). Caradocian, Urals.

Ainoa Mannil, 1958.

A. maeruensis Mannil, 1958. D2b (Middle Caradocian), Estonia.

Holia Bradley, 1930.

H. magnaspina Bradley, 1930. Kimmswick Limestone (Lower Caradocian), Minnesota.

H. cimelia Whittington and Evitt, 1953. Edinburg Limestone (Lower Caradocian), Virginia.

H. secristi Whittington and Evitt, 1953. Lincolnshire Limestone, (Upper Llandeilian) Virginia.

Nieszkowskia Schmidt, 1881.

N. cephaloceras (Nieszkowski, 1857). Llandeilian, Estonia.

N. ahti Öpik, 1928. C2 (Lower Caradocian), Estonia.

N. ahtioides Mannil, 1958. D1 (Middle Caradocian), Estonia.

N. capitalis Öpik, 1930. C2-3 (Lower Caradocian), Estonia.

N. cephaloceras longispina Thorslund, 1940. Chasmops Limestone, (Lower Caradocian) Sweden.

N. limuca Mannil, 1958. D2b (Middle Caradocian), Estonia.

N. mars Hudson, 1905. Chazyan, N.E. North America.

N. norvegica Nikolaisen, 1961. 4aB (Lower Caradocian), Norway.

N. numitor (Billings, 1866). Richmondian (Ashgillian), Quebec.

N. osmussaarensis Mannil, 1958. C1b (Lower Caradocian), Estonia.

N. satyrus (Billings, 1865). Chazyan, N.E. North America.

N. tallinnensis Mannil, 1958. C1c (Llandeilian), Estonia.

N. unica (Thomson, 1857). Lower Caradocian, Girvan Area.

N. variolaris (Linnarsson, 1869). Lower to Middle Caradocian, Sweden.

Pandaspinapyga Esker and Levin, 1964.

P. projecta (Esker, 1961). Kimmswick Limestone (Lower Caradocian), Missouri.

P. salsa Esker, 1964. Bromide Formation (Lower Caradocian) Oklahoma.

P. stubblefieldi (Bancroft, 1949), Harnagian (Lower Caradocian), Shropshire.

Youngia Lindström, 1885.

Y. trispinosa (Young, 1968). Penkill Group (Upper Llandoverian), Girvan Area.

Y. alaica Weber, 1932. Upper Silurian, Turkestan.

Y. douglasi Lamont, 1948. Llandoverian, Girvan Area.

Y. globiceps Lindström, 1885. Wenlockian, Gotland.

Y. inermis Lindström, 1885. Wenlockian, Gotland.

Y. moroides (Marr and Nicholson, 1888). Skelgill Beds (Lower Llandoverian) N. England.

Y. uralica Tschernyschew, 1893. Lower Devonian, Urals.

?Y. aspera (Weber, 1948). Upper Ordovician, Karatao, U.S.S.R.

?Y. canadensis (Billings, 1866). Ashgillian, Anticosti.

?Y. yakolevi (Weber, 1948). Upper Ordovician, Karatao, U.S.S.R.

?Hadrohybus Raymond, 1925.

H. dunbari Raymond, 1925. Normanskill Formation, (Lower Caradocian) Newfoundland.

Subfamily DEIPHONINAE Raymond, 1913.

Deiphon, Barrande, 1850.

D. forbesi Barrande, 1850. Wenlockian, Bohemia.

D. americana Weller, 1907. Wenlockian, Illinois.

D. angelini Warburg, 1925. Leptaena Limestone (Ashgillian), Sweden.

D. barrandei Whittard, 1934. Wenlockian, Shropshire.

D. circularis sp. nov. Upper Llandoverian, Shropshire.

D. dikella Whittard, 1934. Lower Llandoverian, South Wales.

D. globifrons Angelin, 1854. Wenlockian, Gotland.

D. longifrons Whittard, 1934. Upper Llandoverian, New York State.

D. pisum Foerste, 1894. Lower Silurian, Ohio.

Sphaerocoryphe Angelin, 1854.

S. dentata Angelin, 1854. Upper Ordovician, Sweden.

S. akimbo Tripp, 1967. Stinchar Limestone (Lower Caradocian), Girvan

S. arachniformis Bradley, 1930. Kimmswick Limestone (Lower Caradocian), Missouri.

S. atlantiades Öpik, 1937. E (Upper Caradocian), Estonia.

S. carinae Lindström, 1953. Lower Caradocian, Sweden.

S. erratica Mannil, 1958. F1 (Ashgillian), Estonia.

S. goodnovi Raymond, 1905. Chazyan (Middle Ordovician), New York State.

S. globiceps (Portlock, 1843), , Ireland.

S. hastata Begg, 1940. Superstes Shales (Lower Caradocian) Girvan Area.

S. hubneri Schmidt, 1881. C3 (Lower Caradocian), Estonia.

S. major Ruedemann, 1901. Trentonian (Middle Caradocian), New York State.

S. maquoketensis Slocum, 1913. Lower Ashgillian, Iowa.

S. psiles Tripp, 1954. Superstes Shales (Lower Caradocian), Girvan Area.

S. punctata (Angelin, 1854). Leptaena Limestone (Ashgillian), Sweden.

S. robustus Walcott, 1875. Trentonian (Middle Caradocian) Cincinnatti.

S. saba Tripp, 1962 Confinis Flags. (Lower Caradocian) Girvan Area.

S. salteri Billings, 1866. Ashgillian, Anticosti.

S. schmidti Mannil, 1958. F1a (Ashgillian), Estonia.

S. thomsoni Reed, 1906. Drummock Group (Ashgillian), Girvan Area.

? *S. cranium* (Kutorga, 1854) C1 (Lower Caradocian), Estonia.

Hemisphaerocoryphe Reed, 1896.

H. pseudohemicranium (Nieszkowski, 1859). Llanvirnian, Estonia.

H. granulata (Angelin, 1854). Leptaena Limestone (Ashgillian), Sweden.

H. inflata Nikolaison, 1961. Lower Caradocian, Norway.

H. pseudohemicranium dolichocephala (Schmidt, 1881). C3 (Caradocian), Estonia.

?*Ovalocephalus* Koroleva, 1959.

O. kelleri Koroleva, 1959. Middle Ordovician, Northern Kazakhstan.

Subfamily AREIINAE Prantl and Přibyl, 1947.

Areia Barrande, 1872.

A. bohemica Barrande, 1872. Králův Dvůr Beds (Ashgillian), Bohemia.

A. fritschi Barrande, 1872. Dobrotivá Beds (Llandeilian), Bohemia.

?A. suecica Olin, 1906. Ashgillian, Sweden.

Areiaspis Přibyl and Vaněk, 1964b.

A. barrandei (Perner, 1918). Šárka Beds (Llanvirnian), Bohemia.

APPENDIX 1b.

Nomina nuda listed with species in alphabetical order

Nomina nuda.

Actinopeltis caudata Lu, 1959.

Sphaerexochus conusoides Koroleva, 1953.

Cheirurus lunshanensis Grabau.

Ceraurinus punctatus Chugaeva, 1961.

Cheirurus sinicus Lu, 1959.

Crotalocephalus sternbergi racemifer Přibyl and Vaněk, 1964a.

APPENDIX 1c.

Species of doubtful position within the Cheiruridae listed alphabetically under genera.

Cheirurus bocagei Delgado, 1908.

A fragment of a cranidium figured, impossible to place from the illustration.

Cheirurus durocheri Roualt, 1847.

Publication not seen.

Cheirurus radiatus Lisogor, 1954.

A fragment of a pygidium of Middle Ordovician age showing three pairs of possibly long spines radially disposed. This species does not fit any described genus.

Cheirurus solitarius Billings, 1866.

Not figured and impossible to place from the short description.

Cheirurus venceslasi Delgado, 1908.

A poorly illustrated pygidium of Middle Ordovician age most closely resembling *Xystocrania*.

Cheirurus weberi Lomovitskaya

Publication not seen.

Ceraurinella peregrinus Dean, 1966.

This Arenigian species described from France appears not to belong to *Ceraurinella* as Dean believed. Its eleven thoracic segments have pleurae which are not furrowed, which would seem to exclude it from the Cheirurinae. The pygidium with large anterior spines and gradational posterior pairs of spines resembles that of early Ceraurinellids or

Bartoninids but this could be a case of parallel evolution of this species (which more probably is a Cyrtometopinid belonging to a new genus) and some of the Cheirurinae.

Ceraurinus biformis Maksimova, 1955.

Publication unobtainable.

Ceraurinus borealicus Balashova, 1960.

Publication unobtainable.

Ceraurinus kluevkaensis Balashova, 1960.

Publication unobtainable.

Ceraurinus nordicus Balashova, 1960.

Publication unobtainable.

Ceraurinus tamyricus Balashova, 1960.

Publication unobtainable.

Ceraurus hydei Weller, 1907.

Dr. Richardson of the Field Museum of Natural History kindly sent casts of the Holotype of this species. It is a very poor specimen showing a cephalon similar to that of Iuba, eleven thoracic segments of the type of the subfamily Cheirurinae, and a pygidium with an axis showing three rings, and a long pair of anterior spines. Behind this the pygidium is damaged so that the other spines (if any) are not visible. Mr. Mikulic of Milwaukee has informed me that he is dealing with this species and it is not considered further here.

<u>Typhloniscus</u> <u>princeps</u> Reed, 1908.

This specimen has not been seen by the author. It is a blind form of the Ashgillian Sholeshook Limestone, and as such does not fit the diagnosis of <u>Typhloniscus</u>, or of <u>Lehua</u> to which genus Barton (1916) referred it.

'<u>Eccoptochile</u>' <u>pectinatus</u> Salter MS.

This specimen is described in Chapter IV. It is probably a Cyrtometopinid belonging to an undescribed genus.

<u>Nieszkowskia</u> <u>kochii</u> Boll.

This species is listed by Reed (1896) in dealing with <u>Cheirurus</u>. No other reference to the species has been found.

<u>Sphaerocoryphe</u> <u>euurus</u> Kutorga, 1854.

From the illustration in Kutorga, it is impossible to place this species. It possibly belongs to <u>Pseudosphaerexochus</u>.

<u>Prosopiscus</u> <u>cheiruroides</u> Mansuy, 1920.

The poor illustrations of the fragments of this species indicate that it may be a Cheirurid. It possibly belongs to the Pilekiinae.

APPENDIX 1d.

Forms referred to the family Cheiruridae which are here considered to belong elsewhere.

Cheirurus singularis Howell and Sanford, 1947.

From the description and illustration of the species it is evident that it is the cephalon of a *Calymene*. It probably belongs to the pygidia described in the same paper as *Calymene niagarensis*.

Ceraurus rarus Walcott, 1877.

According to Raymond and Barton (1913) this specimen is the free cheek of an Encrinurid.

Ceraurinus longifrons Troedsson, 1929 pars.

The pygidium attributed to this species by Troedsson belongs to a species of *Remipyga*. The cephala with unfurrowed glabellae are of uncertain affinities.

Onycopyge liversidgei Woodward, 1880.

Considered to constitute a new monotypic subfamily of the Encrinuridae (See Chapter IV).

Hammatocnemis tetrasulcatus Kielan, 1960.

Possibly a new monotypic family. See Chapter III.

ADDENDUM.

Since the completion of the typing of this thesis, the following species has come to my notice.

Crotalocephalus copiosus (Haas, 1968). Lower Soganli Shale, (Siegenian), North western Turkey.

HAAS, W. 1968. Trilobiten aus dem Silur und Devon von Bithynien (NW-Türkei). *Palaeontogr.* 130 A. 60-207, pls. 26-37, 61 textfigs., 3 tables.

A PRELIMINARY ACCOUNT OF THE

TRILOBITES OF THE LLANDOVERIAN OF THE TYPE AREA.

A PRELIMINARY ACCOUNT OF THE

TRILOBITES OF THE LLANDOVERIAN OF THE TYPE AREA

This study, like that compsising the main part of this thesis, was suggested by Dr. J. Shirley. The trilobites of the Upper Ordovician, and also of the Wenlockian of the Welsh Borders and Wales are well known and illustrated, but no work has ever been published on the trilobites of the Llandoverian of the type area, and it is 30 years since Whittard published his work on the Upper Valentian trilobites of Shropshire.

To date, no more than a start has been made on this work. About three weeks have been spent in the field in the Llandovery area, and a collection of trilobites made. In addition, the trilobites in Prof. O. T. Jones's collection from the area have been looked at and noted down.

Trilobites are not very common in the Llandoverian rocks of the type area, and it is this which is probably the major cause of their not having been described. However, patience at many localities in the area is rewarded with the finding of fragments of trilobites usually preserved as internal and external moulds.

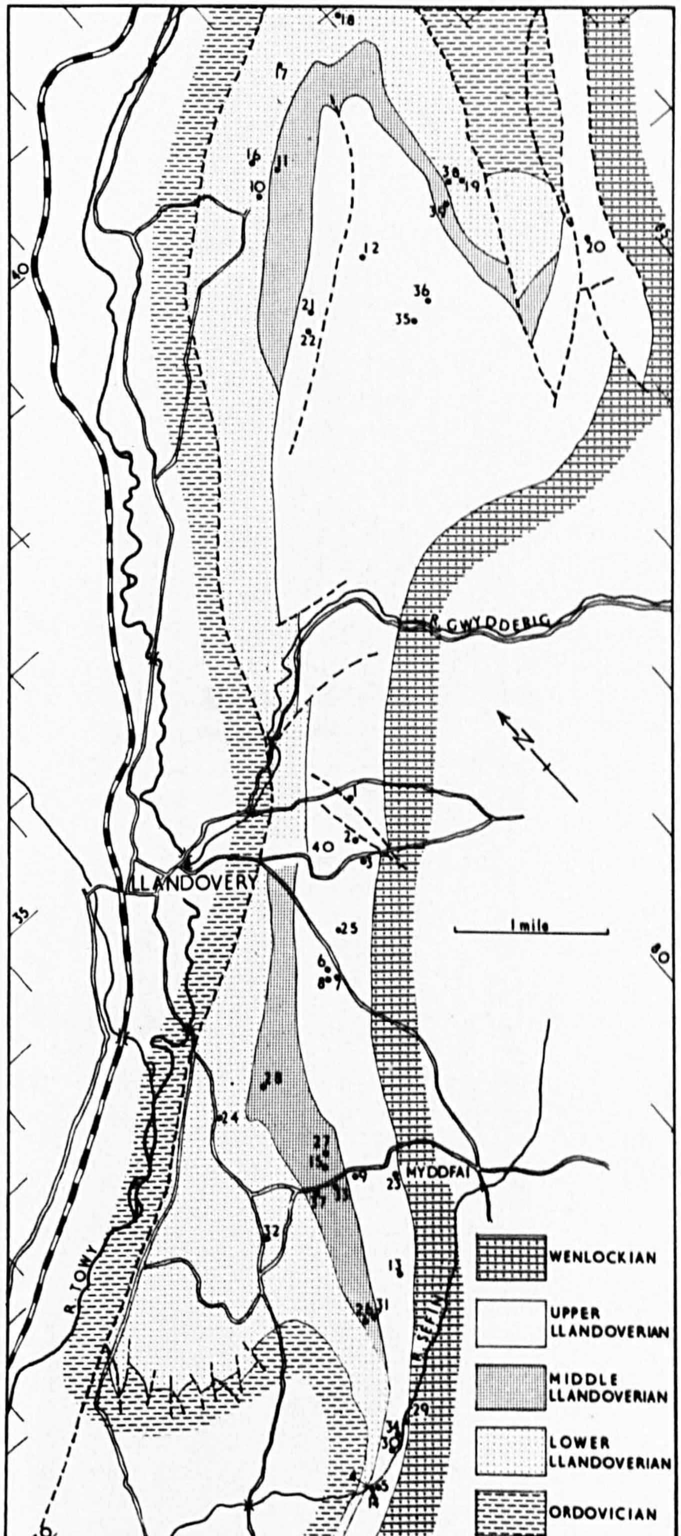
In common with all the fossils in the Llandoverian of the type area, the trilobites are rarest in the Lower Llandoverian only some 15 fragments as yet having been found which are identifiable at the generic level. The Middle Llandoverian has yielded some 25 specimens, but in the Upper Llandoverian the trilobites are most common, about 130 specimens, some complete, having been found.

As yet, few determinations beyond the generic level have been attempted. About 12 genera are represented of which three (Acernaspis, Encrinurus and Calymene) account for about 60% of the specimens.

Text figure 15 shows the 40 trilobite localities in relation to the subdivisions of the Llandoverian as published by Jones in 1925 and 1949. The appendix which follows, lists these localities with their grid reference, horizon and the genera with the number of fragments found there. Internal and external moulds of the same fragments are counted as one unit, as are individual moulds where the other was not found. Any fragment of a trilobite is counted as a unit so that no distinction is made between a complete specimen and a single thoracic segment, for example.

Text figure 15.

Map of the Llandovery District with the trilobite localities shown in relation to the subdivisions of the Llandoverian.



Text figure 15

APPENDIX

APPENDIX

All grid references should be preceeded by the letters SN.

Locality 1.	78783373.	Ca.	Acernaspis sp. nov. A	6
			Encrinurus sp. nov. A	6
			Calymene cf. replicata	3
			Bartoninus cf. elongatus	2
			Leonaspis sp. nov. A.	2
			Indet.	9
Locality 2.	78483338.	Ca.	Encrinurus sp. nov. A	2
			Indet.	1
Locality 3.	78263324.	C_3.	Leonaspis sp.	1
Locality 4.	74192816.	C_1.	Acernaspis sp. nov. A	1
			Encrinurus sp. nov. A	12
			Calymene replicata	11
			Bartoninus cf. elongatus	3
			Proetus sp.	1
			Illaenus sp. nov.	2
			Acasteid	1
			Lichid	1
			Indet.	1
Locality 5.	74202812.	C_1.	Calymene cf. replicata	3
Locality 6.	77453237	C_4.	Acernaspis sp.	1
			Encrinurus sp.	1
			Calymene sp.	1
			Leonaspis sp.	1
Locality 7.	77473229.	C_5.	Leonaspis sp.	2
			Indet.	2
Locality 8.	77393236.	C_5.	Leonaspis sp.	1
			Proetus sp.	1
			Indet.	3
Locality 9.	76083091.	C_1.	Acernaspis sp.	1
Locality 10.	82283902.	Ac.	Indet.	1

Locality 11.	82743911	Ba.	Encrinurus sp. nov. B	2
			Calymene sp. nov. A	4
			Leonaspis sp.	1
			Indet.	1
Locality 12.	82603790.	Cb.	Encrinurus sp.	1
			Calymene sp.	1
Locality 13.	75952960	C_4.	Indet.	1
Locality 14.	74142810	C_1.	Leonaspis sp. nov. A	1
			Proetus sp.	1
			Zelliskellinid	1
			Indet.	2
Locality 15.	76113111.	B_1.	Encrinurus sp. nov. B	1
Locality 16.	83503925.	Ac.	Acernaspis sp. nov. B	2
			Calymene sp.	2
			Proetus sp.	1
Locality 17.	83433999.	Ab.	Acernaspis sp.	1
			Proetus sp.	1
Locality 18.	84023995.	Ac.	Illaenus sp. nov.	1
Locality 19.	83683788.	Ac.	Calymene sp.	1
			Indet.	1
Locality 20.	84493656.	Ca.	Indet.	3
Locality 21.	81803779.	Ca.	Leonaspis sp.	3
Locality 22.	81673762.	Ca.	Leonaspis sp.	1
Locality 23.	76583050.	C_5.	Acernaspis sp.	1
			Calymene sp.	1
			Bartoninus sp.	2
			Youngia sp.	1
			Indet.	1
Locality 24.	75603222.	A_3.	Calymene sp.	1
Locality 25.	77733275.	C_4.	Acernaspis sp.	1
			Encrinurus sp. nov. A	8
			Bartoninus sp.	1
			Illaenus sp.	3

Locality 26.	75392950.	B_1.	Encrinurus sp.	1
			Calymene sp.	1
Locality 27.	76123132.	B_3.	Acernaspis sp.	1
			Indet.	1
Locality 28.	76213209.	B.	Encrinurus sp.	1
			Bartoninus sp.	1
			Illaenus sp.	1
			Indet.	1
Locality 29.	74762832.	C_1.	Acernaspis sp. nov. A	2
			Encrinurus sp.	1
Locality 30.	74502823.	C_1.	Acernaspis sp. nov. A	2
			Calymene replicata	3
			Homalonotus sp.	1
			Indet.	6
Locality 31.	75512951	B_1.	Leonaspis sp.	1
			Homalonotus sp.	1
Locality 32.	75113084.	A_3.	Acernaspis sp.	1
			Calymene sp.	1
Locality 33.	76013091.	B_3.	Encrinurus sp.	1
Locality 34.	74622828.	C_1.	Acernaspis sp.	1
			Dalmanites sp.	1
Locality 35.	82603704.	Cb.	Illaenus sp.	1
Locality 36.	82763711.	Ca.	Leonaspis sp.	1
Locality 37.	75793098.	B.	Calymene sp.	1
Locality 38.	83513794.	Ac.	Calymene sp.	1
Locality 39.	83553776.	B.	Leonaspis sp.	1
Locality 40.	'Near Troed-y-rhiw',	C_1.	1 mile ESE of Llandovery	
			Homalonotus sp.	1

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PLATES.

Plate 1.

Cheirurus centralis Salter, 1853.

Figures 1-2. *Cheirurus centralis*, BU 61 (ex Ketley 264); figured Salter, 1864, Pl. 6, figs. 11a and b. Woolhope Shale, Malvern, Worcs. 1. Dorsal view, x3. 2. Reverse view of 1. x3.

Figure 3. *Cheirurus centralis*. Lectotype GSM 36099; figured Salter, 1853, pl. 2, fig. 16. Wenlock Shale, Nelson's Tower Wood, Llandeilo, Carms. Internal mould of pygidium, x2.

Figure 4. *Cheirurus centralis*, SM A28582; Wenlock Shale, Dudley, Worcs. x2.

Figure 5. *Cheirurus centralis*. BU 410 (ex Hollier); figured Salter, 1864, Pl. 6, fig. 9. Wenlock Shale, Dudley, Worc. x2.

Figure 6. *Cheirurus centralis*, BM 44228; Wenlock Limestone, Malvern, Worc. x2.

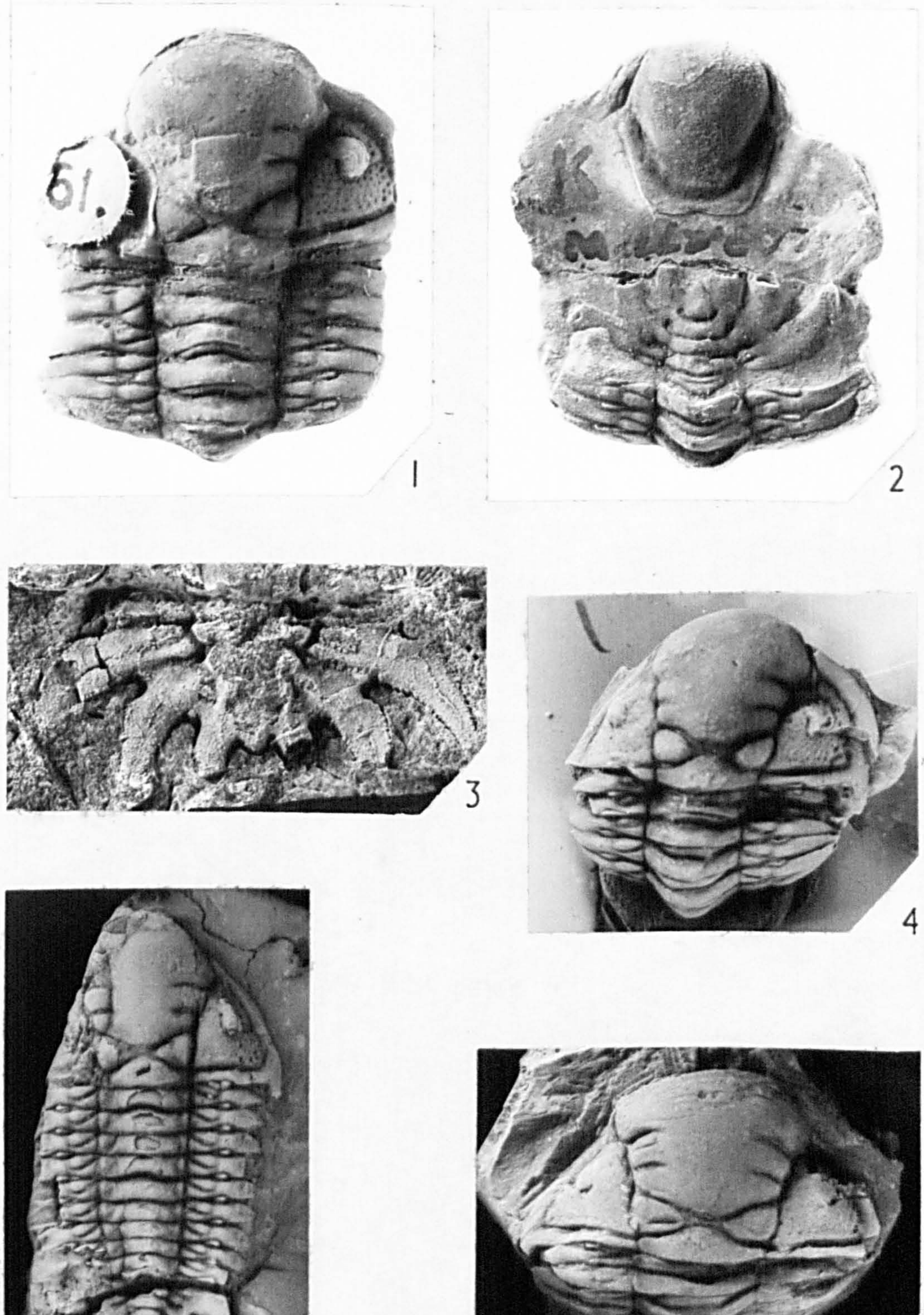

Plate 1

Plate 2.

Cheirurus longifrons sp. nov.

Cheirurus centralis Salter, 1853.

Cheirurus latiaxis sp. nov.

Figure 1. *Cheirurus longifrons*, Holotype GSM 36283; Wenlock Limestone, Malvern, Worcs. x2.

Figure 2. *Cheirurus centralis*, BU 268; Wenlock Shale, Malvern, Worcs. x2.

Figure 3. *Cheirurus centralis*, BM 59012; Wenlock Shale, Dudley, Worcs. x2.

Figure 4. *Cheirurus latiaxis*. Holotype BM I13649; Wenlock Shale, Malvern, Worcs. x2.

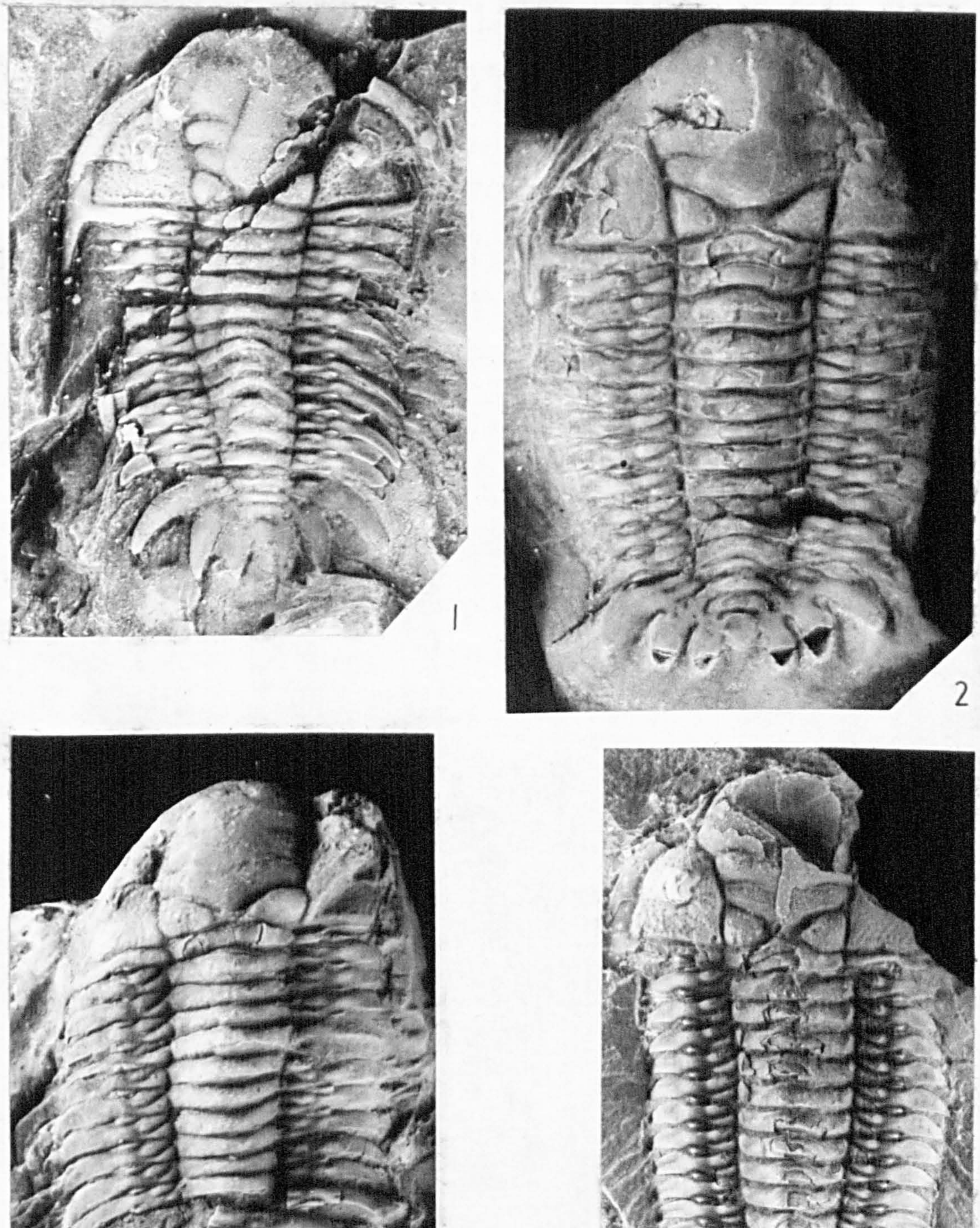

Plate 2

Plate 3.

Cheirurus cf. *insignis* Beyrich, 1845.

Cheirurus longifrons sp. nov.

Cheirurus centralis Salter, 1853.

Cheirurus inusitatus sp. nov.

Figure 1. *Cheirurus* cf. *insignis*, OUM C187; Wenlock Shale, Malvern Tunnel, Herefordshire. x2. Mentioned McKerrow *et al*. 1956, p. 506.

Figure 2. *Cheirurus longifrons*, GSM 36097; Wenlock Shale, Wyche, Malvern, Worcs. x3.

Figure 3. *Cheirurus centralis*, BU 62 (ex Ketley 263); figured Salter, 1864, Pl. 6, fig. 12. Woolhope Shale, Malvern, Worcs. x3.

Figures 4-5. *Cheirurus centralis*, GSM 36065; Woolhope Beds, Worcester Railway, Malvern, Worcs. 4. Lateral view, x2. 5. Dorsal view x2.

Figure 6. *Cheirurus inusitatus*, Holotype GSM 36094; Wenlock Shale, Wyche, Malvern, Worcs. x2.

Figure 7. *Cheirurus inusitatus*, BM It2274; Wenlock Shale, Dudley, Worcs. x2.

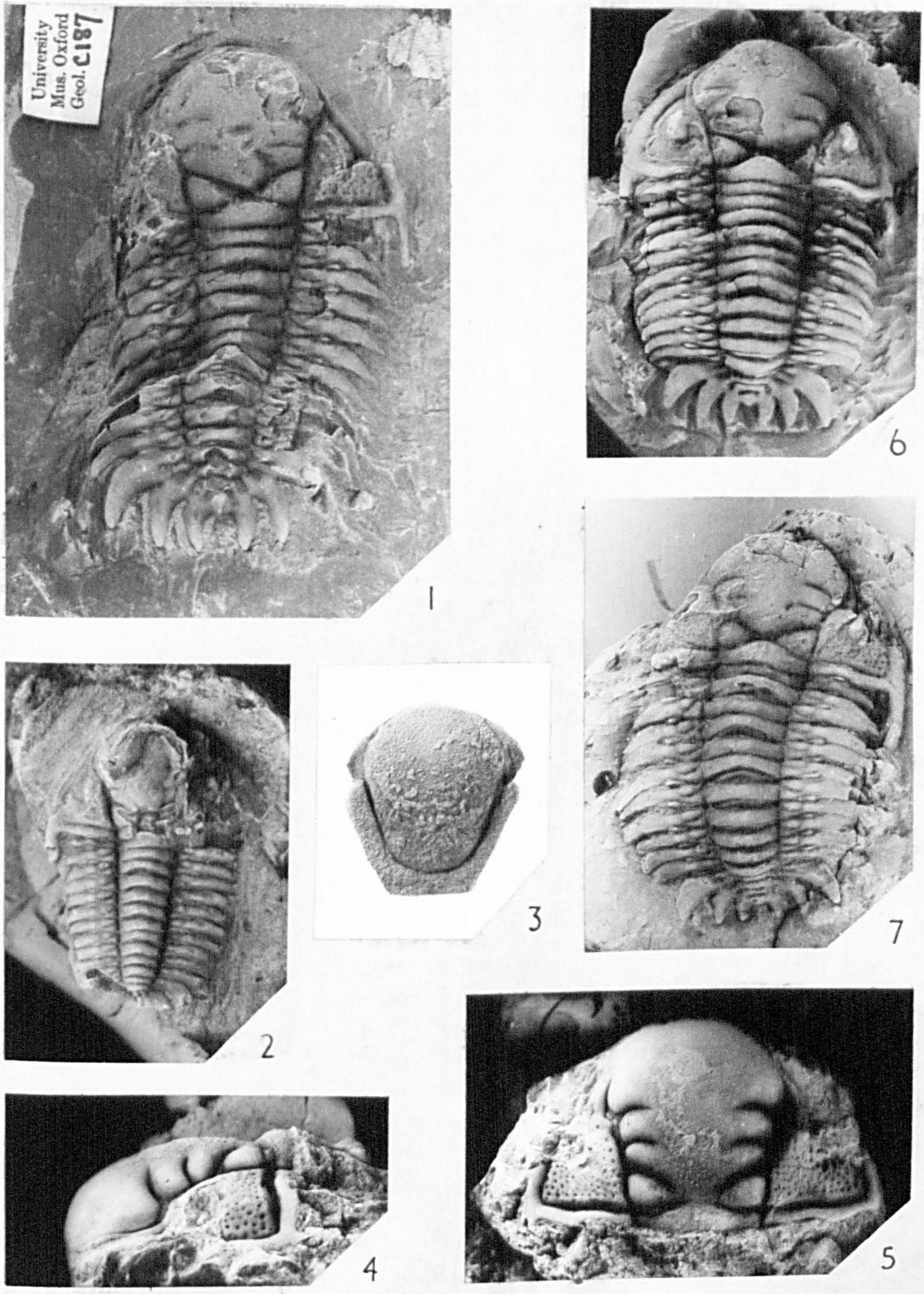

Plate 3

Plate 4.

Cheirurus postremus sp. nov.

?Crotalocephalina sp.

Cheirurus longifrons sp. nov.

Figures 1-2. Cheirurus postremus, Holotype SM A38677; Upper Coniston Flags, Helm Knot, Dent. 1. Dorsal view, x2. 2. Anterolateral view, showing eye ridge. x2.

Figures 3-4. ?Crotalocephalina sp. NU S451/1; high Lower Eltonian, Millichope, Salop. 3. Dorsal view, x6. 4. Lateral view x6.

Figures 5-6. Cheirurus longifrons, GSM 36103; Wenlock Limestone, Malvern, Worcs. 5. Dorsal view, x3. 6. Reverse view of 5 showing pygidium and part of hypostoma, x3.

Figures 7-8. Cheirurus postremus, BM 42905; Upper Silurian (?Kirkby Moor Flags), Benson's Knot, Kendal. 7. Dorsal view, x2. 8. Anterolateral view showing eye ridge, x3.

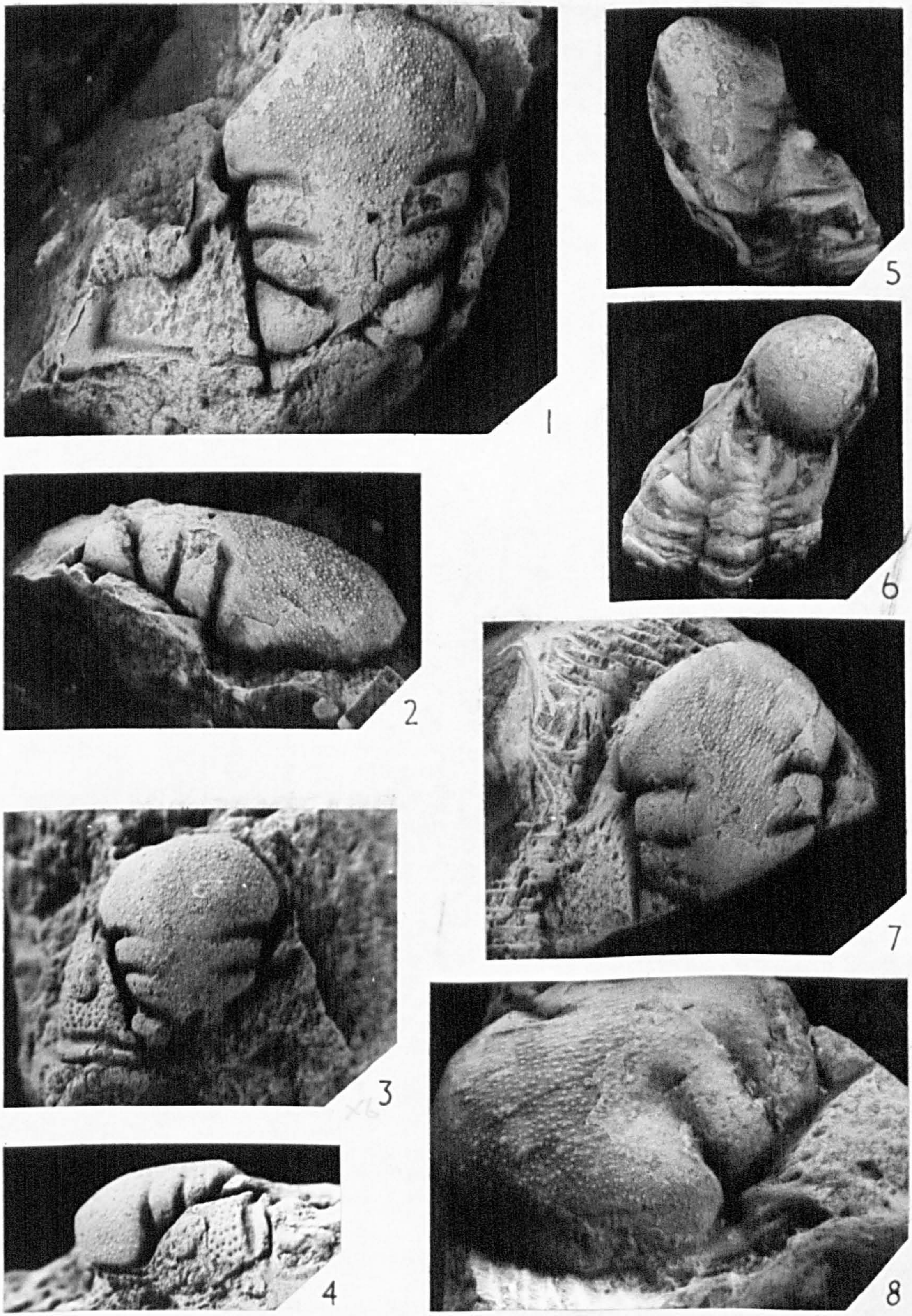

Plate 4

Plate 5.

Iuba retrospinosa gen. et sp. nov.

Figure 1. *Iuba retrospinosa*, BU 60 (ex Ketley 267); figured Salter, 1864, Pl. 6, fig 10. Wenlock Limestone, Dudley, Worcs. x2.

Figure 2. *Iuba retrospinosa*, GSM 33085; figured Salter, 1853, Pl. 2, fig. 3. Wenlock Limestone, Dudley, Worcs. x6.

Figure 3. *Iuba retrospinosa*, BM 1551; Wenlock Shale, Dudley, Worcs. ventral view of pygidium showing extent of doublure. x4.

Figure 4. *Iuba retrospinosa*, Holotype BU 413 (ex Holcroft 239); Wenlock ?Limestone, Dudley, Worcs. x2.

Figures 5-6. *Iuba retrospinosa*, BU 415 (ex Holcroft 208); Wenlock ?Limestone, Dudley, Worcs. 5. Ventral view of hypostoma. x2. 6. Lateral view. x2.

Figure 7. *Iuba retrospinosa*, BM It2246; Wenlock Limestone, Dudley Worcs. x2.

Figure 8. *Iuba retrospinosa*, SM A28583; Wenlock Shale, Dudley, Worcs. x4.

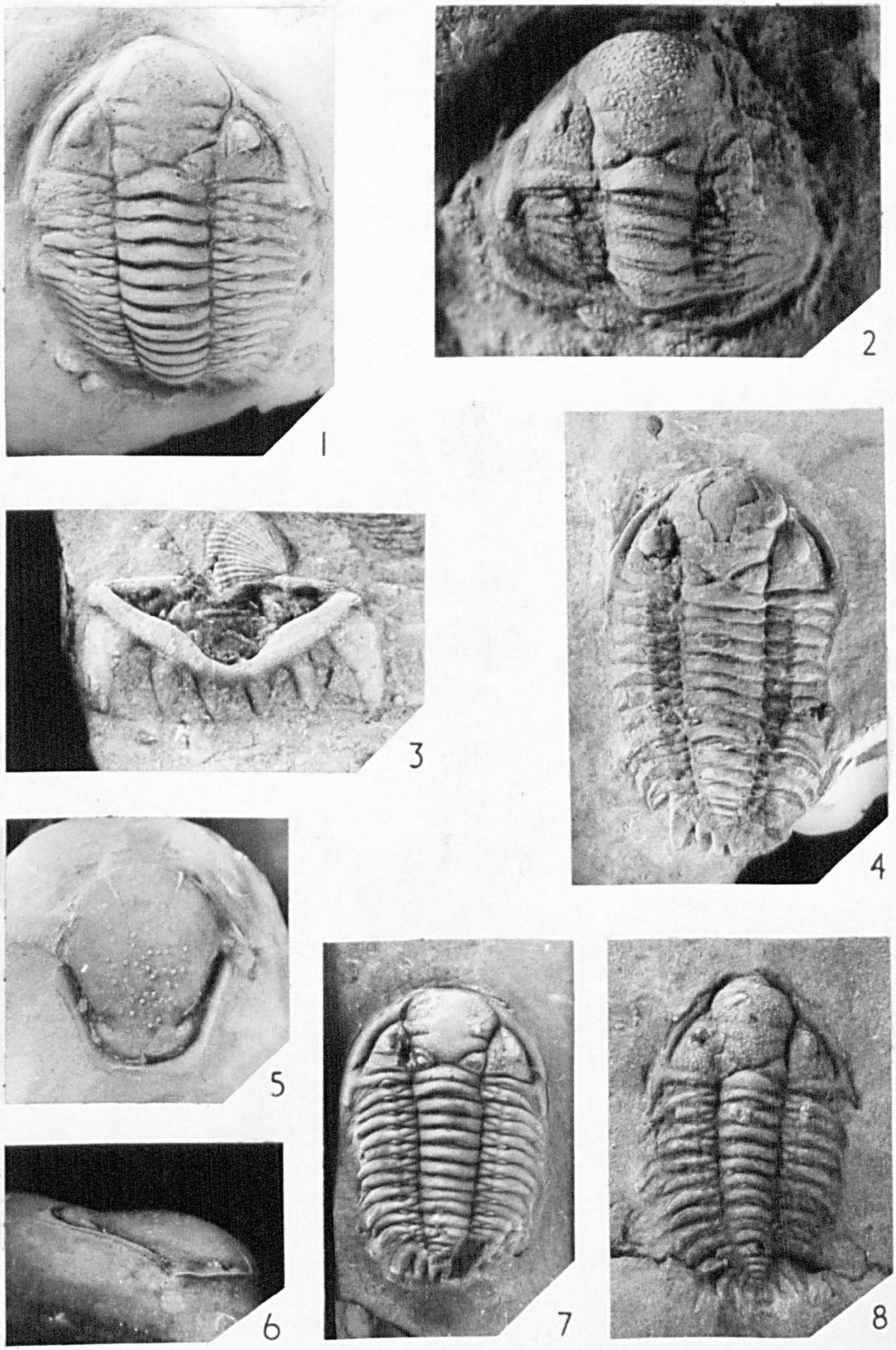

Plate 5

Plate 6.

<u>Iuba</u> <u>retrospinosa</u> gen. et. sp. nov.

Figure 1. <u>Iuba</u> <u>retrospinosa</u>, BU Ketley 396; Wenlock Limestone, Dudley, Worcs. x2.

Figure 2. <u>Iuba</u> <u>retrospinosa</u>, BU Ketley 575; Wenlock Limestone, Dudley, Worcs. x2.

Figure 3. <u>Iuba</u> <u>retrospinosa</u>, BM It2245; Wenlock Limestone, Dudley, Worcs. x2.

Figure 4. <u>Iuba retrospinosa</u>, SM A28581; Wenlock Shale, Dudley, Worcs. x2.

Figure 5. <u>Iuba</u> <u>retrospinosa</u>, BU Ketley 266; Wenlock Shale, Dudley, Worcs. x2.

Figure 6. <u>Iuba</u> <u>retrospinosa</u>, SM A10252; Wenlock Shale, Dudley, Worcs. x3.

Figufe 7. <u>Iuba</u> <u>retrospinosa</u>, BM It2255; Wenlock Limestone, Dudley, Worcs. x2.

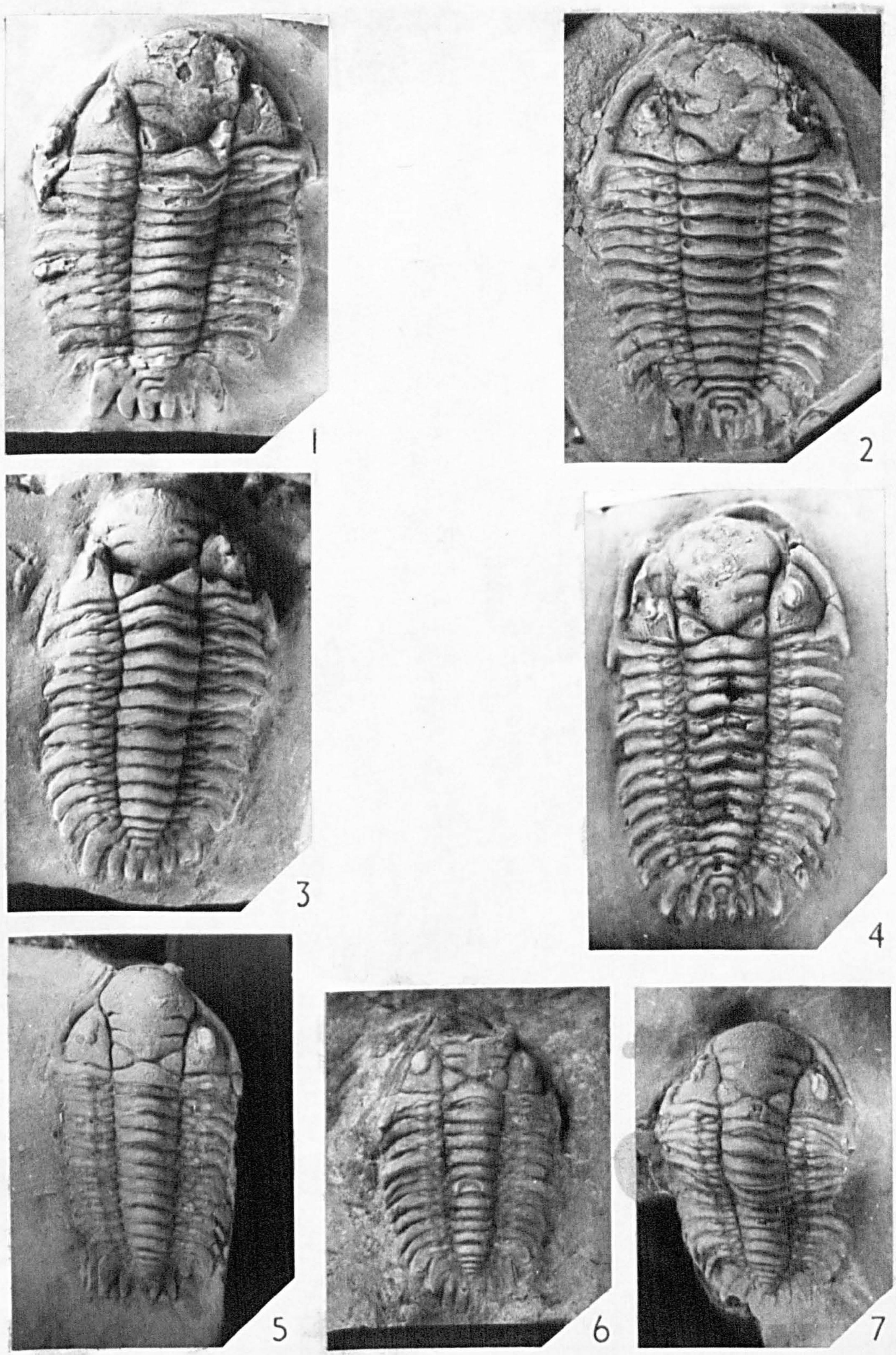

Plate 6

Plate 7.

Iuba gen. nov. sp. A.

Iuba wychensis gen. et sp. nov.

Iuba retrospinosa gen. et sp. nov.

Figures 1-2. *Iuba* sp. A., NU S579/3; high Lower Eltonian, Upper Westhope, Salop. 1. Dorsal view of broken cranidium, x6. 2. Anterolateral view, x6.

Figure 3. *Iuba?wychensis*, OUM C13172a; Purple Shales, Wall-Under-Haywood, Salop. (SO 51209276). Internal mould of small cranidium, x20.

Figures 4-5. *Iuba wychensis*, OUM C6543 a & b Holotype, Wyche Beds (C_6-Upper Llandoverian), Old Storridge Common Area, (SO 74055167), Salop. 4. Latex cast of external mould C6543b, x6. 5. Damaged internal mould, C6543a, x6.

Figure 6. *Iuba retrospinosa*, BU Ketley 338; Wenlock Shale, Dudley, Worcs, x2.

Figure 7. *Iuba retrospinosa*, SM A28585; Wenlock Shale, Dudley, Worcs. x2.

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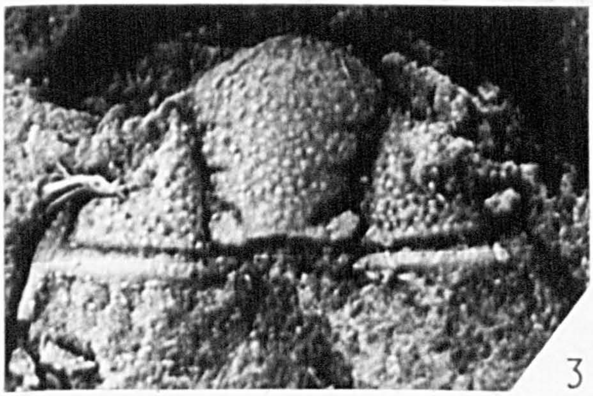

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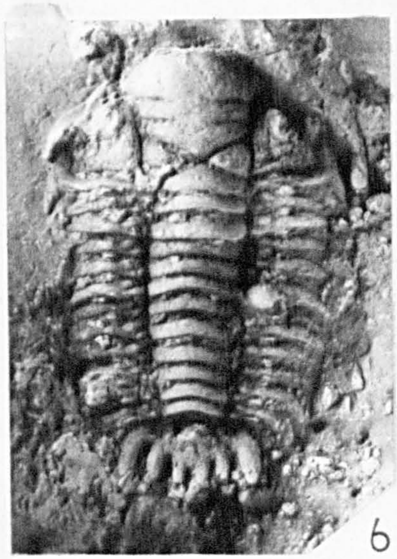

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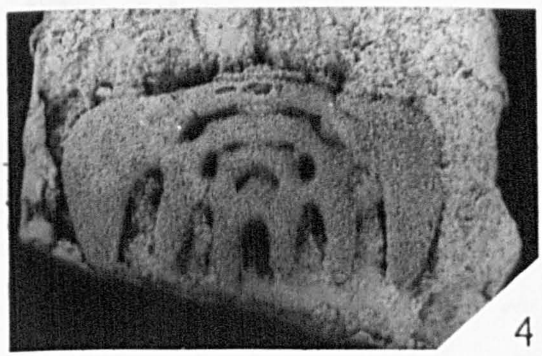

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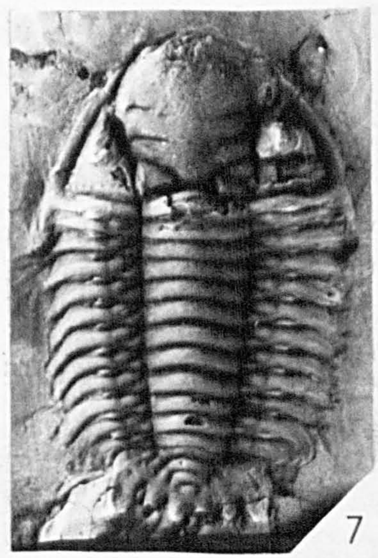

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Plate 7

Plate 8.

Bartoninus elongatus (Reed, 1931).

Figure 1. Bartoninus elongatus, Paralectotype HM A1073; figured Reed, 1931; Pl. IV, fig. 6. Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figures 2-3. Bartoninus elongatus, Paralectotype HM A1072; figured Reed, 1931, Pl. IV, figs. 5 & 5a. Saugh Hill Group, Newlands, Girvan Ayrshire. 2. Dorsal view of internal mould, x3. 3. Anterolateral view of same, x3.

Figures 4-6. Bartoninus elongatus, HM A1045; figured Reed, 1934 (as type of Cheirurus conjunctus, BG 1198) Pl. IV, fig. 1. Saugh Hill Group, Newlands, Girvan, Ayrshire. 4. Dorsal view of latex cast of external mould, x2½. 5. Anterolateral view of same, x2½. 6. Enlarged view of posterior part of right fixed cheek (Latex cast of external mould) showing pitting and tuberculation, x6.

Figure 7. Bartoninus elongatus. Lectotype HM A1074; figured Reed, 1931, Pl. IV, fig. 7. Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figure 8. Bartoninus elongatus. BM In43714; Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of internal mould with free cheeks in place, x3.

Figure 9. Bartoninus elongatus, Paralectotype HM A1075; figured Reed, 1931, Pl. V, fig. 4. Saugh Hill Group, Newlands, Girvan, Ayrshire. Ventral view of internal mould, x3.

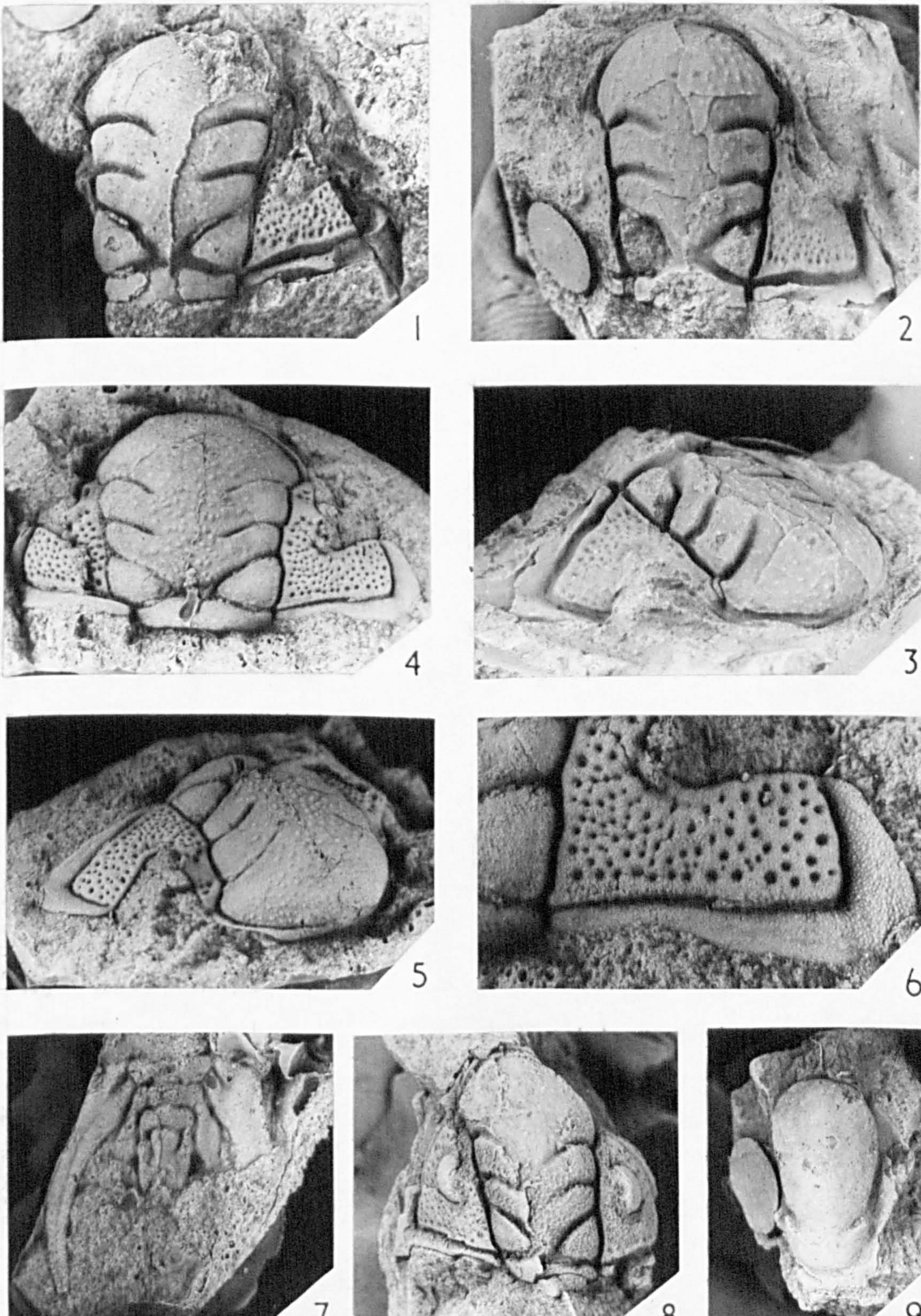


Plate 8

Plate 9.

Bartoninus elongatus (Reed, 1931).

Figures 1-2. Bartoninus elongatus, HM A5714B; Newlands Sandstone, Newlands, Girvan, Ayrshire. 1. Dorsal view of internal mould, x2½. 2 Anterolateral view of same, x2½.

Figures 3-4. Bartoninus elongatus, BM In43711; Saugh Hill Group, Newlands, Girvan, Ayrshire. 3. Dorsal view of internal mould, x2. 4. Dorsal view of latex cast of external mould, x2.

Figures 5-6. Bartoninus elongatus, HM A772; Saugh Hill Group, Newlands, Girvan, Ayrshire. 5. Dorsal view of internal mould of small individual, x10. 6. Anterior view of same showing continuous preglabellar furrow, x10.

Figure 7. Bartoninus elongatus, BM In43719; Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of internal mould of small individual, x6.

Figure 8. Bartoninus elongatus, BM In43728; Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of latex cast of external mould, x3.

Figure 9. Bartoninus elongatus, BM In43717; Saugh Hill Group, Newlands, Girvan, Ayrshire. Ventral view of internal mould, x3.

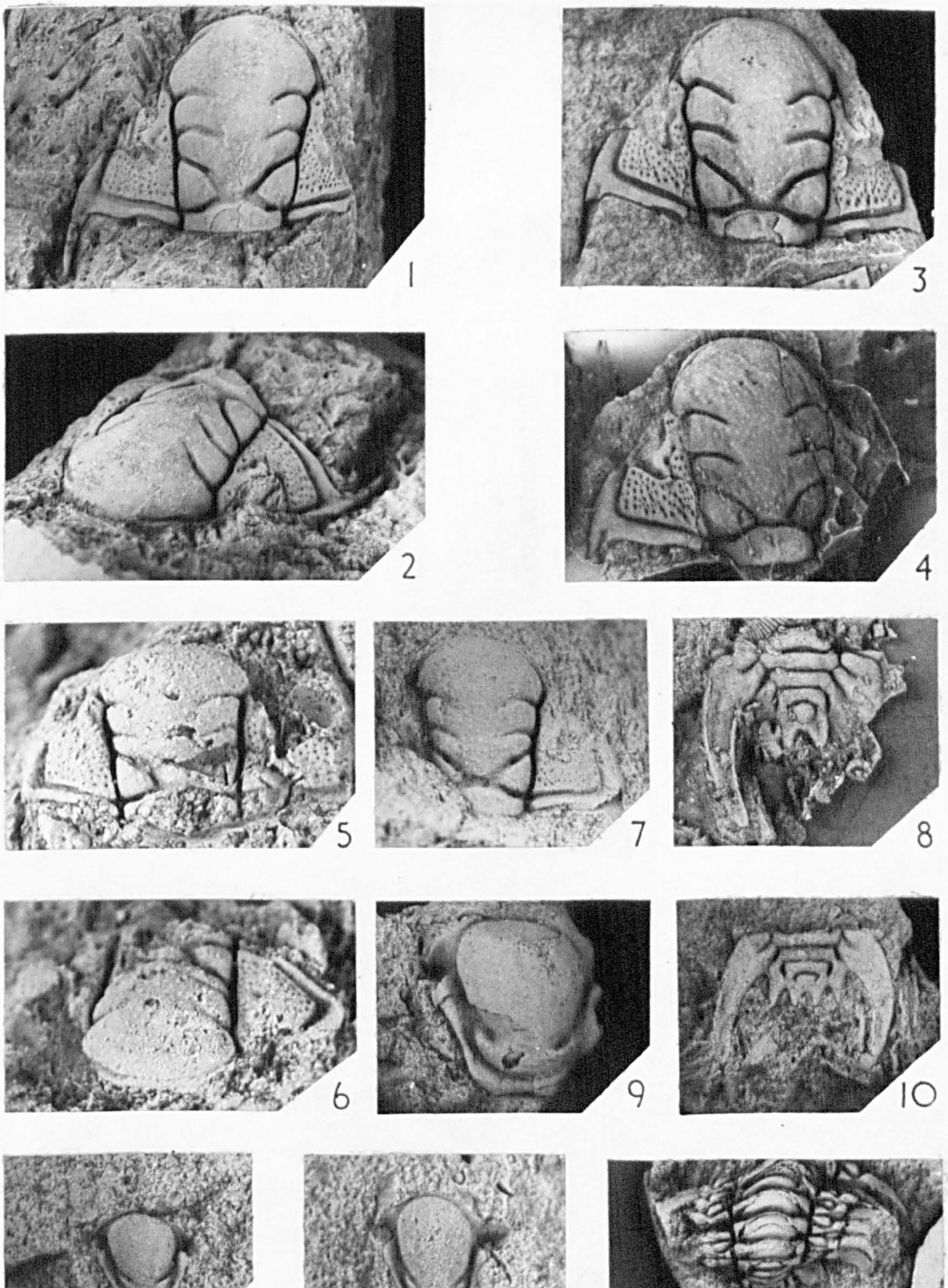


Plate 9

Plate 10.

Bartoninus skelgillensis sp. nov.

Figures 1-2. Bartoninus skelgillensis, Paratype NU LS2/21; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland. 1. Dorsal view of internal mould, x4. 2. Anterolateral view of same, x4.

Figure 3. Bartoninus skelgillensis, NU LS2/23; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland, Dorsal view of internal mould, x4.

Figure 4. Bartoninus skelgillensis, Holotype NU LS2/27; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland. Dorsal view of internal mould, x8.

Figures 5-6. Bartoninus skelgillensis, NU LS2/26; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland, 5. Dorsal view of internal mould, x4. 6. Anterolateral view of same, x4.

Figure 7. Bartoninus skelgillensis, NU LS2/24; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland. Ventral view of latex cast of external mould, x4.

Figure 8. Bartoninus skelgillensis, NU LS2/25; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland, Dorsal view of internal mould x3.

Figure 9. Bartoninus skelgillensis, NU LS2/20; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland, Ventral view of latex cast of external mould, x4.

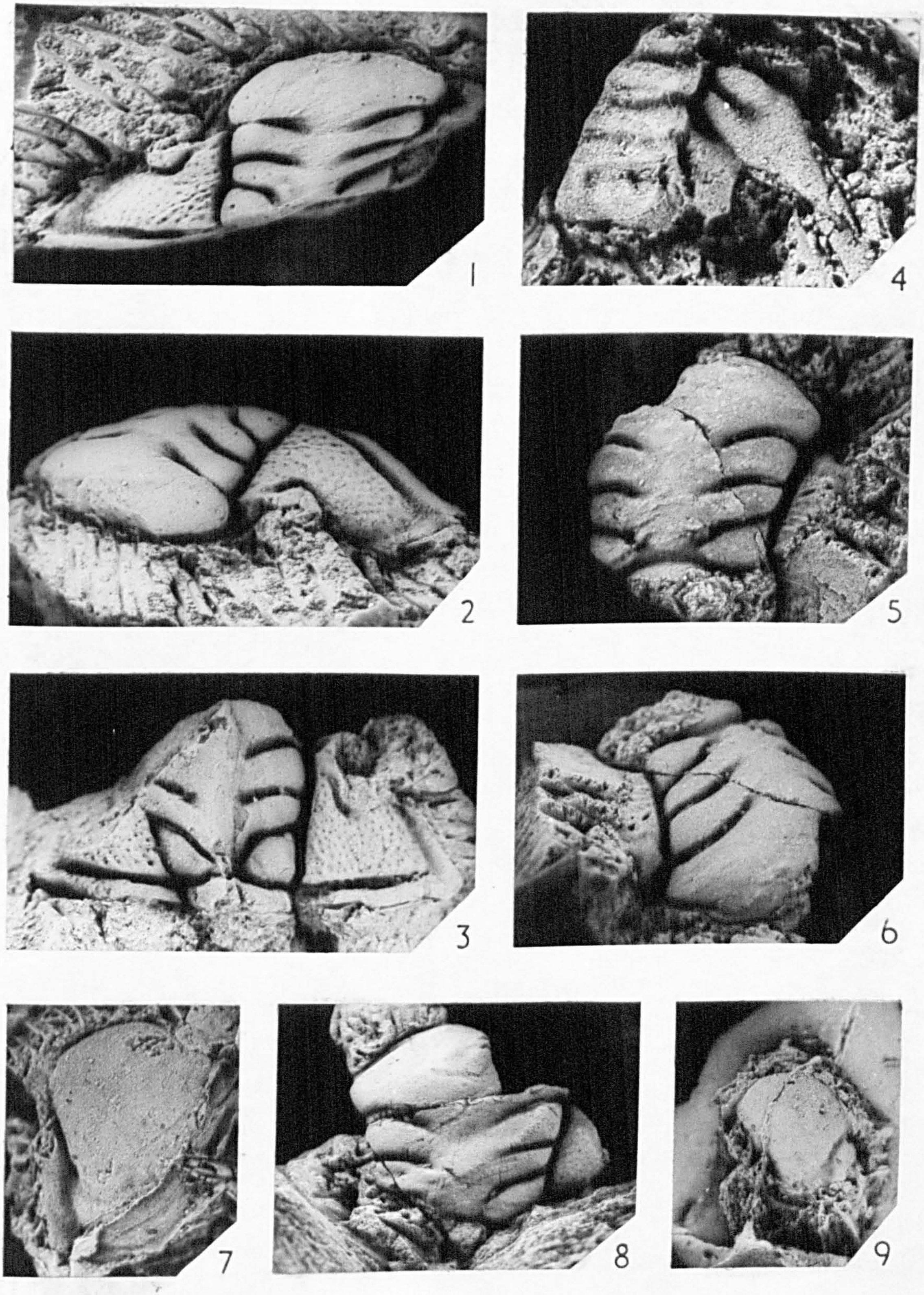


Plate 10

Plate 11.

Bartoninus sholeshookensis sp. nov.

Figure 1. Bartoninus sholeshookensis, MU L11655; Sholeshook Limestone, Prendergast Place, Haverfordwest, Pembrokeshire. Dorsal view of latex cast of external mould, x1.

Figures 2-3. Bartoninus sholeshookensis, Holotype BM In16399; Sholeshook Limestone, Farmyard east of Prendergast Place, Haverfordwest, Pembrokeshire. 2. Latex cast of external mould, x1. 3. Internal mould, x1.

Figure 4. Bartoninus sholeshookensis, GSM 24530; figured Salter, 1846, Pl. VII, fig. 4. Sholeshook, Haverfordwest, Pembrokeshire. Dorsal view of internal mould, x1.

Figure 5. Bartoninus sholeshookensis, BM I16400; Sholeshook Limestone, Farmyard east of Prendergast Place, Haverfordwest, Pembrokeshire. Dorsal view of internal mould, x1.

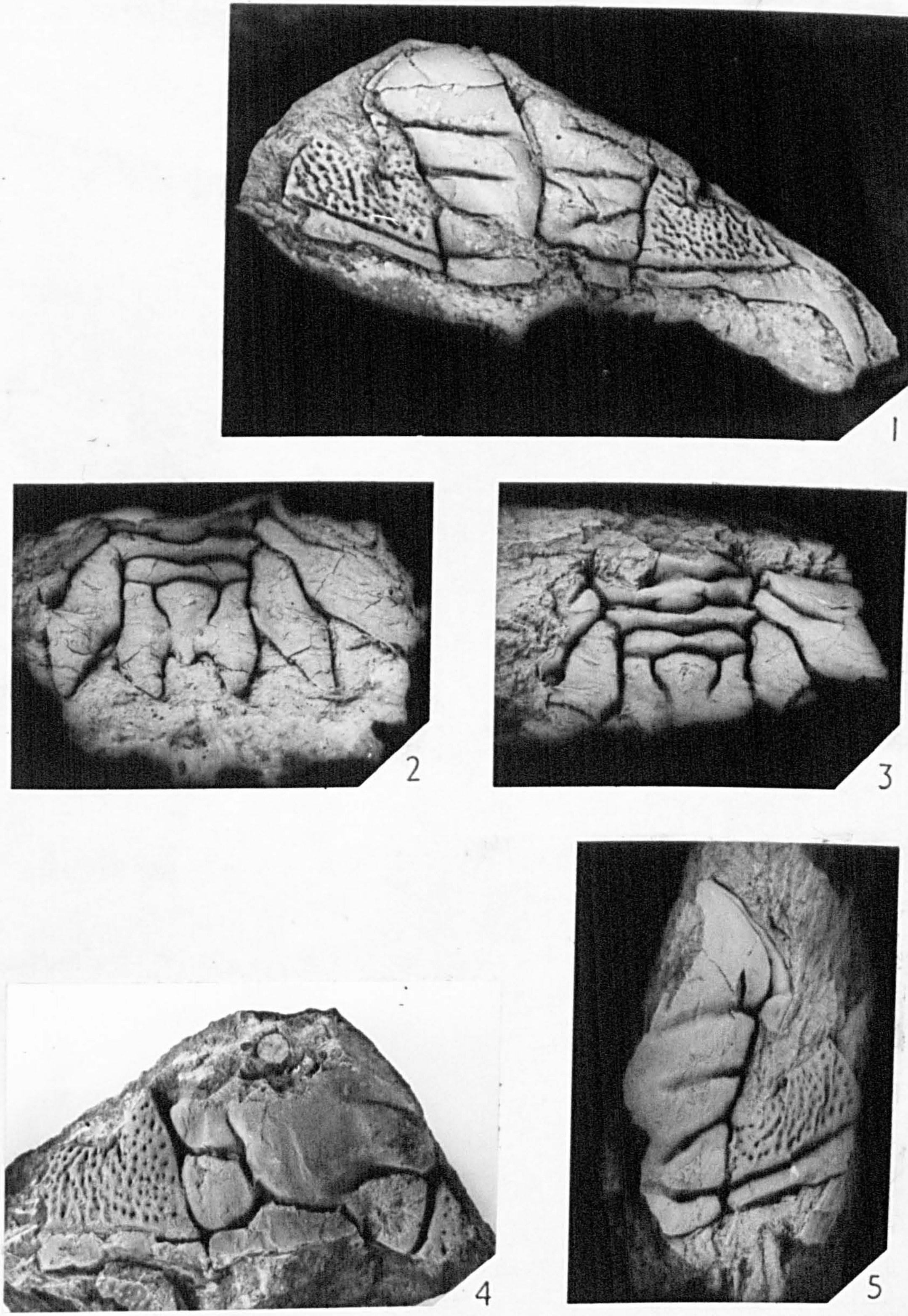


Plate II

Plate 12.

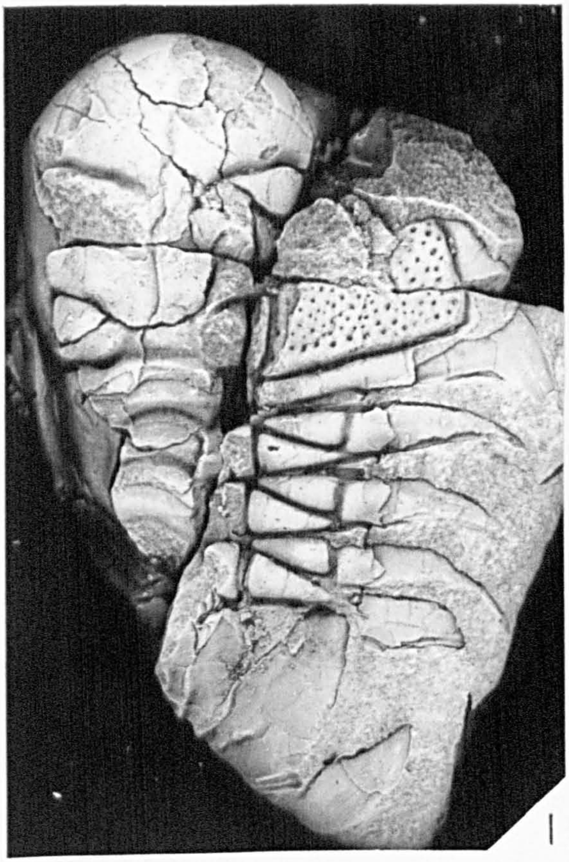
Bartoninus girvanensis sp. nov.

Figufe 1. Bartoninus girvanensis, BM In23408/1; Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayrshire. Dorsal view of internal mould, x1.

Figure 2. Bartoninus girvanensis, BM In23407/2; Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayreshire. Dorsal view of internal mould, x1.

Figure 3. Bartoninus girvanensis, Holotype BM In23407/1; Starfish Bed, Ardmillan Series, Drummock Group, Thriave Glen, Girvan, Ayrshire. Dorsal view of internal mould, x1.

Figure 4. Bartoninus girvanensis, BM In23407/3; Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayrshire. Dorsal view of internal mould of parts of six thoracic segments, x1.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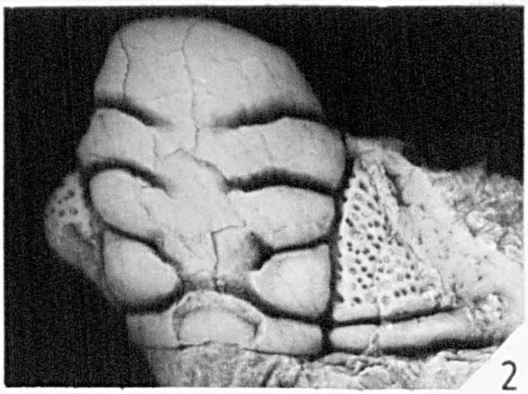
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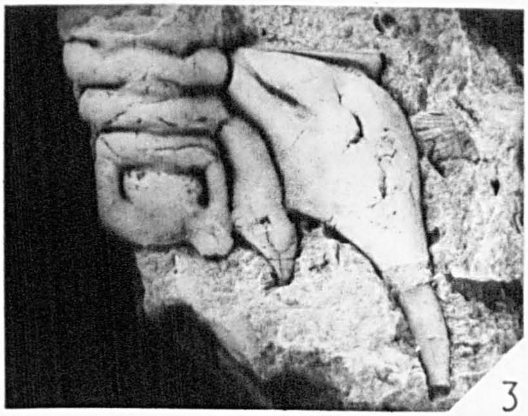
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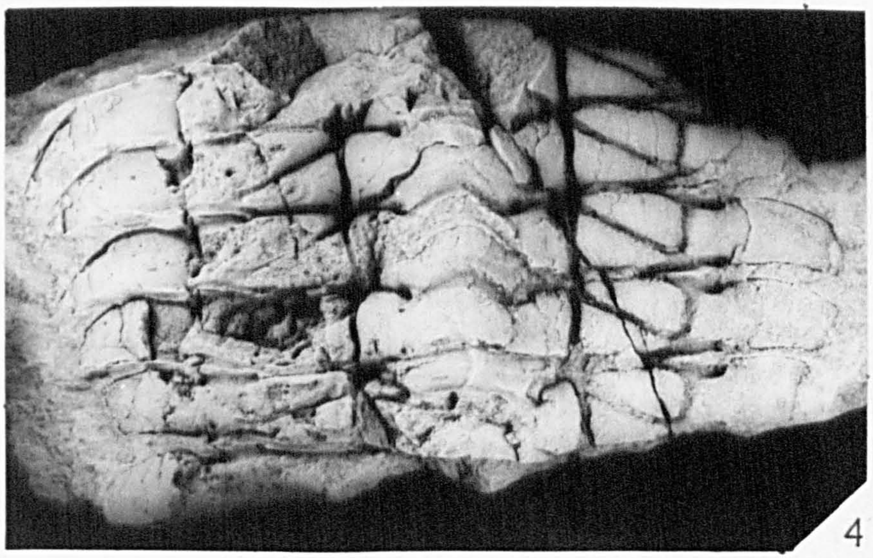
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Plate 12

Plate 13.

Bartoninus girvanensis sp. nov.

Bartoninus williamsii (M'Coy, 1849).

Figure 1. Bartoninus girvanensis, BM In23424; Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayrshire. Ventral view of internal mould of hypostoma, x1.

Figures 2-3. Bartoninus girvanensis, BM In23408/2; Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayrshire. 2. Ventral view of latex cast of external mould of pygidial doublure, x1¼. 3. View of same pygidium, showing internal mould of part of the dorsal surface, and external mould of proximal part of doublure with tuberculate surface (Pits on external mould), x2½.

Figures 4-5. Bartoninus girvanensis, BM In23409; Starfish Bed, Ardmillan Series, Drummock Group, Thraive Glen, Girvan, Ayrshire. 4. Dorsal view of internal mould, x1. 5. Anterolateral view of same, x1.

Figure 6. Bartoninus williamsii, Lectotype SM A10309; figured M'Coy, 1851, Pl. 1F, figs. 13, 13a & b; figured Salter, 1864, Pl. 5, fig. 4; Schists at Golen Goed, Lower Llandoverian, Myddfai, near Llandovery, Carmarthenshire. Dorsal view of badly distorted internal mould, x2.

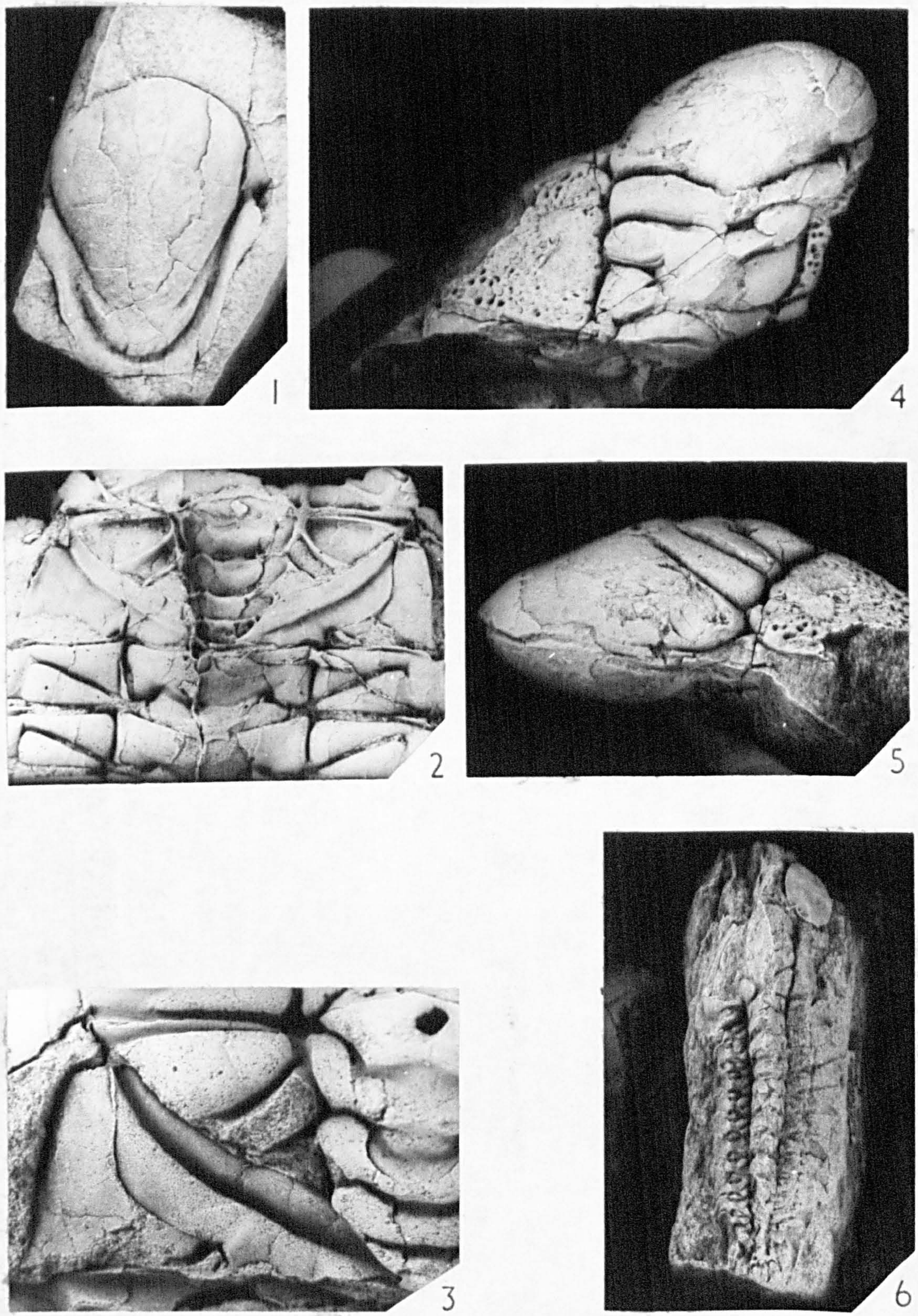

Plate 13

Plate 14.

Bartoninus keisleyensis (Reed, 1896a)

Figures 1-2. Bartoninus keisleyensis, SM A11854; Keisley Limestone, Keisley, Westmorland. 1. Dorsal view of internal mould, shell preserved in places, x2. 2. Anterolateral view of same, x2.

Figures 3-4. Bartoninus keisleyensis, SM A11846; figured Reed, 1896a, Pl. XX, fig. 7; Keisley Limestone, Keisley, Westmorland. 3. Dorsal view of internal mould, flattened dorsoventrally, x2. 4. Anterolateral view of same, x2.

Figure 5. Bartoninus keisleyensis, SM A11855; Keisley Limestone, Keisley, Westmorland. Dorsal view of internal mould with shell preserved in places, x2.

Figure 6. Bartoninus keisleyensis, SM A11849; figured Reed, 1896a, Pl. XX, fig. 9. Keisley Limestone, Keisley, Westmorland. Ventral view of internal mould with shell preserved in places, x2.

Figure 7. Bartoninus keisleyensis, Lectotype SM A11847; figured Reed, 1896a, Pl. XX, fig. 8. Keisley Limestone, Keisley, Westmorland. Dorsal view of internal mould, x2.

Figure 8. Bartoninus keisleyensis, Paralectotype SM A11848; Keisley Limestone, Keisley, Westmorland. Dorsal view of pygidium with shell preserved, x2.

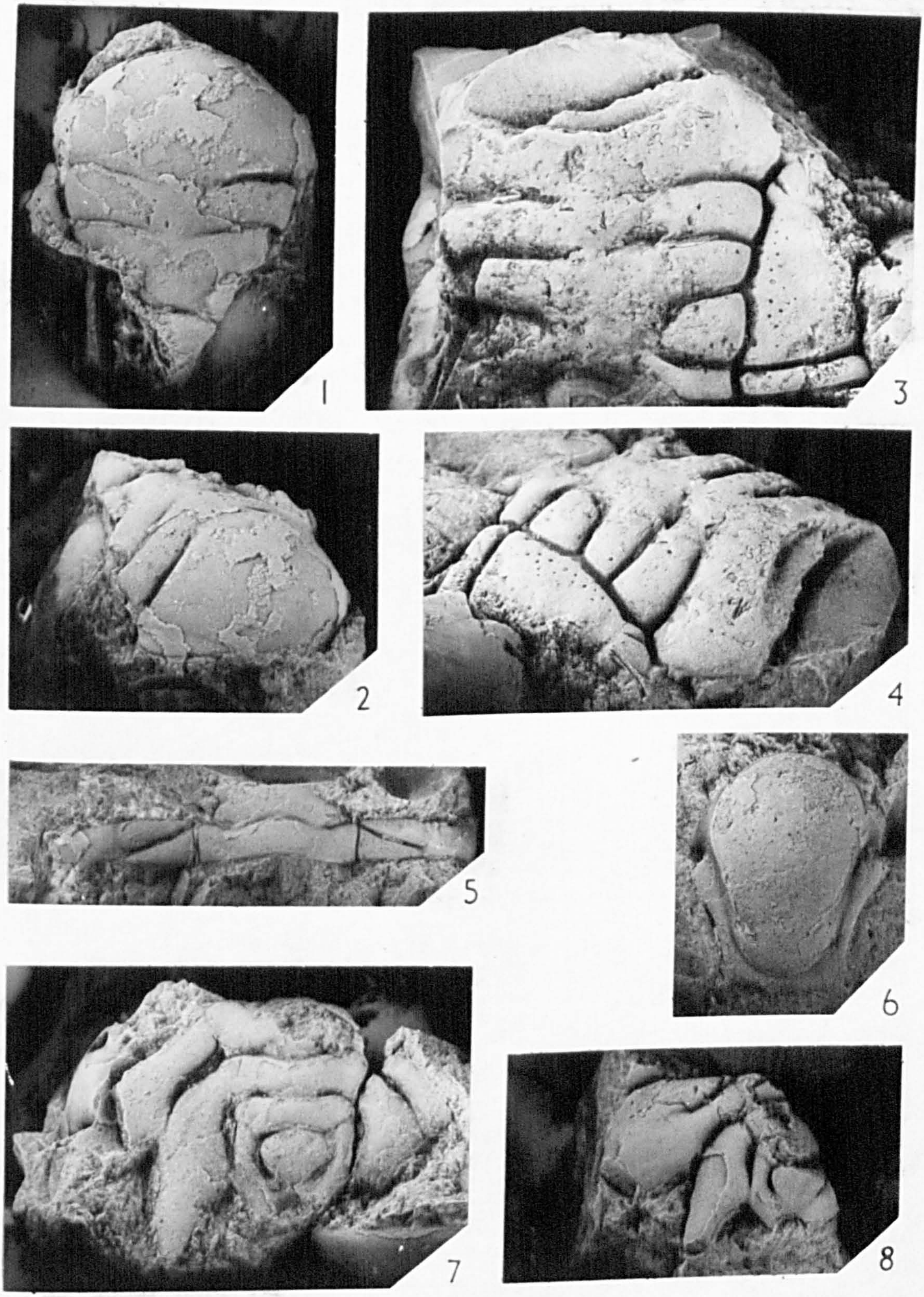

Plate 14

Plate 15.

Bartoninus keisleyensis (Reed, 1896a).

Bartoninus cf. *glaber* (Angelin, 1854).

Figure 1. *Bartoninus keisleyensis*, SM A11842; Keisley Limestone, Keisley, Westmorland. Dorsal view of fragmentary glabella, shell preserved in places, x1½.

Figures 2-3. *Bartoninus keisleyensis*, SM A11850; Keisley Limestone, Keisley, Westmorland. 2. Dorsal view of internal mould shell preserved in places, x2. 3. Anterolateral view of same, x2.

Figures 4-5. *Bartoninus* cf. *glaber*, RSM 1870 12 891C; Chair of Kildare, Ireland. 4. Dorsal view of internal mould,shell preserved in places, x2. 5. Anterior view of same, x2.

Figures 6-7. *Bartoninus* cf. *glaber*, SM A11859; Keisley Limestone, Keisley, Westmorland. 6. Dorsal view of internal mould shell preserved in places, x2. 7. Anterior view of same, x2.

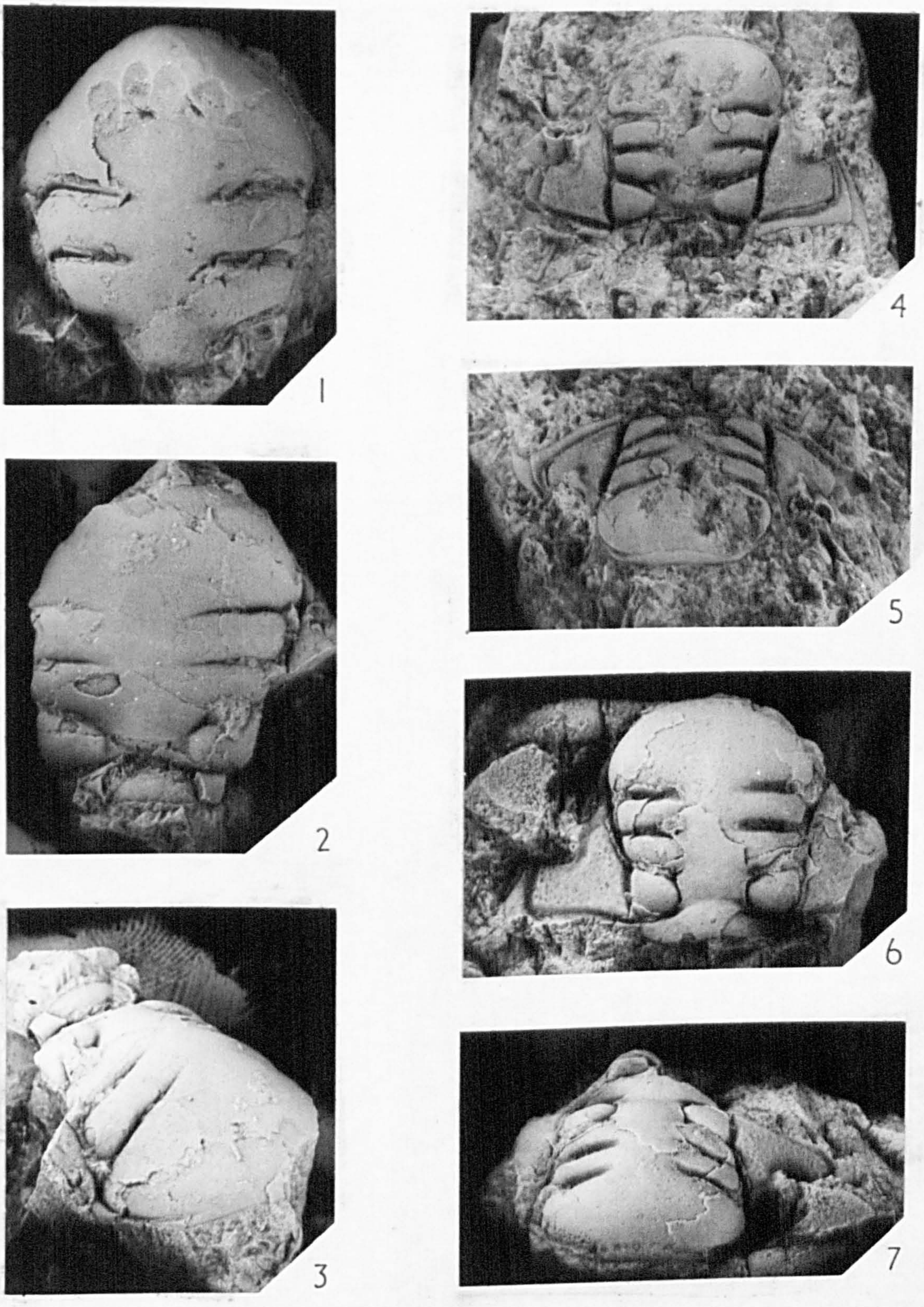

Plate 15

Plate 16.

<u>Bartoninus</u> <u>gelasinosus</u> (Portlock, 1843).

?<u>Bartoninus</u> sp.

<u>Bartoninus</u> cf. <u>keisleyensis</u> (Reed, 1896a).

Figures 1-2. <u>Bartoninus</u> <u>gelasinosus</u>, Lectotype GSM 35373; figured Portlock 1843, Pl. III, fig. 4a; figured Salter, 1864, Pl. 5, fig. 7. 'Caradoc', Tyrone, Ireland. 1. Dorsal view of internal mould, x1½. 2. Anterior view of same, x1½.

Figure 3. <u>Bartoninus</u> <u>gelasinosus</u>, GSM 35374; figured Portlock, 1843 (as <u>Arges</u> <u>planospinosus</u>), Pl. V, fig. 9b: figured Salter, 1864, Pl. 5, fig. 8. 'Caradoc', Tyrone, Ireland. Dorsal view of internal mould, x2.

Figure 4. <u>Bartoninus</u> <u>gelasinosus</u>, GSM 35375; figured Portlock, 1843 (as <u>Arges</u> <u>planospinosus</u>), Pl. V, fig. 9a; Dorsal view of internal mould. 'Caradoc', Tyrone, Ireland, x2.

Figure 5. ?<u>Bartoninus</u> sp. GSM 35376 and 35378; figured Portlock, 1843, Pl. III, fig. 4b. 'Caradoc', Tyrone, Ireland. Dorsal view of internal mould, x1½.

Figure 6. <u>Bartoninus</u> <u>cf</u>. <u>keisleyensis</u>, RSM 1870 12 891A; Chair of Kildare, Kildare, Ireland. Ventral view of external mould, shell removed in places, x1½.

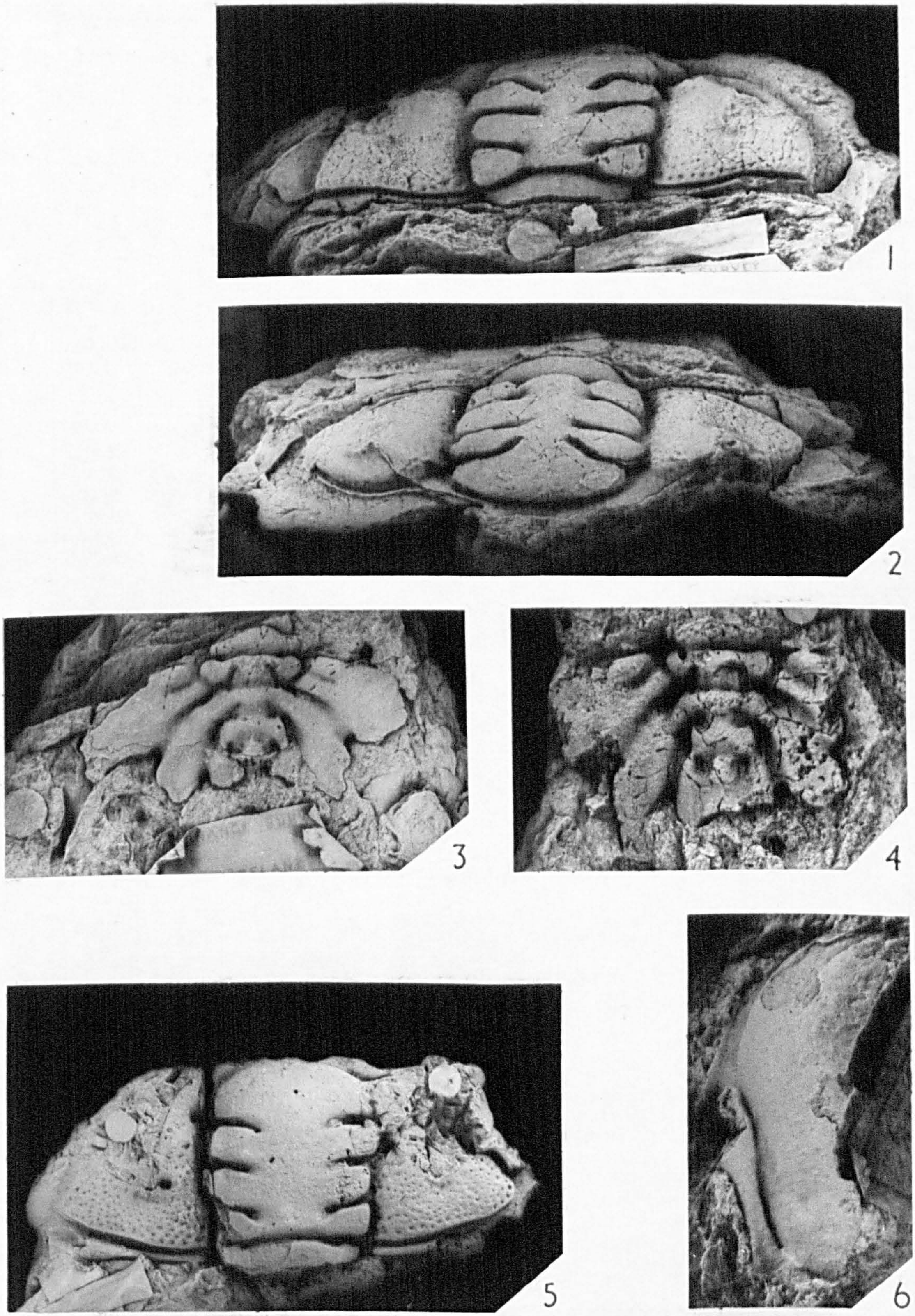

Plate 16

Plate 17.

Bartoninus acanthodes (Marr and Nicholson, 1888).

Bartoninus elongatus (Reed, 1931).

Bartoninus aff. elongatus. (Reed, 1931).

Bartoninus sholeshookensis sp. nov.

Figure 1. Bartoninus acanthodes, Paralectotype SM A40325; figured Marr and Nicholson, 1888, Pl. XVI, fig. 7; zone of Phacops glaber, Skelgill, near Ambleside, Westmorland; Dorsal view of internal moulds of two cranidia, lower right hand one being paralectotype, x4.

Figure 2. Bartoninus acanthodes, Lectotype SM A40330; figured Marr and Nicholson 1888, Pl. XVI, fig. 8; zone of Phacops glaber, Skelgill, near Ambleside, Westmorland. Dorsal view of internal mould, x4.

Figure 3. Bartoninus elongatus, BM In43728; Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figure 4. Bartoninus elongatus, BM In23415; Saugh Hill Group, Newlands, Girvan, Ayrshire; Dorsal view of internal mould, x3.

Figures 5-6. Bartoninus aff. elongatus, GSM OTJ612; Lower Llandoverian, Priory Hill Railway Cutting, Haverfordwest, Pembrokeshire. 5. Dorsal view of internal mould, x3. 6. Anterior view of same, x3.

Figure 7. Bartoninus sholeshookensis, BM In54453a; Old quarry by north side of track, 300 ft. north east of Vaynor Farm, ½ mile west

of Llanddowror, Carmarthenshire. Dorsal view of internal mould of pygidial axis, x3.

Figure 8. *Bartoninus sholeshookensis*, GSM 24572; figured Salter, 1846, Pl. 7, fig. 5; Robeston Wathan Limestone, Robeston Wathan, Carmarthenshire. Dorsal view of internal mould, x2.

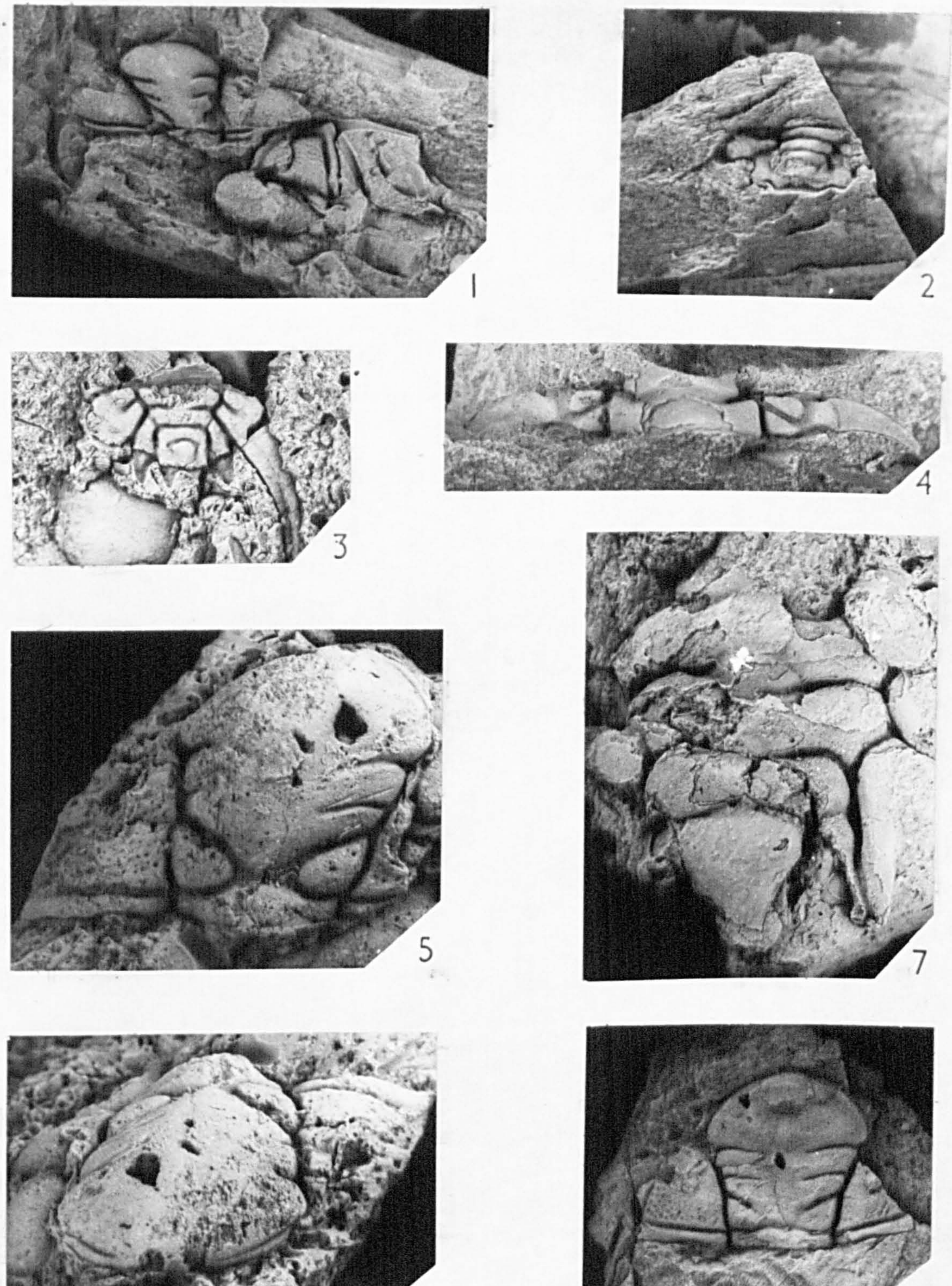

Plate 17

Plate 18.

Bartoninus craigensis (Tripp, 1954).

Bartoninus susceptus (Reed, 1931).

Bartoninus girvanensis. sp. nov.

Figure 1. Bartoninus craigensis, GSM 35380; figured Salter, 1864, Pl. 5, fig. 6; Craighead, Girvan, Ayrshire. Dorsal view of internal mould, x2.

Figure 2. Bartoninus susceptus, BM In 23426; figured Reed, 1906 (as Cheirurus gelasinosus), Pl. XVIII, fig. 6. Stinchar Limestone, Barr Series, Craighead, Girvan, Ayrshire, x1½.

Figures 3-4. Bartoninus craigensis, BM In23420; Stinchar Limestone, Barr Series, Craighead, Girvan, Ayrshire. 3. Dorsal view, x3. 4. Anterior view, x3.

Figures 5-6. Bartoninus girvanensis, BM In 41338; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. 5. Dorsal view of internal mould, x3½. 6. Enlarged view of internal mould of visual surface, x10.

Figures 7-8. Bartoninus susceptus, Lectotype BM In23425; figured Reed, 1906 (as Cheirurus gelasinosus), Pl. XVIII, fig. 5. Stinchar Limestone, Barr Series, Craighead, Girvan, Ayrshire. 7. Dorsal view of internal mould, x1½. 8. Lateral view showing distorted left cheek, x1½.

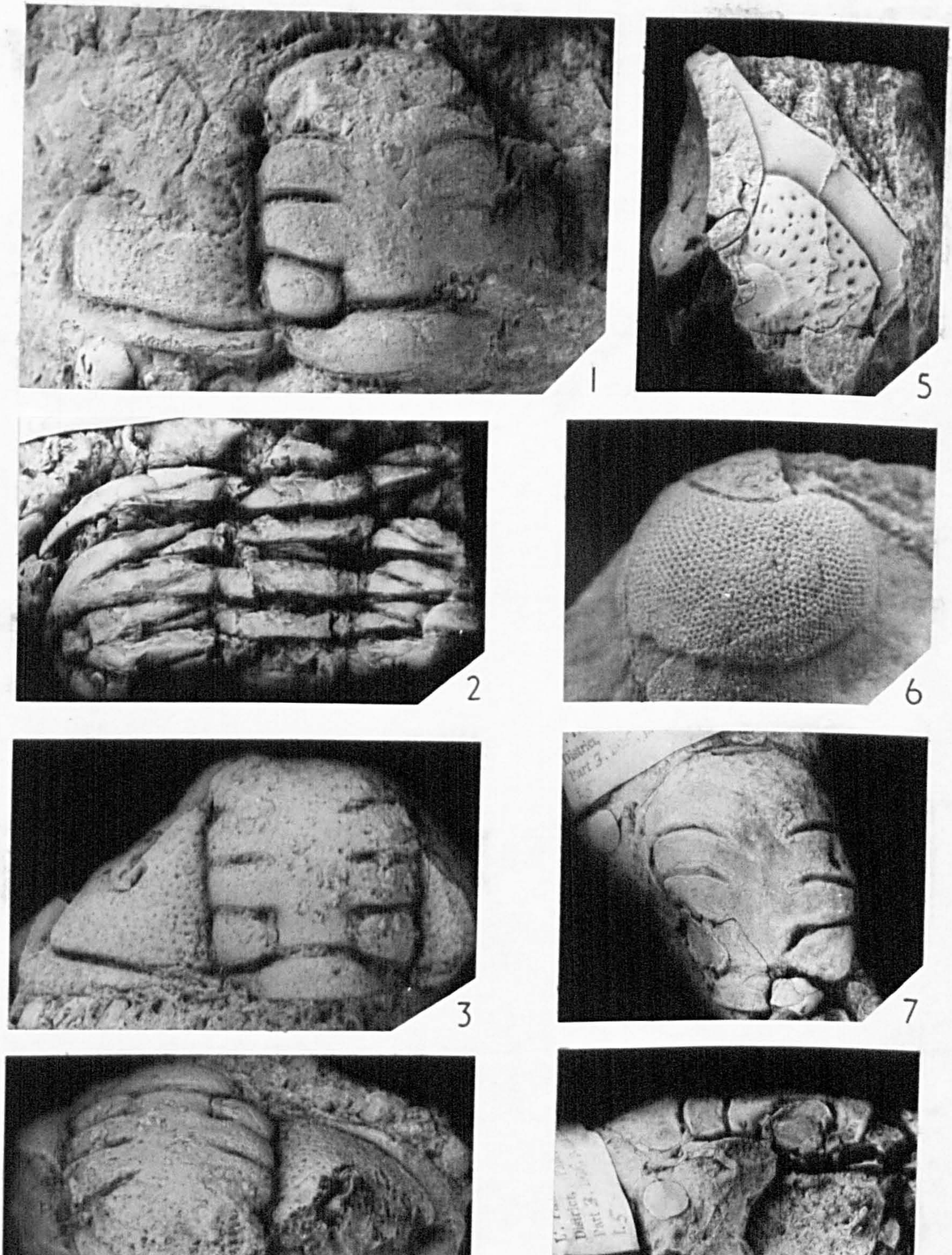

Plate 18

Plate 19.

Bartoninus cf. keisleyensis

Bartoninus elongatus (Reed, 1931)

Bartoninus skelgillensis sp. nov.

Figure 1. Bartoninus cf. keisleyensis, GSM 35369; figured Salter, 1864, Pl. 5, fig. 2. Chair of Kildare Limestone, Kildare, Ireland. Dorsal view, x2.

Figure 2. Bartoninus cf. keisleyensis, GSM 35383; figured Salter, 1864, Pl. 5, fig. 12. Chair of Kildare Limestone, Kildare, Ireland. Dorsal view of latex cast of external mould, x3.

Figure 3. Bartoninus elongatus, BM In23417; Saugh Hill Group, Newlands, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figures 4-5. Bartoninus skelgillensis, NU LS2/17; Upper Skelgill Beds, Skelgill, near Ambleside, Westmorland. 4. Dorsal view of latex cast of external mould, x4. 5. Anterolateral view of same, x4.

Figures 6-7. Bartoninus elongatus, BM In43722; Saugh Hill Group, Newlands, Girvan, Ayrshire. 6. Ventral view of internal mould, x3. 7. Lateral view of same, x3.

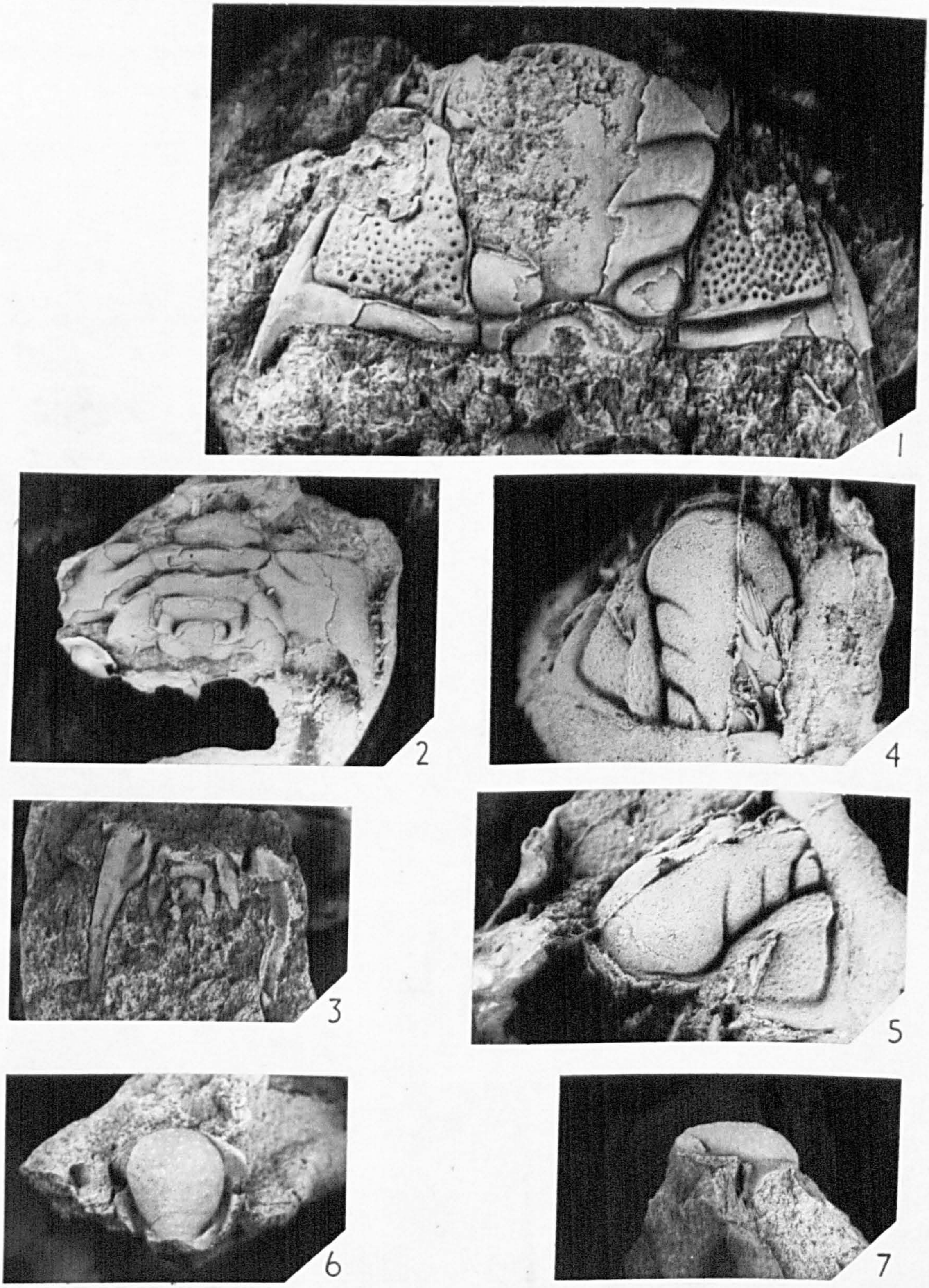

Plate 19

Plate 20.

<u>Cheiruretaerus</u> <u>falcatus</u> gen. et sp. nov.

<u>Cheirurus</u> <u>centralis</u> Salter, 1853.

Figure 1. <u>Cheiruretaerus</u> <u>falcatus</u>, BU 417 (ex Holcroft 322); 'Upper Silurian' (?Lower Ludlovian), Sedgley, Staffordshire. Dorsal view, posterior part of thorax turned down, x2.

Figures 2-3. <u>Cheiruretaerus</u> <u>falcatus</u>, Holotype BU 420 (ex Holcroft 186); 'Upper Silurian' (?Lower Ludlovian), Sedgley, Staffordshire. 2. Dorsal view of cephalon and anterior part of the thorax, x2. 3. Reverse view of 2, showing most of thorax and the pygidium, x2.

Figure 4. <u>Cheiruretaerus</u> <u>falcatus</u>, BU 418 (ex Holcroft 368); 'Upper Silurian' (?Lower Ludlovian), Sedgley, Staffordshire. Dorsal view, cephalon damaged and turned down, x2.

Figure 5. <u>Cheiruretaerus</u> <u>falcatus</u>, BU 419 (ex Hollier); Lower Ludlovian, Dudley District, Worcestershire. Dorsal view, x2.

Figures 6-7. <u>Cheirurus</u> <u>centralis</u>, GSM 38262; figured Salter, 1853, Pl. II, figs. 11-13. Dormington Wood, Woolhope, Herefordshire. 6. Lateral view, x2. 7. Ventral view, x2.

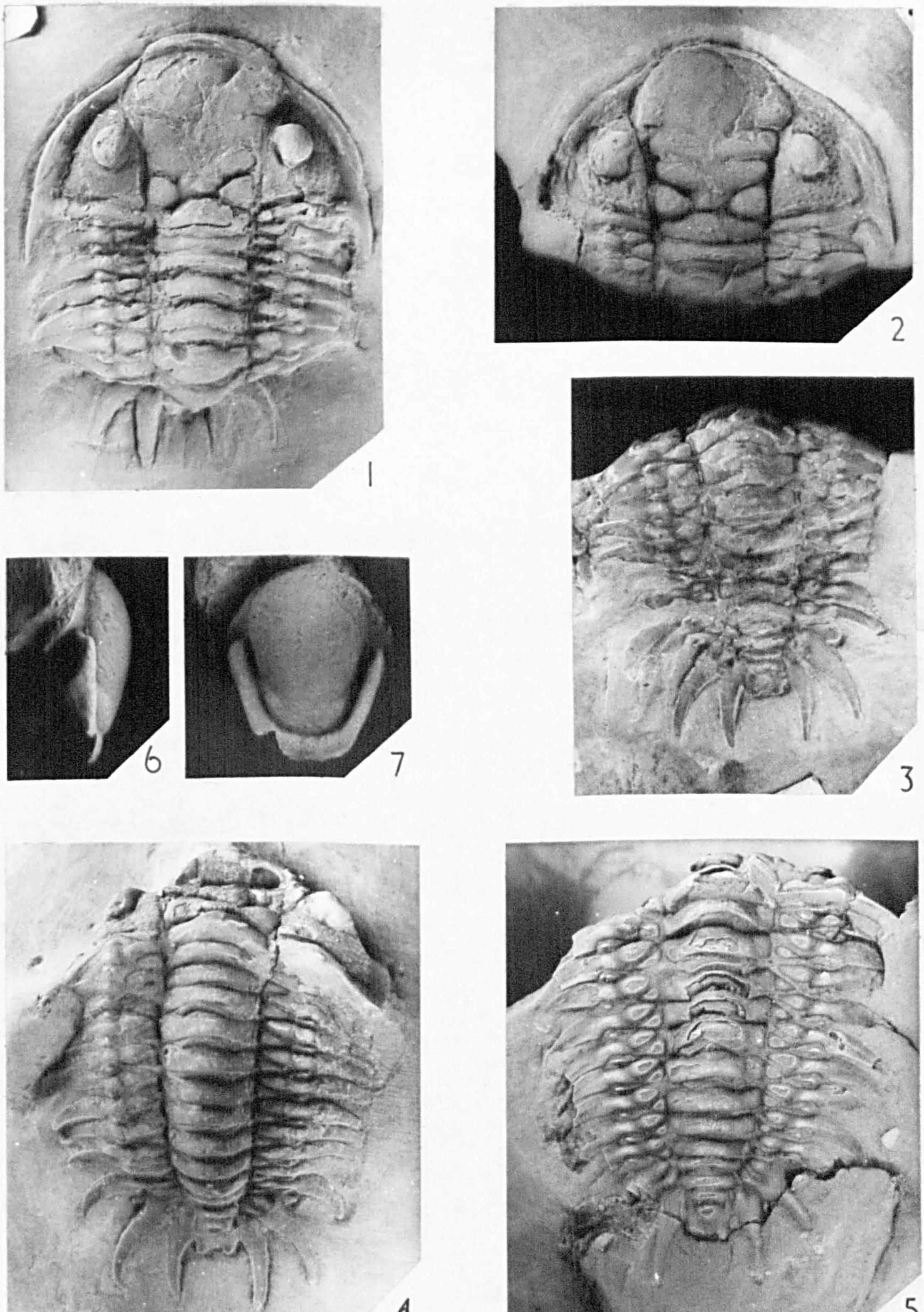

Plate 20

Plate 21.

Cheiruretaerus sp. A.

?*Cheiruretaerus* sp. B.

?*Cheirurus* sp.

Pseudocheirurus sp. A.

Pseudocheirurus sp. B.

?*Macrogrammus* sp.

Figures 1-2. ?*Cheiruretaerus* sp. B., BM In48514; Wenlock Limestone, Locality unknown. 1. Dorsal view of internal mould, x2. 2. Anterolateral view of same x2.

Figures 3-4. *Cheiruretaerus* sp. A., BM I1479; Wenlock Limestone, Malvern, Worcestershire. 3. Dorsal view of internal mould, x1. 4. Anterolateral view of same, x1.

Figure 5. ?*Cheirurus* sp., SM A40883; Wenlock Shale, Left Bank of River Severn, 300 yds south-east of Buildwas Church (Abbey), Shropshire. Dorsal view, x2.

Figures 6-7. *Pseudocheirurus* sp. A., BM In23423; Upper Llandoverian, Camregan Group, Bargany Pond Burn, Girvan, Ayrshire. 6. Dorsal view of damaged external mould, x2. 7. Anterolateral view of same, x2.

Figures 8-9. ?*Macrogrammus* sp., GSM 16193; figured Reed, 1906, (as *Cheirurus gelasinosus* var ?.), Pl. XVIII, fig. 7. 'Bala', Balclatchie, Girvan, Ayrshire. 8. Dorsal view, x3. 9. Anterior view, x3.

Figures 10-11. ?Macrogrammus sp., RSM 1889 91 32B; Horizon unknown, Balclatchie, Girvan, Ayrshire. 10. Dorsal view, x4. 11. Anterior view, x4.

Figures 12-13. Pseudocheirurus sp. B., BM In23418; Lower Tarranon, Penkill Group, Penwhapple Glen, Girvan, Ayrshire. 12. Dorsal view, x2. 13. Lateral view, x2.

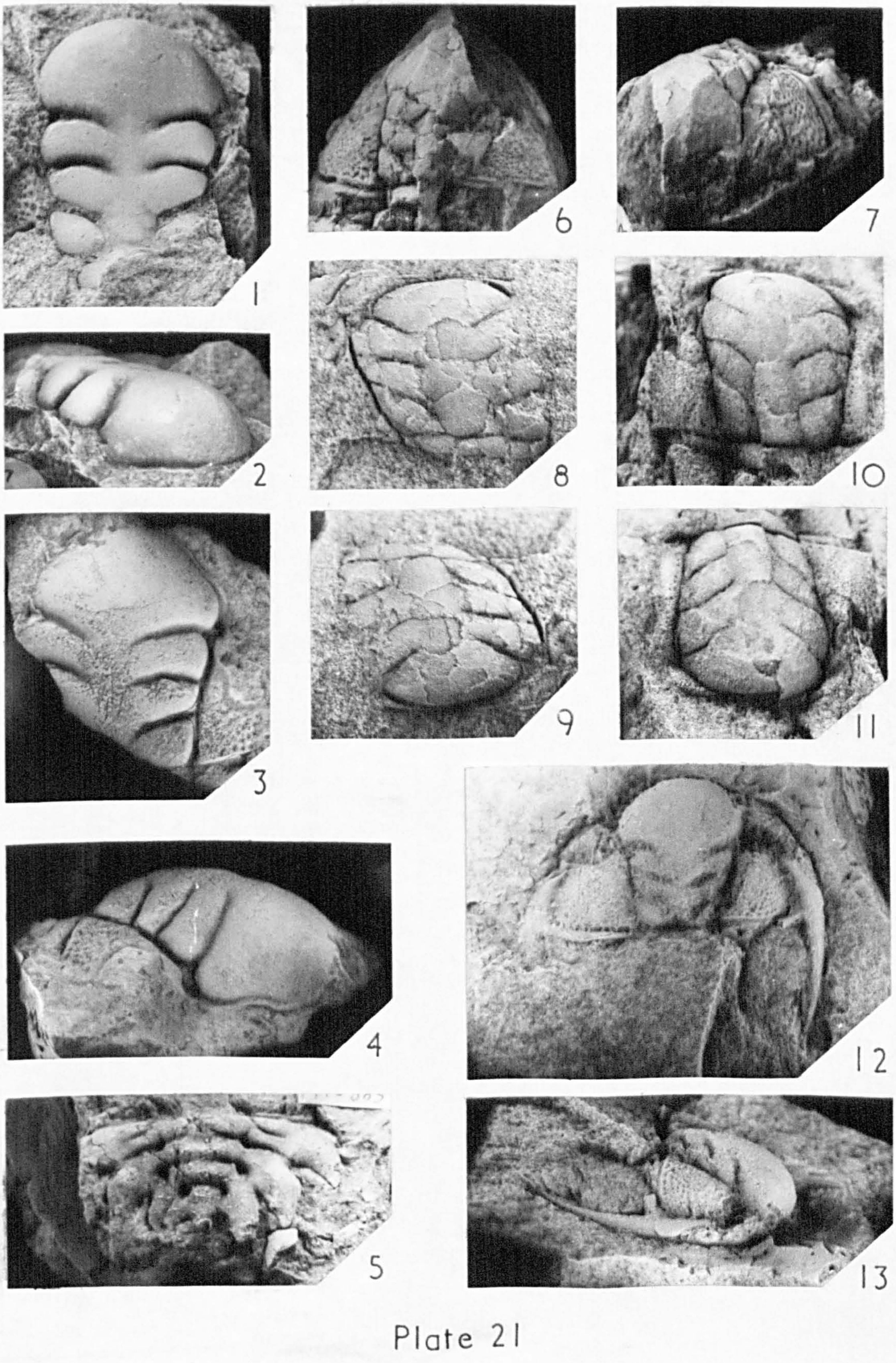

Plate 21

Plate 22.

Setacauda cancrura (Salter, 1853).

Figures 1-2. *Setacauda cancrura*, SM A11870; figured Reed, 1896a (as syntype of *Cheirurus* (*Pseudosphaerexochus*) *subquadratus*), Pl. XX, fig. 11; Keisley Limestone, Keisley, Westmorland. 1. Dorsal view of internal mould, shell preserved in places, x3. 2. Lateral view of same, x3.

Figures 3-4. *Setacauda cancrura*, SM A11869; Keisley Limestone, Keisley, Westmorland. 3. Dorsal view, x3. 4. Lateral view of same, x3.

Figures 5-6. *Setacauda cancrura*, SM A11874; Keisley Limestone, Keisley, Westmorland. 5. Dorsal view of internal mould, x2. 6. Lateral view of same, x2.

Figure 7. *Setacauda cancrura*, GSM 35379; Keisley Limestone, Keisley, Westmorland. Dorsal view, x3.

Figure 8. *Setacauda cancrura*, GSM 35368; Chair of Kildare Limestone, Kildare, Ireland. Dorsal view, x3.

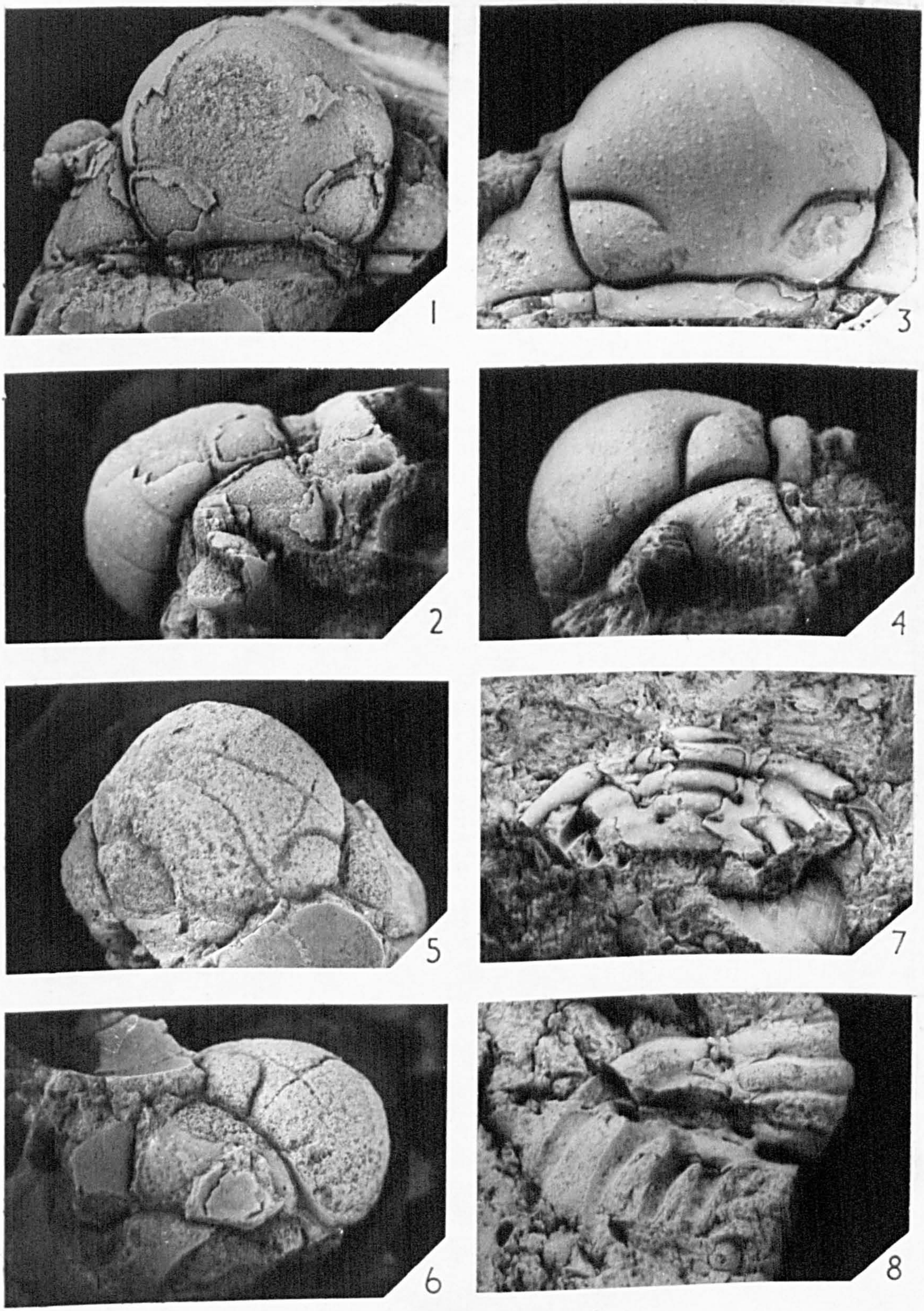

Plate 22

Plate 23.

Setacauda cancrura (Salter, 1853).

Pseudosphaerexochus sp. A.

Figures 1-2. Setacauda cancrura, SM A11872; Keisley Limestone, Keisley, Westmorland. 1. Dorsal view of internal mould, x3. 2. Lateral view of same, x3.

Figure 3. Setacauda cancrura, SM A11893; Keisley Limestone, Keisley, Westmorland, Dorsal view, x3.

Figure 4. Setacauda cancrura, RSM 1870 12 1173A; Chair of Kildare Limestone, Kildare, Ireland. Anterolateral view, x2.

Figure 5. Pseudosphaerexochus sp. A., SM A9584; Ashgillian Limestone Dyke, Railway cutting 2000' south of Horton in Ribblesdale Railway Station, Yorkshire. Palpebral view, x6.

Figure 6. Setacauda cancrura, Lectotype GSM 35367; figured Salter, 1864, Pl. 5, fig. 15. Chair of Kildare Limestone, Kildare, Ireland. Dorsal view of weathered internal mould, x2.

Figures 7-8. Setacauda cancrura, SM A11866; Keisley Limestone, Keisley, Westmorland. 7. Dorsal view, x3. 8. Anterolateral view, x3.

Figure 9. Pseudosphaerexochus sp. A., SM A9583; Ashgillian Limestone Dyke, Railway cutting 2000' south of Horton in Ribblesdale Railway Station, Yorkshire. Dorsal view, x10.

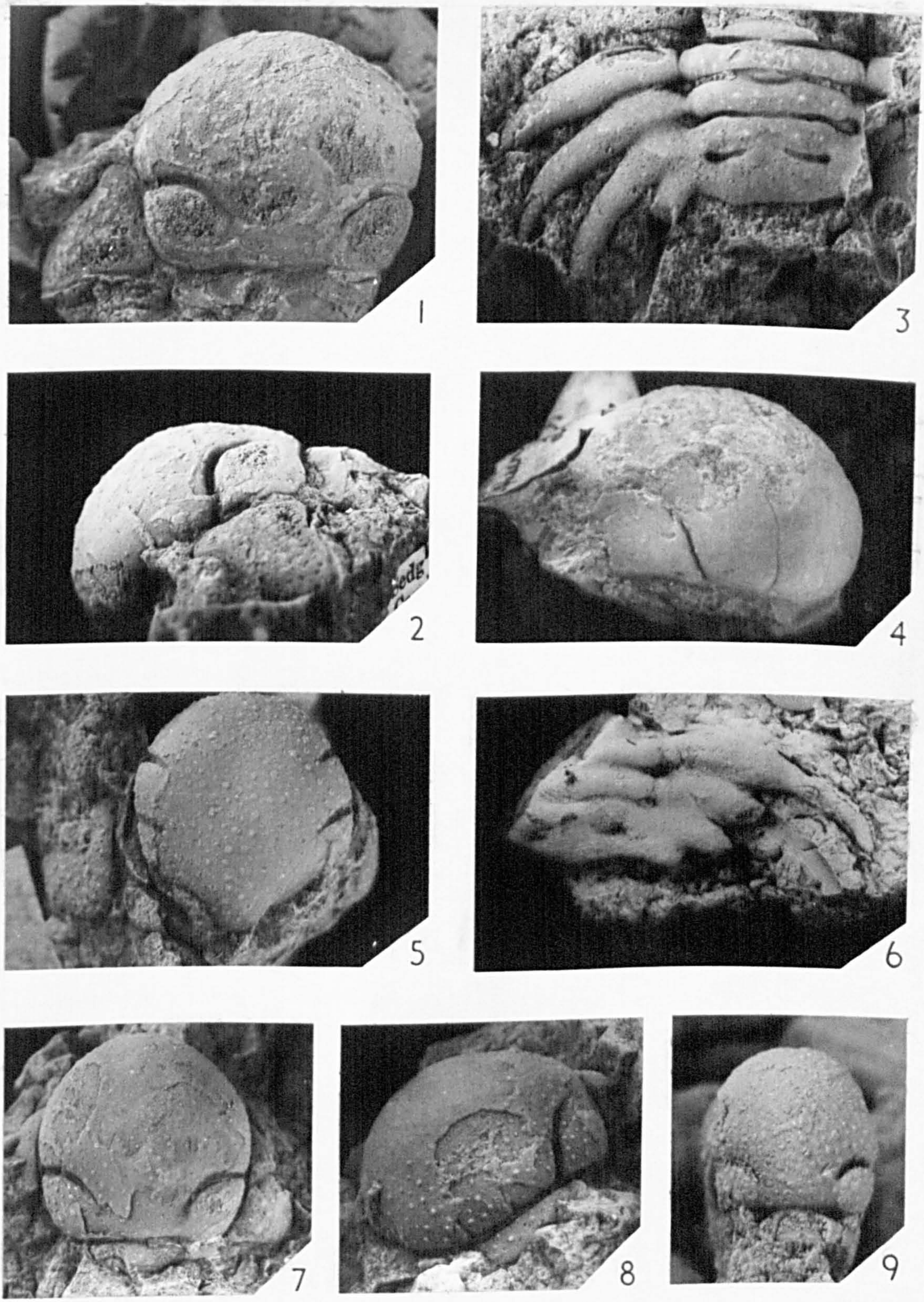

Plate 23

Plate 24.

Pseudosphaerexochus girvanensis sp. nov.

Figures 1-2. Pseudosphaerexochus girvanensis, RSM 1859 33 206; Drummock Group, Ladyburn, Girvan, Ayrshire. 1. Dorsal view of internal mould, x2. 2. Lateral view of same, x2.

Figure 3. Pseudosphaerexochus girvanensis, HM A558; Starfish Bed No. 1, Ladyburn, Girvan, Ayrshire. Ventral view of hypostoma, x3.

Figure 4. Pseudosphaerexochus girvanensis, HM A2993; Starfish Bed No. 1, Ladyburn, Girvan, Ayrshire. Dorsal view of internal mould, shell preserved in places, x3.

Figure 5. Pseudosphaerexochus girvanensis, BM In43057/1; Starfish Bed, Drummock Group, Ladyburn, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figure 6. Pseudosphaerexochus girvanensis, BM In43057; Starfish Bed, Drummock Group, Ladybrun, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figures 7-9. Pseudosphaerexochus girvanensis, Holotype HM A846/3; Starfish Bed No. 1, Ladyburn, Girvan, Ayrshire. 7. Dorsal view, x2. 8. Lateral view of same, x2. 9. Anterolateral view of free cheek showing arrangement of lenses in eye, x10.

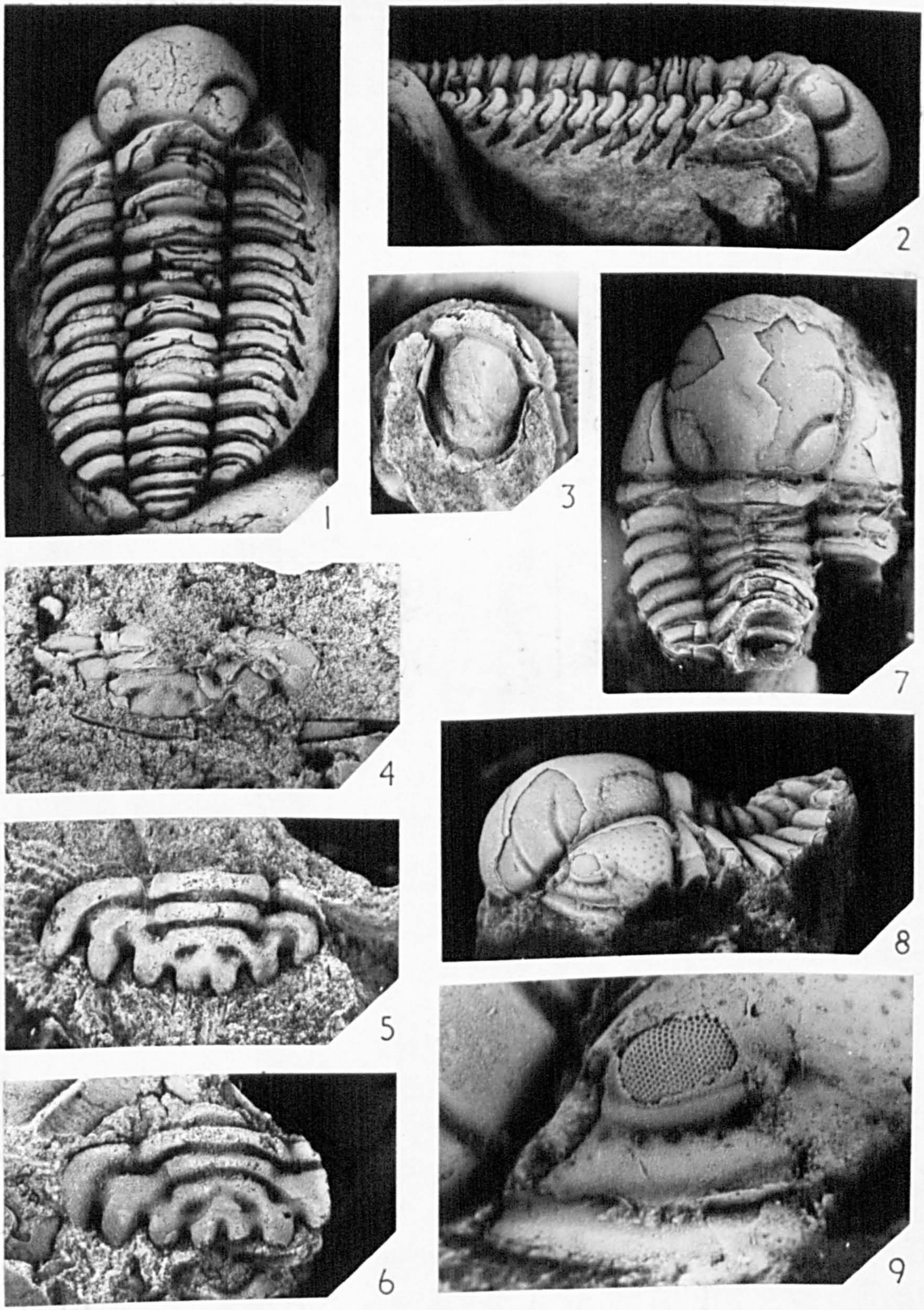

Plate 24

Plate 25.

Pseudosphaerexochus girvanensis sp. nov.

Setacauda cancrura (Salter, 1853).

Figures 1-3. Pseudosphaerexochus girvanensis, HM A993; Starfish Bed, Ladyburn, Girvan, Ayrshire. 1. Dorsal view of internal mould, x3. 2. Lateral view of same, x3. 3. Palpebral view of same, x3.

Figure 4. Pseudosphaerexochus girvanensis, HM A3005; Upper Drummock Group, South Threave Glen, Girvan, Ayrshire. Ventral view of hypostoma, x3.

Figures 5-6. Pseudosphaerexochus girvanensis, HM A3657; Starfish Bed, Ladyburn, Girvan, Ayrshire. 5. Dorsal view of internal mould, x3. 6. Lateral view of same, x3.

Figures 7-8. Pseudosphaerexochus girvanensis, HM A1050; Upper Drummock Group, Starfish Bed, Ladyburn, Girvan, Ayrshire. 7. Palpebral view of internal mould, x3. 8. Anterior view of same, x3.

Figure 9. Setacauda cancrura, SM A11863; Keisley Limestone, Keisley, Westmorland. Ventral view of hypostoma, x3.

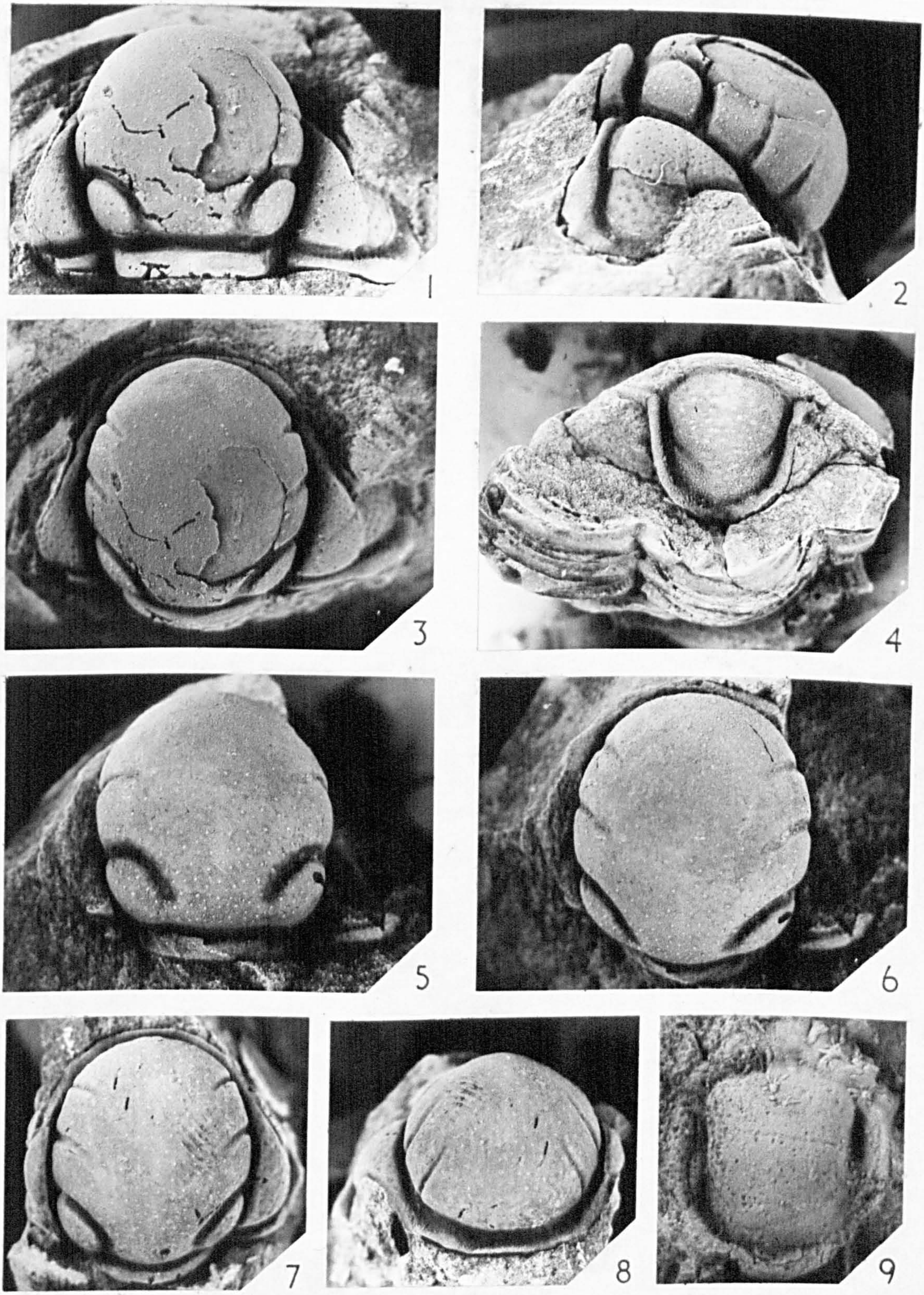

Plate 25

Plate 26.

Pseudosphaerexochus juvenis (Salter, 1848).

Pseudosphaerexochus sp. B.

Figures 1-2. *Pseudosphaerexochus juvenis*, GSM Pg136; Sholeshook Limestone, Prendergast Place, Haverfordwest, Pembrokeshire. 1. Dorsal view of internal mould, x1½. 2. Lateral view of same, x1½.

Figure 3. *Pseudosphaerexochus juvenis*, Lectotype GSM 24534; figured Salter, 1848, Pl. VII, figs, 1. 1a. Whittington 1965, Pl. XII, figs. 2, 4, 8. Sholeshook Limestone, Sholeshook, Haverfordwest, Pembrokeshire. Dorsal view of internal mould, x2.

Figure 4. *Pseudosphaerexochus juvenis*, Paralectotype GSM 24536; figured Salter, 1848, Pl. VII, fig. 3. Sholeshook Limestone, Sholeshook, Haverfordwest, Pembrokeshire. Dorsal view of internal mould, x4.

Figure 5. *Pseudosphaerexochus juvenis*, Paralectotype GSM 24535; figured Salter, 1848, Pl. VII, fig. 4. Sholeshook Limestone, Sholeshook, Haverfordwest, Pembrokeshire. Dorsal view of internal mould, x2.

Figures 6-7. *Pseudosphaerexochus juvenis*, NU LZ/1; Sholeshook Limestone, Prendergast Place, Haverfordwest, Pembrokeshire. 6. Dorsal view of internal mould, x2. 7. Lateral view of same, x2.

Figures 8-10. *Pseudosphaerexochus* sp. B., HM A3638; 7' above Starfish Bed No. 3, Ladyburn, Girvan, Ayrshire, 8. Dorsal view of internal mould, x3. 9. Palpebral view of same, x3. 10. Lateral view of same, x3.

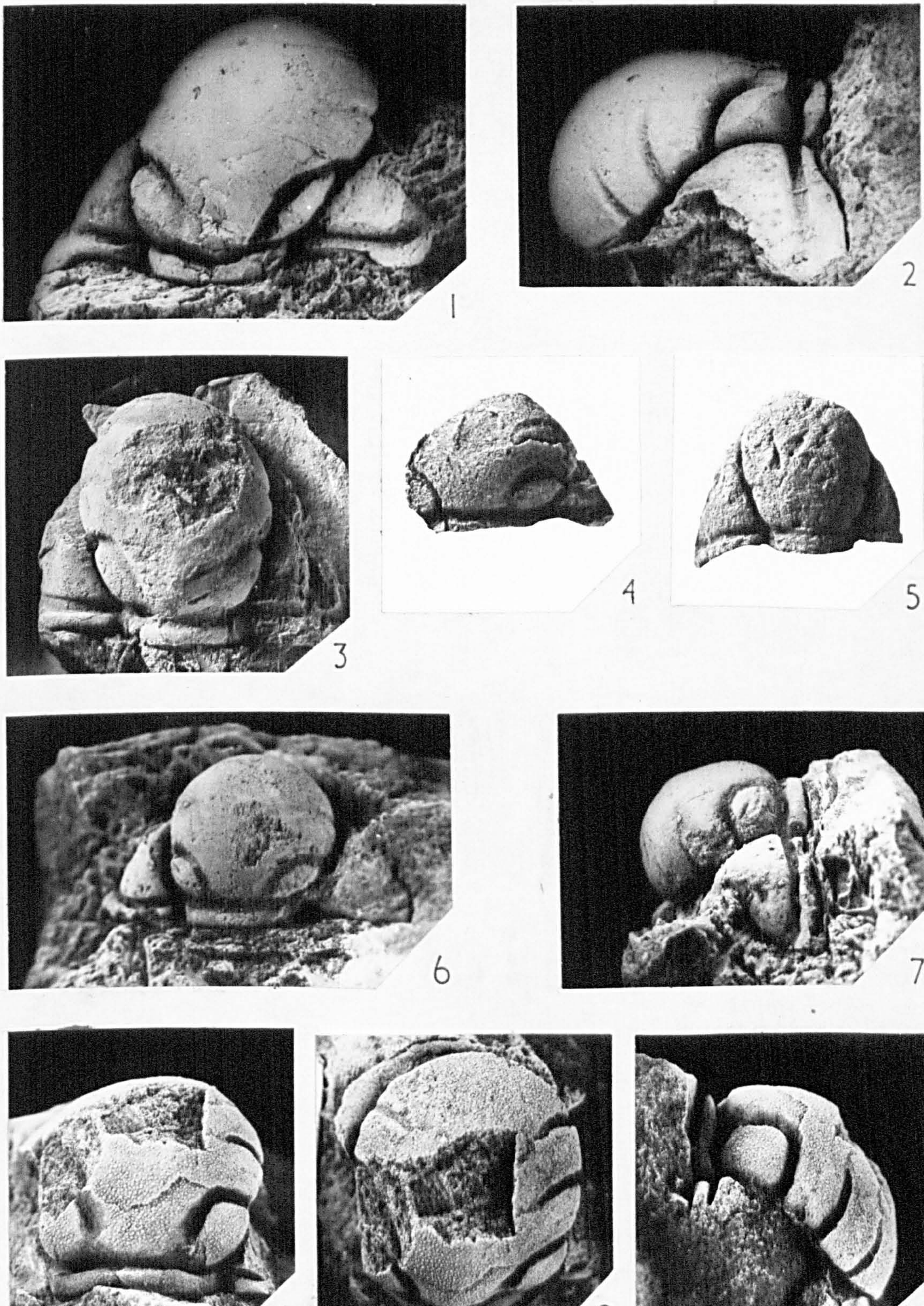

Plate 26

Plate 27.

Stubblefieldia verrucosa sp. nov.

Pseudosphaerexochus consimilis sp. nov.

Figures 1-3. *Stubblefieldia verrucosa*, BM In47201; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. 1. Dorsal view of internal mould, x3. 2. Palpebral view of same, x3. 3. Lateral view of same, x3.

Figure 4. *Stubblefieldia verrucosa*, BM In47170; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figure 5. *Stubblefieldia verrucosa*, Holotype, BM In47164; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. Dorsal view of internal mould, x3.

Figures 6-8. *Pseudosphaerexochus consimilis*, BM In47165; Starfish Bed, Upper Drummock Group, Ladyburn, Girvan, Ayrshire. 6. Dorsal view of internal mould, x2½. 7. Palpebral view of same, x2½. 8. Lateral view of same, x2½.

Figures 9-11. *Pseudosphaerexochus consimilis*, Holotype HM A1049; Starfish Bed, Upper Drummock Group, Ladyburn, Girvan, Ayrshire. 9. Dorsal view of external mould, x2. 10. Palpebral view of same, x2. 11. Lateral view of same, x2.

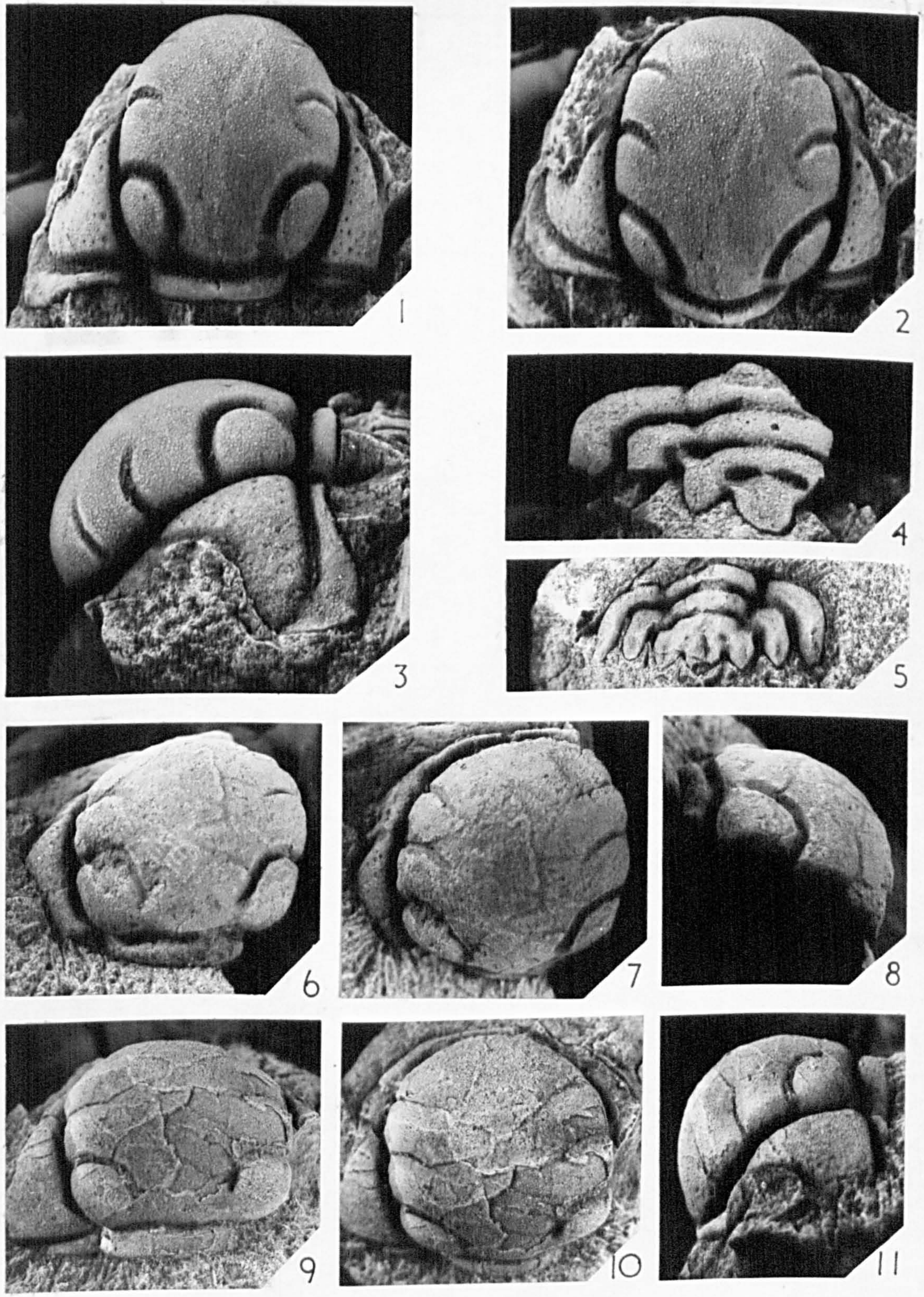

Plate 27

Plate 28.

Placoparina sedgwicki (M'Coy, 1849)

'Eccoptochile'pectinatus Salter MS.

Figure 1. Placoparina sedgwicki, GSM 92927; figured Whittard, 1958 Pl. XV, fig. 11. Shales interbedded with Stapeley Volcanic Group, Nind Quarry, near Linley, Shropshire. Dorsal view of external mould, x2

Figure 2. Placoparina sedgwicki, GSM 69897; figured Whittard, 1940, Pl. VI, fig. 7. Boat Level Adit, Brookleas Coppice, Leigh, Shropshire. Dorsal view of external mould, x4.

Figure 3. Placoparina sedgwicki, GSM 92928; figured Whittard, 1958, Pl. XV, fig. 10. Shales interbedded with Stapeley Volcanic Group, Nind Quarry, near Linley, Shropshire. Dorsal view of external mould, x2

Figure 4. Placoparina sedgwicki, GSM 92926A; figured Whittard, 1958, Pl. XV, fig. 6. Shales interbedded with Stapeley Volcanic Group, Nind Quarry, near Linley, Shropshire. Dorsal view of external mould, x2.

Figure 5. 'Eccoptochile' pectinatus, GSM 35241-2; Llanvirnian, Cefn Gwynlle, Shelve, Shropshire. Dorsal view of damaged external mould, x4.

Figure 6. 'Eccoptochile' pectinatus, GSM 69759; Llanvirnian, Cefn Gwynlle, Shelve, Shropshire. Dorsal view of pygidium, x4.

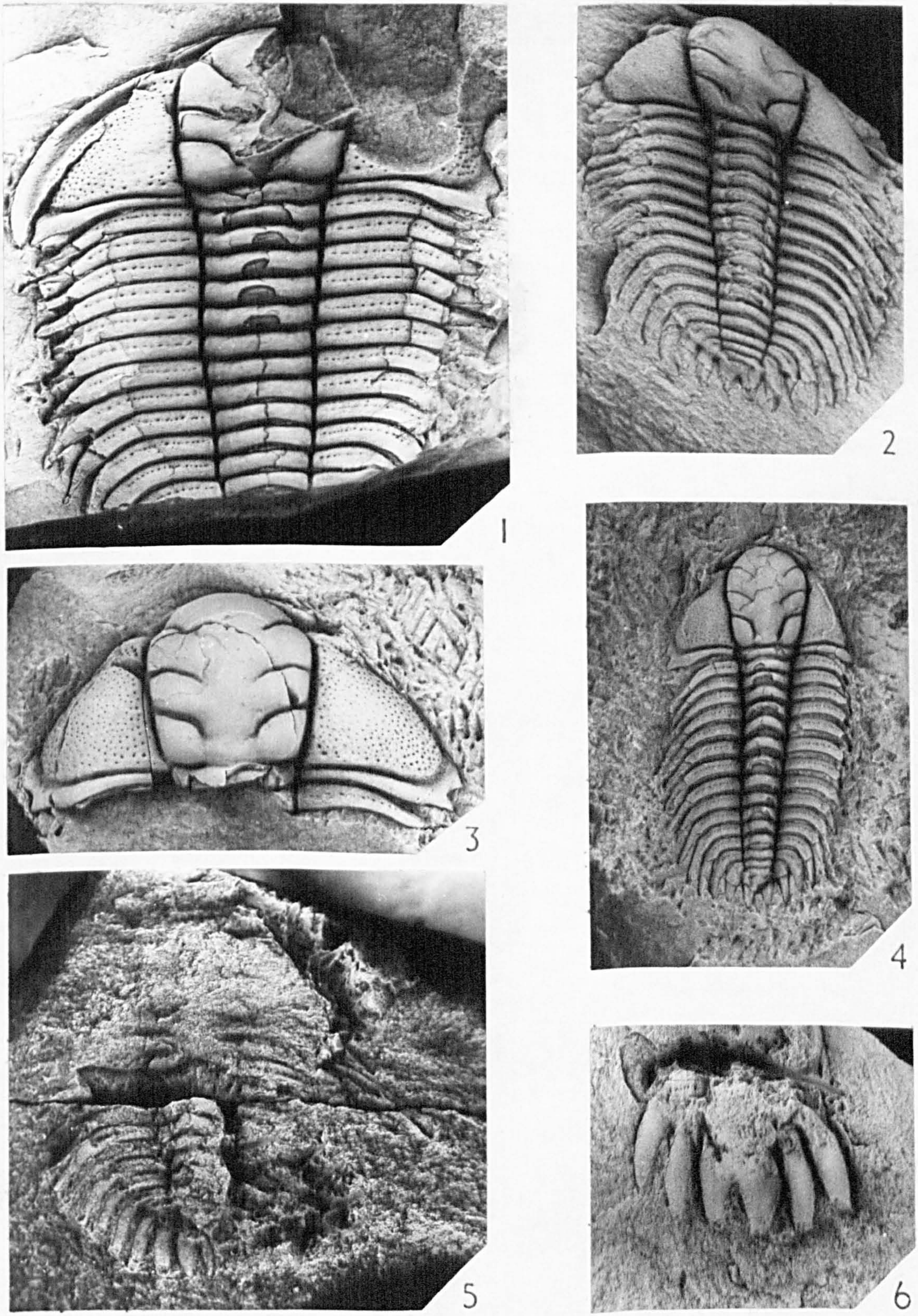

Plate 28

Plate 29.

Sphaerexochus mirus Beyrich, 1845.

Figures 1-3. *Sphaerexochus mirus*, BM It2461; Wenlockian, Komorau, Bohemia. 1. Dorsal view of internal mould, x3. 2. Lateral view of same, x3. 3. Anterior view of same, x3.

Figures 4-5. *Sphaerexochus mirus*, BM 23774; Wenlockian, Komorau, Bohemia. 4. Dorsal view of internal mould, x2. 5. Lateral view of same, x2.

Figure 6. *Sphaerexochus mirus*, BM It2459; Wenlockian, Komorau, Bohemia. Ventral view of hypostoma, shell missing from most of median body, x5.

Figures 7-8. *Sphaerexochus mirus*, BM It2462. Wenlockian, Komorau, Bohemia. 7. Dorsal view, shell preserved in places, x2. 8. Lateral view of same, x2.

Figure 9. *Sphaerexochus mirus*, BM It2456; Wenlockian, Komorau, Bohemia. Dorsal view of internal mould, x2.

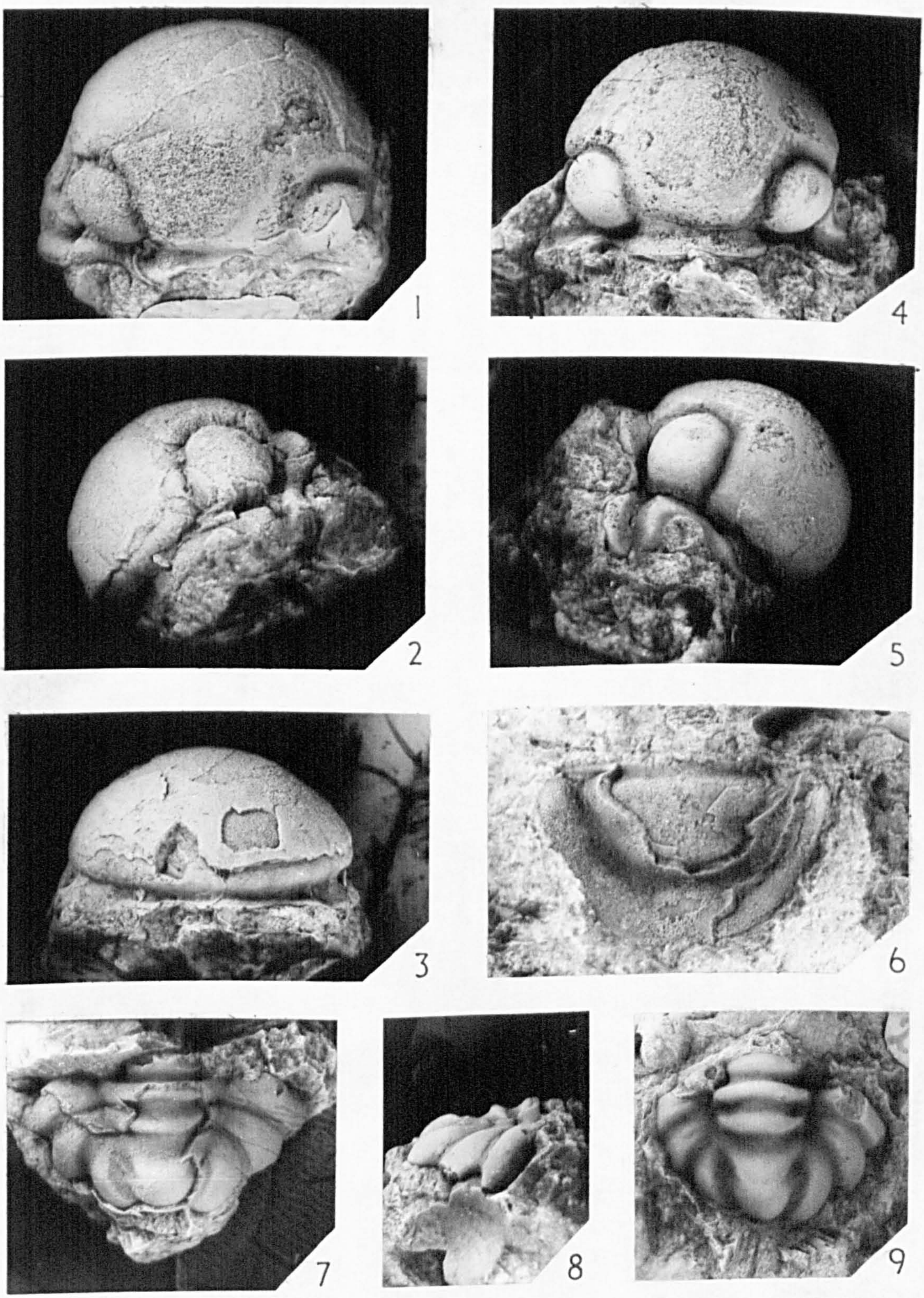

Plate 29

Plate 30.

Sphaerexochus aff. mirus Beyrich, 1845.

Figures 1-2 Sphaerexochus aff. mirus, BU Ketley 272; Wenlock Limestone, Dudley, Worcestershire. 1. Dorsal view, x2. 2. Lateral view of same, x2.

Figure 3. Sphaerexochus aff. mirus, SM A28592; Wenlock Shale, Malvern, Worcestershire. Dorsal view, x2.

Figures 4-5. Sphaerexochus aff. mirus, GSM 33105; Wenlock Limestone, Dudley, Worcestershire. 4. Anterior view of enrolled specimen, x2. 5. Lateral view of same, x2.

Figures 6-7. Sphaerexochus aff. mirus, SM A28595; Wenlock Shale, Malvern, Worcestershire. 6. Dorsal view, x2. 7. Lateral view, x2.

Figure 8. Sphaerexochus aff. mirus, SM A28602; Wenlock Limestone, Dudley, Worcestershire. Lateral view, x2.

Figure 9. Sphaerexochus aff. mirus, BU Ketley 382; Wenlock Shale, Dudley, Worcestershire. Dorsal view, x2.

Figures 10-11. Sphaerexochus aff. mirus, NU T7546; Wenlock Limestone, Dudley, Worcestershire. 10. Dorsal view of single segment, x3. 11. Lateral view of same, x3.

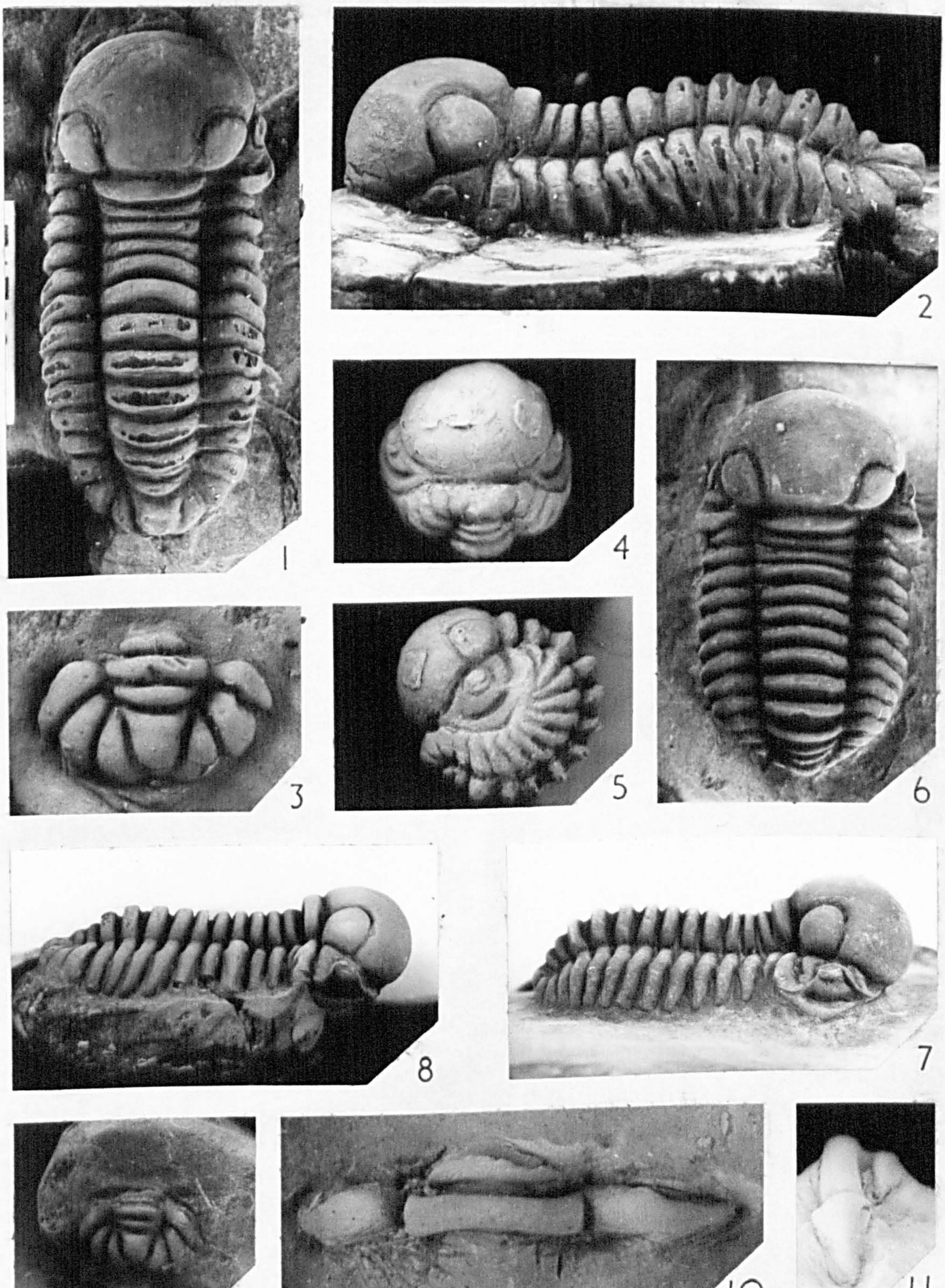

Plate 30

Plate 31.

Sphaerexochus aff. *mirus* Beyrich, 1845.

Figures 1-2. *Sphaerexochus* aff. *mirus*, GSM 36322; Wenlock Limestone, Trindle, Dudley, Worcestershire. 1. Dorsal view, x2. 2. Lateral view of same, x2.

Figure 3. *Sphaerexochus* aff. *mirus*, GSM 36121; Wenlock Shale, Wych, Malvern, Worcestershire. Dorsal view, x2.

Figure 4. *Sphaerexochus* aff. *mirus*, SM A28591; Wenlock Shale, Malvern, Worcestershire. Dorsal view, x2.

Figure 5. *Sphaerexochus* aff. *mirus*, BU Ketley 185; Wenlock Shale, Dudley, Worcestershire. Dorsal view, x2.

Figures 6-7. *Sphaerexochus* aff. *mirus*, BU Ketley '15'; Wenlock Shale, Dudley, Worcestershire. 6. Dorsal view, x2. 7. Anterior view, x2.

Figure 8. *Sphaerexochus* aff. *mirus*, BU Ketley 384; Wenlock Shale, Dudley, Worcestershire. Dorsal view, x2.

Figure 9. *Sphaerexochus* aff. *mirus*, BU Ketley 328; Wenlock Shale, Dudley, Worcestershire. Dorsal view, x2.

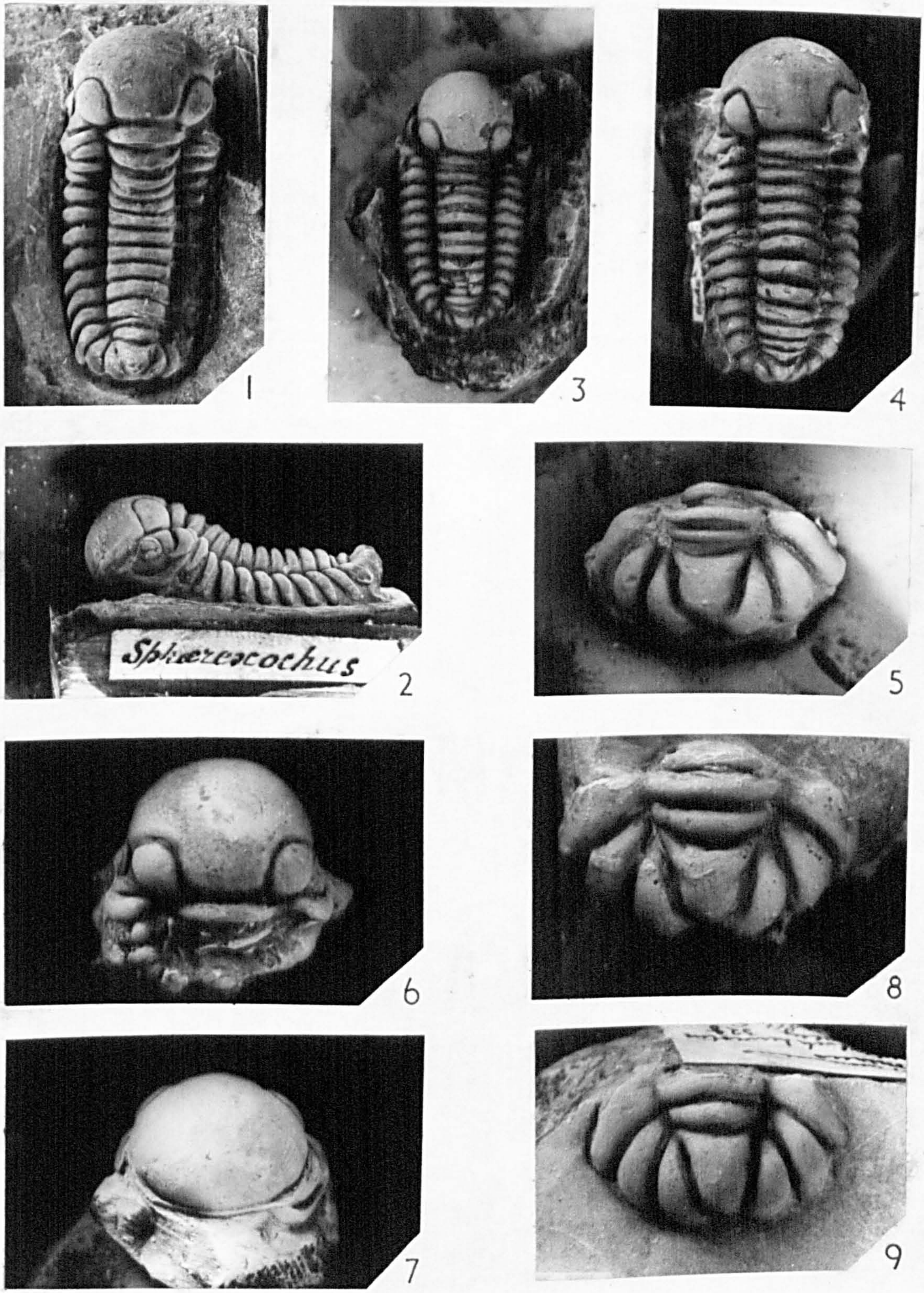

Plate 31

Plate 32.

Sphaerexochus balclatchiensis Reed, 1914.

Figures 1-2. *Sphaerexochus balclatchiensis*, Paralectotype BM In23535a; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 1. Dorsal view of internal mould, x2. 2. Lateral view of same, x2.

Figures 3-4. *Sphaerexochus balclatchiensis*, Paralectotype BM In23533a; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 3. Dorsal view of internal mould, x2. 4. Lateral view of same, x2.

Figures 5-6. *Sphaerexochus balclatchiensis*, Lectotype BM In23532; figured Reed, 1934, Pl. VIII, fig. 2. Balclatchie Group, Balclatchie, Girvan, Ayrshire. 5. Dorsal view of internal mould, x2. 6. Dorsal view of external mould (Latex cast), x2.

Figures 7-9. *Sphaerexochus balclatchiensis*, BM In23539; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 7. Dorsal view of internal mould, x2. 8. Lateral view of same, x2. 9. Dorsal view of external mould, (Latex cast), x2.

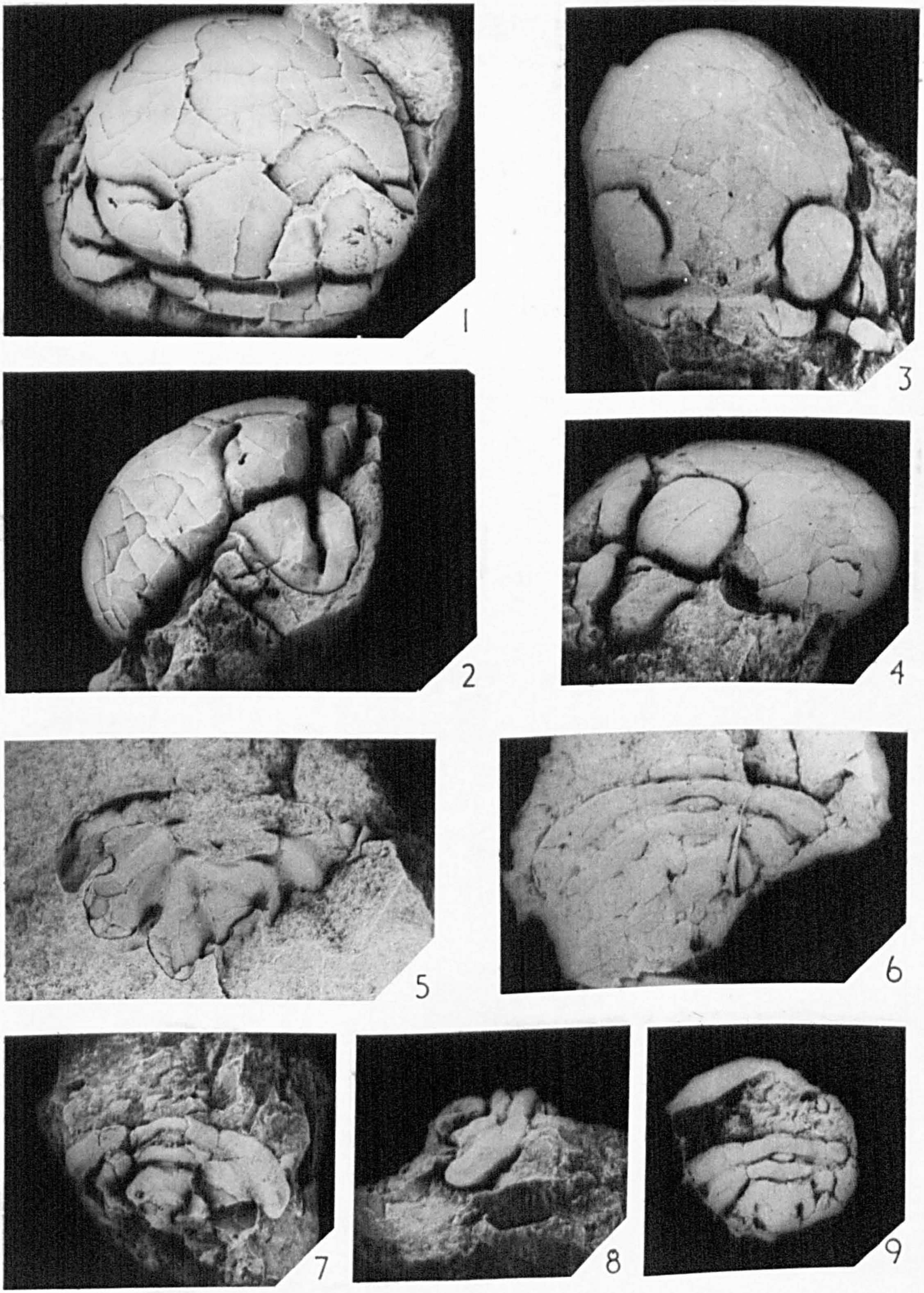

Plate 32

Plate 33.

Sphaerexochus balclatchiensis Reed, 1914.

Albaedes shallochensis gen. nov. (Reed, 1935)

Figures 1-2. *Sphaerexochus balclatchiensis*, Paralectotype BM In23537; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 1. Dorsal view of internal mould, x2. 2. Lateral view of same, x2.

Figures 3-4. *Sphaerexochus balclatchiensis*, Paralectotype BM In23534; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 3. Dorsal view of internal mould, x4. 4. Lateral view of same, x4.

Figures 5-6. *Sphaerexochus balclatchiensis*, Paralectotype BM In23536; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 5. Dorsal view of internal mould, x3. 6. Lateral view of same, x3.

Figures 7-8. *Sphaerexochus balclatchiensis*, Paralectotype BM In23538; Balclatchie Group, Balclatchie, Girvan, Ayrshire. 7. Lateral view of thoracic segment, x2. 8. Dorsal view of same, x2.

Figures 9-10. *Albaedes shallochensis*, Lectotype BM In36969; figured Reed, 1935, Plate 1, figs. 20-20a. Whitehouse Group, Whitehouse Bay, Ayrshire. 9. Dorsal view of pygidium and posterior part of thorax, x5. 10. Dorsal view of specimen, x2.

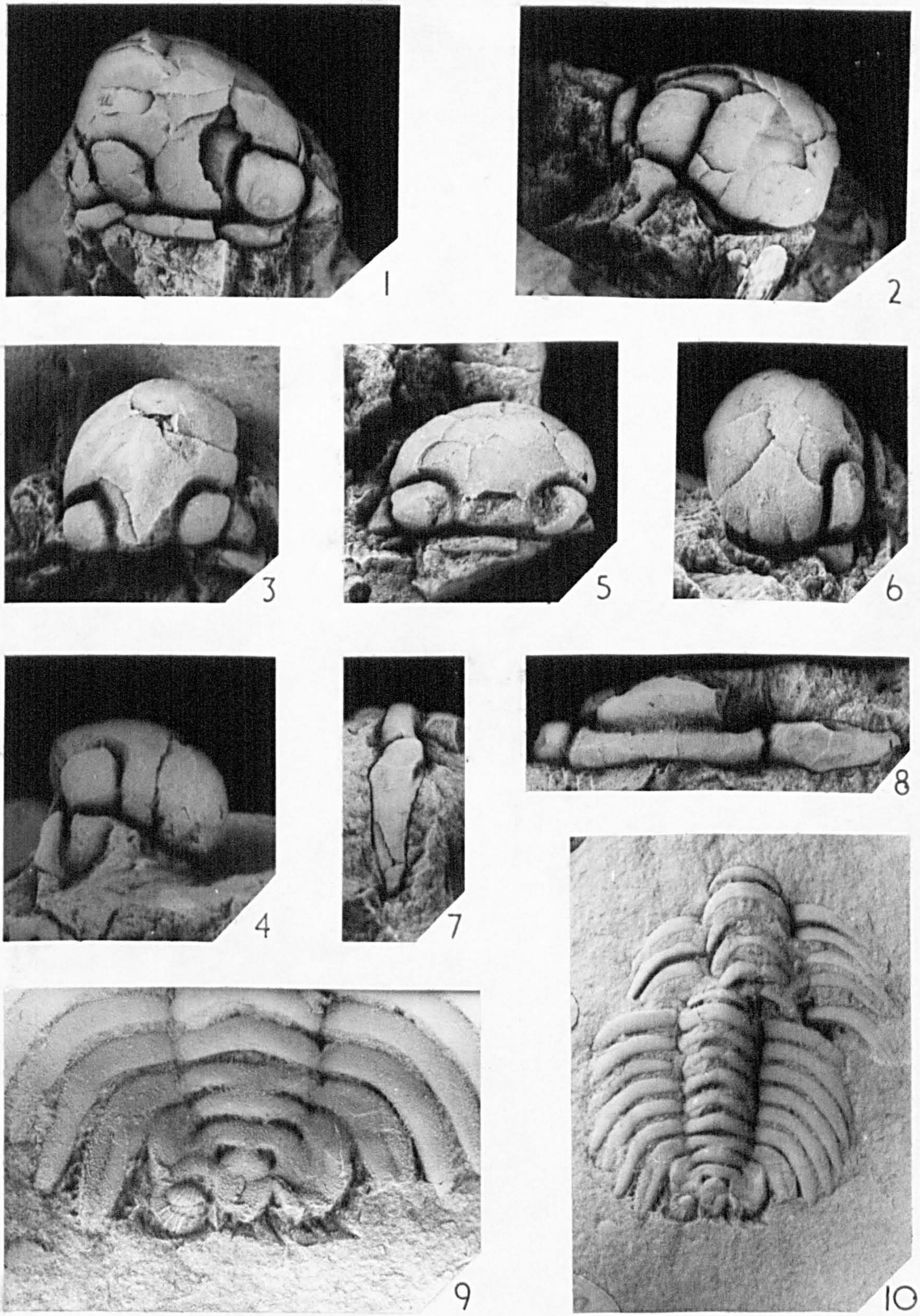

Plate 33

Plate 34.

Sphaerexochus calvus M'Coy, 1849.

Figures 1-2. Sphaerexochus calvus, RSM 1870 12 1173D; Chair of Kildare Limestone, Kildare, 1. Dorsal view, x3. 2. Lateral view of same, x3.

Figures 3-4. Sphaerexochus calvus, RSM 1870 12 1173G; Chair of Kildare Limestone, Kildare. 3. Dorsal view of internal mould, x3. 4. Lateral view of same, x3.

Figures 5-6. Sphaerexochus calvus, RSM 1870 12 1173E; Chair of Kildare Limestone, Kildare. 5. Dorsal view, x3. 6. Lateral view of same, x3.

Figure 7. Sphaerexochus calvus, RSM 1870 12 1173C; Chair of Kildare Limestone, Kildare. Dorsal view, x4.

Figure 8. Sphaerexochus calvus, RSM 1870 12 893A; Chair of Kildare Limestone, Kildare. Dorsal view, x4.

Figures 9-10. Sphaerexochus calvus, RSM 1870 12 1173F. Chair of Kildare Limestone, Kildare. 9. Dorsal view of internal mould, shell preserved in places, x3. 10. Lateral view of same, x3.

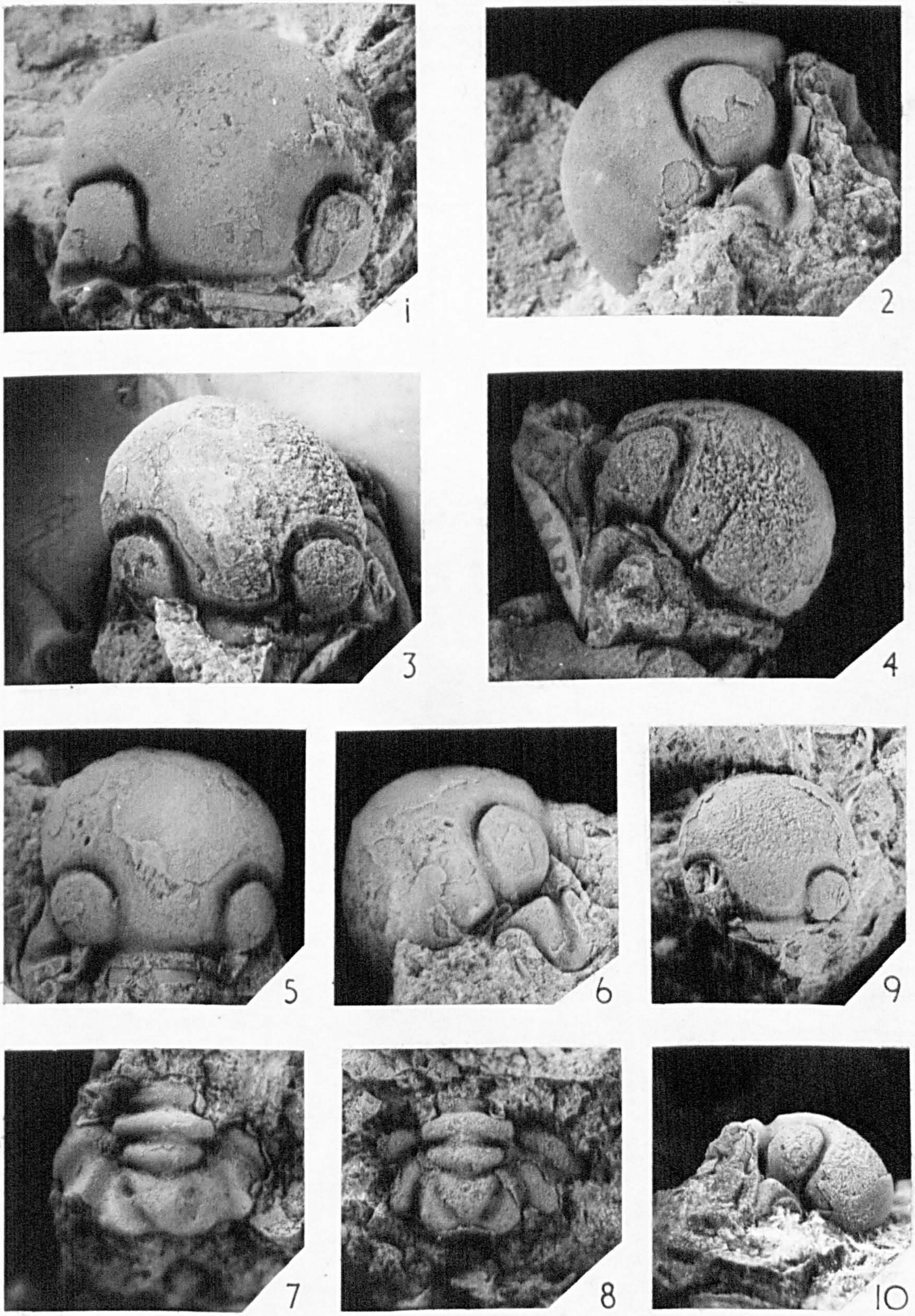

Plate 34

Plate 35.

Deiphon barrandei Whittard, 1934.

Figure 1. Deiphon barrandei, BU 63 (ex Ketley 299); Wenlock Limestone, Dudley, Worcestershire. Anterior view, x3.

Figure 2. Deiphon barrandei, GSM 58952; Wenlock Limestone, Dudley, Worcestershire. Anterior view, x3.

Figure 3. Deiphon barrandei, SM A3298; Wenlock Limestone, Dudley, Worcestershire. Dorsal view, x3.

Figures 4-6. Deiphon barrandei, SM A3294; Wenlock Limestone, Dudley, Worcestershire. 4. Dorsal view, x3. 5. Lateral view, x3. 6. Anterior view, x3.

Figure 7. Deiphon barrandei, SM A3303; Wenlock Limestone, Dudley, Worcestershire. Dorsal view showing part of thorax, x3.

Figure 8. Deiphon barrandei, SM A3304; Wenlock Shale, Dudley, Worcestershire. Dorsal view, x3.

Figure 9. Deiphon barrandei, SM A3301; Wenlock Limestone, Dudley, Worcestershire. Dorsal view, x3.

Figure 10. Deiphon barrandei, SM A3295; Wenlock Limestone, Dudley, Worcestershire. Dorsal view of fragmentary pygidium, x3.

Figure 11. _Deiphon barrandei_ Paratype SM A3296; figured Whittard, (as D. _forbesi_ var. _barrandei_) Plate XVI, fig. 3. Wenlock Limestone, Dudley, Worcestershire. Dorsal view of pygidium, x3.

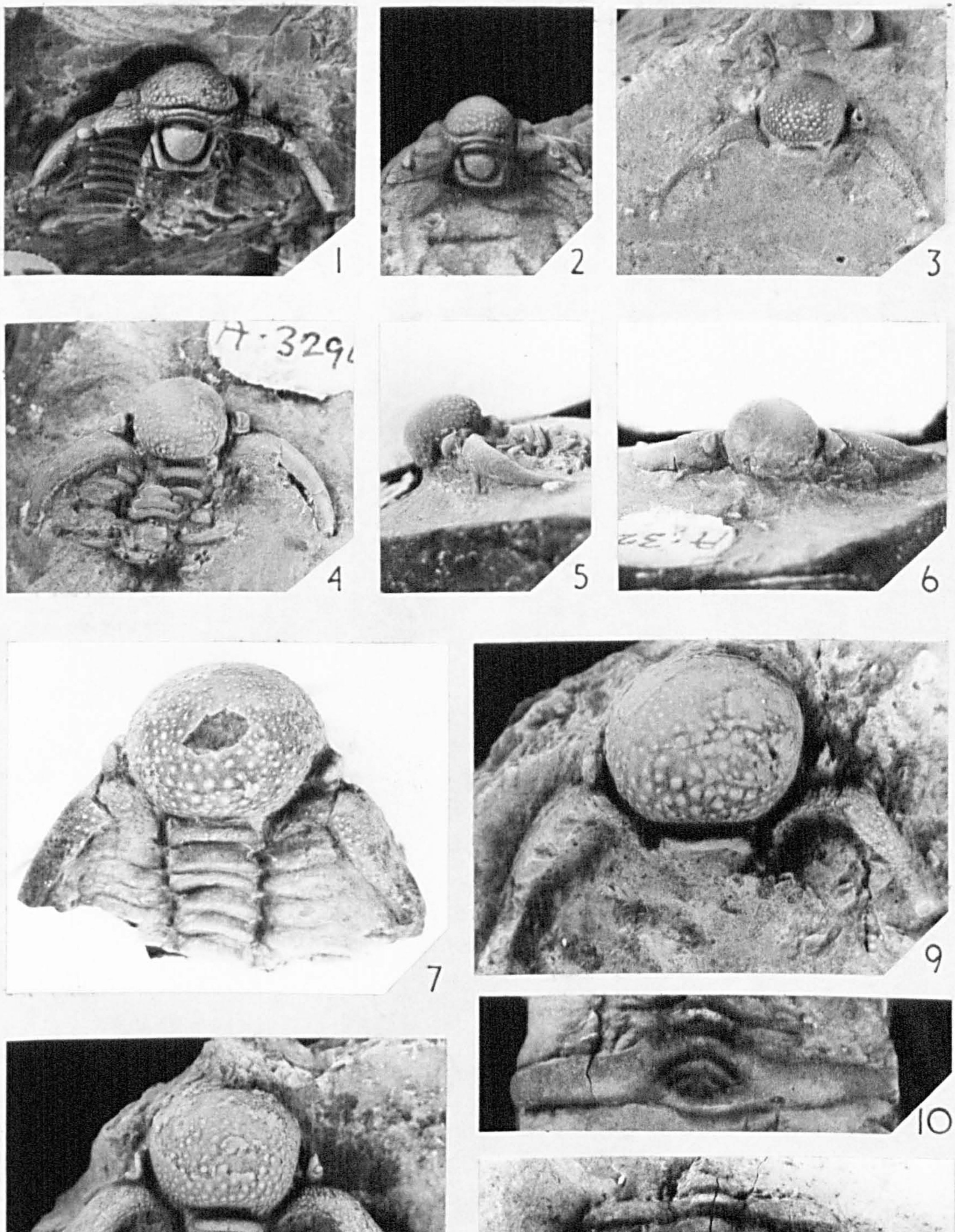

Plate 35

Plate 36.

<u>Deiphon</u> <u>barrandei</u> Whittard, 1934.

<u>Deiphon</u> <u>forbesi</u> Barrande, 1850.

<u>Deiphon</u> <u>circularis</u> sp. nov.

Figure 1. <u>Deiphon</u> <u>barrandei</u>, BU Ketley 309; Wenlock Limestone, Dudley, Worcestershire. Dorsal view, x3.

Figure 2. <u>Deiphon</u> <u>barrandei</u>, BU Ketley 131; Wenlock Limestone, Dudley, Worcestershire. Dorsal view, x3.

Figure 3. <u>Deiphon</u> <u>barrandei</u>, SM A3311; figured Salter, 1864, Pl. 7. fig. 11. Wenlock Limestone, Dudley, Worcestershire. Dorsal view, x3.

Figures 4-5. <u>Deiphon</u> <u>forbesi</u>, SM A3309; Etage E1, zone of <u>Cyrtograptus</u> <u>murchisoni</u>, Listice, Bohemia. 4. Dorsal view, x3. 5. Anterolateral view, x3.

Figure 6. <u>Deiphon</u> <u>forbesi</u>, SM A3308; Etage E1, zone of <u>Cyrtograptus</u> <u>murchisoni</u>, Listice, Bohemia. Dorsal view, x3.

Figures 7-9. <u>Deiphon</u> <u>circularis</u>, Holotype OUM C14771; Venusbank Formation, Upper Llandoverian, Josey's Wood, SJ 36560213, Shropshire. 7. Palpebral view, x3. 8. Dorsal view, x3. 9. Anterior view, x3. Internal mould.

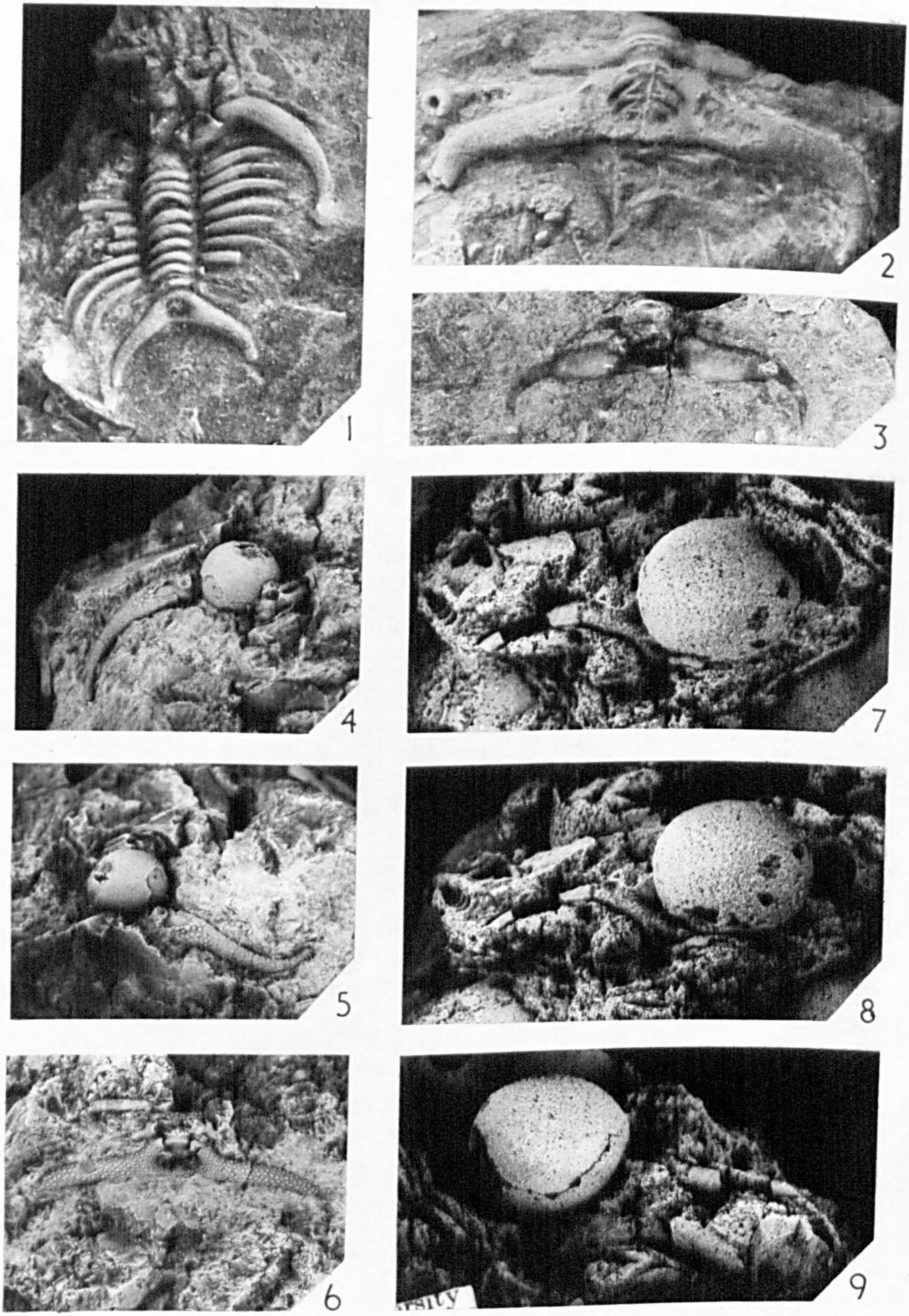

Plate 36

Plate 37.

Sphaerocoryphe thomsoni (Reed, 1906).

Sphaerocoryphe globiceps (Portlock, 1843).

Figure 1. *Sphaerocoryphe thomsoni*, BM In23467; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. Latex cast of near complete specimen, dorsal view, x3.

Figures 2-3. *Sphaerocoryphe thomsoni*, BM In23469; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. 2. Internal mould, dorsal view, x3. 3. Latex cast of external mould of same, x3.

Figures 4-5. *Sphaerocoryphe thomsoni*, BM In23465; Starfish Bed, Drummock Group, Thraive Glen, Girvan, Ayrshire. 4. Dorsal view of internal mould, x5. 5. External mould of same, latex cast, x5.

Figure 6. *Sphaerocoryphe globiceps*, Lectotype GSM 35462; figured Portlock 1843 (as *Ceraurus globiceps*) Pl. 1, figs 7a-c; Salter, 1864, Pl. 7, fig. 21. Desertcraight, Tyrone. Dorsal view of poor external mould, x4.

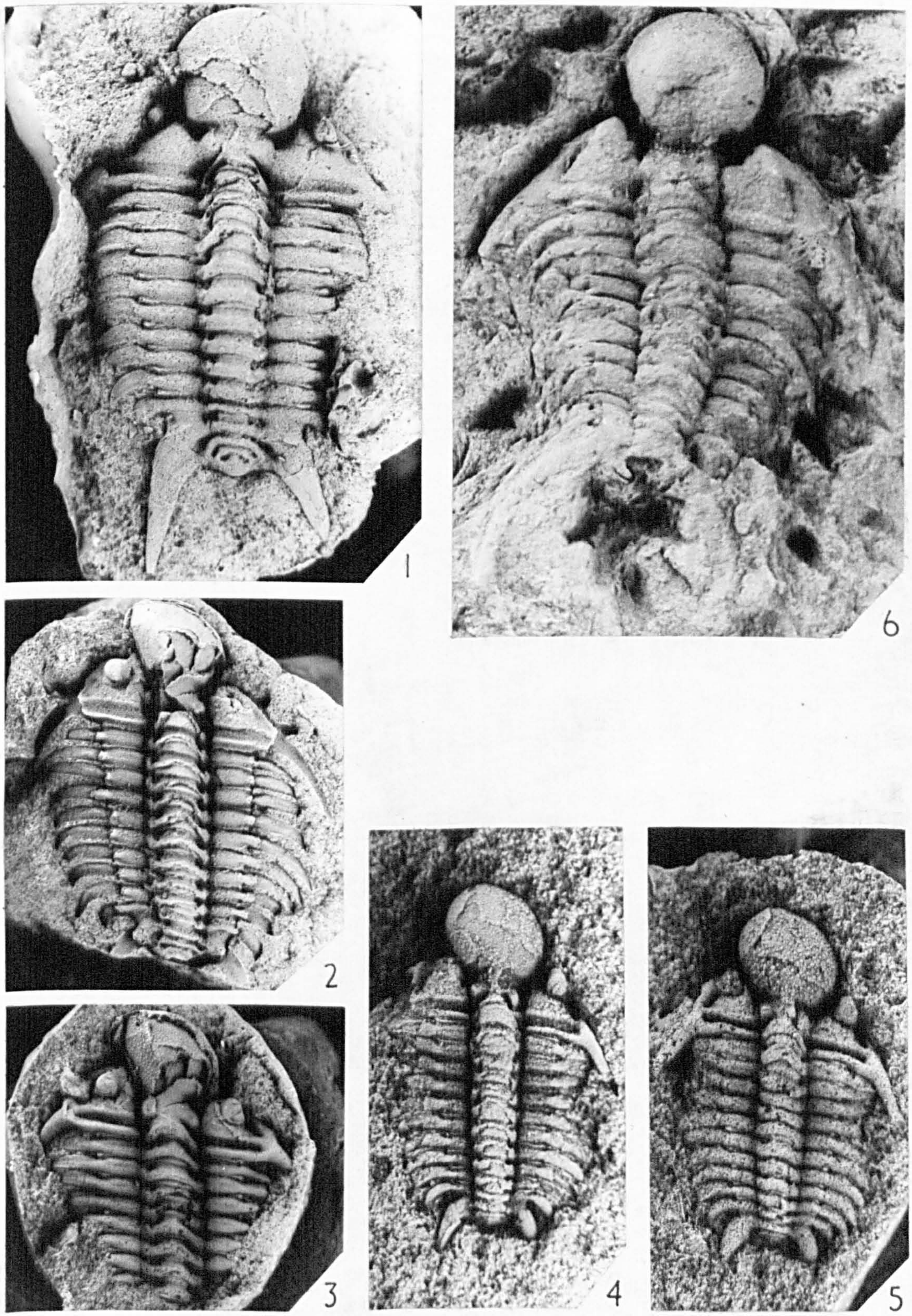

Plate 37

Plate 38.

Youngia trispinosa (Young, 1868).

Figures 1-2. *Youngia trispinosa*, Lectotype HM A52/1; figured Young, 1868, Pl. 1, figs. 4-5. Penkill Group, Penkill, Girvan, Ayrshire. 1. Dorsal view of internal mould, x3. 2. Lateral view of same, x3.

Figure 3. *Youngia trispinosa*, BM In23492; Penkill Group, Penkill, Girvan, Ayrshire. Dorsal view, x3.

Figures 4-5. *Youngia trispinosa*, BM In23493; figured Nicholson and Etheridge, 1878, Pl. VII, figs. 15-16. Penkill Group, Penkill, Girvan, Ayrshire. 4. Dorsal view, x1½. 5. Lateral view of same, x1½.

Figures 6-7. *Youngia trispinosa*, BM In23495; Penkill Group, Penkill, Girvan, Ayrshire. 6. Dorsal view of internal mould shell preserved in places, x2. 7. Lateral view of same, x2.

Figure 8. *Youngia trispinosa*, BM In23496; figured Nicholson and Etheridge, 1878, Pl. VII, fig. 14. Penkill Group, Penkill, Girvan, Ayrshire. Dorsal view, x2.

Plate 38

Plate 39.

Youngia trispinosa (Young, 1868).

Figures 1-2. *Youngia trispinosa*, BM In23499; figured Reed, 1906, Pl. XIX, fig. 9. Penkill Group, Penkill, Girvan, Ayrshire. 1. Dorsal view, x2. 2. Lateral view, x2.

Figure 3. *Youngia trispinosa*, BM In23491; figured Nicholson and Etheridge, 1878, Pl. VII, fig. 10. Penkill Group, Penkill, Girvan, Ayrshire. Dorsal view, x2.

Figure 4. *Youngia trispinosa*, BM In23500; figured Reed, 1906, Pl. XIX, fig. 10. Penkill Group, Penkill, Girvan, Ayrshire. Dorsal view of internal mould, x1½.

Figures 5-6. *Youngia trispinosa*, BM In23498; figured Reed, 1906, Pl. XIX, fig. 8. Penkill Group, Penkill, Girvan, Ayrshire. 5. Dorsal view of internal mould, x2. 6. Lateral view of same, x2.

Figure 7. *Youngia trispinosa*, BM In23502; figured Reed, 1906, Pl. XIX, fig. 12. Penkill Group, Penkill, Girvan, Ayrshire. Dorsal view of axial portion of thoracic segment referred tothis species, x3.

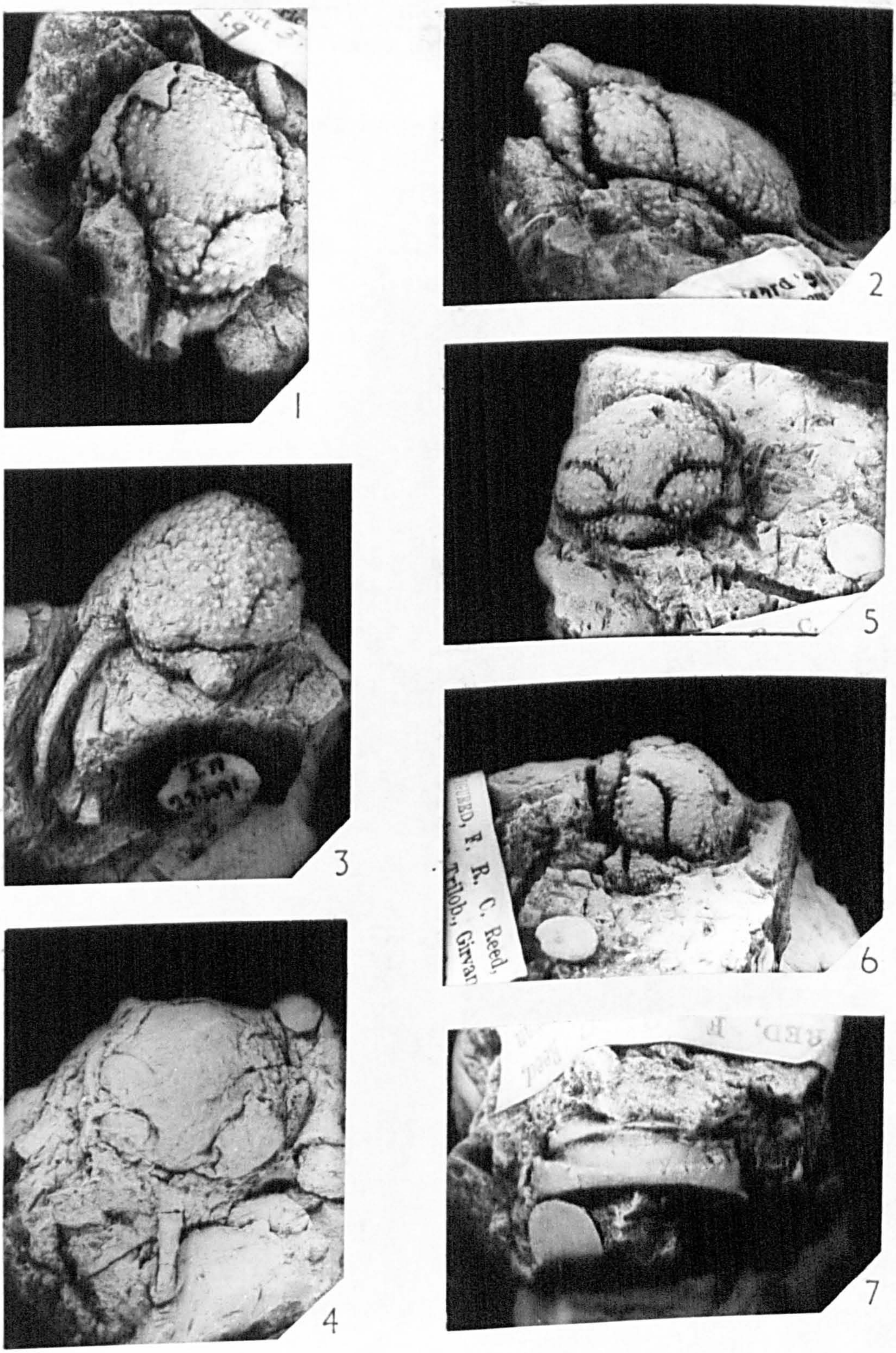

Plate 39

Plate 40.

Onycopyge liversidgei Woodward, 1880.

Youngia moroides (Marr and Nicholson, 1888).

Youngia aff. trispinosa (Young, 1868).

Figures 1-3. Onycopyge liversidgei, Lectotype BM I107a & b; figured Woodward, 1880, p. 98; Whittard, 1934, Pl. XVI, figs. 10-11. 'Silurian', near Bombala, New South Wales. 1. Dorsal view of damaged external mould, x3. 2. Dorsal view of cephalon, x3. 3. Lateral view of same, x3.

Figures 4-5. Youngia moroides, SM A40326b; figured Marr and Nicholson, 1888, Pl. XVI, fig. 10. Phacops glaber zone, Middle Skelgill Beds, Skelgill, near Ambleside, Westmorland, 5. Latex cast of external mould, smaller specimen of two on same block, x6. 6. Latex cast of external mould, x3.

Figures 6-7. Youngia aff. trispinosa, HM A1111. Saugh Hill Group, Newlands, Girvan, Ayrshire. 6. Dorsal view of internal mould, x8. 7. Anterolateral view of same, x8.

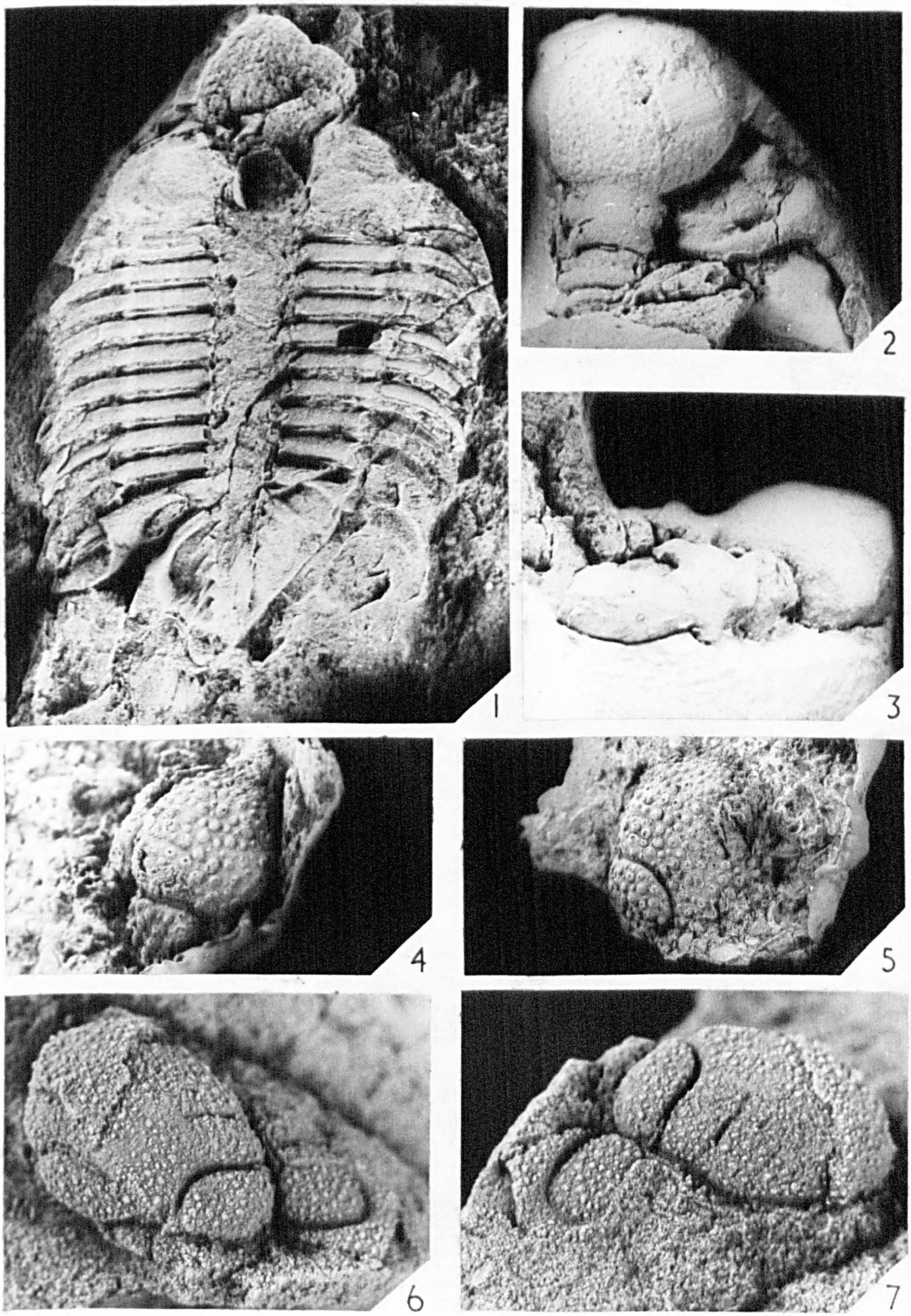

Plate 40