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A STUDY OF THE MORPHOLOGY AND PHYLOGENY OF THE FAMILY HARPETIDAE HAWLE AND CORDA, 1847 (TRILOBITA)

ABSTRACT

The present paper deals with the morphological, phylogenetic and taxonomic problems of the trilobites of the family *Harpetidae* HAWLE et CORDA, 1847. This family is divided into three subfamilies—*Harpetinae* HAWLE et CORDA, 1847, *Eoharpetinae* PŘIBYL et VANĚK, 1981 and *Dolichoharpetinae* PŘIBYL et VANĚK, 1981. These comprise nineteen genera and subgenera. Six new harpetids species or subspecies are described.

PREFACE

Among the Lower Palaeozoic trilobites, the unique position of the family *Harpetidae* HAWLE et CORDA, 1847 is particularly striking. Its morphology, phylogeny, taxonomy and palaeo-ecology are dealt with in this paper. The genus *Harpes* was described in 1839 by GOLDFUSS. Later, HAWLE and CORDA (1847) established the group "*Harpides*" for this genus, also including in it the genus *Harpides*, described by BEYRICH in the year 1846, which today is assigned to the family *Harpididae* (recte *Harpidetidae* WHITTINGTON, 1950). In 1854, ANGELIN described the genus *Arraphus*, introducing for it the family *Arraphidae* into which he included — in addition to the type genus *Arraphus* ANGELIN, 1854 — the genus *Harpes* GOLDFUSS, 1839. *Arraphidae* is a subjective synonym of the family *Harpetidae* HAWLE et CORDA, 1847 established earlier. In 1885, NOVÁK had erected for the species *Harpes primus* BARRANDE, a new genus, *Harpina*, which RAYMOND (1905) gave a new name, *Eoharpes*, because of the homonymy with *Harpina* BURMEISTER, 1844 (*Coleoptera*) and

Harpina BÖCK, 1870 (Crustacea). In 1898, JONES and WOODWARD described a further new genus of this family, designating it *Hibbertia*. Since that time, during more than forty years, nobody dealt in greater detail with the generic taxonomy of the family *Harpetidae*. It was not until 1948 that LAMONT described three new harpetid genera from the Ordovician and Silurian of Scotland (*Dubhglasina*, *Metaharpes* and *Scotoharpes*). After a year, WHITTINGTON (1949) introduced a further new genus, *Dolichoharpes*, and in 1950 (a) he published a monograph on the British harpetids, establishing the new genera *Aristoharpes*, *Lioharpes*, *Paraharpes*, *Platyharpes* and *Selenoharpes*. But in the same year (1950b) WHITTINGTON himself abolished the validity of the genus *Platyharpes*, as it is a younger synonym of *Hibbertia* JONES et WOODWARD, 1898. Furthermore, in 1963 Whittington proposed that *Aristoharpes* WHITTINGTON, 1950 should be regarded as a synonym of *Selenoharpes*. From the Lower Tremadocian of Argentina, the so far known oldest representative of the family *Harpetidae* — *Australoharpes* — has been described by HARRINGTON and LEANZA (1957). Furthermore, new generic taxa of the family *Harpetidae* were established in 1963 by VANĚK, namely the genera *Bohemoharpes*, *Fritchaspis*, *Kielania* and *Reticuloharpes*. In 1973, NORFORD pointed out that *Scotoharpes* has priority over *Aristoharpes* and *Selenoharpes*, and both these genera are later subjective synonyms of *Scotoharpes*. Recently, a further genus *Harpesoides* KOROLEVA, 1978 described from the Upper Ordovician of Kazakhstan (U.S.S.R.) was added to them. *Harpesoides* might be identical with the genus *Paraharpes* WHITTINGTON, 1950. In 1981 PRIBYL and VANĚK divided the family *Harpetidae* into three subfamilies (*Harpetinae*, *Eoharpetinae* and *Dolichoharpetinae*) and described six new taxa: *Bohemoharpes* (*Declivoharpes*), *B.* (*Unguloharpes*), *Helioharpes*, *Kielania* (*Lowtheria*), *Thorslundops* and *Wegelinia*.

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GENERAL CHAPTERS

1. Origin of the family *Harpetidae* HAWLE et CORDA, 1847

In the Lower Ordovician the family under consideration already had distinctive morphological features, so that it may be assumed that its evolution was very long, beginning at the latest in the Upper Cambrian. The hitherto known earliest representative of this family, the genus *Australoharpes* HARRINGTON et LEANZA, 1957, first occurred in the Lower Tremadocian of Argentina. We start from its morphological features, gradually following up the evolution of the whole family. But this genus has so far been known from isolated cephalon only. In its morphology, in addition to the conspicuous brim [synapomorphic feature, existing in all the representatives of the studied family], a large preglabellar boss, elongately tetragonal, is striking. The glabella is narrowly conical with one pair of lateral glabellar furrows (1S) and lobes (1L). Alae are semicircular and small. The genal roll is narrow and brim broad; fringe with

a girder extending to tips of prolongations. Between the genicranidium and genal prolongations, an elongately subtrigonal depression — a relic of free genae — is developed. In our opinion, this depression (a relic of free genae) is of a considerably morphologic-phylogenetic importance. Some features distinctive of the genus *Australoharpes* also exist in the Lower and Middle Cambrian representatives of the family *Conocoryphidae* ANGELIN, 1854, particularly in the genus *Ctenocephalus* HAWLE et CORDA, 1847. The latter genus also has a conspicuous preglabellar boss and a conical glabella. Axial furrows, bounding laterally the glabella, widen sideways (tr.) at their posterior margins, so that they resemble wide semicircular depressions from which alae may have arisen (probably in harpetid trilobites). Fixigenae are rimmed anteriorly by a marked anterior border. On the genae of some representatives of *Ctenocephalus*, especially of the nominate subgenus, arcuate ridges occur on fixigenae; the part of the genae between fixigenae and the anterior border furrow slopes abruptly toward the anterior margin of cephalon. Librigenae are small, consisting practically of long pointed genal spines widening only (tr.) at the base. In comparing the morphological structure of the exoskeleton of *Australoharpes* and *Ctenocephalus* (Fig. 1), we concluded that *Ctenocephalus* most probably represents a morphological circle of ancestors from which the family *Harpetidae* later split off. The preglabellar boss as well as the narrow and conical glabella and the posterior widening of axial furrows indicating the later origin of alae are analogous in both these genera. The arcuate ridges on fixigenae and their anteriorly sloping parts in *Ctenocephalus* gave rise to the genal roll in the *Harpetidae*. In *Ctenocephalus*, from the anterior border of cranium the typical harpetid brim with rim originated. The librigenae of *Ctenocephalus*, provided with elongate genal spines, have also been preserved as relics in *Australoharpes*. It is just the above-mentioned elongately subtrigonal small depression of characteristic shape, which may be regarded as a trace of the spines. Thus, the brim in *Harpetidae* became hypertrophic having taken the function of a widened alimentary caeca which may probably also have formed part of an "auxiliary respiratory system". During the phylogenetic evolution this brim also surrounded librigenae with which it fused into brim and genal prolongations. When we consider the morphology and the origin structure of cephalon to be applied to *Harpetidae*, we assume that a hypothetical congruent link between *Conocoryphidae* and *Harpetidae* existed, namely in the sense that later a form may be found, in which the anterior marginal border (or brim) would be considerably widened while the other conocoryphid (recte ctenocephalid) features would remain preserved (see Fig. 1). In contrast to *Conocoryphidae*, harpetid have eyes¹⁾ which are lacking in the representatives of the family *Conocoryphidae*, although in their place crescentic tubercles appear, simulating palpebral lobes, to which "eye ridges" are directed (e. g. in *Conocoryphe* (C.) *feralsensis* COURTESOLE, 1967, C. (C.) *pseudooculata* MIQUEL, 1905, *Conocoryphid* sp. A-cf. FRITZ, 1973) and a complicated structure of caeca. In both *Conocoryphidae* and *Harpetidae*, the high number of thoracic segments, their configuration, the small pygidium and the homologous shape of hypostome (see Figs. 1 and 2) testify to their phylogenetic relationship. But it is not possible to pass unnoticed that *Conocoryphidae* occurred — in so far as it has been recognized — in the Lower and Middle Cambrian only (in the *Paradoxides forchhammeri* Biozone-teste KOROBOV, 1973). As has already been mentioned, the representatives of *Harpetidae* did not appear until the Lower Tremadocian. For this reason, a fairly long time interval existed between the times of occurrence of the two families, lasting during the whole Upper Cambrian. But we believe that in the future, well preserved specimens of the hypothetical Upper Cambrian forms may be found, which would furnish evidence of a continuous phylogenetic evolution. In this statement, we essentially agree with the opinion of HENNINGSMOEN (1951, p. 194) who assumed a close phylogenetic

1) The eyes of harpetid trilobites have 2 to 3 small elliptical lenses whose longer axis is horizontal. According to CLARKSON (1975, p. 9) "harpid (recte harpetid) eyes could perhaps be regarded as an independent evolutionary experiment towards a schizochroal condition, but their structure is so different from that of phacopid eyes that it would be unwise to term them schizochroal."

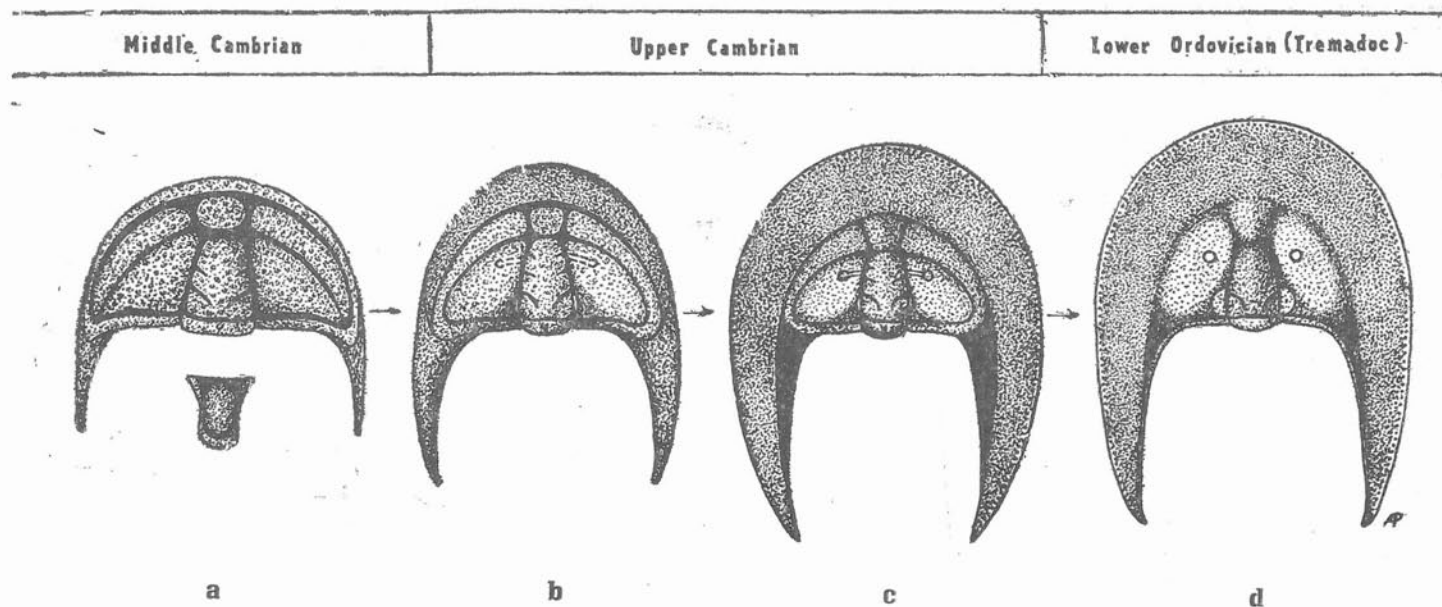


Fig. 1

a — *Ctenocephalus* (*Ctenocephalus*) *coronatus*. Jince Beds. Middle Cambrian, Paradoxides [Eccaparadoxides] pusillus Biozone. Skryje near Týřovice (Bohemia). x2.5 b — Hypothetical descendent of *Conocoryphidae*. x2.5. c — Hypothetical ancestor of *Harpetidae*. x3.0. — d — *Australoharpes depressus*. Lower Tremadoc [Lower Ordovician], Kainella meridionalis Biozone. Argentina. x3.5.

Eoharpetinae	Dolichoharpetinae	Harpetinae
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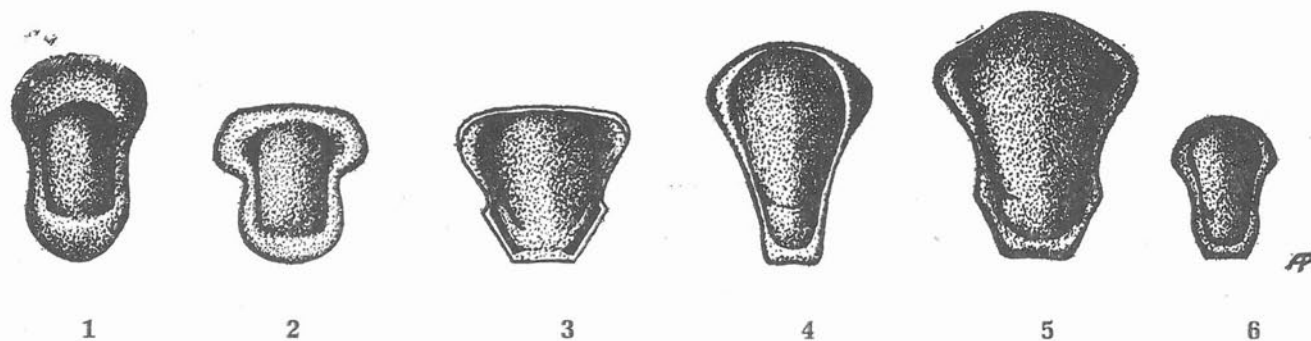


Fig. 2

1. *Eoharpes primus*, Šárka Formation. Llanvirnian, Ordovician, Osek near Rokycany (Bohemia). x5.4. — 2. *Paraharpes hornei*, Ashgillian, Upper Ordovician, Scotland. x6.0. 3. — *Dolichoharpes* aff. *reticulatus*. Esbataottine Formation, Middle Ordovician, Canada, x7.5. 4. — *Bohemoharpes* (*Unguloharpes*) *ungula ungula*. Kopanina Formation, Silurian. x5.0. 5. — *Lioharpes* (*Lioharpes*) *venulosus venulosus*. Koněprusy Limestone, Praha Formation. Lower Devonian. x3.5. 6. — *Kielania* (*Kielania*) *dorbygnyana*. Dvorce, Prokop Limestone, Praha Formation, Lower Devonian. x5.0.

relationship between *Harpetidae* and *Conocoryphidae*. Should *Conocoryphidae* of the suborder *Ptychopariina* really be distant phylogenetic ancestors of the family *Harpetidae*, then the establishment of the suborder *Harpina* by WHITTINGTON (1959) may be regarded as superfluous.

During the evolution of the family *Harpetidae*, ranging from the Lower Ordovician to the Upper Devonian, there existed, on the whole, a distinct tendency of glabella and glabellar furrows to increase and become more expressive, as well as an increase in number of thoracic segments. In most Silurian and Devonian harpetid genera, the girder does not extend to the tips of prolongations and meets the internal rim at some distance behind the posterior border. The *Harpetinae* sometimes tended toward considerable vaulting of the cephalic brim; the limit types are represented by *Wegelinia* and *Kielania*.

2. The morphology and terminology of the family *Harpetidae*

In designating the individual morphological elements of a harpetid cephalon we used the terminology according to WHITTINGTON [1949, 1950a], HENNINGSMOEN (1951) and the "Treatise" (1959). We may note that with regard to our interpretation of the harpetid structure of the cephalon of *Ctenocephalus* morphology as mentioned above in chapter 1, the facial suture (or more accurately its relic) runs within the harpetid cephalon, i. e. there where the girder extends. The latter played an important role in the system of alimentary caeca and thus the original course of facial suture became less perceptible. In our opinion, the marginal suture of the harpetid brim is not homologous to facial suture of other trilobite groups; it may also have had another function and origin. The caecal morphology in *Harpetidae* is shown in Fig. 3.

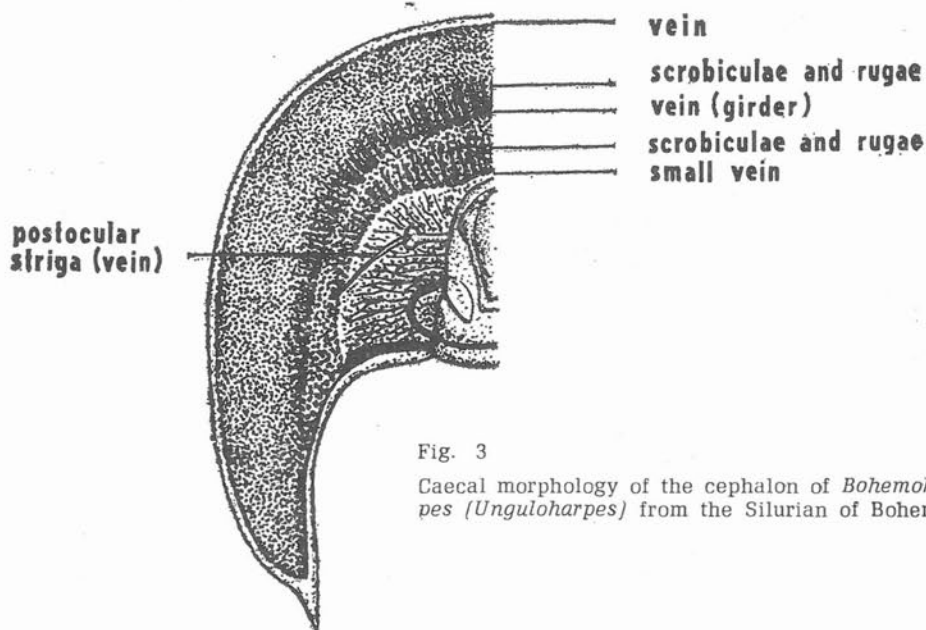


Fig. 3

Caecal morphology of the cephalon of *Bohemoharpes* (*Unguloharpes*) from the Silurian of Bohemia.

The main vein of the caecal alimentary apparatus probably ran through the girder. The secondary branching of the veins and ridges extends on genal lobes, genal roll and brim in the shape of radial ridges or fine veinlets. In some taxa having a post-ocular striga, the latter may also actually be a vein. Between the veins, scrobiculae

and rugae are scattered. Fine pores on cephalia (not perforation), on glabella and genae of the representatives of the family *Harpetidae* are, in our opinion, cuticular alveoles from which cellular excrescences in the shape of setae may have run, developed analogously in many groups of recent arthropods as integumentary sensory organs. When these fine pores are examined in greater detail in the representatives of some species (e. g. *Bohemoharpes ungula*, *Lioharpes venulosus*, *L. crassimargo*, *Helioharpes transiens*, *Reticuloharpes reticulatus* etc.) a certain variability appears as to their number per one mm², within a range of 10 to 30 pores. The setae from these pores possibly belong to the sensory tactile organs. The established varying density of pores (i. e. the density of the setae growing from them) agrees with the conditions in recent insects and arthropods where setae also vary in one and the same species, even within one locality. In *Harpetidae*, the hypostome is also located near the inner margin of the lower lamella of genal roll as already RICHTER (1921), WHITTINGTON (1950a) and others have noticed. RICHTER (1921, pl. 16, fig. 1) assumes the existence of a hypothetical ventral membrane connecting the inner margin of the lower lamella of the genal roll with the anterior margin of hypostome. However, for the present we have no evidence of such a membrane, but judging by the Bohemian species, in which hypostome has been preserved "in situ", the existence of such a membrane is very probable. According to the above statements, we remark that within the *Conocoryphidae* (e. g. in *Conocoryphe* and *Ctenocephalus*) too, the hypostome is distant from the posterior margin of rostral plate, and even in this case it is necessary to assume the presence of a membrane linking the rostral plate with the hypostome. Preglabellar boss appears to a greater or lesser extent in almost all representatives of the family *Harpetidae*, be it in the shape of a moderate elevation running along sagittal axis of the genal roll, and bounded by a shallow depression extending exsagittally at lateral margins (e. g. in *Lioharpes*, *Reticuloharpes* etc.), or in the form of sagittal broadening of genal roll (e. g. in *Bohemoharpes crassifrons* etc.).

3. The morphological criteria used for the classification of the *Harpetidae*

The majority of the criteria for classifying this family, which to a certain extent is morphologically fairly uniform, have been evaluated by WHITTINGTON (1950a). We add some notes to his conclusions. The measurement of the parameres (sag.) of cephalia, brim and genal prolongations has shown that the values obtained may be used for characterizing species as well as genera.

Index. Sagittal length of cephalon to the sagittal length of the brim in various species, if followed up in time succession, may indicate a mutually close affinity and phyletic relationship between the individual taxa. In contrast, the index of sagittal length of cephalon to the exsagittal length of brim prolongations is a very constant feature; it can therefore be used for a generic diagnosis. In order to determine both these indexes we measured complete cephalia of the individual representatives of the family (no less than 3 specimens), considering them to be flat surfaces (not taking their convexity into consideration). For example, the real sagittal length of the brim is not taken into account when the brim is concave or convex. The length of brim and genal prolongations was measured by drawing a straight line through the posterior border of cephalon, and from this line the length of brim and genal prolongations was measured up to their terminal tips, irrespective of a higher or lower convexity or concavity. The average several measurements in the individual species served then as the basis for calculating the indexes.

The configuration of the cephalic brim as well as the shape and structure of glabella, the caecae on genae and preglabellar field, and the shapes of hypostomes were taken as the basis for the division of the family *Harpetidae* into three subfamilies - *Harpetinae*, *Eoharpetinae* and *Dolichoharpetinae*. As the specific features of *Harpetidae* representatives we assume:

- (1) Sagittal length of the cephalon and the genal and brim prolongations,
- (2) sagittal length of the glabella,
- (3) the situation of eyes, and the length of eye ridges,
- (4) convexity of the genal roll and,
- (5) the various convexity or concavity of the brims and their different pitting.

4. Evolution of harpetid trilobites

Australoharpes is the hitherto earliest known representative of the *Harpetidae*. It has been found not only in the Lower Tremadocian of Argentina, but has also been reported by PETRUNINA (1966) from the Tremadocian²⁾ of the Saiano-Altai area of the U.S.S.R. This genus still retains many features of its ctenocephalid ancestors (see the chapter on the origin of the whole family) which in younger genera and subgenera already are less pronounced (relic of a boss, relic of librigena etc.). For the present we assign *Australoharpes* (with some hesitation) to the subfamily *Eoharpetinae*. This subfamily has so far been established for several genera, which have been found in the Ordovician and Lower Silurian of Europe, North and South America, Australia and Asia(?). With regard to their morphological configuration of the exoskeleton, particularly the structure of hypostome, and also to the arrangement of girder, which extends to tips of prolongations, we recognize within this subfamily two evolutionary lineages; the main evolutionary lineage (*Paraharpes-Hibbertia-Thorslundops*) and the lateral blind lineage with *Eoharpes*. The former evolutionary lineage begins with *Paraharpes* widespread in the Ordovician from the Llandeillan to the Ashgillian. During the Caradocian, the genus *Hibbertia* may have split off from this evolutionary lineage, and later the genus *Thorslundops* also derived from it. In the Ashgillian the latter was already extinct. The Upper Ordovician genus *Wegelinia* may also belong to this evolutionary lineage. In contrast, the evolutionary lineage of the genus *Hibbertia* probably continued up to the Llandoveryan. This lineage of evolution consisted of the genera *Paraharpes-Hibbertia-Thorslundops-Wegelinia*. It is characterized not only by large alae and large preoccipital glabellar lobes but also, particularly, by a fringe with a girder extending to tips of the genal prolongations. The overwhelming majority of the representatives of this evolutionary lineage lived during the Ordovician.

Within the nominate subfamily *Harpetinae*, for the time being, we have recognized 12 genera and subgenera, where (in the overwhelming majority) a hypostome is known (Fig. 2). The morphological structure of hypostome together with further features of the dorsal exoskeleton is useful in solving essential problems of the phyletic relationship between the individual genera. In addition to the above-mentioned genus *Australoharpes* (from which for the present we do not derive any generic or subgeneric taxon of the nominate subfamily), the genus *Scotoharpes* appears in the Lower Ordovician (Arenigian) of the Asaphid faunal palaeoprovince. The latter genus was widespread biostratigraphically because it persisted over a long time-span from the Lower Ordovician (Arenigian) to the Upper Silurian (probably Wenlockian or even Ludlovian).³⁾

The configuration of the hypostome and the dorsal exoskeleton of *Scotoharpes* shows its close relationship to *Bohemoharpes* which at the outset of the Silurian (Llandoveryan) may have arisen from it. In *Bohemoharpes* a markedly concave brim developed, and the pair of muscle scars near 1S of lateral glabellar furrows becomes more conspicuous. The pitting on the brim becomes finer and denser. The nominate subgenus

²⁾ From the Tremadoc Ceratopyge Limestones of Scania, Sweden, part of a harpetid fringing has been found by MOBERG and SEGERBERG (1906). WHITTINGTON (1950b) determined it as "*Harpes*" (*s. l.*) *sp. ind.* This fragment most likely does not belong to the genus *Australoharpes*.

³⁾ The biostratigraphic range of this genus is essentially at variance with all our so far obtained experience with harpetid trilobites and especially the time-spans of their occurrence. For this reason we studied in detail the individual representatives of this genus, seeking some criteria for their classification (e.g. restitution of *Selenoharpes* Whittington for the Ordovician representatives), but we failed so far to find any. On the incomplete material available, mostly cephalons only, we did not discover — except for some small deviations — any constant features which would be useful for classification. Such a deviation could be observed in the Ordovician representatives earlier referred to *Scotoharpes*, which have on the glabella a 1S of lateral glabellar furrows shifted little sideways, and whose brim is broader (sag.) Perhaps later finds of more complete specimens, particularly those with a hypostome or the entire number of segments, will enable a satisfactory classification.

Bohemoharpes (*Bunemoharpes*) is phyletically directly linked up with the subgenus *Bohemoharpes* (*Unguloharpes*). The latter probably split off soon after the origin of the nominate subgenus. In *Bohemoharpes* (*Unguloharpes*) the brim becomes narrower and its semicircular outline passes into a horseshoe-shape. Alae decrease and one pair of lateral muscle scars near 1S becomes still more pronounced, and finally, in the Lower Devonian (Lochkovian), a further subgenus *Bohemoharpes* (*Declivoharpes*) arose from *Bohemoharpes* (*Unguloharpes*). In it, in spite of some new morphological features, its origin from *Bohemoharpes* (*Unguloharpes*) may be distinctly recognized. *B. (Bohemoharpes)* has been known to occur as early as in the Lower Silurian (Llandovery), and from that time its evolution continued up to the Lower Devonian (Lochkovian). *B. (Unguloharpes)* occurred continuously from the Kopaninian to the Přídolian (Upper Silurian) from where we know so far its youngest representative. *B. (Declivoharpes)* has hitherto been known from the Lochkovian. The last member of this evolutionary lineage, probably derived from *Bohemoharpes* (*Unguloharpes*) is represented by *Lioharpes* (*Fritchaspis*) which begins to appear as early as in the Lochkovian. It is actually the youngest hitherto found harpetid of this separate evolutionary lineage, as the last representative of it is known from the Upper Devonian (Frasnian). *Lioharpes* (*Fritchaspis*) in the Pragian gave rise to the nominate subgenus *Lioharpes* (*Lioharpes*). According to the general structure of cephalon, it may be assumed that the genus *Dubhglasina*, insufficiently known, may have evolved from *Scotoharpes*. *Dubhglasina* occurred as early as in the Middle Ordovician (Caradocian). This evolutionary "trend" within the nominate subfamily is expressed by several synapomorphic features common in the pertinent genera:

- (a) considerably analogous structure of hypostome,
- (b) relatively small alae,
- (c) fine and comparatively dense pitting of brim,
- (d) muscle scars near the 1S are small and shallow,
- (e) fringe with girder curving behind genal angles as to meet the internal rim.

It is not excluded that the lateral branch of this evolutionary lineage appeared as late as in the Upper Silurian of the Italian Alps, probably in the Ludlovian, from where GORTANI (1909) described a very fragmentary remain of a cephalon with brim broken off. We assign tentatively this fossil remain, according to its conical carinate glabella, to the genus *Reticuloharpes* [*R. (?) forojuliensis*]. The younger representatives of this genus may be followed up to the Middle Devonian (Givetian). *Helioharpes* may have had common origin with *Reticuloharpes*; at the outset of the Devonian the former genus probably derived from the morphological circle of forms close to those of *Reticuloharpes*. This assumption is supported by the fairly large pits on brim of both above-mentioned genera. In spite of this, no clear rather close affinities have so far been recognized. The genus *Harpes* also shows certain phylogenetic relations to *Reticuloharpes*, but on the assumption only, that Gortani's Upper Silurian species *R. (?) forojuliensis* belongs really to *Reticuloharpes*, which in such a case would be a stratigraphically and phylogenetically older genus than *Harpes*. However, the typical representatives of the latter genus are restricted to the Middle Devonian (Eifelian) where undoubted representatives of *Reticuloharpes* also occurred. The representatives of this lateral evolutionary lineage of *Harpetinae* and a little younger and earlier extinct, in the Givetian have the following synapomorphic features in common:

- (a) considerably analogous structure of hypostome,
- (b) large and conspicuous alae, partly depressed so as to appear as subdivided into two parts,
- (c) coarse and widely spaced pits on brim,
- (d) frequent presence of rows of large pits along the external rim and girder at the internal margin of the brim and on preglabellar field,
- (e) large muscle scars near 1S of glabellar furrows, which are obvious, conspicuous, fairly deep, the same as the preoccipital glabellar lobes,
- (f) in the Silurian and Devonian, representatives of the genera *Harpes*, *Helioharpes* and *Reticuloharpes* have the fringe with girder incurved behind genal angles so as to meet the internal rim, but not extending to the tips of prolongations.

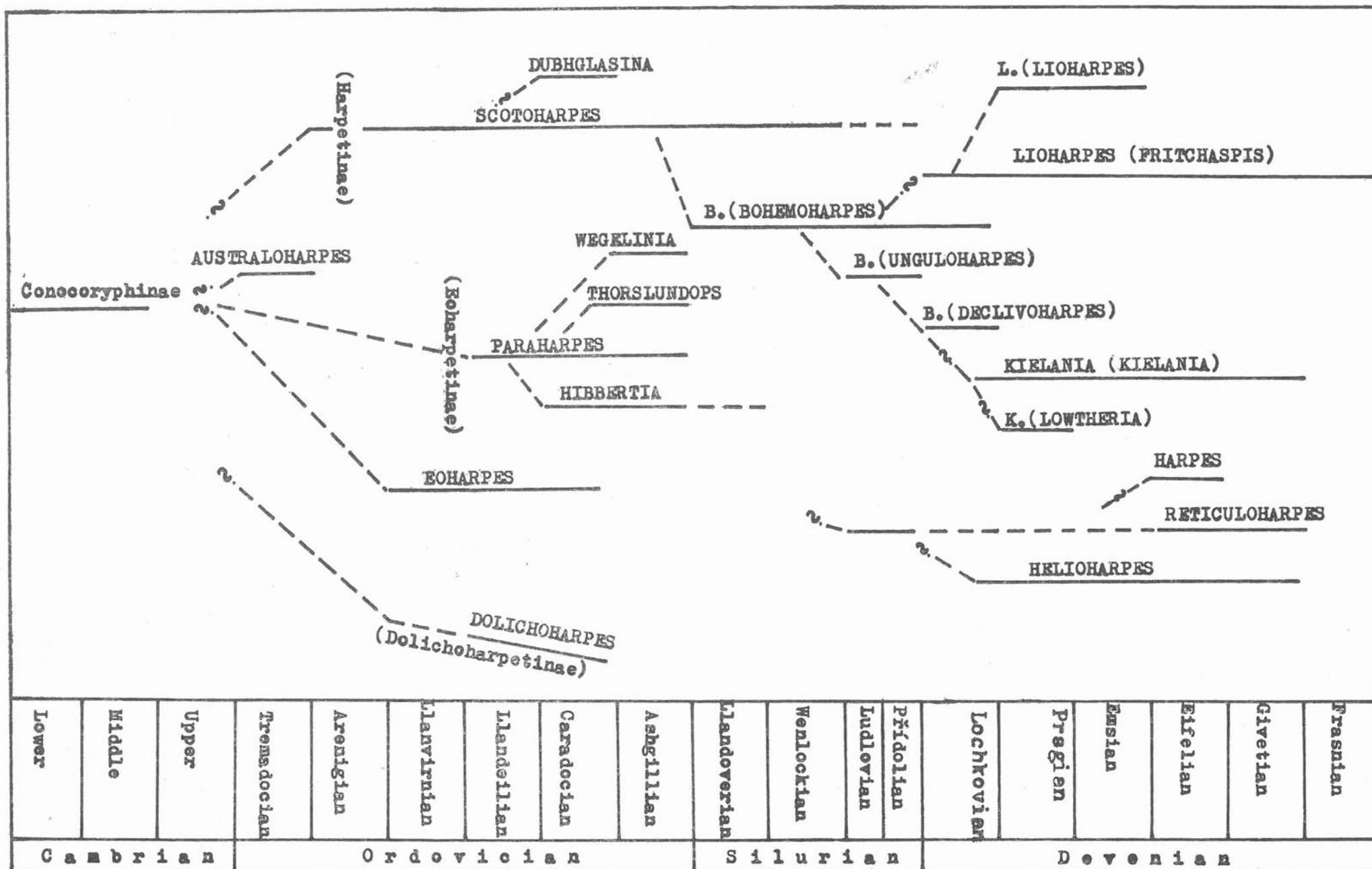
The *Reticuloharpes-Harpes* lateral lineage, cannot be distinguished from the *Scotoharpes-Bohemoharpes* lineage so as to separate this lineage and refer it to a higher systematic unit. In spite of that in the Ordovician and the Siluro-Devonian evolutionary lineages several different characteristic features exist, we leave this problem open, because the hypostomes and complete exoskeletons of these representatives of this lineage have not hitherto been recognized.

There are still the genera *Wegelinia* and *Kielania* [recte *K. (Kielania)* and *K. (Lowtheria)*] to be mentioned within this family. For the present the problem of the origin of both these taxa is fairly unclear. *Wegelinia* occurring in the Upper Ordovician (Ashgillian) has a strikingly large alae and also large muscle scars near 1S. Its fringe with the girder extent to the tips of genal prolongations and sloping of the brim differ in both these genera. In our opinion, *Wegelinia* may have represented a lateral blind and terminal evolutionary branch which split off from the evolutionary lineage of *Eoharpetinae*, the genus *Wegelinia* not showing any rather close relationship to *Kielania*. On the other hand the genus *Kielania* appeared in the Lower Devonian (Lochkovian) and continued to the Middle Devonian (Srbiskian). It is distinguished by small alae, different structure of hypostome, small muscle scars near 1S and by a girder not extending to tips of prolongations. From above differences, *Kielania* should most probably belong to the *Scotoharpes-Bohemoharpes* evolutionary lineage.⁴⁾ But it differs from it in that some representatives of the subgenus *K. (Kielania)* have a somewhat coarser and less dense pits on the brim which culminate in the subgenus *K. (Lowtheria)* whose general outline of cephalon is partly reminiscent of that in *Reticuloharpes*. Within the genus *Kielania*, two small evolutionary lineages may be distinguished — the main with *K. (K.) obuti* — *K. (K.) dorbigniana* and *K. (K.) novaki*, possibly also with *K. (K.) convexa* and *K. (K.) kayseri*, and the lateral branch which gave rise to *K. (K.) waageni*. It is possible that *Kielania* essentially represents homeomorphologically very similar taxa whose phylogenetic origin was different. As the dorsal and ventral exoskeletons of *Kielania* are known in part only, this problem could not so far be solved in greater detail. Species of *K. (Kielania)* could be derived with a certain doubt, i. e. species with finely pitted brim, small alae and hypostomes close to those of *Bohemoharpes* and *Lioharpes* from the wider circle of some forms of the genus *Bohemoharpes*, and perhaps also from a hitherto unknown taxon of *B. (Declivoharpes)*, fairly suggesting *K. (Kielania)* by its broad brim sloping forwardly. In contrast, *K. (Lowtheria)*, due to its strikingly large, widely spaced pits on the brim and the pyriform shape of cephalon, forms a separate group. It is problematic whether its derivation from the *Scotoharpes-Bohemoharpes* evolutionary lineage would be correct. The third subfamily, *Dolichoharpetinae*, has been established for the genus *Dolichoharpes* coming from the Ordovician of North America and Europe (Llandeilo-Caradoc). In our opinion, its phylogenetic origin may probably have been close to the genus *Paraharpes*, particularly according to the analogous structures of the girder, which extend to tips of prolongations. This subfamily may have originated from a so far not definable common circle of harpetid forms. For the present we regard *Dolichoharpes* as a very specialized genus, which, from the taxonomic-systematic point of view, should be separated as an independent subfamily.

From the above statements it follows that the phylogenetic evolution at the beginning of the two main lineages of evolution within *Harpetidae* took place in the Ordovician outside the Barrandian Basin (Bohemia), possibly outside the Selenopeltis faunal palaeoprovince, as in this time-span the overwhelming majority of harpetid trilobites were found in the Bathyrud and Asaphid faunal palaeoprovinces as well as in the younger warm-water Remopleuridid palaeoprovince lying north of the cool-water Selenopeltis faunal palaeoprovince. It was not until the Silurian that sea water became considerably warmer, which was due to orogenetic and epeirogenetic processes and shifting of the pole by the continental drift and thus also of the climatic zones. During the Llandovery, immigration of harpetids set in, directed from western and northern regions

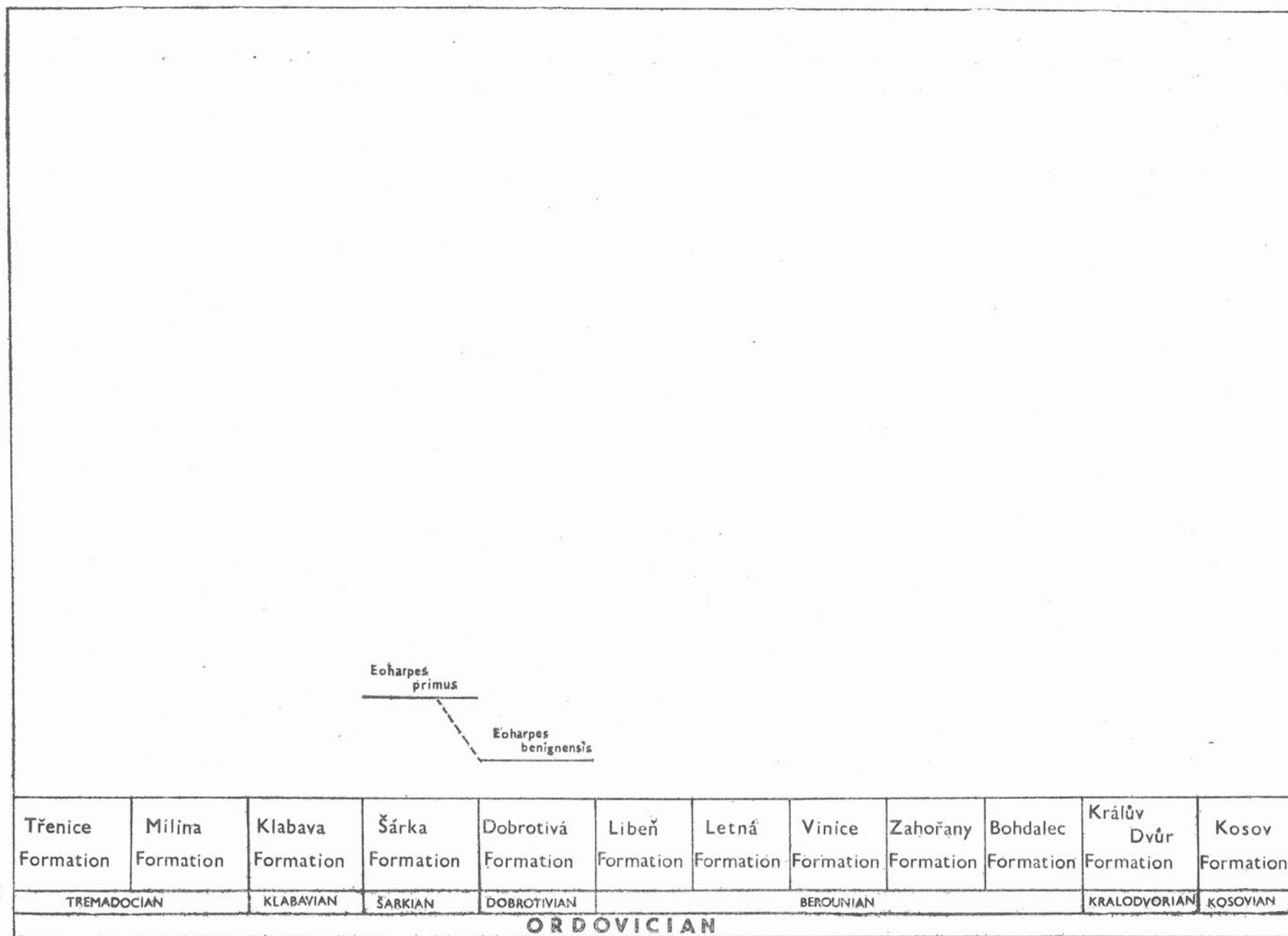
⁴⁾ Perhaps the morphological similarity of the cephalon of both mentioned genera (*Wegelinia* and *Kielania*) were more strongly influenced by palaeo-ecologic factors than by close phylogenetic relationships.

Tab. I.
Outline of the evolution of the representatives of the family *Harpetidae* and their stratigraphic distribution



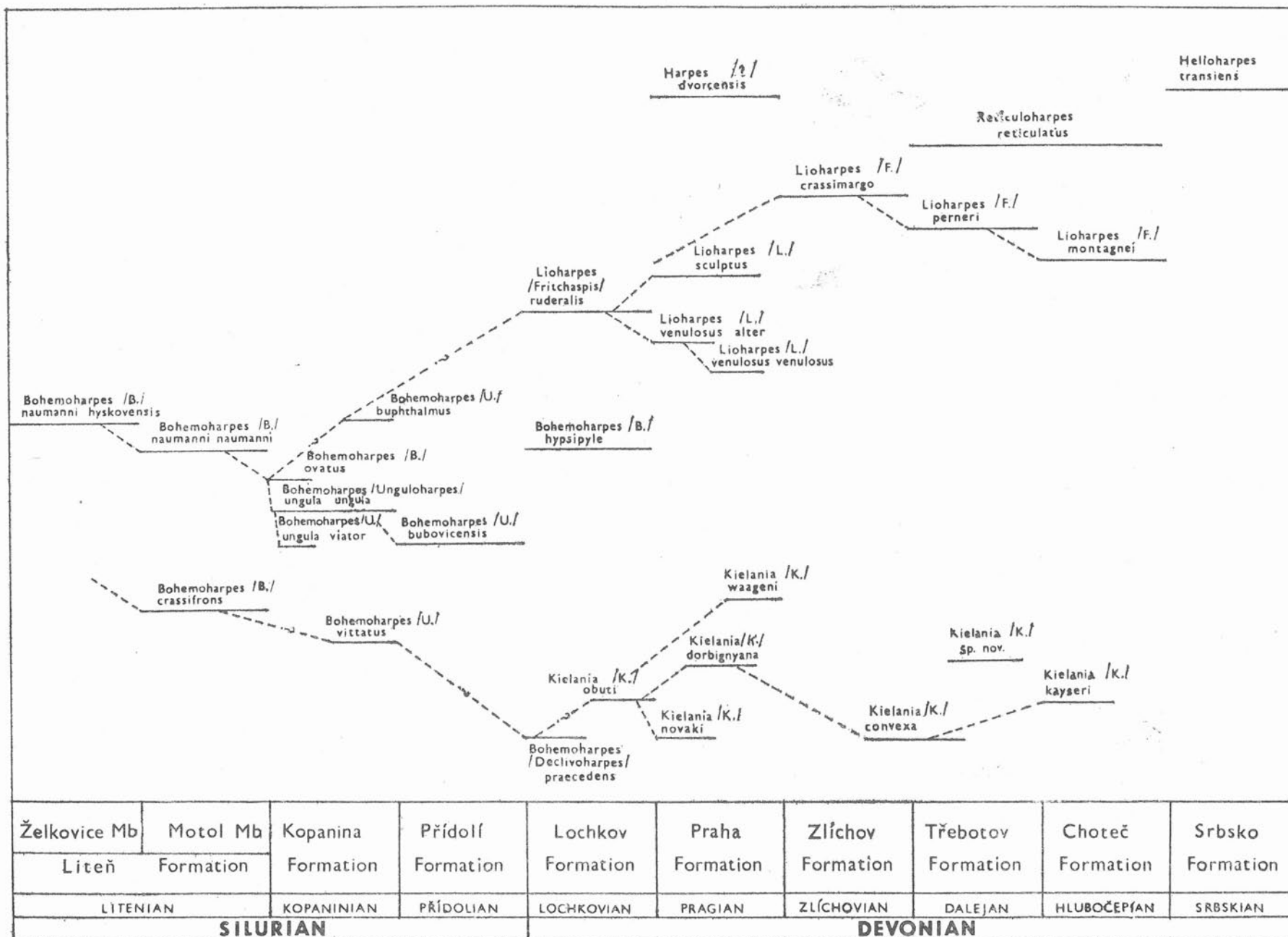
Tab. II.

Outline of the evolution of the Bohemian representatives of the family *Harpetidae* and their stratigraphic distribution



Tab. III.

Outline of the evolution of the Bohemian representatives of the family *Harpetidae* and their stratigraphic distribution



to central Europe (mainly into the Bohemian area) forming part of the Pacific-Mediterranean faunal palaeoprovince. In this relatively free space with a low selection pressure, the immigrating harpetids found an optimal living environment, to which they responded by considerable speciation and radiation. During Silurian-Middle Devonian times, the Barrandian Basin became an optimal space for innumerable populations of *Harpetinae*.

The evolution and palaeogeographic distribution of the subfamily *Dolichoharpetinae* and the genus *Dolichoharpes* took place in the Lower and Middle Ordovician of North America and western Europe, i. e. in the Bathyrud faunal palaeoprovince. Only the representatives of the genus *Eoharpes* (from the subfamily *Eoharpetinae*) lived during their phylogenetic evolution in Llanvirn-Caradoc time in the cool-water of the Sele-nopeltis faunal palaeoprovince. It could not hitherto be solved from where they penetrated into this faunal palaeoprovince.

5. Notes on the ontogeny of harpetid trilobites

The ontogenetic development of the family *Harpetidae* has so far been very imperfectly known. Thus we confine ourselves to some notes resulting from the systematic study of this trilobite group. In juvenile ephebic specimens, boss is more distinct than that of the holaspid ones. On the meraspis specimens, of which a very small number has hitherto been known and which are rather poorly preserved [e. g. ontogenetic stage 2 of *Kielania* (K.) *novaki* and 5 to 7 stages of the meraspis period of *Helioharpes radians*], a boss is not visible. The meraspis stage of *K. (K.) novaki* has a narrow and long glabella extending to a relatively narrow, but not elevated genal roll. The brim slopes moderately forward, but not so much as in the case in adult specimens of this species. Eyes inconspicuous; it seems that they are lacking throughout which is a marked difference from the meraspis stages of the representatives of the family *Trinucleidae* having conspicuous eye tubercles. The absence of eyes(?) in the meraspis stages of harpetids may suggest similar characters in their phylogenetic ancestors, namely that of the family *Conocoryphidae* (see the chapter on the origin of the *Harpetidae*). Alae are inconspicuous, small, semicircular in outline. In *K. (K.) novaki*, the second thoracic segment projects into a spine. Pygidium is indistinctly segmented. Brim and genal roll are faintly pitted (comp. PRANTL et PRIBYL, 1954, Pl. 8, fig. 4). In the German specimens of the species *Helioharpes radians* too, a narrow and long glabella is striking, as well as inconspicuous small alae. The girder is pronounced, the same as the pits of the brim and genal roll. Thoracic pleurae are obliquely out on their distal ends.

It is very difficult to draw any conclusion on the basis of the so far available incomplete material concerning the ontogenetic evolution of *Harpetidae*. But it seems that the convexity and the increase of the relative width (sag.) of the brim was essentially finished at the meraspis/holaspid stage boundary or perhaps even a little sooner, whereas the development of the alimentary caecal apparatus lasted longer, up to the holaspid stage. This fact may be observed particularly on *Bohemoharpes* (*Unguloharpes*) *ungula unguia*, *Lioharpes* (L.) *venulosus* and L. (*Fritchaspis*) *montagnei*, in which younger, ephebic individuals have a less differentiated "alimentary caeca" which is also less perceptible than that in fully adult specimens.

6. Palaeo-ecological notes

(a) Geographical distribution in the various palaeoprovinces

Many palaeontologists have already studied the mode of life of these particular forms of trilobites, considerably differing from the other trilobite families. Recently, especially RICHTER (1920, 1921), DACQUE (1921), STØRMER (1930), WHITTINGTON (1950 a-b-c), PRANTL and PRIBYL (1954) and BERGSTRÖM (1973) focused their studies on this subject. *Australoharpes* is the earliest known harpetid occurring in the Lower Tremadocian of Argentina (and ? U. S. S. R.), in the Olenid faunal palaeoprovince (sensu WHITTINGTON and HUGHES, 1974), whereas in the Rasettiid fauna palaeoprovince no finds of harpetid trilobites have as to now been made. Thus, it seems that is the Olenid faunal palaeoprovince where the evolution of harpetid taxa may have begun. But FORTEY (1975) regards the Olenid community defined by him on Spitsbergen as a deep-water one and therefore independent of the boundaries of the faunal palaeoprovinces demarcated by Whittington and Hughes.

Harpetids became widespread (in the Arenig) especially in the Bathyrud and Asaphid faunal palaeoprovince. In the Palaeozoic of Bohemia (the Barrandian Basin) harpetids occur for the first time in Sárkian Stage as a part of the Llanvirnian trilobite immigration (*Eoharpes*) which did not link up with any of their former occurrence. This is their first appearance in the whole Selenopeltis faunal palaeoprovince. It is not until the Caradocian that harpetids became more widespread, not only in the area of the present-day British Isles (partly belonging to the cool-water Selenopeltis faunal palaeoprovince), but also in the other palaeoprovinces. The Silurian and Devonian times are characterized by their almost world-wide distribution. But they could not so far be found in the Devonian cool-water Malvino-Kaffric faunal palaeoprovince of South America, South Africa and western Antarctica where, however, many other, probably warm-water, trilobites are lacking too or are represented poorly only. Such are e. g. *Scutelluidae*, *Cheiruridae* etc. In the regions of the Malvino-Kaffric palaeoprovince, the wide distribution of trilobites in the superfamily *Dalmanitacea* is striking.

b) Mode of life

The typical configuration of cephalon in harpetid trilobites, particularly the hypertrophic "alimentary" apparatus (caeca on genal roll, and brim) characterized them as unique stenophagous alimentary specialists. A liquid fairly important for their digestive processes probably streamed through the system of small channels (veins and tube-like channels) perceptible on vertical cross-sections through the brim (comp. RICHTER, 1921, Pl. 16). On the other hand, it is clear that the animal did not die when part of the brim [sometimes fairly large] was broken off in any manner. The injury cicatrized and a callus formed, which furnishes evidence of the vitality of the individual. With regard to our opinion on the function of the brim as a hypertrophic "alimentary" caeca, we do not accept the views of some palaeontologists considering the brim of the cephalon of harpetid trilobites to be a kind of "plough" serving for burrowing into sea bottom (DOLLO, 1909, STAFF and RECK, 1911 etc.). We are rather inclined to assume that the brim worked (in its secondary function) as an alleviating hydrostatic device (ROUAULT, 1847, RICHTER, 1921) which could also be important in pressing the exoskeleton on to the sea bottom. It is possible that part of genal and brim caecae also had a respiratory function as has been pointed out by JELL [1978]. According to the occurrence of harpetid trilobites in various lithological types of rocks, these trilobites often also occurred in coarse organodetrital sediments. It cannot be assumed that burrowing was their most frequent mode of life, as the brim would have been injured much more often than in the cases which can be assumed according to the factological material. We therefore believe that most representatives of harpetid trilobites may be regarded as vagrant benthic to nektobenthic forms often moving on the sea bottom or floating above it. We regard PRANTL and PŘIBYL'S (1954) view as probable that harpetid trilobites swam with the dorsal side of the exoskeleton turned downward. Even in this case the pitted brim, according to hydrodynamic laws, would have had the function of a floatation device. We assume that the characteristic position of harpetids on the sea bottom, evidently a quiet "rest" position is demonstrated by specimens of *Bohemoharpes* (*Unguloharpes*) *ungula unguis* or *Lioharpes* (*Lioharpes*) *venulosus venulosus*, i. e. cephalon touching the sea bottom by its outer margins of the brim, similarly as did several first pairs of appendages under thoracic segments. But a fairly great part of thorax and pygidium was somewhat distant from the bottom, being directed obliquely upward (see Pl. 4, fig. 2). It is very probable that the representatives of harpetid with flat or concave brims, (e. g. *Bohemoharpes*, *Scotoharpes* etc.) lived in a somewhat different palaeo-ecological environment than the representatives of *Wegelinia* or *Kielania* with convex brims sometimes obliquely sloping anteriorly, most likely being dependent on different food. It seems that this is attested by a relatively lower number of thoracic segments. It is also probable that *Wegelinia* and *Kielania* were less mobile than the other harpetids, and may have remained for relatively longer time on one and the same spot, being pressed to the bottom. Several principles may be derived from the stratigraphic and geographic distribution of harpetid trilobites in the Barrandian of Bohemia where their occurrence in Silurian and Devonian sediments is incontestably optimal as compared with other localities throughout the world; up to the present time, from this area more than 25 harpetid species have been described.

(1) The areas of occurrence of coeval species do not overlap each other. Even if an overlap exists, one of the species is oppressed so as to become defensive and finally to disappear from the assemblage. This interspecific competition may be seen in the occurrence of the Silurian species *Bohemoharpes* (*B.*) *naumanni naumanni* and *B.* (*B.*) *crassifrons* in the uppermost layers of the Liteň Formation. Whereas *B.* (*B.*) *naumanni naumanni* occurs in tuffaceous shales and tuffaceous micritic limestones in the surroundings of Loděnice (i. e. Loděnice, Sedlec, Záhrabská, Svätý Jan pod Skalou), *B.* (*B.*) *crassifrons* is restricted to tuffaceous organodetrital limestones from the immediate neighbourhood of Lištice (Lištice, Kozel hill.). *B.* (*Unguloharpes*) *ungula ungula* and *B.* (*U.*) *vittatus* occur in similarly delimited areas in the upper layers of the Kopanina Formation (Horizon with *Prionopeltis archiaci*). The populations of *B.* (*U.*) *ungula ungula* are widespread almost throughout the Kopanina Formation, in the organodetrital as well as mud limestones. In contrast, *B.* (*U.*) *vittatus* is restricted to the near environs of Lochkov and near the Malá Chuchle locality where *B.* (*U.*) *ungula ungula* is lacking. Similar conditions probably also exist in the middle layers of the Kopanina Formation (in the Horizon with *Ananaspis fecunda*) where in some localities only *B.* (*U.*) *ungula ungula* appears but in other such, as e. g. Prague-Jinonice, Řeporyje, Tachlovice etc. only *B.* (*U.*) *bupthalmus* is present. There are still more striking relationships of harpetid species to their defined areas of occurrence as is the case in the Dvorce-Prokop Limestone (Praha Formation). There occur *Kielania* (*K.*) *waageni*, *K.* (*K.*) *dorbignyana*, *K.* (*K.*) *novaki*, *Harpes* (?) *dvorcensis* and *Lioharpes* (*L.*) *sculptus*, but in different areas, sometimes overlapping each other. For instance, *K.* (*K.*) *waageni* is present in proximity to Malá Chuchle, *K.* (*K.*) *dorbignyana* near Braník, Hlubočepý and Lochkov. *K.* (*K.*) *novaki* may be found in the vicinity of Smíchov (Konvářka locality) and Klukovice. *Lioharpes* (*L.*) *sculptus* is occurring in the environs of Tetín (Dánil hill). *Harpes* (?) *dvorcensis* has hitherto been known only from Praha-Podolí. Noteworthy also is the occurrence of *Kielania* (*K.*) *kayseri* and *Lioharpes* (*Fritchaspis*) *montagnei* in the Acanthopyge Limestone (Hlubočepian). In relation to the latter species, *K.* (*K.*) *kayseri* is distinctly defensive and rapidly disappears altogether from the trilobite assemblage in the Acanthopyge Limestone.

In our opinion, the common occurrence of *Reticuloharpes reticulatus* and *Kielania* (*K.*) *convexa* in the Suchomasty Limestone [e. g. the "Mramorová stěna" at the Zlatý kůň locality near Koněprusy etc.] forms part of a thanatocoenosis. From the lithological character of these limestones [coarse-organodetrital with streaks of mud], the mode of preservation of organic remains as well as the shares of the individual faunal group we conclude that during the sedimentation of the Suchomasty Limestone, this thanatocoenosis was washed down to this place from variously distant areas.

(2) Dependence on facies, i. e. on the character of the substrate, is relatively slight in the Bohemian species. In an area where during a certain time-span only one species lived, its populations are widespread throughout the Barrandian region [e. g. *Eoharpes benignensis* in the Dobrotivá Formation], is represented not only in mudstones and shales but also in the iron ore horizon and sandstones; *Lioharpes* (*Fritchaspis*) *crassimargo* occurs in mud-as well as organodetrital facies [mainly in limestones] of the Zlíšov Formation. *L.* (*F.*) *montagnei* has been found in the organodetrital and mud sediments of the Choteč Formation.

(3) *Lioharpes* (*Lioharpes*) *venulosus venulosus* is very common in the Koněprusy Limestone in the Koněprusy bioherm. In some cases, its remains of lumachelles comprise several tens of specimens. Their exoskeletons, particularly cephalons, are small to medium in size (maximum width 40 or 50 mm). But on Plešivec hill at Měňany, at a short distance from here, lying outside the bioherm area proper, the remains of this subspecies are rarer but larger in size. For instance several cephalons are known whose brim is broken off, and their sizes very around 70–90 mm. It is clear that the intraspecific competition in the bioherm proper was more intense than outside it.

(4) From the Kosov area near Beroun [Barrande's „Dlauhá Hora" locality], among other fossils, a large number of complete exoskeletons of *Bohemoharpes* (*Unguloharpes*) *ungula ungula* are known. Most of them are enrolled, similarly as the representatives of other groups of trilobites found in this locality, e. g. *Leonaspis leonhardi*, *Ceratocephala verneuxi*, *Pseudocheirurus beyrichi*, *Otarion diffractum*, *Cornuproetus* (*Inter-*

proetus intermedius, *Eremiproetus* (*Remacutanger*) *senex* etc. We assume that in this locality (which can no longer be studied due to continuing quarry operations in the large Kosov quarry — KDC quarry) a sudden anastrophic extermination of the whole trilobite assemblage occurred. However, we could not so far find out which were the causes of it. Perhaps (?) the chemical products of sudden submarine volcanic eruptions may have played a role here.

7. Pathological and other phenomena on the exoskeletons of harpetids

As we have mentioned in the preceding chapter, a broken off part of cephalic brim is a frequent phenomenon in harpetid trilobites. Most individuals injured in this way have been found only in the Barrandian region. For example, in *Lioharpes* (*L.*) *venulosus venulosus*, *L. (Fritchaspis) crassimargo*, *Bohemoharpes (Unguloharpes) ungula ungula* and *B. (U.) ungula viator*, only the middle part of the brim remained preserved, whereas lateral parts are mostly lacking (see PRANTL and PRIBYL, 1954, Pl. 2, fig. 23, Pl. 6, figs. 2—3). Another specimen of *Lioharpes (L.) venulosus venulosus* has the brim broken off on the right side (comp. Pl. 4, fig. 4). On the cephalon of *Eoharpes benignensis*, almost half of the left part of lateral brim is lacking (see PRANTL and PRIBYL, 1954, Pl. 10, fig. 3). This injury could be outlined if girder was not affected, and the margins of the broken off brim were cicatrized by callus. In the Palaeozoic of Bohemia the above-mentioned injury and regeneration of the brim was stated in *Lioharpes (L.) venulosus venulosus*. In the genus *Kielania* such an injury has not been found. Of the species occurring outside Bohemia we know analogous cases of injuries in *Wegelinia wegelinii* where brim prolongation on the left side of cephalon was broken off evidently by a hit from outside (comp. text-fig. 14, fig. 7); the callus, formed on the wound, linked up irregularly with the marginal rim. In this case too, the presence of callus testifies to the fact that the individual outlived the injury. A similarly wounded and cicatrized specimen has been recognized in *Bohemoharpes (Unguloharpes) ungula viator* from the Silurian of Bohemia (see Pl. 2, fig. 1). We assume that the outer injury of the brim may be due to several causes:

[1] The injury may have arisen during periodical ecdysis (moulting); although this interpretation seems very attractive, we have not found similar injuries in small-sized early holaspis specimens. With regard to that the development of the caecal apparatus was completely finished as late as in the holaspis stage (see Chapter 5), it could also be assumed that only after the completed development that ecdysis became more difficult, and in this way injuries of the above described kind could take place.

[2] Injury of the brim by a mechanical cause, e. g. a hit on a firm object, by fall of a hard object etc. We consider such a case to be very probable, particularly for the reason, that injury of brim of this type is most frequent in *Lioharpes (L.) venulosus venulosus* living on the Koněprusy bioherm and its surroundings where the fairly great amount of organodetrital material, by its movement (landslide, collapse etc.), led to an injury of a relatively fine brim.

[3] Injury of brim by attack of a predator. This last possibility cannot be precluded completely, but for the present we regard it as purely hypothetical.

In addition to the above-mentioned injuries of brims, we also know some cases of neoplasm on the exoskeletons which are of bacterial origin. For instance, in *Bohemoharpes (Unguloharpes) ungula ungula*, the brim on the right side of cephalon is strikingly swollen so that the original concave character of the brim became strongly affected (see Pl. 8, fig. 1). This neoplasm may be due to inner causes, most probably to an inner pathological process. On one well preserved complete dorsal exoskeleton of the same species, there is on the right side of the brim, a large suboval swell with a peripheral wall and a central caving about 1 mm² in size; in its vicinity, the pits are somewhat larger. This anomalous elevation (comp. Pl. 1, figs. 1—2) points to parasitism on the exoskeleton of the host, but neither the type of the parasite, nor its influence on the host could so far be found out. Probably a neoplasm of parasitic origin may be involved (see also SNAJDR, 1978).

SYSTEMATIC DESCRIPTION

Order *Ptychopariida* SWINNERTON, 1915

Suborder *Ptychopariina* RICHTER, 1913 (= *Harpina* WHITTINGTON, 1950)

Superfamily *Conocoryphacea* ANGELIN, 1854

Family *Harpetidae* HAWLE et CORDA, 1847

Synonym. *Arraphidae* ANGELIN, 1854

For usage and spelling of this name (*Harpetidae*) see Bull. zool. Nom., 1971, 28, pp. 56—58; 1972, 29, pp. 2, 108; 1973, 30, p. 3. (See BEU, 1971; RHEDER, 1972, 1973).

Type genus. *Harpes* Goldfuss, 1843, from the Middle Devonian (Eifelian), F.R.G.

Diagnosis. See WHITTINGTON, 1950 a, pp. 4—5.

Discussion. In our opinion, this family should be divided into three independent subfamilies, *Harpetinae* HAWLE et CORDA, 1847, *Eoharpetinae* PŘIBYL et VANĚK, 1981 and *Dolichoharpetinae* PŘIBYL et VANĚK, 1981.

Stratigraphic range. From the Lower Ordovician (Tremadoc) up to the Upper Devonian (Frasnian). The representatives of this family are distributed in almost all Lower Palaeozoic regions of the world.

Harpetinae HAWLE et CORDA, 1847

Type genus. *Harpes* GOLDFUSS, 1843; Middle Devonian (Eifelian), F. R. G.

Diagnosis (emended here). Cephalon with brim horseshoe-like to pyriform in outline. Glabella with 1—3 pairs of lateral glabellar furrows (1S—3S). A pair of oval muscle scars. Alae usually not depressed, and weakly subdivided into two crescentic portions. Brim concave; the pitting of the upper lamella is dense and fine, or coarse and widely spaced. Girder meeting internal rim behind posterior border and not extending to tips of prolongations. Hypostome elongated, inversely pyriform, with convex anterior margin and well developed anterior lateral wings. Lateral border narrow. Posterior border short (tr), concave or straight, sometimes ended by two points. Thorax of 16 to 29 segments. Pygidium transversely elongated. Axis of 2—10 rings and 3—8 pleural ribs on pygidial fields.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.27—4.41; Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 0.91 to 1.47.

Discussion. We included into the subfamily *Harpetinae* most of the known harpetid genera, namely: *Bohemoharpes* VANĚK, 1963, *Dubhglasina* LAMONT, 1948, *Harpes* GOLDFUSS, 1839, *Helioharpes* PŘIBYL et VANĚK, 1981, *Kielania* VANĚK, 1963, *Lioharpes* WHITTINGTON, 1950, *Reticuloharpes* VANĚK, 1963 and *Scotoharpes* LAMONT, 1948.

Stratigraphic range. From the Lower Ordovician (Arenigian) up to the Upper Devonian (Frasnian); the representatives of the genera

of *Harpetinae* are widespread in almost all the Lower Palaeozoic regions of the world (in Europe, Asia, North America, Australia, Greenland etc.).

Bohemoharpes VANĚK, 1963

Type species. Originally designated by VANĚK (1963), *Harpes naumanni* BARRANDE, 1852; Silurian (Litenian), Bohemia.

Discussion. Within the genus *Bohemoharpes* we distinguish in addition to the nominate subgenus *B. (Bohemoharpes)* VANĚK, 1963 two subgenera: *B. (Unguloharpes)* PŘIBYL et VANĚK, 1981 and *B. (Declivoharpes)* PŘIBYL et VANĚK, 1981.

Bohemoharpes (Bohemoharpes) VANĚK, 1963

Type species. *Harpes naumanni* BARRANDE, 1852; Silurian (Litenian), Bohemia.

Diagnosis. See VANĚK, 1963, p. 227.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.25—2.81. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.10 to 1.34.

Discussion. *B. (Bohemoharpes)* is closely related to *Scotoharpes* and from the phyletic point of view may have derived from the latter genus. *B. (Bohemoharpes)* differs from *Scotoharpes* in a strikingly broad concave brim of cephalon and in the absence of two or three pairs of very shallow pit-like areas between eye ridges and one pair (1S) of lateral glabellar furrows. In both above-mentioned genera the pre-occipital pair of lateral glabellar furrows is arcuately bent forwards, but in *Bohemoharpes* there is a shallow oval muscle scar near this pair of furrows (1S). The genicranidium of the latter genus is longer (sag.) and narrower (tr.) than that of *Scotoharpes*. *B. (Bohemoharpes)* bears a more finer and denser pitting on the surface of the upper lamella of brim. In contrast, the pygidium of *Scotoharpes* has strongly curved pleural furrows.

Other species. *Bohemoharpes (B.) crassifrons* (BARRANDE, 1846), *B. (B.) hypsipyle* sp. n., *B. (B.) naumanni hyskovensis* ŠNAJDR, 1978, *B. (B.) ovatus* BOUČEK, 1935.

Stratigraphic range. From the Silurian (Llandovery) to the Lower Devonian (Lochkovian), Bohemia.

Bohemoharpes (Unguloharpes) PŘIBYL et VANĚK, 1981

Type species. *Trilobites ungula* STERNBERG, 1833; Silurian (Kopaninian), Bohemia.

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 188.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.22—3.95. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.06 to 1.18.

Other species. *Bohemoharpes (Unguloharpes?) acuminatus* (LINDSTRÖM, 1885), *B. (U.) bubovicensis* sp. n., *P. (U.) buphthalmus* (BOUČEK, 1935), *B. (U.) gracilis* (MÜNSTER, 1840), *B. (U.) ungula viator* subsp. n., *B. (U.) vittatus* (BARRANDE, 1852), *B. (U.?) wilkenstii* (MÜNSTER, 1840).

Stratigraphic range. Upper Silurian (Litenian = Wenlockian to Přídolian); Bohemia, Gotland, Germany (F.R.G.), Austria.

Bohemoharpes (*Declivoharpes*) PŘIBYL et VANĚK, 1981

Type species. *Harpes dvorcensis praecedens* PRANTL et PŘIBYL, 1954; Lower Devonian (Lochkovian), Bohemia.

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 188.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.95; another index not measurable [Holotypus B. (D.) *praecedens* only!].

Type species only — *Bohemoharpes* (*Declivoharpes*) *praecedens* (PRANTL et PŘIBYL, 1954); Lower Devonian (Lochkovian), Bohemia.

Dubhglasina LAMONT, 1948

Type species. Originally designated by LAMONT (1948). *Dubhglasina aldonsensis* LAMONT, 1948; Middle Ordovician (Lower Caradocian), Scotland.

Diagnosis. See TRIPP, 1976, pp. 391—392.

Indexes impossible to be measured (Holotype of *Dubhglasina aldonsensis* only!).

Discussion. *D. aldonsensis* is so far very insufficiently known, as its cephalon is incomplete. This poorly known genus is distinguished from *Scotoharpes*, according to LAMONT 1948, p. 4 by "absence of deep furrow between outer and inner parts of cheeks in front of glabella, by poorer development of alae and by absence thereon of bifurcating suture lines; also by absence of "genal caecum" running postero-laterally from eye". This genus is distinguished from all harpetid genera by the great width of the brim anteriorly, the small glabella, and the weak development of the occipital segment (cf. TRIPP, 1976, p. 391).

Type species only — *Dubhglasina aldonsensis* LAMONT, 1948. Middle Ordovician (Lower Caradocian), Scotland.

Harpes GOLDFUSS, 1939

Type species. Originally designated by GOLDFUSS (1839), *Harpes macrocephalus* GOLDFUSS, 1839; Middle Devonian (Eifelian). Germany (F. R. G.).

Diagnosis. See WHITTINGTON, 1950a, p. 14.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.96. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.47.

Discussion. *Harpes* is probably related to *Reticuloharpes*, which also possesses some rows of coarse pits between the genal roll and brim, and larger alae. *Harpes* differs from the latter genus in a different outline of cephalon and the structure of brim and glabella; it has large eye tubercles placed relatively more anteriorly as compared with those in *Reticuloharpes*. The similarities between *Harpes* and *Reticuloharpes* suggest that this harpetid evolutionary lineage may have been derived from a *Reticuloharpes* — like ancestor.

Other species. *Harpes macrocephalus manceaui* PILLET, 1972, *H. ormistoni* sp. n., *H. polaris* MAKSIMOVA, 1977, *H. rouvillei* FRECH, 1887, *H. whidbornei* WHITTINGTON, 1950. With some doubt, we place here the species *H. (?) dvorcensis* PRANTL et PŘIBYL, 1954.

Stratigraphic range. Lower (?) and Middle Devonian (Pragian (?) to Eifelian). (?) Bohemia, Canadian Arctic Islands, England, France, Novaya Zemlja in U.S.S.R., Germany (F.R.G.).

Helioharpes PŘIBYL et VANĚK, 1981

Type species. *Harpes perradiatus* RICHTER et RICHTER, 1943; Middle Devonian (Eifelian), Morocco.

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 189.

Indexes. Length (sag.) of cephalon/Length (sag.) brim = 3.12–3.14. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 2.08 to 2.10.

Discussion. *Helioharpes* may be readily distinguished from all known genera of *Harpetinae* by its different pitting of brim arranged into radial rows with ridges forming a coarse polygonal network. This genus differs from the similar genus *Reticuloharpes* in a horseshoe-shaped, broadly semicircular outline of cephalon, a conical long glabella with faint 1S and an indistinct pair of glabellar muscle scars; alae are much smaller and indistinct. Also the presence of ridges forming a coarse polygonal network on the surface of the upper lamella of the brim is a further distinct feature. All these differences allow *Helioharpes* to be separated from all other genera of *Harpetidae*.

Other species. *Helioharpes* (?) *koeneni* (WEDEKIND, 1914), *H. pyrenaicus* (BARROIS, 1886), *H. radians* (RICHTER, 1863) (syn. = *Harpes asinus* SCHWARZBACH, 1950 — juvenile specimens), *H. transiens* (BARRANDE, 1872), *H. sp. n.* (cf. ERBEN, 1950, p. 30, Text-figs. 2a–c; ALBERTI, 1969, 22, fig. 4).

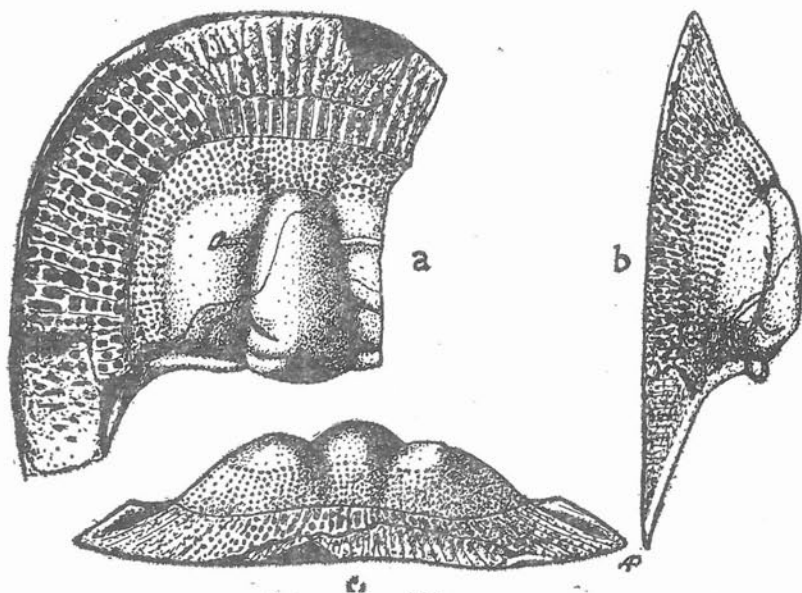


Fig. 4

Helioharpes perradiatus. Middle Devonian (Eifelian), Morocco. (After R. et E. Richter, 1943, Text-figs. 2a–c. a — Incomplete cephalon, dorsal view. x2.7. b — Ibidem, lateral view. x2.7. c — Ibidem, anterior view. x2.7.

Stratigraphic range. Lower (?) to Middle Devonian (Siegenian (?) to Givetian). Bohemia, France, Germany (F.R.G.), Morocco.

Kielania VANĚK, 1963

Type species. Originally designated by VANĚK (1963), *Harpes waageni* PRANTL et PRIBYL, 1954; Lower Devonian (Pragian), Bohemia.

Discussion. *Kielania* is divided into two separate subgenera: *Kielania* (*Kielania*) VANĚK, 1963 and *K. (Lowtheria)* PRIBYL et VANĚK, 1981.

Kielania (Kielania) VANĚK, 1963

Type species. *Harpes waageni* PRANTL et PRIBYL, 1954; Lower Devonian (Pragian), Bohemia.

Diagnosis. See VANĚK, 1963, pp. 228—229.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.21—3.23. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.34 to 1.37.

Discussion. Differentiating features between *K. (Kielania)* and *K. (Lowtheria)* are discussed at the latter taxon. *Wegelinia* differs from *Kielania* in the broader and more vaulted brim, but slowly inclining to the anterior margin of cephalon. On glabella, medial tubercle is lacking; alae are well defined, large. Genal roll not reaching to glabella. Eye tubercles large, placed on the end of the short eye ridges.

Other species. *Kielania (K.) convexa* (HAWLE et CORDA, 1847), *K. (K.) dorbignyana* (BARRANDE, 1846), *K. (K.) kayseri* (NOVÁK 1890), *K. (K.) novaki* (PRANTL et PRIBYL, 1954), *K. (K.) obuti* sp. n., *K. (K.) stenolimbata* MAKSIMOVA, 1979, *K. (K.) superna* MAKSIMOVA, 1979, *K. (K.) aff. waageni* (cf. LÜTKE, 1965, p. 192, Text-fig. 14, Pl. 20, fig. 1), *K. (K.) sp.* (cf. HOLZAPFEL, 1895, Pl. 1, fig. 1), *K. (K.) sp. n.* (cf. MAKSIMOVA, 1960, p. 24, Pl. 6, figs. 5a—b), *K. (K. ?) sp. n.* (cf. Pl. 6, fig. 4 in this paper).

Stratigraphic range. From the Lower Devonian to Middle Devonian (Lochkovian to Givetian); Bohemia, Germany (F.R.G.), Ural and Altai in U.S.S.R

Kielania (Lowtheria) PRIBYL et VANĚK, 1981

Type species. *Kielania triabsidata* ORMISTON, 1971; Lower Devonian (Siegenian), Lowther Island, Canada.

Diagnosis. See PRIBYL et VANĚK, 1981, p. 189.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.21. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.22.

Discussion. *K. (Lowtheria)* differs from the related nominate subgenus in the pyriform outline of cephalon, broad and vaulted glabella with pronounced glabellar lobation and three pairs of expressive lateral glabellar furrows 1S—3S, in deep subtriangular alae and strongly convex broad genal roll and brim with pits equal in size.

Type species only — *Kielania (Lowtheria) triabsidata* Ormiston, 1971; Lower Devonian (Siegenian), Lowther Island, Canada.

Lioharpes WHITTINGTON, 1950

Type species. Originally designated by WHITTINGTON (1950a), *Harpes venulosus* HAWLE et CORDA, 1847; Lower Devonian (Pragian), Bohemia.

Discussion. Within the genus *Lioharpes* we distinguish, in addition to the nominate subgenus *L. (Lioharpes)*, another subgenus *Lioharpes (Fritchaspis)*.

Lioharpes (Lioharpes) WHITTINGTON, 1950

Type species. Originally designated by WHITTINGTON (1950a), *Harpes venulosus* HAWLE et CORDA, 1847; Lower Devonian (Pragian), Bohemia.

Diagnosis. See WHITTINGTON, 1950a, pp. 12—13.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.43—3.45. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.31 to 1.32.

Discussion. *Lioharpes (Fritchaspis)* is closely related to *L. (Lioharpes)* but differs from it in a slightly convex to flat brim, a relatively longer and narrower glabella, smaller alae and oval shallow muscle scars near the 1S of lateral glabellar furrows. Genal roll bears fine pits; on the surface of brim are larger pits and radial ridges. On the other hand, the hypostomes of the two compared subgenera are very similar; we therefore consider *Fritchaspis* only as a subgenus of the genus *Lioharpes*.

Other species. *Lioharpes (Lioharpes) sculptus* (HAWLE et CORDA, 1847), *L. (L.) venulosus alter* subsp. n., *L. (L.) venulosus caillaudi* PILLET, 1972, *L. (L.) sp. n.* (cf. ANCYGIN, 1977, p. 113, Pl. 42, figs. 7—11), *L. (L?) sp.* (cf. ANCYGIN, 1977, p. 114, Pl. 42, figs. 12—13), *L. (L?) sp.* (cf. ALBERTI, 1981, p. 181, Pl. 3, figs. 21—22).

Stratigraphic range. Lower Devonian (Pragian) only; Bohemia, France, Ural in U.S.S.R. and Germany (F.R.G.).

Lioharpes (Fritchaspis) VANĚK, 1963

Type species. Originally designated by VANĚK (1963), *Harpes montagnei* HAWLE et CORDA, 1847; Middle Devonian (Hlubočepian), Bohemia.

Diagnosis. See VANĚK, 1963, p. 228.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.14—3.16. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.24 to 1.26.

Discussion. The features which differentiate this subgenus from *L. (Lioharpes)* have been discussed in the remarks on the nominate subgenus. *Reticuloharpes* and *Helioharpes* are distinguished from *L. (Fritchaspis)* by the different outline of cephalon and very sparse large pits on the surface of brim. In contrast, the genus *Bohemoharpes* has a concave brim slanting forward [*Bohemoharpes (Declivoharpes)*.]

Other species. *Lioharpes (Fritchaspis) altaicus* (WEBER, 1932), *L. (F.) bischoffi* (ROEMER, 1852), *L. (F.) crassimargo* (VANĚK, 1963), *L. (F.) hastatus* (LÜTKE, 1965), *L. (F.) neogracilis* (RICHTER et RICHTER, 1924), *L. (F.) perneri* (PRANTL et PŘIBYL, 1954), *L. (F.) pruniformis* (ALBERTI, 1969), *L. (F.) ruderalis* (HAWLE et CORDA, 1847), *L. (F.) ve-*

netus (GORTANI, 1915), *L. (F.) sp.* (cf. ALBERTI, 1969, p. 486, Pl. 42, fig. 8).

Stratigraphic range. Lower Devonian (Lochkovian) up to Upper Devonian (Fransian); Bohemia, Italy, Germany (F.R.G.) and Altai in U.S.S.R.

Reticuloharpes VANĚK, 1963

Type species. Originally designated by VANĚK (1963), *Harpes reticulatus* HAWLE et CORDA, 1847; Upper Lower Devonian (Dalejan), Bohemia.

Diagnosis. See VANĚK, 1963, p. 229.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.86—2.89. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 0.90 to 0.91.

Discussion. The mutual relationship between *Reticuloharpes*, *Lioharpes* (*Fritchaspis*) and *Helioharpes* has been discussed in the remarks to the above-mentioned taxa. *Reticuloharpes* is probably related to *Harpes* which also possesses large alae, but differs from the latter genus in the different outline of cephalon and the structure of brim and glabella.

Other species. *Reticuloharpes escoti* (BERGERON, 1887), *R. fornicatus* (NOVÁK, 1890), *R. (?) forojuliensis* (GORTANI, 1909), *R. (?) ny-mageensis* (FLETCHER, 1975), *R. socialis* (HOLZAPFEL, 1895), *R. (?) sp.* (cf. ORMISTON, 1971, p. 36, Pl. 4, figs. 1—2, 4—5; ORMISTON, 1972, Pl. 1, fig. 8), *R. (?) sp.* (cf. HOLZAPFEL, 1895, p. 45 (partim), Pl. 2, fig. 3. Non Pl. 1, fig. 1 = *Kielania (K.) sp. n.*; Non Pl. 2, fig. 1 = Lectotypus of the species *R. socialis*), *R. (?) sp.* (cf. CHLUPÁČ, 1969, p. 90, Pl. 11, fig. 4), *R. sp.* (cf. WEBER, 1932, p. 4, Pl. 1, figs. 21a—b, 30a—b), *R. sp.* (cf. WEBER, 1932, p. 3, Pl. 1, figs. 22a—c).

Stratigraphic range. From the Upper Silurian (?) to Middle Devonian (Givetian). Australia, Bohemia, Canada, France, Italy, Moravia, Turkestan (in U.S.S.R.), Germany (F.R.G.).

Scotoharpes LAMONT, 1948

Type species. Originally designated by LAMONT (1948), *Scotoharpes domina* LAMONT, 1948. Lower Silurian (Upper Llandovery), Scotland.

Synonyms. *Aristoharpes* WHITTINGTON, 1950 (subj.).

Selenoharpes WHITTINGTON, 1950 (subj.).

Diagnosis. See NORFORD, 1973, p. 11.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.64—2.66. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.16 to 1.17.

Discussion. As pointed out by NORFORD (1973), *Aristoharpes* WHITTINGTON, 1950 and *Selenoharpes* WHITTINGTON, 1950 are junior synonyms of *Scotoharpes* LAMONT, 1948. The latter genus occurring within a long stratigraphic time-span, which lasted from the Lower Ordovician (Arenig) to the Upper Silurian. In harpetids such a wide stratigraphic range is quite uncommon. Due to our imperfect knowledge of exoskeleton of *Scotoharpes* it is not possible to subdivide this genus into two separate subgenera. This genus is probably closely related to *Bohemoharpes*, the latter being undoubtedly its descendent. The differences

between *Scotoharpes* and *Bohemoharpes* have already been discussed in the remarks on the last named genus.

Other species. *Scotoharpes aduncus* FORTEY, 1980, *S. consuetus* (BILLINGS, 1866), *S. excavatus* (LINNARSSON, 1875), *S. filiarus* DEAN, 1979, *S. fragilis* (RAYMOND, 1925), *S. granti* (BILLINGS, 1865), *S. judex* (MARR et NICHOLSON, 1888), *S. latior* (POULSEN, 1934), *S. tobulatus* (CHUGAEVA, 1975), *S. loma* LANE, 1972, *S. molongloensis* CHATTERTON et CAMPBELL, 1980, *S. pansa* (MAKSIMOVA, 1960), *S. raaschi* NORFORD, 1973, *S. rotundus* (BOHLIN, 1955), *S. sanctacrucensis* (KIELAN, 1960), *S. sinensis* (GRABAU, 1925), *S. singularis* (WHITTINGTON, 1965), *S. sombrero* OWEN, 1981, *S. (?) spasskii* (EICHWALD, 1840), *S. taimyricus* (BALASHOVA, 1959), *S. tatoungensis* (CHANG et FAN, 1960), *S. telleri* (WELLER, 1907), *S. thorslundi* nom. nov.⁵), *S. (?) trinucleoides* (ETHERIDGE et MITCHELL, 1917), *S. vitilis* (WHITTINGTON, 1963), *S. willsi* (WHITTINGTON, 1950), *S. youngi* (REED, 1914), *S. sp.* (cf. NORFORD, 1973, p. 22, Pl. 2, fig. 6), *S. (?) sp.* (cf. WHITTINGTON, 1950a, p. 48, Pl. 7, fig. 13), *S. (?) sp.* (cf. PILLET in BORDET-CAVET-PILLET, 1960, p. 12, Pl. 1, fig. 6; Text-fig. 5d), *S. (?) sp.* (cf. DEAN, 1970, p. 3, Pl. 1, figs. 5, 6, 10), *S. (?) sp.* (cf. BATES, 1968, p. 183, Pl. 13, figs. 1, 2, 5, 6), *S. (?) sp.* (cf. KOBAYASHI et HAMADA, 1971, p. 121, Pl. 21, fig. 20), *S. sp.* (cf. OWEN et BRUTON, 1980, p. 21, Pl. 6, fig. 10), *S. (?) sp.* (cf. THOMAS, 1978, p. 53, Pl. 14, figs. 5a—c), *S. (?) sp.* (cf. INGHAM, 1970, p. 38, Pl. 5, figs. 21—22), *S. sp.* (cf. ROSS, 1972, p. 36, Pl. 10, figs. 7—8), *S. sp.* (cf. LANE, 1979, p. 24, Pl. 5, figs. 3—6).

Stratigraphic range. From the Lower Ordovician (Arenigian) to the Upper Silurian (Ludlovian). Australia, Canada (British Columbia, Newfoundland), China, England, Greenland, Japan, Nepal, Norway, Poland, Scotland, Spitsbergen, Sweden, U.S.A. (Nevada), U.S.S.R. (Estonia, Kazakhstan, Taimyr) etc.

Eoharpetinae PŘIBYL et VANĚK, 1981

Type genus. *Eoharpes* RAYMOND, 1905. Upper part of the Lower Ordovician (Sárkian), Bohemia.

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 191.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.13—2.19. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 0.95 to 1.92.

Discussion. *Eoharpetinae* has been established for the genera *Eoharpes*, *Hibbertia*, *Paraharpes*, *Thorslundops* and *Wegelinia*. The oldest genus *Australoharpes* has been introduced into this subfamily only with some hesitation. This subfamily, especially with regard to the different morphology of hypostome and other features of cephalon, does not show

⁵) THORSLUND [1940] described from the Ordovician (Chasmops Group) of Sweden a new species *Harpes concavus*. As this name is a later homonym of the earlier name *Harpes concavus* HAWLE et CORDA, 1847 [= *Bohemoharpes* (U.) *ungula unguia*], the new name *S. thorslundi* nom. nov. has been used here. The holotype of *S. thorslundi* is represented by a cephalon described by THORSLUND [1940] on p. 152 and figured on pl. 11, figs. 16—18.

any close phylogenetic relationships to the other harpetid subfamilies. The genera of this subfamily form one of the main evolutionary lineages of the harpetid trilobites which began to exist in the Lower Ordovician. Stratigraphic range. Lower Ordovician (Lower Tremadocian) to the Lower Silurian (?Llandovery). Argentina, Bohemia, Canada, England, France, Germany (F.R.G.), Ireland, Norway, Scotland, U.S.S.R. (Estonia, Saiano-Altai region), and Australia.

Eoharpes RAYMOND, 1905

Type species. Originally designated by RAYMOND (1905), *Harpes primus* BARRANDE, 1872. Upper Lower Ordovician (Šárkian), Bohemia.

Diagnosis. See WHITTINGTON, 1948, p. 223.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.86—2.87. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 1.35 to 1.42.

Discussion. The synonymy for this genus was given by WHITTINGTON (1948) and by PRANTL et PŘIBYL (1954). This genus includes six distinctive species; the one from Germany (F.R.G.) is not very well known. These species are distributed in the Selenopeltis faunal palaeo-province only. *Eoharpes* differs from all known genera of *Harpetinae* and *Dolichoharpetinae* in the low convexity of the anterior part of glabella, different shape of hypostome as well as the lower number of thoracic segments.

Other species. *Eoharpes benignesis* (BARRANDE, 1872), *E. cristatus* ROMANO, 1975, *E. guichenensis* HENRY et PHILLIPOT, 1968, *E. sp.* (cf. RICHTER et RICHTER, 1954, p. 14, Pl. 1, fig. 5) etc.

Stratigraphic range. Upper Lower Ordovician to Middle Ordovician (Llanvirnian to Caradocian); Bohemia, France, Portugal, Germany (F.R.G.).

Australoharpes HARRINGTON et LEANZA, 1957

Type species. Originally designated by HARRINGTON et LEANZA (1957). *Australoharpes depressus* HARRINGTON et LEANZA, 1957. Ordovician (Lower Tremadocian), Argentina.

Diagnosis. See HARRINGTON et LEANZA, 1957, p. 195.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = ca 2.45. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = ca 1.92.

Discussion. This oldest harpetid genus differs from all known genera of *Harpetidae* in a very broad horseshoe-shaped brim, slightly convex semioval cephalon and in its swollen subtrigonal boss in the sag. part of genicranidium. A subtrigonal depression, a relic of librigenae, is also very characteristic. Eye ridge absent.

Other species. *A. (?) pospelovi* PETRUNINA (1966 — listed, MS).

Stratigraphic range. Lower Ordovician (Tremadocian). Argentina and (?) Saiano-Altai region in U. S.S.R. See postscript on the p. 39.

Hibbertia JONES et WOODWARD, 1898

Type species. Originally designated by JONES and WOODWARD, 1898. *Hibbertia orbi-*

cularis JONES et WOODWARD, 1898 [= *Harpes flanaganii* PORTLOCK, 1843]. Middle Ordovician (Caradocian), Ireland.

Synonyms. *Platyharpes* WHITTINGTON, 1950 (obj.).

?*Metaharpes* LAMONT, 1948 (subj.).

Diagnosis. See WHITTINGTON, 1950a, pp. 10—11.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.24—2.27. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 0.93 to 0.95.

Discussion. *Platyharpes* WHITTINGTON, 1950 is a synonym of *Hibbertia* JONES et WOODWARD, 1898. Into the synonymy of the latter genus we tentatively place *Metaharpes* LAMONT, 1948, which has been described by LAMONT according to an isolated brim only. However, a decision could be taken only after a direct comparison of the type specimens of the species of both the genera (*Hibbertia* and *Metaharpes*). The genus *Paraharpes* is very similar to *Hibbertia* and may be its direct ancestor. The generic features of the cephalon of the two above-mentioned genera are similar; only the outline of cephalon, the width of the brim and genal roll are different.

Other species. *Hibbertia* (?) *amibouei* (LAMONT, 1948), *H. balclatchiensis* (WHITTINGTON, 1950), *H. trippi* (WHITTINGTON, 1950), *H. whittingtoni* TRIPP, 1965, *H. sp.* (cf. TRIPP, 1976, p. 391, Pl. 4, figs. 23—24), *H. sp.* (cf. TRIPP, 1976, p. 391, Pl. 4, fig. 25a—b).

Stratigraphic range. From the Middle Ordovician (Caradocian) to the (?) Lower Silurian (Llandovery). Ireland, Scotland.

Paraharpes WHITTINGTON, 1950

Type species. Originally designated by WHITTINGTON, 1950a. *Harpes (Eoharpes) hornei* REED, 1914. Upper Ordovician (Ashgillian), Scotland.

Diagnosis. See WHITTINGTON, 1950a, p. 11.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.16—3.19. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 0.95 to 0.97.

Discussion. Into the synonymy of the genus *Paraharpes* we place *Harpesoides* KOROLEVA, 1978. *Paraharpes* is probably closely related to *Hibbertia*, but differs from it in the oval outline of cephalon, broader genal roll and somewhat narrower flat brim with rather larger pits, and greater number of thoracic segments.

Other species. *Paraharpes anticostiensis* (TWHENHOFEL, 1928), *P. costatus* (ANGELIN, 1854), *P. inghami* OWEN, 1981, *P. karamolensis* (KOROLEVA, 1978), *P. necopinus* (KOROLEVA, 1978), *P. ottawaensis* (BILLINGS, 1865), *P. ruddyi* WHITTINGTON, 1950, *P. similis* NIKOLAISEN, 1965, *P. valcourensis* (SHAW, 1968), *P. whittingtoni* McNAMARA, 1979, *P. sp. n.* (cf. SCHMIDT, 1894, p. 69, Pl. 5, figs. 10—18; WIMAN, 1908, p. 139, Pl. 8, fig. 24), *P. sp.* (cf. SHAW, 1968, p. 55, Pl. 7, fig. 8), *P. sp.* (cf. BOLTON, 1981, Pl. 6, fig. 15).

Stratigraphic range. From the upper Lower Ordovician (Llanvirnian) to Upper Ordovician (Ashgillian). Canada, England, Norway, Scotland, Sweden, U.S.A. (New York, Vermont), U.S.S.R. (Estonia, Kazakhstan).

Thorslundops PŘIBYL et VANĚK, 1981

Type species. *Harpes dalecarlicus* THORSLUND, 1930. Middle Ordovician (Viruan), Sweden.

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 190.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 2.13. Another index not measurable photometrically.

Discussion. The related genus *Hibbertia* differs from *Thorslundops* in the characters of glabella and genal roll; eye tubercles are smaller. The radial ridges at the boundary between the brim and cheek roll are not present. The brim prolongations are narrower and tapering rapidly posteriorly.

Other species. *T. (?) sp.* (cf. KIELAN, 1960, p. 159, Pl. 32, fig. 7), *T. sp.* (cf. OWEN, 1981, p. 33, Pl. 8, fig. 2).

Stratigraphic range. Middle Ordovician (Caradocian) to Upper Ordovician (Ashgillian). Norway, Sweden.

Wegelinia PŘIBYL et VANĚK, 1981

Type species. *Harpes wegeli* ANGELIN, 1854. Upper Ordovician (Ashgillian), Sweden.

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 190.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.90—3.10. Another index not measurable photometrically.

Discussion. As pointed out above (p. 19) in the discussion on *Kielania* this genus resembles *Wegelinia*, but differs from the latter genus in the narrower (sag.) and less convex brim, which is steeply inclined outward. On glabella, there is a small medial node developed on the anterior margin. Alae ill-defined, narrow; genal roll reaches to glabella; eyes very small, placed at the end of prominent eye ridges. Girder not extending to tips of prolongations. By the above-mentioned features *Wegelinia* is distinguished from other Ordovician genera of *Harpetidae*. Type species only — *Wegelinia wegeli* (ANGELIN, 1854). Upper Ordovician (Ashgillian). Norway, Sweden.

Dolichoharpetinae PŘIBYL et VANĚK, 1981

Type genus. *Dolichoharpes* WHITTINGTON, 1949. Middle Ordovician (Caradocian), North America (Missouri).

Diagnosis. See PŘIBYL et VANĚK, 1981, p. 191.

Indexes. Length (sag.) of cephalon/Length (sag.) of brim = 3.83—3.88. Length (sag.) of cephalon/Length (exsag.) of brim prolongations = 0.50 to 0.53.

Discussion. The configuration of the cephalon, especially of the narrow brim, broad genal roll, glabella and hypostome, and the coarse reticulation on the surface of cephalon distinctly differentiate *Dolichoharpetinae* from all representatives of *Harpetinae* and *Eoharpetinae*. The low number of thoracic segments of the subfamily suggests the genus *Kielania* having an almost identical number of thoracic segments; however, the cephalon of *Dolichoharpes* is strikingly different.

Stratigraphic range. This monotypic subfamily has been established only for the genus *Dolichoharpes* Whittington, 1949 occurring

in the Lower and Middle Ordovician. Canada (Baffin Island), England, Ireland, U.S.A., U.S.S.R.

Dolichoharpes WHITTINGTON, 1949

Type species. Originally designated by WHITTINGTON (1949). *Eoharpes uniserialis* RAYMOND, 1925. Middle Ordovician (Caradocian), U. S. A. (Missouri).

Diagnosis. See WHITTINGTON, 1950a, pp. 7—9.

Other species. *Dolichoharpes arcticus* WHITTINGTON, 1954, *D. dentoni* (BILLINGS, 1863)⁶⁾, *D. doranni* (PORTLOCK, 1843), *D. escanabae* (HALL, 1851), *D. proclivus* ESKER, 1964, *D. reticulatus* WHITTINGTON, 1949⁷⁾, *D. rutrellus* (CLARKE, 1897), *D. (?) villosus* KOROLEVA, 1978, *D. sp.* (cf. CHATTERTON et LUDWIGSEN, 1976, p. 41, Pl. 7, figs. 1—36; Pl. 22, fig. 5), *D. sp.* (cf. SHAW, 1968, p. 55, Pl. 7, figs. 1—6, 10—11; Non Pl. 7 = otarionid hypostome), *D. sp.* (cf. DEAN, 1979, p. 5, Pl. 1, figs. 2—3; Pl. 2, fig. 8), *D. sp.* (cf. PŘIBYL et VANĚK, 1981, Pl. 1, fig. 3).

Stratigraphic range. Lower Ordovician (Llanvirnian) to Middle Ordovician (Caradocian). Baffin Island (Canada), England, North Ireland, U.S.A. (Oklahoma, Virginia, Missouri, New York) and U.S.S.R. (?) (Kazakhstan).

Descriptions of new species and subspecies of

Harpetidae

Bohemoharpes (*Bohemoharpes*) *hypsipyle* sp. n.

(Pl. 3, figs. 1—4)

Derivatio nominis. *Hypsipyle* — the name is derived from the Greek mythology. Holotype. Incomplete cephalon, figured here on Pl. 3, figs. 1—4. (NM, L 18297).

Stratum typicum et locus typicus. Lochkov Formation (Lochkovian), Lower Devonian; Měňany near Beroun (outcrop in the cut of the road to Koněprusy), Bohemia.

Material. 3 cephalons.

Diagnosis. Cephalon semicircular. Glabella long and tr. narrow. Brim broad (sag.), concave, with pitting very fine and dense. External rim strongly swollen.

Description. Cephalon semicircular in outline. Greatest width of the cephalon at the posterior margin. Genicranidium moderately convex. Glabella ovoid, vaulted and widest at preoccipital glabellar lobes 1L; only 1S of furrows is visible. Preglabellar field extremely short

⁶⁾ DEMOTT (1963) (teste CHATTERTON et LUDWIGSEN, 1976, p. 43) pointed out that the species *D. escanabae*, *D. dentoni*, *D. rutrellus* and *D. uniserialis* coming from strata of Trenton age are synonymous. Because *D. uniserialis* is probably the best known of these four species, CHATTERTON et LUDWIGSEN (1976) suggested to retain the name *D. uniserialis*. They remark to this serious nomenclatoric and taxonomic problem: "On the basis of usage, should these forms all prove to be synonymous, it would at present appear to be preferable to retain the name *D. uniserialis*. This taxonomic problem will, however, need to be sorted out a later date by somebody who is able to compare all of the types."

⁷⁾ SHAW (1974, p. 26) included into the synonymy of the species *D. reticulatus* WHITTINGTON, 1949 two further species — *D. proclivus* ESKER, 1964 and tentatively *D. arcticus* WHITTINGTON, 1954.

(sag.), sloping anteriorly. Occipital ring convex, with small median node. Occipital furrow obvious, straight. Alae small, subtriangular, well perceptible, moderately convex. Alar furrow fine and visible. Eye tubercles rather large, elevated. Eye ridge faint, transverse, reaching to axial furrows. Genal roll vaulted, separated from genae by a row of large pits. Brim broad (sag.), concave, slightly wider sagittally than laterally; external rim strongly swollen. At the genal roll/brim boundary one row of radially arranged ridges. The latter are thin, irregular, reaching to external rim. On the surface of genae, venation and sparse pits. Brim pitting is very fine and dense. Other parts of exoskeleton not known.

Size of the holotype (in mm). Length (sag.) of cephalon — 25.2; length (sag.) of brim — 7.3; length (sag.) of glabella — 13.0; tr. width of cephalon at the posterior margin (estimate) — 42.0.

Discussion. The closely related species *B. (B.) ovatus* (BOUČEK, 1935) differs from *B. (B.) hypsipyle* sp. n. in a shorter (sag.) and broader (tr.) glabella, smaller alae, moderately convex genal roll with narrower (sag.) and less concave brim. The genal caeca on genae in *B. (B.) ovatus* is indistinct, almost imperceptible.

Occurrence. See "Stratum typicum and locus typicus".

Bohemoharpes (Unguloharpes) bubovicensis sp. n.

(Pl. 9, fig. 5)

Derivatio nominis. *Bubovicensis*—the name is derived from the Bubovice near Beroun locality where the specimens of this species were found.

Holotype. Incomplete cephalon, figured here on Pl. 9, fig. 5. (ÚG, JV 534).

Stratum typicum et locus typicus. Přídolí Formation (lower and middle layers) (Přídolí), Upper Silurian; Bubovice (small quarry at the road leading from Bubovice to Loděnice, Bohemia).

Material. 28 incomplete cephalons.

Diagnosis. Cephalon horseshoe-shaped in outline. Glabella ovoid, slightly carinate. Brim narrow (sag.), slightly sloping forward, very finely and densely pitted. External rim raised.

Description. Cephalon horseshoe-shaped in outline. Width of the cephalon about $\frac{1}{4}$ of its sag. length. Glabella ovoid, vaulted, slightly carinate, with 3 pairs of glabellar furrows 1S—3S, of which the 1S and 2S are very short. Preoccipital furrows of 1S shallow, arcuate. Near the 1S of lateral furrows a pair of muscle-scars is slightly visible. Preglabellar field absent. Occipital ring convex, with small median node shifted to anterior margin. Alae semicircular, moderately vaulted; alar furrows deeply impressed. Eye tubercles well visible, elevated, shifted to the anterior part of glabella. Eye ridges faint, inconspicuous, reaching to axial furrows. Genal roll distinct and moderately vaulted, in sag. axis reaching to glabella. Brim relatively narrow (sag.), slightly sloping forward. External rim raised. At the genal roll/brim boundary a row of radially divergent ridges extends to $\frac{1}{3}$ the width (tr.) of the brim. The surface of genal lobes bears well visible venation and rather large pits. Brim very finely and densely pitted. Other parts of exoskeleton not known.

Size of the holotype (in mm). Length (sag.) of cephalon — 15.0;

length (sag.) of brim — 5.0; length (sag.) of glabella — 8.0; tr. width of cephalon at the posterior margin — 22.0.

Discussion. *Bohemoharpes (Unguloharpes) buphthalmus* (BOUČEK, 1935) is related to *B. (U.) bubovicensis* sp. n. It differs from the latter species (*bubovicensis*) chiefly in the sag. narrower and more concave brim, shorter (sag.) and broader (tr.) glabella and alae which are smaller and less convex. Further more, there is a longer (exsag.) space between the genal roll and eye tubercles. Occipital ring is narrower and moderately convex. The pitting of brim is much finer. *B. (U.) ungula* (STERNBERG, 1833) differs from *B. (U.) bubovicensis* sp. n. in the sag. narrower concave brim with finer pits, the radial ridges which at the genal roll/brim boundary are shorter and less conspicuous. In the sag. axis of genal roll, there is a conspicuous relic of a boss. The preglabellar field is longer in the direction of sag. axis. Eyes smaller and shifted a little farther from glabella; the latter is longer (sag.) and narrower, without an obvious carina having an inconspicuous median tubercle in the anterior part. The occipital ring is narrower (sag.) in *B. (U.) ungula* than in *B. (U.) bubovicensis*. In *B. (U.) ungula* alae are smaller, flat, delimited by a shallower alar furrow.

Occurrence. See "Stratum typicum et locus typicus" and Kosov hill near Beroun (quarry KDC), Zadní Kopanina and Praha 5-Butovice, "Na hradišti" locality.

Bohemoharpes (Unguloharpes) ungula viator subsp. n.

(Pl. 2, figs. 1—6)

Derivatio nominis. *Viator* (Latin) — pilgrim, after the geographical occurrence of this subspecies.

Holotype. Cephalon figured here on Pl. 2, figs. 3—5. (NM, L 15419).

Stratum typicum et locus typicus. Kopanina Formation (Kopaninlan). Horizon with *Cromus beaumonti*, Upper Silurian; Zadní Kopanina, outcrops in the Zmrzlík, Bohemia.

Material. 10 cephalons.

Diagnosis. The subspecies of *B. (Unguloharpes) ungula* (STERNBERG, 1833) is characterised by the following features: tr. broader glabella with a well-defined carina, preoccipital glabellar furrows 1S transversally longer and large, ovoid lateral muscle scars near these furrows; alae larger, semicircular. On genae, venation clearly visible, and behind the eyes an expressive postocular striga. Preglabellar field absent. Genal roll more vaulted than that in *B. (U.) ungula ungula*, and anteriorly broader in sag. axis, displaying a conspicuous relic of boss; the brim is sag. narrower and less concave. The posterior border of cephalon is broader and deeper impressed. Other parts of exoskeleton unknown.

Size of holotype (in mm). Length (sag.) of cephalon — 11.0; length (sag.) of brim — 3.2; length (sag.) of glabella — 6.0; width (tr.) of cephalon at the posterior margin — 19.8.

Discussion. This new subspecies agrees in most characters of cephalon with the *B. (U.) ungula ungula* but differs from it in various features mentioned above.

Occurrence. See "Stratum typicum et locus typicus" and Kosov hill near Beroun (quarry KDC).

Kielania (Kielania) obuti sp. n.

[Pl. 8, figs. 4—5; Pl. 9, fig. 4]

Derivatio nominis. Named in honour of the outstanding Russian palaeontologist Prof. A. M. Obut, Novosibirsk (U. S. S. R.)

Holotype. Cephalon, figured here on Pl. 8, figs. 4B, 5B. (ÚUG, JV 2166).

Stratum typicum et locus typicus. Lochkov Formation (Lochkovian), Lower Devonian; Černá rokle at Kosoř near Praha, Bohemia.

Material. 2 cephalons, 1 isolated brim.

Diagnosis. Cephalon elongated-oval, convex. Glabella narrow, elongated, slightly carinate. Brim moderately convex, sloping forward and sideward, with dense and fine pits. External rim narrow and prominent.

Description. Cephalon elongated-oval, almost horseshoe-shaped in outline, convex. Glabella moderately convex, narrow, elongated, slightly carinate, standing above the level of genal lobes, with 3 pairs of lateral glabellar furrows 1S—3S. Only the short preoccipital pair of lateral furrows (1S) is well defined; it is slanting to sag. axis. Occipital furrow shallow, almost straight; occipital ring narrow, widening in the middle, with a small medial node at the anterior margin. Axial furrows narrowing, obvious. Genal lobes convex, with eye tubercles located near the anterior part of glabella. Slightly perceptible short eye ridges run out from the eyes, straight to glabella. Alae small, semicircular, smooth, ill-defined by alar furrow. Preglabellar field very short (sag.). Genal roll rather arched in front, narrow, with a relic of boss in the sag. axis, and not reaching to glabella. The pitting on the genal roll regular, fine, with radially arranged tiny ridges, mainly in the anterior and lateral margins of genae. Posterior border narrow, convex. Fringe with girder meeting internal rim behind posterior border. Brim moderately convex, width of about $\frac{1}{3}$ the maximum length of cephalon, sloping forward and sideward; external rim narrow, prominent. The upper lamella of the brim bears dense and fine pits between larger ones, and very fine, somewhat irregularly anastomosing veins sometimes reaching to the external rim. Brim and genal prolongations gradually narrowing distally, turn quickly sideward taking an almost vertical position. Other part of the exoskeleton unknown.

Size of holotype (in mm). Length (sag.) of cephalon — 6.8; length (sag.) of brim — 2.4 (estimate); length (sag.) of glabella — 3.0; width (tr.) of cephalon at the posterior margin — 9.0.

Discussion. The taxon most resembling our new species is *K. (K.) dorbignyana* (BARRANDE, 1846), which differs from *K. (K.) obuti* sp. n. in a shorter and broader glabella without carina and preoccipital furrows 1S which are more obvious, bent forward, as well as in the well developed preglabellar field, and more prominent eye ridges. *K. (K.) obuti* has a longer glabella, less convex genal roll, and finer pits on the brim as well as equally-sized ones on genal roll. This new species is the oldest representative of the genus *Kielania*.

Occurrence. See "Stratum typicum et locus typicus".

Lioharpes (Lioharpes) venulosus alter subsp. n.

(Pl. 4, figs. 5—6)

Derivatio nominis. From Latin *alter*, meaning second, according to the occurrence in the Koněprusy area, where the second representative of the subgenus *L. (Lioharpes)* has been found.

Holotype. Cephalon figured here on Pl. 4, figs. 5—6. (NM, L 18295).

Stratum typicum et locus typicus. Vinařice Limestone (Pragian), Lower Devonian; the quarry on Homolák hill near Vinařice, Bohemia.

Material. 5 cephalons.

Diagnosis. *L. (L.) venulosus alter* subsp. n. differs from *L. (L.) venulosus venulosus* (Hawle et Corda) mainly in the distinctly ovoid glabella without carina, narrower (exsag.) posterior genal border and more concave brim; radial ridges running from genicranidium to brim are shorter and less conspicuous. Genal roll narrower. The pitting on brim and genal roll is finer and denser as well as the granulation on the surface of cephalon.

Size of the holotype (in mm). Length (sag.) of cephalon — 20.3; length (sag.) of brim — 9.0; tr. width of cephalon at the posterior margin — 40.1 (estimate).

Discussion. This new subspecies may be compared only with *L. (L.) venulosus caillaudi* PILLET, 1972 and *L. (L.) venulosus venulosus* (HAWLE et CORDA, 1847). The former subspecies differs from *L. (L.) venulosus alter* in having a distinctly elongated glabella with carina in sag. axis, in less concave to flat brim, a sag. longer preglabellar field. The pitting on the upper lamella of the brim is more similar to the pitting of the nominate subspecies. The shape of alae and the radially arranged ridges of caeca are also rather equal to those in *L. (L.) venulosus venulosus* than to those of *L. (L.) venulosus alter*.

Occurrence. See "Stratum typicum et locus typicus" and Plešivec hill near Měňany (isolated boulders) and "Čertovy schody" near Koněprusy (isolated boulders).

Lioharpes (Lioharpes) sculptus (HAWLE et CORDA, 1847)

(Pl. 5, figs. 1—4, 7)

1847 *Harpes sculptus* sp. n.; HAWLE et CORDA, p. 163.

1970 *Lioharpes (Fritchaspis) sculptus* (HAWLE et CORDA); HORNÝ et BASTL, p. 280. Holotype. By monotypy — incomplete cephalon with some thoracic segments described by HAWLE et CORDA (1847) on p. 163. The holotype is figured here on Pl. 5, figs. 1—3, (NM, No. 212/67).

Stratum typicum et locus typicus. Dvorce-Prokop Limestone (Pragian), Lower Devonian; Damil hill near Tetín, Bohemia.

Material. 6 cephalons.

Diagnosis. Cephalon reversed U-shaped. Glabella suboval, carinate. Brim narrow, concave, with very fine and sparse pits. External rim prominent.

Description. Cephalon reversed U-shaped, moderately convex. Glabella suboval in shape, elongate, carinate, widest across lateral lobes at 1L. Only 1S furrows deeply impressed; the furrows delimit rounded subtriangular small 1L. Preglabellar field short (sag.) and sloping anteriorly. Occipital ring arched, slightly convex; occipital furrow deep. Alae small, slightly convex dorsally, and semicircular in outline. Alar

furrows narrow, distinct. Eye tubercles clearly protruding. Eye ridge short. Genal roll conspicuous and slightly vaulted, separated from the genal lobes by a row of large pits. Brim narrow (sag.), concave dorsally; external rim prominent. On the brim/genal roll boundary, radial ridges appear, some of them are more prominent than the remaining ones. These ridges extend to $\frac{1}{3}$ of the width of brim. On the surface of genal roll and brim very fine and sparse pits. Posterior genal border prominent. Number of thoracic segments unknown. We know only some anterior segments (on the holotype). Axis narrow and slightly convex, separated from pleurae by shallow axial furrows. Pleurae flat, relatively narrow, bearing pleural furrows.

Size of the holotype (in mm). Length (sag.) of cephalon — 16.0 (estimate); length (sag.) of brim — 6.0 (estimate); length (sag.) of glabella — 8.0 (estimate); tr. width of cephalon at the posterior margin — 22.0.

Discussion. *L. (Lioharpes) venulosus venulosus* (HAWLE et CORDA) is close to *L. (L.) sculptus* (HAWLE et CORDA), but differs from it in having large pits on genal roll and brim, sag. shorter preglabellar field and larger alae; a relic of boss in the axis of genal roll is more conspicuous. Radial ridges on the genal roll are larger and longer than those on *L. (L.) venulosus venulosus*. The brim is relatively narrower. *L. (L.) venulosus alter* subsp. n. is also similar to *L. (L.) sculptus*, but differs from it in a shorter and broader glabella, and shorter preglabellar field, but alae are larger and more expressive. The surface of the brim is covered with larger relatively sparse pits, and distinct radial ridges devoid of venation. *L. (L.) venulosus caillaudi* PILLET also has the cephalic structure very similar to *L. (L.) sculptus*, but alae are larger, eyes are shifted toward glabella and axial and alar furrows are deeply incised. The pitting on the brim in the latter species is denser and finer.

Occurrence. See "Stratum typicum et Locus typicus" and Klukovice near Praha, so-called "Červený lom" (Loděnice Limestone) and Praha-Smíchov, Konvářka (Dvorce-Prokok Limestone).

Lioharpes (Fritchaspis) crassimargo (VANĚK, 1963)

[Text-fig. 9, figs. 1—3; Text-fig. 10, figs. 1—5]

? *Harpes crassimargo* sp. n.; NOVÁK, unpublished manuscript (nomen nudum!).

1954 *Harpes montagnei* HAWLE et CORDA; PRANTL et PŘIBYL, Pl. 3. fig. 13; Pl. 6, fig. 4. [Non Pl. 2, figs. 3—4; Pl. 3, fig. 7; Pl. 7, figs. 2, 4 [= *L. (Fritchaspis) montagnei*].

1954 *Harpes aff. montagnei* HAWLE et CORDA; PRANTL et PŘIBYL, pp. 33, 89—90, 144—145.

1963 *Fritchaspis crassimargo* sp. n.; VANĚK, p. 228.

Holotype. Originally designated by VANĚK (1963) as fig. 4 on Pl. 6 in PRANTL and PŘIBYL's paper (1954).

Stratum typicum et locus typicus. Zlíchov Formation (Zlíchovian), Lower Devonian; Choteč, in the valley of the Choteč brook, at the weekend cottages, Bohemia. Material. 30 cephalons, 1 genicranidium and 1 incomplete thorax.

Diagnosis. Cephalon horseshoe-shaped in outline. Glabella conical, slightly carinate. Brim broad, concave, with large pits, arranged in some incomplete diagonal rows. At the external margin of the cephalic rim one concentric row of rather large pits. External rim broad and raised.

Description. Cephalon horseshoe-shaped in outline, with genicranidium slightly vaulted, slowly sloping to brim. Glabella conical, slightly carinate, occupying $\frac{2}{3}$ of the length of genicranidium, with 3 pairs of lateral glabellar furrows 1S—3S; 1S is longest, very obvious, turning forward and bounding a pair of oval muscle scars. Occipital ring considerably prominent, raised and broadened medially, with a small median node. Axial furrows narrow and deep. Alae rather marked, semicircular, in front extending into a narrow subtrigonal processus reaching to the 2S. Genal lobes approximately as broad as glabella, but less convex, sloping to the anterior and posterior margins of cephalon. At the frontal part of glabella, on genal lobes, a pair of short and little distinct eye ridges extends to protruding eyes composed of two lenses. Genal roll broadest sagittally and tapering to the lateral margins of genae. Pits on genal roll large and sparse, the larger pits are irregularly spread on the boundary between the genal roll and very narrow preglabellar field; a regular row of the pits demarcates the genal roll and brim. Brim broad (sag.), concave. External rim broad and raised. From the genal roll radially arranged ridges extend onto brim, some of them (approximately each fifth) reaching to half the length of brim. The upper lamella of brim is covered with large pits, in some arranged in complete diagonal rows. At the external margin of the cephalic rim one concentric row of rather large pits. The surface of glabella bears very fine and sparse granulation. A small tubercle lies at the frontal margin of glabella (visible only on well-preserved specimens). On the surface of genal lobes very fine pits aligned diagonally and reaching to the posterior margin of these lobes. Thorax imperfectly known. Axis moderately convex, narrow, sag. short, bounded by axial furrows. Pleurae straight, occupying $\frac{4}{5}$ of the segments, but at the outer margins they are obliquely bent backward. Pleural furrows distinct, bisecting the pleurae into two equal bands. Surface of thorax smooth. The other parts of exoskeleton are unknown.

Size of the holotype (in mm). Length (sag.) of cephalon — 28.5; length (sag.) of brim — 10.0; length (sag.) of glabella — 14.2; width (tr.) of cephalon at the posterior margin — 30.4 (estimate).

Discussion. NOVÁK (MS) recognized taxon as an independent species and designated it preliminarily as *Harpes crassimargo*. PRANTL and PŘIBYL (1954) compared this species with "*Harpes*" *montagnei* HAWLE et CORDA and included the eighth types of the species "*H.*" *crassimargo* given in NOVÁK's manuscript into the synonymy of "*H.*" *montagnei*. The validity of this species has been accepted by VANĚK (1963), who selected the holotype, but did not give a description. Thus, we give here a detailed description of this species. *L. (F.) crassimargo* is closely related to *L. (F.) montagnei* (HAWLE et CORDA) but differs from it in broader (tr.) and shorter (sag.), slightly carinate glabella, occipital ring enlarged (sag.) in the middle, and conspicuous short alae. Preglabellar field is also shorter. Eyes are larger, prominent. Brim slightly concave. On the surface of genicranidium and brim, minute pits lie between the reticulation and the radially arranged ridges on the upper lamella of brim; the characters of genal caeca in the two above-mentioned

species are different. A similar species *L. (F.) hastatus* (LÜTKE, 1965) from Germany (F.R.G.) has broader (tr.) and longer glabella, its genicranidium is more convex and the brim vaulted. The impressions of genal caeca are also entirely different.

Occurrence. See "Stratum typicum et locus typicus" and Praha-Hlubočepy, abandoned quarry "U kapličky" and small abandoned quarry near Sv. Prokop, Švagerka near Zlíchov — all belonging to the lower and upper layers of the Zlíchov Formation; furthermore the Praha-Klukovice and Čeřinka (hill) near Butovice (Chýnec Limestone) and the Zlatý kůň hill at Koněprusy (Suchomasty Limestone, lower layers).

Harpes ormistoni sp. n.

(Text-fig. 15, fig. 1)

1967 *Harpes macrocephalus* GOLDFUSS; ORMISTON, p. 50, Pl. 4, figs. 4—7.

1967? *Harpes* sp. indet.; ORMISTON, p. 52, Pl. 4, figs. 8—9.

Derivatio nominis. Named in honour of Dr. A. R. Ormiston of Tulsa (Oklahoma), who was the first to publish a description of this species.

Holotype. Cephalon figured by ORMISTON (1967) on Pl. 4, fig. 4. (Geol. Surv. of Canada, No. 18116).

Stratum typicum et locus typicus. Blue Fiord Formation (Middle Devonian); S. E. Svendsen Peninsula, Ellesmere Island, Canada.

Diagnosis. *H. ormistoni* sp. n. differs from *H. macrocephalus* GOLDFUSS, 1839, in more backward shifted eyes, tr. shorter alae and in genal and brim prolongations convergent to sag. axis. External rim is markedly broad. Postocular striga narrow, obvious, beginning at the base of eye tubercles, turning slightly downward, strongly backward and running subparallel to the inner margin of the genal lobe, and disappearing opposite the farthest rear part of the alar furrow.

Description. See ORMISTON, 1967, p. 50.

Size of holotype (in mm). Length (sag.) of cephalon — 32.0 (estimate); length (sag.) of brim — 7.5 (estimate); length (sag.) of glabella — 15.8 (estimate); width (tr.) of cephalon at the posterior margin — 40.0 (estimate).

Discussion. ORMISTON (1967) described under the name *Harpes macrocephalus* three cephalons from the Blue Fiord Formation of the Ellesmere Island, and under the same *Harpes* sp. indet. a well-preserved thorax and one cephalon from the unnamed Middle Devonian limestone of the Princess Royal Islands, Canada. It may be assumed that all the specimens mentioned are conspecific and belong to the new species of *Harpes*. From ORMISTON's illustration (1967, Pl. 4, figs. 4—7) we recognize that this Canadian species belongs to the new species, which is closely related to *H. macrocephalus* GOLDFUSS, 1839 from the Middle Devonian of Germany, especially in the shape of the cephalon and thorax, but it is distinguished from it by more backward shifted eyes, shorter alae and genal roll and brim prolongations convergent to sag. axis; also a narrow postocular striga is present. Compared with other species of *Harpes*, *H. ormistoni* sp. n. is readily recognizable by more backward shifted eyes, sag. elongated glabella as well as by a long brim and genal prolongation, converging to sag. axis of exoskeleton.

Occurrence. "Stratum typicum et locus typicus" and Twilight

Creek, Bathurst Island. Perhaps also the specimens from the unnamed Middle Devonian limestone of the largest of the Princess Royal Islands belong here.

INDETERMINABLE SPECIES OF HARPETID GENERA

Names of species and authors:	Remarks
<i>Arraphus corniculatus</i> ANGELIN, 1854, p. 86, Pl. XLI, fig. 6.	The holotype of this species is probably lost. It is very difficult to determine this species according to Angelin's original description and illustration of the genicranidium and to assign it to any harpetid genus. <i>Arraphus corniculatus</i> is therefore a <i>nomen dubium</i> only.
<i>Harpes costatus</i> var. <i>acuta</i> WEBER, 1948, p. 12, Pl. 2, fig. 11.	An incomplete genicranidium very reminiscent of the representatives of the <i>Scotoharpes</i> sp.
<i>Harpes antiquatus</i> BILLINGS, 1859, p. 469, fig. 38.	Billing's original specimen (type) has been lost [teste SHAW, 1968, p. 54]; this specimen may be compared with the species of the genus <i>Scotoharpes</i> .
<i>Harpes bucco</i> BATHER, 1910, p. 116, text-figs. 1—5.	The holotype of <i>Harpes bucco</i> Bather is a fragment of cephalon coming from the Silurian of Carnic Alps. The specimen from the „Roter Kalk“ of the Silurian of the Eastern Alps figured by HERITSCH, figs. 860—861 (1929) is also very fragmentary. It was therefore not possible to assign the species „ <i>H. bucco</i> “ to any genus.
<i>Trinucleus ellipticus</i> MÜNSTER, 1840, p. 46, Pl. 5, fig. 23.	RICHTER et RICHTER (1923, p. 62) as well as HUGHES—INGHAM—ADDISON (1975, p. 593) already called attention to the fact that this species had been established on the fragment of unidentified harpetid (?) trilobite. <i>Nomen dubium!</i>
<i>Trinucleus issedon</i> EICHWALD, 1857, p. 1376, Pl. LII, fig. 29.	This species „ <i>T. issedon</i> “ has also been established on the basis of fragment of the cephalon of an unidentified harpetid. <i>Nomen dubium!</i>
<i>Harpes kyliodorhachis</i> KOBAYASHI et HAMADA, 1972, p. 29, Pl. 3, figs. 11 and 12a—b.	The original illustration by KOBAYASHI and HAMADA (1972) of this species is quite insufficient and does not give a clear idea for a generic designation. Perhaps this species belongs to the genus <i>Helioharpes</i> .
<i>Trinucleus laevis</i> MÜNSTER, 1840, p. 46, Pl. 5, fig. 24.	An incomplete and unrecognizable harpetid genicranidium. <i>Nomen dubium!</i>
<i>Harpes pamiricus</i> BALASHOVA, 1966, p. 231, Pl. 3, fig. 17.	The poor preservation of the cephalon and only part of thorax do not permit to study closely this species and to attempt at a generic determination.
<i>Eoharpes pustulosus</i> [HALL, 1847], p. 246, Pl. LXI, figs. 2a—b.	This HALL'S specimen designated by HALL as <i>Ceraurus? pustulosus</i> has been assigned by RAYMOND et BARTON (1913, p. 542) to the genus <i>Eoharpes</i> . We are of the opinion

Eoharpes cassinensis

(WHITFIELD), 1897, p. 182,
Pl. 5, figs. 3-4.

Eoharpes minnesotensis

(CLARKE), 1894, p. 755, fig. 76.

Harpes pygmaeus

LÜTKE, 1965, p. 194,
Pl. 20, figs. 4-6; Text-fig. 15.

Harpes scanicus

ANGELIN, 1854, p. 86, pl. XLI, figs. 5a-b.

that it is very difficult to assign a single fragment of a spine with an extended base to any harpetid genus. This fragment may belong (according to us) to any cheirurid genus (*Ceraurus*?)

This species may belong to the genus *Scotharpes* (teste FORTEY, 1980).

Original paper and specimen none seen.

This species has been established on the basis of a juvenile specimen of an unidentifiable genus.

The holotype of this species is probably lost (teste WHITTINGTON, 1950b, p. 302). This species may be close related to *Paraharpes costatus* (ANGELIN). Nomen dubium!

Outline of the evolution of the Bohemian representatives of the family *Harpetidae* and their stratigraphic distribution

The oldest known representative of the Ordovician harpetid trilobites in central Bohemia is *Eoharpes primus* (BARRANDE, 1972) occurring in the Šárka Formation (Šárkian). It appears among the first immigrants into the Barrandian intrageosyncline. A further species, *Eoharpes benignensis* (BARRANDE, 1872) links up directly with it. Compared with the earlier species, the brim of the later species is wider (sag.), sloping more steeply forward. Its low-vaulted glabella has a pronounced conical shape. Eyes decrease in size, eye ridges becoming less prominent. In contrast, alae increase and the number of thoracic segments rises. It may be assumed that *E. benignensis* (BARRANDE) from the Dobrotivá Formation (Dobrotivian) is a direct descendent of *E. primus*. Other taxa of the harpetids from the Ordovician of Bohemia are for the present not known. It is not until the Silurian that they appear in the Želkovice Formation (Litenian), i.e. at the time when trilobite fauna intensively migrated into the sedimentary area of central Bohemia. Among numerous taxa newly appearing here during the Silurian, the oldest taxon *Bohemoharpes (Bohemoharpes) naumanni hyskovensis* ŠNAJDR, 1978 has been recognized, from which *Bohemoharpes (Bohemoharpes) naumanni naumanni* (BARRANDE, 1852) probably evolved in the Motol Member (Litenian)⁸. During sedimentation of the lower layers of the Kopanina Formation, in the Horizon with *Cromus beaumonti* (Kopaninian), *B. (B.) naumanni naumanni* (BARR.) may have given rise to *Bohemoharpes (Bohemoharpes) ovatus* (BOUČEK, 1935). Compared with the earlier form *B. (B.) naumanni naumanni* (BARR.), *B. (B.) ovatus* (BOUČ.) has a broad (tr.) and shorter (sag.) glabella, less distinct

⁸) Two specimens figured by BARRANDE (1872) on pl. 12, figs. 18-19, designated by him as *Harpes crassifrons* BARRANDE, should also be assigned to *Bohemoharpes (Bohemoharpes) naumanni naumanni* (BARRANDE).

lateral glabellar furrows of 1p—3p, less convex occipital ring and a narrower (sag.) brim. These features, in which these two species differ, are rather unsubstantial, so that these taxa may be regarded as showing very probably a direct phylogenetic relationship.⁹⁾ It is in the Horizon with *Cromus beaumonti* that *B. (Unguloharpes) ungula ungula* (STERNBERG, 1833) and *B. (U.) ungula viator* subsp. n. appeared for the first time. The first above-mentioned subspecies (*ungula ungula*) has been ascertained also in the Horizons with *Ananaspis fecunda* and *Prionopeltis archiaci*.

A descendent of the *B. (U.) ungula ungula* may possibly be seen in *B. (U.) bubovicensis* sp. n. which has been found in the lower layers of the Přídolí Formation (Přídolian). The above-mentioned taxa probably represented a direct evolutionary lineage. To this lineage we assign the species *B. (U.) buphthalmus* (BOUČEK) restricted to the Horizon with *Ananaspis fecunda* (Kopaninian = Ludlovian). We consider its assumed splitting off from *B. (B.) ovatus* (BOUČEK) to be somewhat problematic; namely, the width (sag.) of the brim in *Bohemoharpes (Unguloharpes) buphthalmus* is fairly reduced, eye ridges are more prominent, and glabella wider (tr.). *Bohemoharpes (Bohemoharpes) hypsipyle* sp. n. from the Lower Devonian (Lochkovian) is not a direct link with the earlier taxa of the subgenus *B. (Bohemoharpes)* which has hitherto been revealed. This species is one of the largest harpetid trilobites of Bohemia.

The second, parallel, although not so diversified evolutionary lineage of bohemoharpetid trilobites begins with *B. (Bohemoharpes) crassifrons* (BARRANDE, 1846) occurring in the Motol Formation (Litenian); biostratigraphically, this species is coeval with *B. (Bohemoharpes) naumanni naumanni* (BARR.). In *B. (B.) crassifrons* (BARR.) the genal roll is strikingly prominent, so that it is very difficult to regard this species as derived from *Bohemoharpes (Bohemoharpes) naumanni hyskovensis* ŠNAJDR from which *B. (B.) naumanni naumanni* (BARR.) probably evolved. *B. (B.) crassifrons* (BARR.) is restricted to the Motol Formation; it is only in the uppermost layers of the Kopanina Formation (Kopaninian), in the Horizon with *Prionopeltis archiaci*, that the latter species has its morphological (but not phylogenetic) successor — *Bohemoharpes (Unguloharpes) vittatus* (BARRANDE, 1852), whose genal roll is narrower (sag.) and less prominent and whose brim is more concave. His eyes are smaller and less protruding. In the Barrandian region, there is a long stratigraphical interval between the occurrence of *B. (B.) crassifrons* and *B. (U.) vittatus*. This gap is too long for assuming that both these species are in "direct phylogenetic relation". But it seems very probable that from the morphological circle of the species *B. (U.) vittatus* the subgenus *Bohemoharpes (Declivoharpes)* subg. n. could have arisen, as we know a typical representative of *B. (Declivoharpes)* only from the Lochkov Formation (Lochkovian, Lower Devonian). In this re-

⁹⁾ The specimen figured by PRANTL and PŘIBYL [1954] on pl. 4, fig. 2, designated as *Harpes naumanni* BARRANDE, should also be assigned to *B. (Bohemoharpes) ovatus* (BOUČEK).

presentative, i.e. *Bohemoharpes (Declivoharpes) praecedens* (PRANTL et PŘIBYL, 1954), the genal roll is still distinctly convex similarly as in the representatives of the group *B. (B.) crassifrons* — *B. (U.) vittatus*, but its eyes are larger, the brim being broad and flat, moderately sloping forward. As has been mentioned in the chapter on the evolution of harpetid trilobites, the morphological circle of an earlier, hitherto not well-known species of the subgenus *Bohemoharpes (Declivoharpes)*, may be the initial circle from which the genus *Kielania* and, particularly, the species *Kielania (Kielania) obuti* sp. n. arose. The latter species is also derived from the uppermost layers of the Lochkovian. However, it has not so far been possible to present proofs for this assumption. In *Kielania (Kielania) obuti* sp. n. the convexity of genal roll becomes suppressed, glabella is longer and the brim is more convex and more steeply sloping forward, but the prominent external rim, newly acquired by *B. (Declivoharpes)*, remains preserved. *Kielania (Kielania) obuti* sp. n. occurring in the Lochkov Formation (Lochkovian) may have given rise to *Kielania (Kielania) dorbignyana* (BARRANDE, 1846) and perhaps to *Kielania (Kielania) novaki* (PRANTL et PŘIBYL, 1954). Together with the latter two species, *Kielania (Kielania) waageni* (PRANTL et PŘIBYL, 1954) occur, whose flat brim, striking obliquely forward, partly suggests rather the initial morphological circle of *B. (Declivoharpes)* than that of *K. (Kielania) obuti*. The species *K. (K.) dorbignyana* (BARR.), *K. (K.) novaki* (PRANTL et PŘIBYL) and *K. (K.) waageni* (PRANTL et PŘIBYL) occur in the Dvorce-Prokop Limestone and Loděnice Limestone facies (Pragian). *Kielania (Kielania) dorbignyana* (BARR.) is morphologically fairly closely related to *Kielania (Kielania) convexa* (HAWLE et CORDA, 1847) from the layers at the Zlichovian/Dalejan boundary. Finally, in the Acanthopyge Limestone (Hlubočepian), *K. (K.) convexa* may have rise (?) to the very rarely occurring species *Kielania (Kielania) kayseri* (NOVÁK, 1890). In addition to these species, we also know a fairly large incomplete brim from the upper layers of the Třeboťov Formation (Dalejan) (see Pl. 6. fig. 4) which we tentatively refer to the genus *Kielania*. This specimen displays large pits on the brim. This feature also exists in some species of this genus outside Bohemia (see the chapter on the evolution of harpetid trilobites). This brim therefore clearly deviates from that of the species with finely perforated brims of the *Kielania (Kielania)* type, which form the main evolutionary lineage of the nominate subgenus. But let us return to the species *Bohemoharpes (Unguloharpes) buphthalmus*, which by its narrower (sag.) brim and a row of large pits at the brim/girder boundary as well as by its short radial ridges on the upper lamella of brim, is very reminiscent of the lower Devonian (Lochkovian) taxon *Lioharpes (Fritchaspis) ruderalis* (HAWLE et CORDA, 1947). Although it could not hitherto be stated whether both these two species link up with each other, it is possible to assume that *L. (Fritchaspis)* may have evolved from the morphological circle of the forms whose morphology approaches that of *Bohemoharpes (Unguloharpes) buphthalmus* (BOUČEK). It is *Lioharpes (Lioharpes) sculptus* (HAWLE et CORDA, 1847) appearing in the Dvorce-Prokop Limestone of Pragian age, which links up directly with *Lioharpes (Fritchaspis) ru-*

deralis (HAWLE et CORDA). *Lioharpes* (*Lioharpes*) *sculptus* (HAWLE et CORDA) has several features assumed by us to exist in its ancestor *Lioharpes* (*Fritchaspis*) *ruderalis*, i.e. narrow (sag.) brim etc. At the same time, from the latter species, *Lioharpes* (*Lioharpes*) *venulosus alter* subsp. n., known from the Vinařice Limestone (Pragian), may have split off this taxon in the overlying Koněprusy Limestone (Pragian) may have transformed into the subspecies *Lioharpes* (*Lioharpes*) *venulosus venulosus* (HAWLE et CORDA, 1847). But it is not excluded that, with regard to some morphological elements of the cephalon (e.g. brim broader (sag.) than that known in *L. (Fritchaspis) ruderalis*) of both last named taxa, that their splitting off may have taken place rather from another morphological circle of the subgenus *Lioharpes* (*Fritchaspis*) than from the circle represented by *Lioharpes* (*Fritchaspis*) *ruderalis*.

In the Dvorce-Prokop Limestone (Pragian), the species *Harpes* ? *dvorcensis* PRANTL et PŘIBYL, 1954 is rarely encountered. For the present, we assign it to the genus *Harpes*, although with doubt. Although *Harpes* ? *dvorcensis* displays a row of large pits at the external rim and at the margin of the preglabellar field, which are similar to the pitting of *Harpes*, its large alae are not bisected, eyes are much smaller, and more distant from the glabella, and two rows of large pits are placed at the girder/brim boundary, whereas in *Harpes* they are reduced to one row. It is not quite excluded that this species might represent a new genus or subgenus of *Harpes*. But for its erection, no sufficient material is available. *Lioharpes* (*Fritchaspis*) *crassimargo* (VANĚK, 1963), known from the Zlíchov Formation (Zlíchovian, Upper Lower Devonian) has no ancestor in the Dvorce-Prokop Limestone, and for the present we do not assume a close affinity between it and *L. (F.) ruderalis* (HAWLE et CORDA). On the other hand, it may be taken into consideration that *L. (F.) crassimargo* (VANĚK) gave rise to *Lioharpes* (*Fritchaspis*) *perneri* (PRANTL et PŘIBYL, 1954) widespread in the younger Třebotov Formation and in the upper portions of the Suchomasty Limestone (Dalejan). The last hitherto known species of this evolutionary line, *Lioharpes* (*Fritchaspis*) *montagnei* (HAWLE et CORDA, 1847), may have originated from the circle of *L. (Fritchaspis) perneri* (PRANTL et PŘIBYL) in the overlying Choteč and Acanthotype Limestones (Choteč Formation, Hlubočepian).

In addition to the above-mentioned harpetid taxa, which in central Bohemia form more or less continuous evolutionary lineages, the advent of two immigrants was revealed. In the Suchomasty Limestone and rarely also in the overlying Acanthopyge Limestones, the species *Reticuloharpes reticulatus* (HAWLE et CORDA, 1847) has been found, which probably had arisen outside the Barrandian region. The second species, *Helioharpes transiens* (BARRANDE, 1872) also occurs rarely in the overlying Middle Devonian layers of Srbsko Formation (Srbskian). It appeared in central Bohemia region, not phyletically linking up with any "endemic" species.

In conclusion we remark that harpetid trilobites, although found in various lithofacies, were relatively rare members of the various assemblages where the number of the species of diverse genera of the families

Iliaenidae, *Scutelluidae*, *Proetidae*, *Otarionidae*, *Odontopleuridae*, *Cheiruridae*, *Phacopidae* and *Dalmanitidae* highly exceeded the number of contemporaneous harpetid trilobites throughout the Silurian-Devonian sedimentation cycle. Harpetids occurred very rarely, so that in a certain assemblage the population of some harpetid taxa became fairly abundant as is the case e.g. in *Lioharpes* (*Lioharpes*) *venulosus venulosus* which became very numerous in the Lower Devonian Koněprusy bioherm (Pragian), or in *Bohemoharpes* (*Unguloharpes*) *ungula ungula* occurring in the Upper Silurian Horizon with *Prionopeltis archiaci* in the Kosov area near Beroun.

POSTSCRIPT

At the time of receiving the first proof of this study we have received from Dr. P. A. Jell from Melbourne his recent publication "Tremadoc trilobites of the Digger Island Formation, Waratah Bay, Victoria" (Memoirs of the Museum of Victoria, Vol. 46, Nos. 1 and 2, pp. 53—88, pls 19—33, 1985). In his paper he described two harpetid genera — *Australoharpes* Harrington and Leanza, 1957 (with two new species) and *Brachyhipposiderus* Jell, 1985 (with the type species only). The both mentioned genera belong probably to the subfamily *Eoharpetinae* Přibyl and Vaněk, 1981.

Jell and Stait published in the same year (1985) another paper entitled "Tremadoc trilobites from the Florentine Valley Formation, Tim Shea Area, Tasmania" (the same Memoirs of the Museum of Victoria, Vol. 46, Nos. 1 and 2, pp. 1—34, pls. 1—13, 1985). In this publication they described and figured a new species of the genus *Scotoharpes* Lamont, 1948 (*S. lauriei* Jell and Stait, 1985). This genus belongs in the subfamily *Harpetinae* Hawle and Corda, 1847.

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STUDIE O MORFOLOGII A FYLOGENEZI ČELEDI HARPETIDAE HAWLE ET CORDA, 1847

Předložená práce shrnuje výsledky našeho studia morfologie, fylogeneze a taxonomie trilobitů čeledi *Harpetidae* HAWLE et CORDA, 1847. Celá práce je rozdělena do tří velkých částí. V části všeobecné je diskutován předpokládaný původ čeledi *Harpetidae* z kambrické čeledi *Conocoryphidae*, především z morfologického okruhu rodu *Ctenocephalus*. Dále jsou uvedeny morfologické znaky, použité pro klasifikaci čeledi *Harpetidae*. V kapitole o evolučním vývoji harpetidních trilobitů je sledován fylogenetický vývoj jednotlivých rodů. Krátce jsou připojeny poznámky k jejich ontogenetickému vývoji. V paleoekologických poznámkách je nejdůležitějším poznatkem vzájemné ekologické vylučování synchronních druhů v barrandienském paleozoiku a jejich teritoriálním omezení. Je věnována též pozornost patologickým a ostatním změnám na kruhových harpetidních trilobitů.

V systematické části práce je zdůvodněno rozdělení čeledi *Harpetidae* HAWLE et CORDA na tři samostatné podčeledi: *Harpetinae* HAWLE et CORDA, 1847, *Eoharpetinae* PŘIBYL et VANĚK, 1981 a *Dolichoharpetinae* PŘIBYL et VANĚK, 1981. Na závěr této systematické kapitoly jsou uvedeny popisy nových nebo až dosud nedostatečně známých taxonů, především z barrandienského siluru a devonu.

Konečně poslední část práce je věnována evolučnímu vývoji českých taxonů a je uvedeno jejich stratigrafické rozšíření. V přehledu lze vyjádřit rozšíření dosud známých barrandienských taxonů následovně:

Ordovik:

Souvrství šárecké (šárecký stupeň, llanvirn): *Eoharpes primus* (BARRANDE)

Souvrství dobrotivské (dobrotivský stupeň, llanillo): *Eoharpes benignensis* (BARRANDE)

Silur:

Souvrství želkovické (liteňský stupeň, llandovery): *Bohemoharpes* (*Bohemoharpes*) *naumanni hyskovensis* SNAJDR

Souvrství liteňské (liteňský stupeň, wenlock); svrchní polohy (biozóny s *Cyrtograptus rigidus* až *Testographus testis*): *Bohemoharpes* (*Bohemoharpes*) *naumanni naumanni* (BARRANDE) a *Bohemoharpes* (*Bohemoharpes*) *crassifrons* (BARRANDE)

Souvrství kopaninské (kopaninský stupeň, spodní budňan-ludlow): horizont s *Cromus beaumonti*: *Bohemoharpes* (*Unguloharpes*) *ungula viator* subsp. n., *B. (U.) ungula ungula* (STERNBERG) a *B. (Bohemoharpes) ovatus* (BOUČEK); horizont s *Ananaspis fecunda*: *Bohemoharpes* (*Unguloharpes*) *ungula ungula* (STERNBERG) a *B. (U.) buphthalmus* (BOUČEK); horizont s *Prionopeltis archiaci*: *Bohemoharpes* (*Unguloharpes*) *ungula ungula* (STERNBERG) a *B. (U.) vittatus* (BARRANDE)

Souvrství přídolské (přídolský stupeň, svrchní budňan); spodní a střední polohy, počínaje biozónou s *Pseudomonoclimacis* (?) *ultima*: *Bohemoharpes* (*Unguloharpes*) *bubovicensis* sp. n.

Devon:

Souvrství lochkovské (lochkovský stupeň, spodní devon): *Bohemoharpes* (*Bohemoharpes*) *hypsipyle* sp. n., *Bohemoharpes* (*Declivoharpes*) *praecedens* (PRANTL et PŘIBYL), *Lioharpes* (*Fritchaspis*) *ruderalis* (HAWLE et CORDA), *Kielania* (*Kielania*) *obuti* sp. n.

Souvrství pražské (pražský stupeň, spodní devon): facie vápenců vinařických: *Lioharpes* (*Lioharpes*) *venulosus alter* subsp. n.; facie vápenců koněpruských: *Lioharpes* (*Lioharpes*) *venulosus venulosus* (HAWLE et CORDA); facie vápenců dvorecko-prokopských: *Lioharpes* (*Lioharpes*) *sculptus* (HAWLE et CORDA), *Kielania* (*Kielania*) *novaki* (PRANTL et PŘIBYL), *K. (K.) waageni* (PRANTL et PŘIBYL), *K. (K.) dorbignyana* (BARRANDE), *Harpes* (?) *dvorcensis* (PRANTL et PŘIBYL); facie vápenců loděnických: *Lioharpes* (*Lioharpes*) *sculptus* (HAWLE et CORDA), *Kielania* (*Kielania*) *novaki* (PRANTL et PŘIBYL); facie vápenců sliveneckých: *Lioharpes* (*Fritchaspis*) *ruderalis* (HAWLE et CORDA)

Souvrství zlíchovské (zlíchovský stupeň, spodní devon): facie typických zlíchovských vápenců, včetně bazálního korálového obzoru: *Lioharpes* (*Fritchaspis*) *crassimargo* (VANĚK); facie vápenců suchomastských (spodní polohy): *Lioharpes* (*Fritchaspis*)

crassimargo [VANĚK], *Reticuloharpes reticulatus* [HAWLE et CORDA], *Kielania* [*Kielania*] *convexa* [HAWLE et CORDA]; facie vápenců chýnických: *Lioharpes* [*Fritchaspis*] *crassimargo* [VANĚK]

Souvrství dalejsko-třebotovské [dalejský stupeň, spodní devon]: facie třebotovských vápenců: *Lioharpes* [*Fritchaspis*] *perneri* [PRANTL et PRIBYL], *Kielania* [*Kielania*?] sp. [sp. n.]; facie vápenců suchomastských [svrchní polohy]: *Reticuloharpes reticulatus* [HAWLE et CORDA], *Lioharpes* [*Fritchaspis*] *perneri* [PRANTL et PRIBYL]

Souvrství chotečské [hlubočepský stupeň, střední devon]: facie chotečských vápenců [svrchní polohy]: *Lioharpes* [*Fritchaspis*] *montagnei* [HAWLE et CORDA]; facie vápenců akanthopygových: *Reticuloharpes reticulatus* [HAWLE et CORDA], *Lioharpes* [*Fritchaspis*] *montagnei* [HAWLE et CORDA], *Kielania* [*Kielania*] *kayseri* [NOVÁ]

Souvrství srbské [srbský stupeň, střední devon]: *Helioharpes transiens* [BARRANDE].

Klíč k určování rodů českých zástupců harpetidních trilobitů (založený na znacích cephalonů)

1. Hlavový lem má obrys téměř uzavřeného kruhu; je konkávně na svém povrchu prohnutý a nese velmi jemné dírkování. Glabela je málo klenutá, nápadně úzká (tr.) a dlouhá (sag.). Alae malé *B. (Bohemoharpes)*

2. Hlavový lem obráceně hruškovitý; je slabě kupředu sklopený a nese velmi hrubé a řídké dírkování. Silně vystouplá glabela je při bázi široká (tr.), dlouhá (sag.) s výrazným sag. kýlem. Nápadné jsou velké alae *Reticuloharpes*

3. Hlavový lem má podkovovitý obrys

a) je téměř plochý nebo nepatrně kupředu sklopený a nese hrubé, velmi řídké dírkování. Glabela slabě klenutá, vpředu se ponořující pod povrch lící. Je úzká (tr.), dlouhá (sag.). Alae jsou malé, nevýrazné *Eoharpes*

b) je téměř plochý a nese hrubé, řídké dírkování, mezi něž jsou umístěna četná anastomosující žebírka a lišty, které plasticky vystupují z povrchu lemu. Glabela mírně klenutá, tr. úzká, sag. dlouhá, s nevýrazným sag. kýlem. Alae jsou dosti malé *Helioharpes*

c) je téměř plochý a nese dosti hrubé a husté dírkování. Glabela ovoidní, klenutá, s naznačeným sag. kýlem. Alae velké *L. (Lioharpes)*

d) je téměř plochý, v okolí sag osy nápadně široký a mírně šikmo kupředu sklopený. Na povrchu nese velmi husté, jemné dírkování. Glabela klenutá, elongátní. Alae dosti velké *B. (Declivoharpes)*

e) je slabě konkávní, s velmi jemným a hustým dírkováním. Glabela nepřilíží klenutá, sag protažená, úzká. Alae dosti malé *L. (Fritchaspis)*

f) je konkávně prohnutý a nese velmi jemná dírkování. Glabela zřetelně klenutá, s naznačeným sag. kýlem. Je tr. široká, sag. krátká. Alae malé *B. (Unguloharpes)*

g) je konvexně vyklenutý nebo ostře kupředu sklopený, ve většině případů s velmi jemným a hustým dírkováním. Glabela je sag. dlouhá a tr. úzká, slabě vyvýšená nad povrch lící. Alae malé *K. (Kielania)*

EXPLANATION OF PLATES AND TEXT-FIGURES

Most of the trilobites figured are in collections of the National Museum of Prague and their numbers are prefixed NM. Other specimens are in collections in the following institutions: Central Geological Survey, Prague (ÚÚG), Geological-Palaeontological Museum of Humboldt University, Berlin (T), Mineralogisk Museum, University of Copenhagen (MMH), Geological Survey of Canada, Ottawa (GSC), Peabody Museum, Yale University (YPM), Geological Institute of the University of Uppsala (GIU), Palaeontological Museum, University of Oslo (PMO), Geological Institute of the University of Rennes (ES), United States National Museum, Washington D. C. (USNM), Museum of Comparative Zoology, Harvard University, Cambridge, Mass., U. S. A. (MCZ), Department of Geology, University of Buenos Aires (GUBA), Geological and Palaeontological Institute of the University of Pisa (MGUP), coll. Dr. Feist, Laboratory of Palaeontology, University of Montpellier (coll. Feist), coll. Dr. Lamont of Carlisle, Penicuik, Scotland (coll. Lamont).

Catalogue numbers are preceded by the appropriate letters as given in parenthesis.

All specimens were whitened with ammonium chloride before photographing. Most of the photographs and all text-figures are the work of Dr. A. Přibyl.

EXPLANATION OF TEXT-FIGURES

Text — fig. 1

Figs. 1—2. *Bohemoharpes (Bohemoharpes) naumanni naumanni* (Barrande, 1852)
Motol Member, Liteň Formation; Cyrtograptus ramosus-C. radians Biozone.
Loděnice near Beroun, Černidla (artificial outcrop), central Bohemia.

1. Cephalon, partly exfoliated, dorsal view. (NM, L 18270). x2,5.
2. Anterior view. x2,5.

Fig. 3. *Bohemoharpes (Bohemoharpes) crassifrons* (Barrande, 1846)
Motol Member, Liteň Formation; Testograptus testis Biozone. Kozel near
Beroun, central Bohemia.

3. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18281). x4,5.

Figs. 4—6. *Bohemoharpes (Bohemoharpes) ovatus* (Bouček, 1935)
Kopanina Formation; Horizon with *Cromus beaumonti*. Řeporyje, old quarry
„Mušlovka“, central Bohemia.

4. Cephalon, partly exfoliated, lateral view. (NM, L 18289). x4,0.
5. Anterior view. x4,0.
6. Dorsal view. x4,0.

Text — fig. 2

Figs. 1—2. *Bohemoharpes (Bohemoharpes) crassifrons* (Barrande, 1846)
Motol Member, Liteň Formation; Testograptus testis Biozone. Kozel near
Beroun (Bohemia).

1. Cephalon, partly exfoliated, dorsal view. Orig. Prantl and Přibyl, 1954, Pl. 3, fig. 4, Pl. 8, fig. 1. (NM, L 6128). Slightly retouched. x2,5.
2. Lateral view. x2,5.

Figs. 3—5. *Bohemoharpes (Unguloharpes) buphthalmus* (Bouček, 1935)
Kopanina Formation; Horizon with *Ananaspis fecunda*, Kosov hill near
Beroun, central Bohemia.

3. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. Orig. Bouček, 1935, Pl. 1, fig. 1. (NM, L 17145). x3,0.
4. Lateral view. x3,0.
5. Anterior view. x3,0.

Fig. 6. *Bohemoharpes (Bohemoharpes) ovatus* (Bouček, 1935)
Kopanina Formation; Horizon with *Cromus beaumonti*. Kosov hill near
Beroun, central Bohemia.

6. Cephalon, partly exfoliated, dorsal view. (NM, L 2862). x2,8.

Text — fig. 3

- Figs. 1—4. *Bohemoharpes (Unguloharpes) vittatus* (Barrande, 1852)
Kopanina Formation; Horizon with *Prionopeltis archiaci*. Lochkov, old abandoned quarry "Orthocerový lůmek", central Bohemia.
1. Cephalon, partly exfoliated, dorsal view. (NM, L 15435). x4,0.
2. Cephalon, partly exfoliated, dorsal view. (NM, L 2779). x3,0.
3. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18285). x3,5.
4. Cephalon, latex cast, dorsal view. (NM, L 18300). x2,5.
- Fig. 5. *Bohemoharpes (Bohemoharpes) crassifrons* (Barrande, 1852)
Motol Member, Liteň Formation; *Testograptus testis* Biozone. Kozel near Beroun (Bohemia).
5. Incomplete genicranidium, internal mould, dorsolateral view. (NM, L 18280). Slightly retouched. x2,5.
- Fig. 6. *Bohemoharpes (Bohemoharpes) ovatus* (Bouček, 1935)
Kopanina Formation; Horizon with *Cromus beaumonti*. Reporyje, old quarry "Mušlovka" (Bohemia).
6. Cephalon, partly exfoliated, dorsal view. Holotype. Orig. Bouček, 1935, Pl. 1, fig. 3. (NM-gypsum cast-sine No). x3,5.

Text — fig. 4

- Figs. 1—2. *Bohemoharpes (Unguloharpes) ungula ungula* (Sternberg, 1833)
Kopanina Formation; Horizon with *Prionopeltis archiaci*. Kosov hill near Beroun (Bohemia).
1. Enrolled specimen, partly exfoliated, ventral view. (NM, L 18299) x5,0.
2. Nearly complete exoskeleton, partly exfoliated, dorsal view. (NM, L 2950). x4,0.
- Figs. 3—5. *Bohemoharpes (Unguloharpes) buphthalmus* (Bouček, 1935)
Kopanina Formation; Horizon with *Ananaspis fecunda*, Kosov hill near Beroun (Bohemia).
3. Incomplete cephalon, partly exfoliated, lateral view. (NM, L 18272). x3,0.
4. Anterior view. x3,0.
5. Dorsal view. x3,0.

Text — fig. 5

- Figs. 1—5. *Lioharpes (Lioharpes) venulosus venulosus* (Hawle et Corda, 1847)
Praha Formation, Koněprusy Limostone. Koněprusy near Beroun, Zlatý kůň hill (Bohemia).
1. Nearly complete exoskeleton, partly exfoliated, dorsal view. (NM, L 547). x2,5.
2. Incomplete cephalon of the young specimen, partly exfoliated, dorsal view. (NM, L 15427). x7,0.
3. Brim with fringe, ventral view. (NM, L 18266). x1,5.
4. Hypostome, internal mould, dorsal view. (NM, L 15424). x10,0.
5. The same hypostome, lateral view. x10,0.

Text — fig. 6

- Figs. 1—6. *Lioharpes (Fritchaspis) ruderalis* (Hawle et Corda, 1847)
Lochkov Formation, Lochkov near Prague (Bohemia).
1. Dorsal view of cephalon with incomplete thorax, partly exfoliated. Orig. Prantl and Přibyl, 1954, Pl. 1, fig. 9 and Pl. 3, fig. 12 (counterpart). (NM, L 6132). Slightly retouched. x2,5.
2. Anterior view. Slightly retouched. x2,5.
3. Dorsal view of incomplete cephalon, partly exfoliated. Orig. Prantl and Přibyl, 1954, Pl. 4, fig. 3. (NM, ČE 1565). x2,5.
4. Lateral view. x2,5.
5. Anterior view. x2,5.
6. Dorsal view of incomplete cephalon, partly exfoliated. (NM, L 15445). x2,5.

Text — fig. 7

- Figs. 1—5. *Lioharpes (Fritchaspis) montagnei* (Hawle et Corda, 1847)

Choteč Formation, Acanthopyge Limestone. Koněprusy near Beroun, small abandoned quarry at Zlatý kůň hill [Bohemia].

1. Dorsal view of incomplete cephalon, partly exfoliated. (NM, L 2992). x2,5.

2. Lateral view. x2,5.

3. Incomplete brim and hypostome, internal mould, dorsal view. (NM, L 15442). x4,0.

4. Dorsal view of incomplete cephalon, partly exfoliated, and hypostome. (NM, L 2993). x1,5.

5. Incomplete cephalon, internal mould, dorsal view. (NM, L 15436). x2,5.

Figs. 6—7. *Lioharpes (Fritchaspis) venetus* (Gortani, 1915)

Middle Devonian, Carnic Alps [Seekopf].

6. Dorsal view of incomplete cephalon, mould. Orig. Gortani, 1915, Pl. 3, fig. 34. (MGUP-sine No). x2,0.

7. Dorsal view of incomplete genicranidium, mould. Orig. Gortani, 1915, Pl. 3, fig. 35. (MGUP-sine No). x2,0.

Text — fig. 8

Figs. 1—2. *Bohemoharpes (Declivoharpes) praecedens* (Prantl et Přibyl, 1954)

Lochkov Formation, Lochkov near Prague, central Bohemia.

1. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. Orig. Prantl and Přibyl, 1954, Pl. 8, fig. 2. (NM, ČE 1568). Slightly retouched. x2,0.

2. Anterior view. x2,0.

Figs. 3—4. *Bohemoharpes (Unguloharpes?) wilkensis* (Münster, 1840)

Upper Silurian, Elbesreuth, Germany [F. R. G.].

3. Incomplete cephalon, partly exfoliated, anterior view. (ÜÜG, JV 432). x5,0.

4. Incomplete cephalon, partly exfoliated, dorsal view. (ÜÜG, JV 428). x5,0.

Fig. 5. *Kielania (Kielania) convexa* (Hawle et Corda, 1847)

Suchomasty Limestone [lower layers]. Koněprusy near Beroun. "Mramorová stěna" at Zlatý kůň hill [Bohemia].

5. Incomplete cephalon of the juvenile specimen, partly exfoliated, dorsal view. (NM, L 18277). x10,0.

Fig. 6. *Kielania (Kielania) dorbignyana* (Barrande, 1846)

Praha Formation, Dvorce-Prokop Limestone. Prague 5-Hlubočepy [Bohemia].

6. Incomplete cephalon of the juvenile specimen, internal mould, dorsal view. (NM, L 15422). x8,5.

Text — fig. 9

Figs. 1—3. *Lioharpes (Fritchaspis) crassimargo* (Vaněk, 1963)

Zlíchov Formation, lower layers, Prague 5-Hlubočepy, old abandoned quarry "U kapličky" [Bohemia].

1. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18273). x6,2.

2. Lateral view. x6,2.

3. Incomplete cephalon with some thoracic segments, partly exfoliated, dorsal view. (NM, L 15426). x2,5.

Figs. 4—5. *Helioharpes* sp. n.

Eifel-Stufe (Middle Devonian), Benneckenstein, "Alte Eiche"-quarry, Unterharz, Germany [F. R. G.].

4. Incomplete cephalon, latex cast, dorsal view. Orig. Erben, 1950,

Text-figs. 2b—2c. (T 311). x1,5.

5. Dorsal view of incomplete cephalon, latex cast. Orig. Erben, 1950,

Text-fig. 2a and orig. Alberti, 1969, Pl. 22, fig. 4a—b. (T 311). x1,5.

Text — fig. 10

Figs. 1—5. *Lioharpes (Fritchaspis) crassimargo* (Vaněk, 1963)

Zlíchov Formation, Choteč near Prague, upper layers [figs. 1—3] and Prague 5-Hlubočepy, old abandoned quarry "U kapličky", lower layers [figs. 4—5]. [Bohemia].

1. Dorsal view of incomplete cephalon, partly exfoliated. Orig. Prantl and

Příbyl, 1954, Pl. 7, fig. 1 as *Harpes ruderalis*. [NM, CE 1567]. Slightly retouched. x2,5.

2. Lateral view. x2,5.

3. Anterior view. x2,5.

4. Dorsal view of incomplete cephalon. [NM, L 15421]. x2,0.

5. Dorsal view of teratological cephalon, partly exfoliated. [NM, L 15443]. x 6,0.

Fig. 6. *Reticuloharpes reticulatus* (Hawle et Corda, 1847)

Choteč Formation, Acanthopyge Limestone, Koněprusy near Beroun, Zlatý kůň hill (Bohemia).

6. Incomplete cephalon, partly exfoliated, dorsal view. [NM, L 18291]. x3,0.

Text — fig. 11

Figs. 1—2. *Kielania (Kielania) convexa* (Hawle et Corda, 1847)

Suchomasty Limestone (lower layers), Koněprusy near Beroun (Bohemia).

1. Incomplete cephalon, partly exfoliated, dorsal view. Paratype. Orig. Prantl and Příbyl, 1954, Pl. 9, fig. 4. [NM, L 6139]. x4,0.

2. Lateral view. Slightly retouched. x4,0.

Figs. 3—4. *Kielania (Kielania) waageni* (Prantl et Příbyl, 1954)

Praha Formation, Dvorce-Prokop Limestone, Prague 5-Malá Chuchle, old abandoned quarry at lane to Slivenec (Bohemia).

3. Cephalon, partly exfoliated, anterior view. Paratype. Orig. Prantl and Příbyl, 1954, Pl. 3, fig. 5. [NM, CF 542]. x4,0.

4. Dorsal view. x 3,0.

Text — fig. 12

Figs. 1—4. *Harpes macrocephalus macrocephalus* Goldfuss, 1839

Eifelian, Gerolstein, Germany [F. R. G.].

1. Incomplete cephalon, partly exfoliated, dorsal view. [ÜÜG, JV 218]. x2,5.

2. Incomplete cephalon, partly exfoliated, anterior view. [ÜÜG, JV 219]. x1,5.

3. The same, dorsal view. x1,5.

4. Incomplete cephalon, partly exfoliated, dorsal view. [ÜÜG, JV 220]. 1:1.

Figs. 5—7. *Harpes rouvillei* Frech, 1887

Upper part of Calcaire à polypiers siliceux s. str. Mont Bataille, Gabrières (Languedoc), France.

5. Incomplete cephalon, latex cast, dorsal view. [Coll. Feist]. x1,75.

6. Incomplete cephalon, latex cast, dorsal view. Neotype [det. dr. Feist]. [Coll. Feist]. x1,75.

7. Incomplete cephalon, latex cast, dorsal view. [Coll. Feist]. x1,75.

Figs. 8—9. *Reticuloharpes reticulatus* (Hawle et Corda, 1847)

Suchomasty Limestone (lower layers), Koněprusy near Beroun.

8. Incomplete cephalon, partly exfoliated, dorsal view. Orig. Novák, 1890, Pl. 3, figs. 17a—17d. [NM, CF 545]. x1,5.

9. Anterior view. x1,5.

Text — fig. 13

Fig. 1 *Dubhglasina aldonsensis* Lamont, 1948

Caradocian, Scotland.

1. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. Orig. Lamont, 1948, Text-fig. 1. [Coll. Lamont]. x1,5.

Figs. 2—3. *Scotoharpes excavatus* (Linnarsson, 1875)

Volkhovian, Cyclopyge stigmata Biozone. Skebro, Resebaek. Denmark.

2. Incomplete cephalon, internal mould, dorsal view. Orig. Poulsen, 1965, Pl. 7, fig. 2. [MMH, 9455]. x3,0.

3. Anterior view. x3,0.

Fig. 4. *Scotoharpes singularis* (Whittington, 1965)

Middle Table Head Formation, Table Cove, Newfoundland, Canada.

4. Incomplete cephalon, dorsal view. Holotype. Orig. Whittington, 1965, Pl. 8, fig. 1. [GSC, 18402]. x3,0.

- Fig. 5. *Scotoharpes vitilis* (Whittington, 1963)
Lower Head, Western Newfoundland, Canada.
5. Cephalon, partly exfoliated, dorsal view. Holotype. Orig. Whittington, 1963, Pl. 2, fig. 7. [GSC, 16176]. x8,0.
- Fig. 6. *Scotoharpes fragilis* (Raymond, 1925)
Middle Ordovician, Boulder in Cow Head Group from Stearing Island, Western Newfoundland, Canada.
6. Latex cast of the external mould of cephalon, dorsal view. Orig. Raymond, 1925, Pl. 1, fig. 11. [YPM, 13036]. x4,5.
- Figs. 7—8. *Eoharpes benignensis* (Barrande, 1872)
Dobrotivá Formation (lower layers). Brandýs nad Labem. Bohemia.
7. Cephalon, internal mould, dorsal view. [ÚUG, JV 657]. x2,0.
8. Anterior view. x2,0.

Text — fig. 14

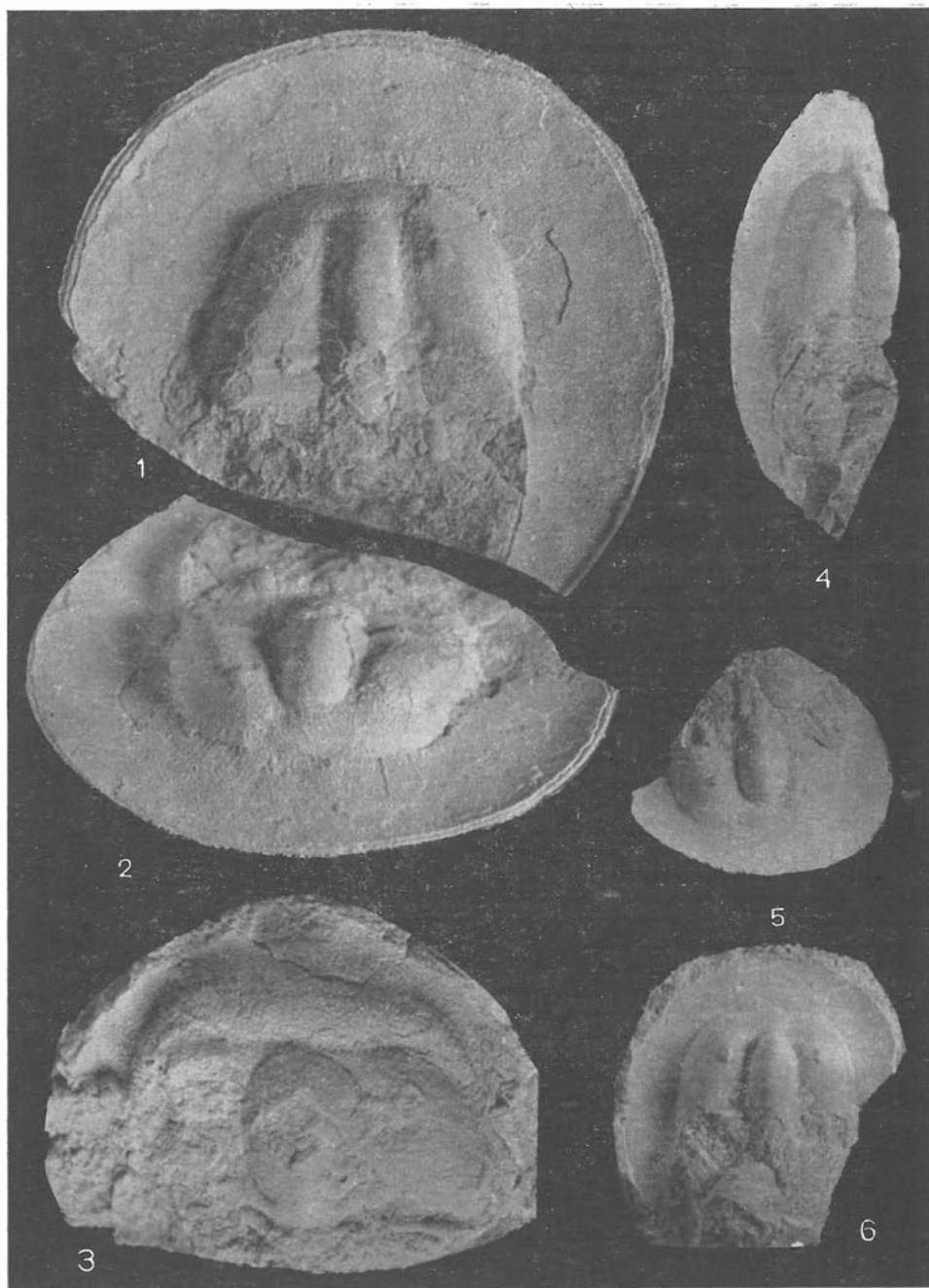
- Fig. 1. *Thorslundops dalecarlica* (Thorslund, 1930)
Viruan. Skälberget, Sweden.
1. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. Orig. Thorslund, 1930, Pl. 4, fig. 1. [GIU, 464]. x1,0.
- Figs. 2—3. *Paraharpes similis* Nikolaisen, 1965
Cyclocrinus Beds. Furuberget in the district of Nes-Hamar, Norway.
2. Incomplete cephalon, latex cast, dorsal view. Holotype. Orig. Nikolaisen, 1965, Pl. 1, fig. 6. [PMO, 38237]. x2,5.
3. Lower lamella of brim and fringe. Paratype. Orig. Nikolaisen, 1965, Pl. 1, fig. 7. [PMO, 73662]. x2,5.
- Figs. 4—6. *Paraharpes costatus* (Angelin, 1854)
Leptaena Limestone, Dalarne, Källholm, Sweden.
4. Cephalon, partly exfoliated, dorsal view. Orig. Warburg, 1925, Pl. 5, fig. 6 and Text-fig. 18. [GIU, 575/D 199]. x1,0.
5. Lateral view. x1,0.
6. Anterior view. x1,0.
- Figs. 7—10. *Wegelinia wegeli* (Angelin, 1854)
Leptaena Limestone. Dalarne, Källholm, Sweden.
7. Teratological cephalon, partly exfoliated, dorsal view. Orig. Warburg, 1925, Pl. 4, figs. 22—23. [GIU, 579]. x1,1.
8. Anterior view. x1,1.
9. Incomplete cephalon, partly exfoliated, dorsal view. Orig. Warburg, 1925, Pl. 4, fig. 21. [GIU, 581]. x1,1.
10. Anterior view. x1,1.

Text — fig. 15

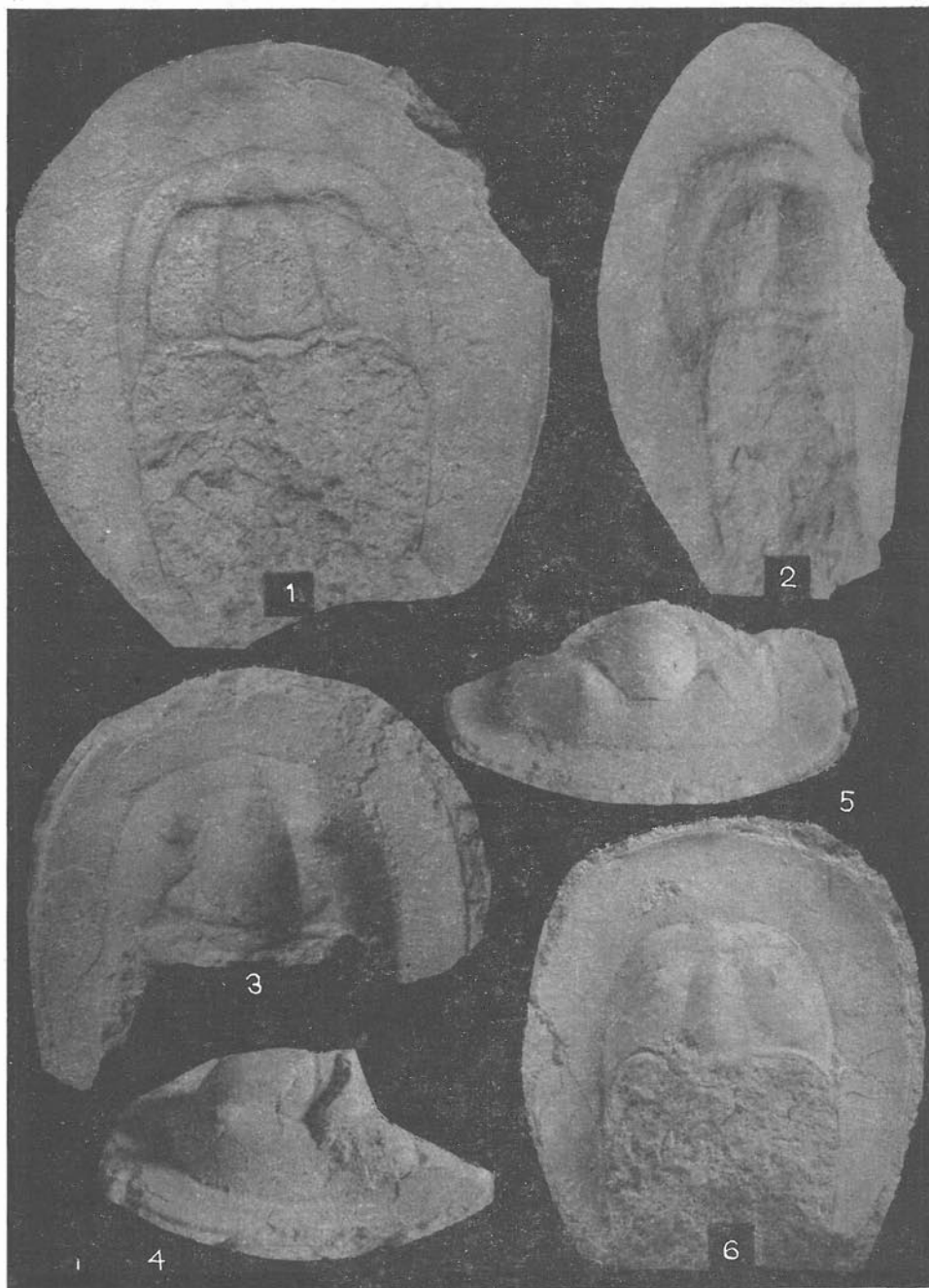
- Fig. 1. *Harpes ormistoni* sp. n.
Blue Fiord Formation. Svendsen Peninsula, Canadian arctic Islands.
1. Latex cast of external mould of entire cephalon. Holotype, dorsal view. Orig. Ormiston, 1967, Pl. 4, fig. 4. [GSC, 18116]. x1,0.
- Fig. 2. *Paraharpes ottawaensis* (Billings, 1865)
Cobourg Beds?. Unspecified locality at Ottawa, Ontario, Canada.
2. Cephalon with some thoracic segments. Dorsal view. Metal replica of holotype. Orig. Billings, 1865, fig. 165. [GSC, 329]. x1,25.
- Fig. 3. *Hibbertia flanaganii* (Portlock, 1843)
Caradocian, Bardehessia Beds. Pomeroy, co. Tyrone.
3. Latex cast of cephalon. Dorsal view. Lectotype. Orig. Whittington, 1950a, Pl. 1, fig. 5. [GSM, 35491]. x1,0.
- Fig. 4. *Scotoharpes domina* Lamont, 1948
Plectodonta aff. canastonensis Beds. Wetherlaw Linn, North Esk Inlier, Midlothian, Scotland.
4. Plaster replica of plasticine, dorsal surface made by Lamont from the holotype, external mould. Orig. Lamont, 1948, fig. 2. x1,5.
- Fig. 5. *Australoharpes depressus* Harrington et Leanza, 1957
Lower Tremadocian, Kainella meridionalis Biozone. Salta, Argentina.

5. Incomplete cephalon, external mould, dorsal view. Holotype. Orig. Har-
rington and Leanza, 1957. Text — fig. 103/2. (GUBA, 4000). x2,0.
- Figs. 6—8. *Kielania (Lowtheria) triabsidata* Ormiston, 1971
Emsian(?), Lowther Island, District of Franklin, Canada.
6. Dorsal view of paratype to show course of girder, internal and external
rims, and nature of pitting. Orig. Ormiston, 1971, Pl. 4, fig. 9. (GSC, 25528).
x1,5.
7. Oblique view of glabellar area of holotype to show pronounced glabellar
lobes, wide alae and fine glabellar ornament. Orig. Ormiston, 1971, Pl. 4,
fig. 2. (GSC, 25527). x2,0.
8. Dorsal view of holotype, Orig. Ormiston, 1971, Pl. 4, fig. 1. (GSC, 25527).
x0,5.
- Text — fig. 16**
- Figs. 1—2. *Eoharpes guichenensis* Henry et Phillipot, 1968
Lower Llandeiliian, Traveusot-en-Guichen (Ille-et-Villaine), France.
1. Incomplete cephalon, internal mould, dorsal view. Holotype. Orig. Henry
and Phillipot, 1968, Pl. 1, fig. 1. (ES sine No.). x2,5.
2. Lateral view. x2,5.
- Figs. 3—4. *Eoharpes benignensis* (Barrande, 1872)
Dobrotivá Formation. Svatá Dobrotivá (Zaječov) (fig. 3) and Prague 6-Vo-
kovice (fig. 4), Bohemia.
3. Incomplete exoskeleton, partly exfoliated, dorsal view. (NM Inv. Nr.
526). x3,2.
4. Incomplete exoskeleton, internal mould, dorsal view. (ÚÜG, JV 6432).
x2,0.
- Fig. 5. *Eoharpes primus* (Barrande, 1872)
Šárka Formation. Osek near Rokycany, Bohemia.
5. Incomplete exoskeleton with hypostome "in situ", internal mould, dorsal
view. (ÚÜG, JV 6433). x3,0.
- Text — fig. 17**
- Figs. 1—2. *Dolichoharpes reticulatus* Whittington, 1949
Basal Edinburg Limestone. Virginia, U. S. A.
1. Incomplete cephalon, dorsal view. Holotype. Orig. Whittington, 1949,
Pl. 2, figs. 2—3. (USNM — sine No.). x2,0.
2. Anterior view. x2,0.
- Figs. 3—6. *Dolichoharpes uniserialis* (Raymond, 1925)
Kimmiswick Limestone. Missouri, U. S. A.
3. Incomplete cephalon, rubber cast of lectotype. Orig. Raymond, 1925,
Pl. 1, fig. 9. (MCZ, 1681). x3,0.
4. Lateral view. x2,0.
5. Incomplete cephalon, lateral view. Paratype. Orig. Raymond, 1925, Pl. 1,
fig. 8. (MCZ, 1682). x3,0.
6. Dorsal view. x3,0.
- Figs. 7—8. *Dolichoharpes* sp. aff. *uniserialis* (Raymond, 1925)
Blackriverian. Oklahoma, U. S. A.
7. Incomplete cephalon with test, anterior view. Orig. Přibyl and Vaněk,
1981, Pl. 1, fig. 3. (ÚÜG, JV 214). x2,0.
8. Dorsal view. x2,0.

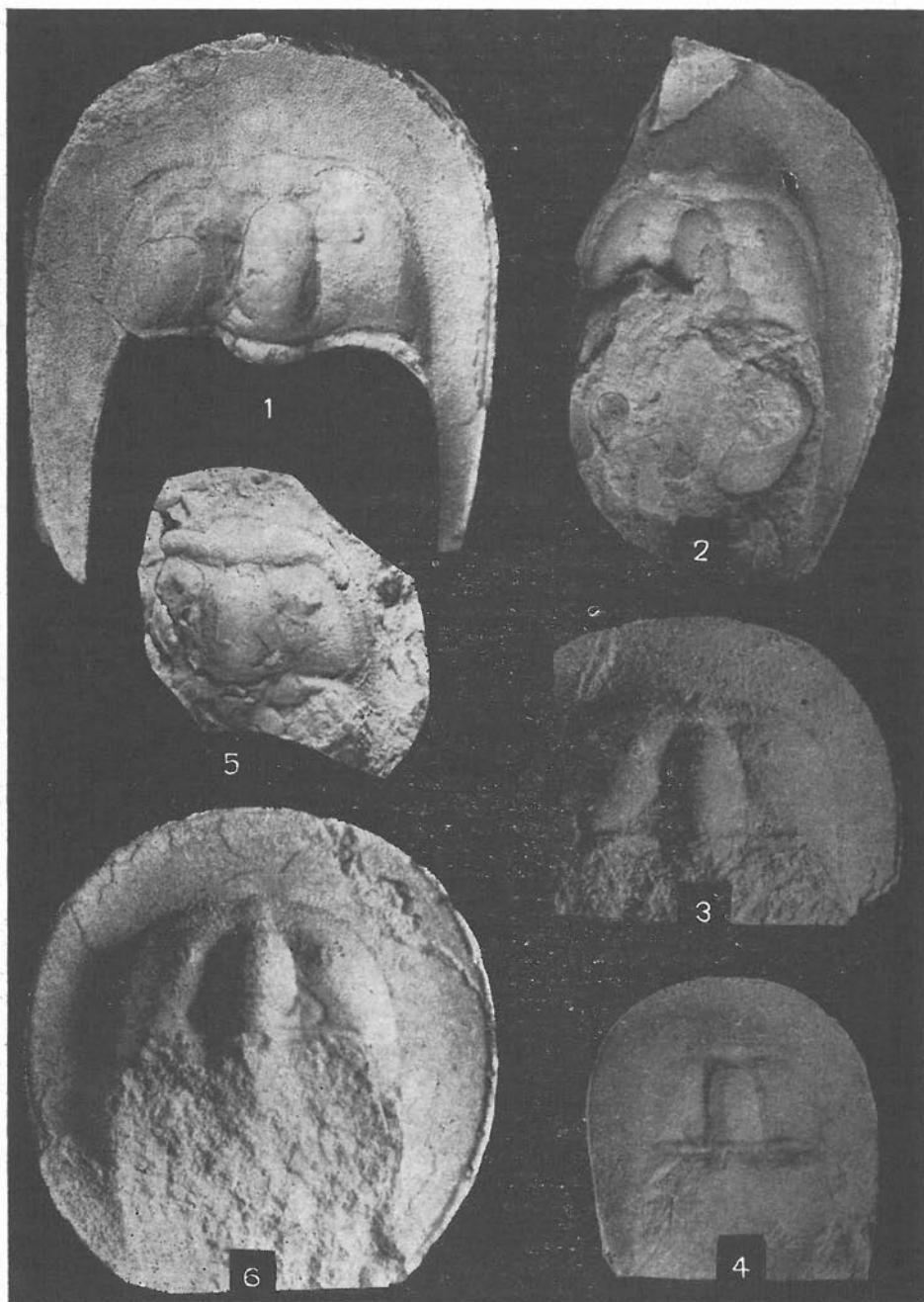
Text-fig. 1



Text-fig. 2



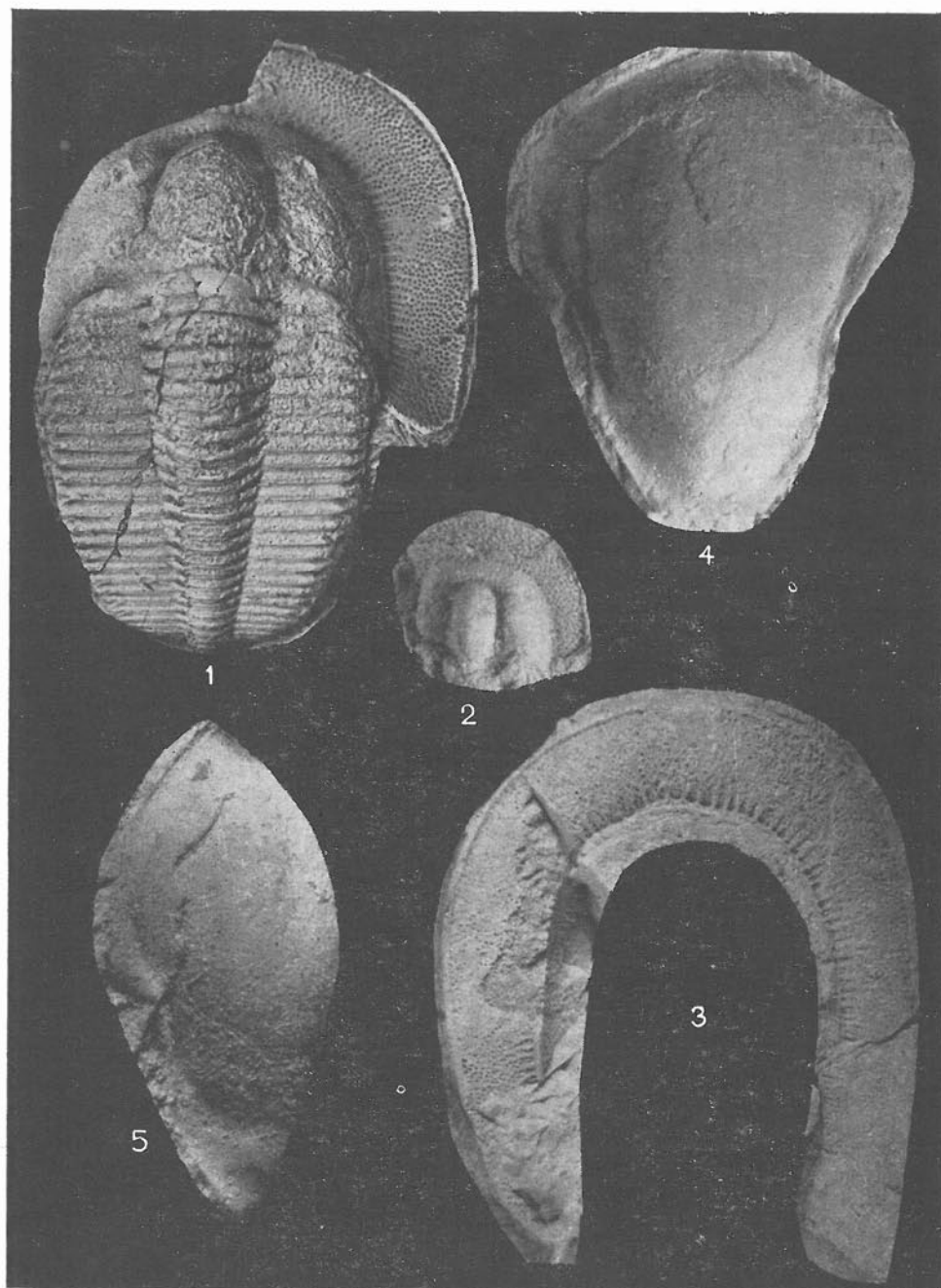
Text-fig. 3



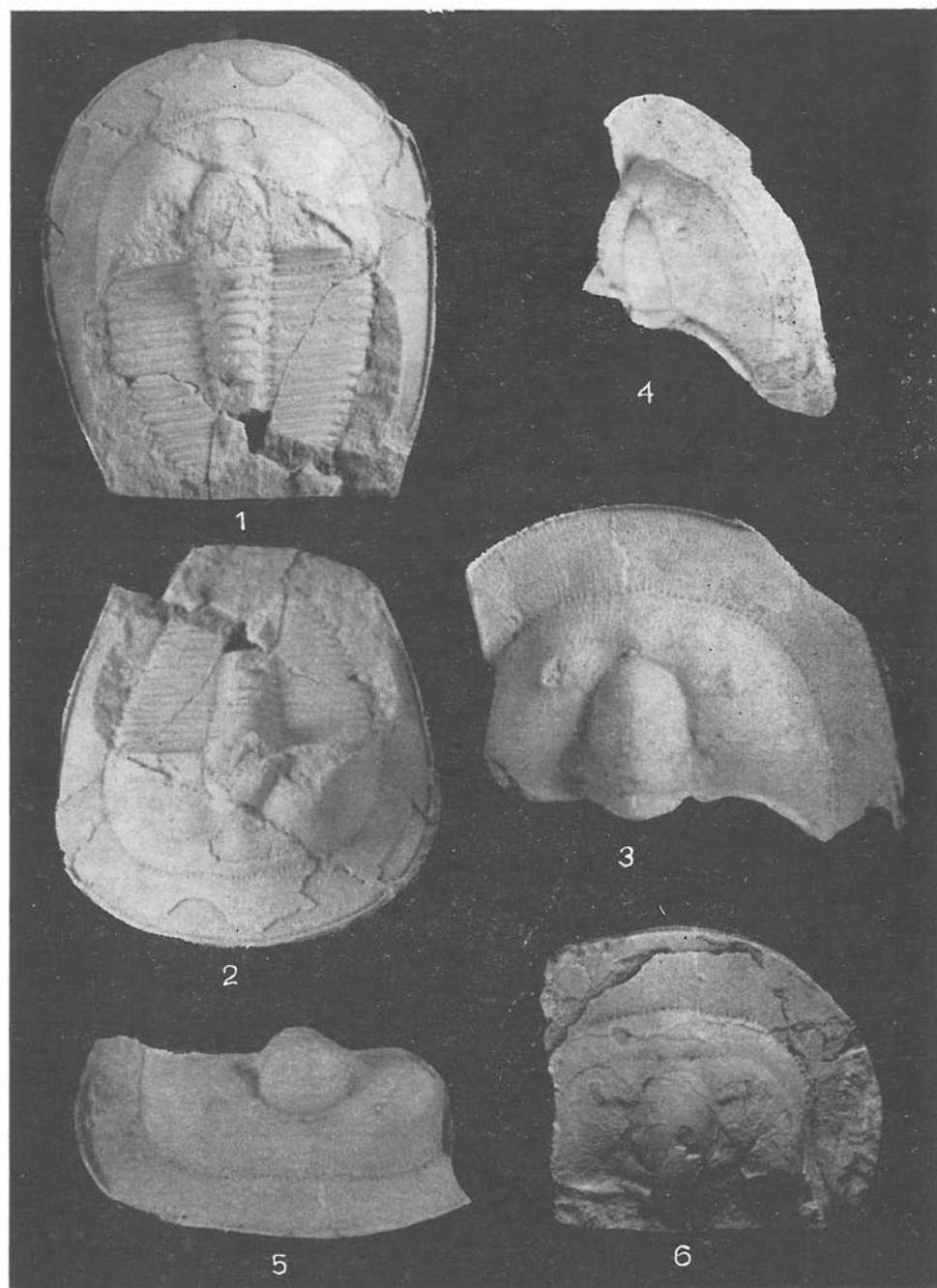
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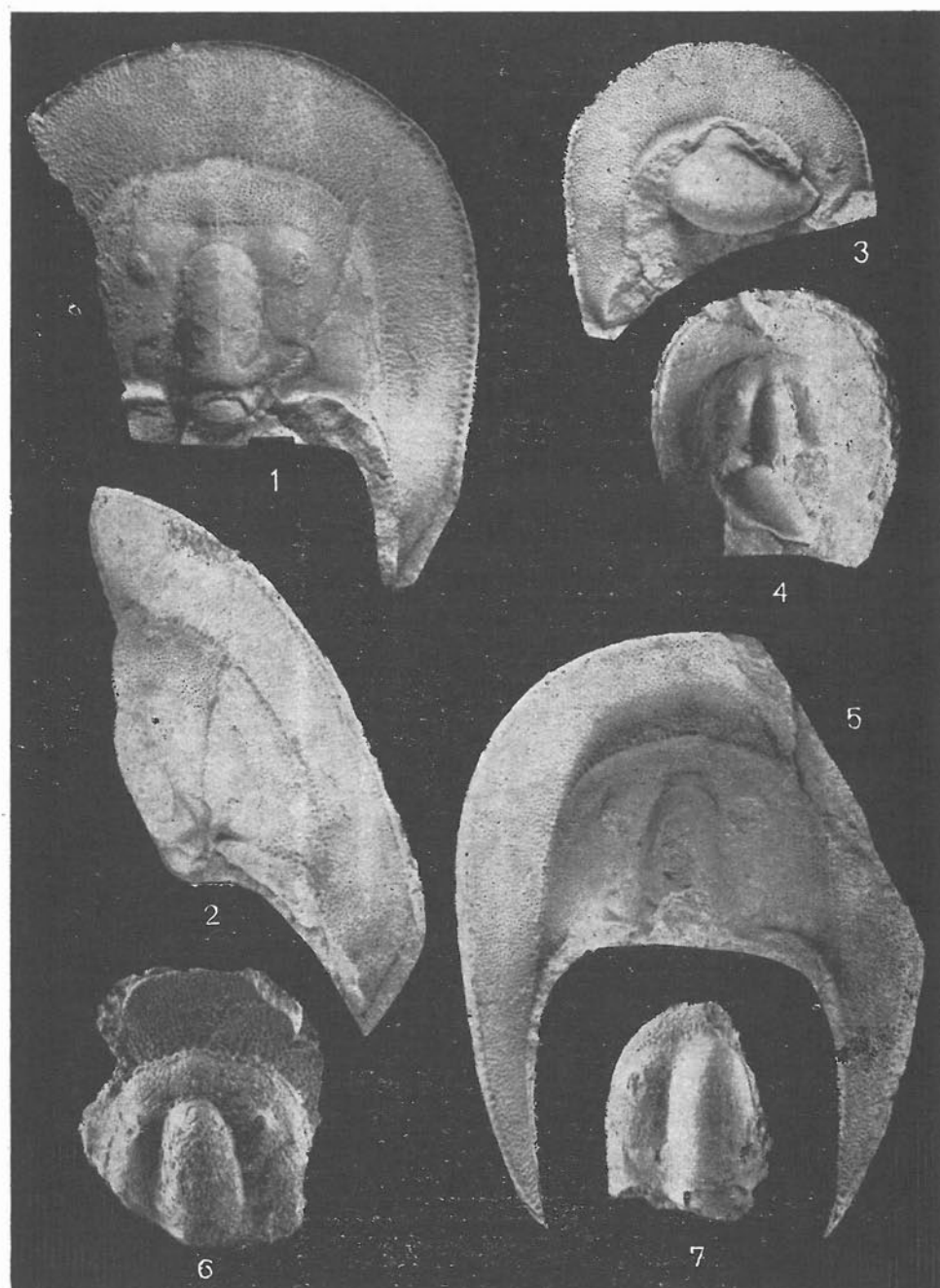
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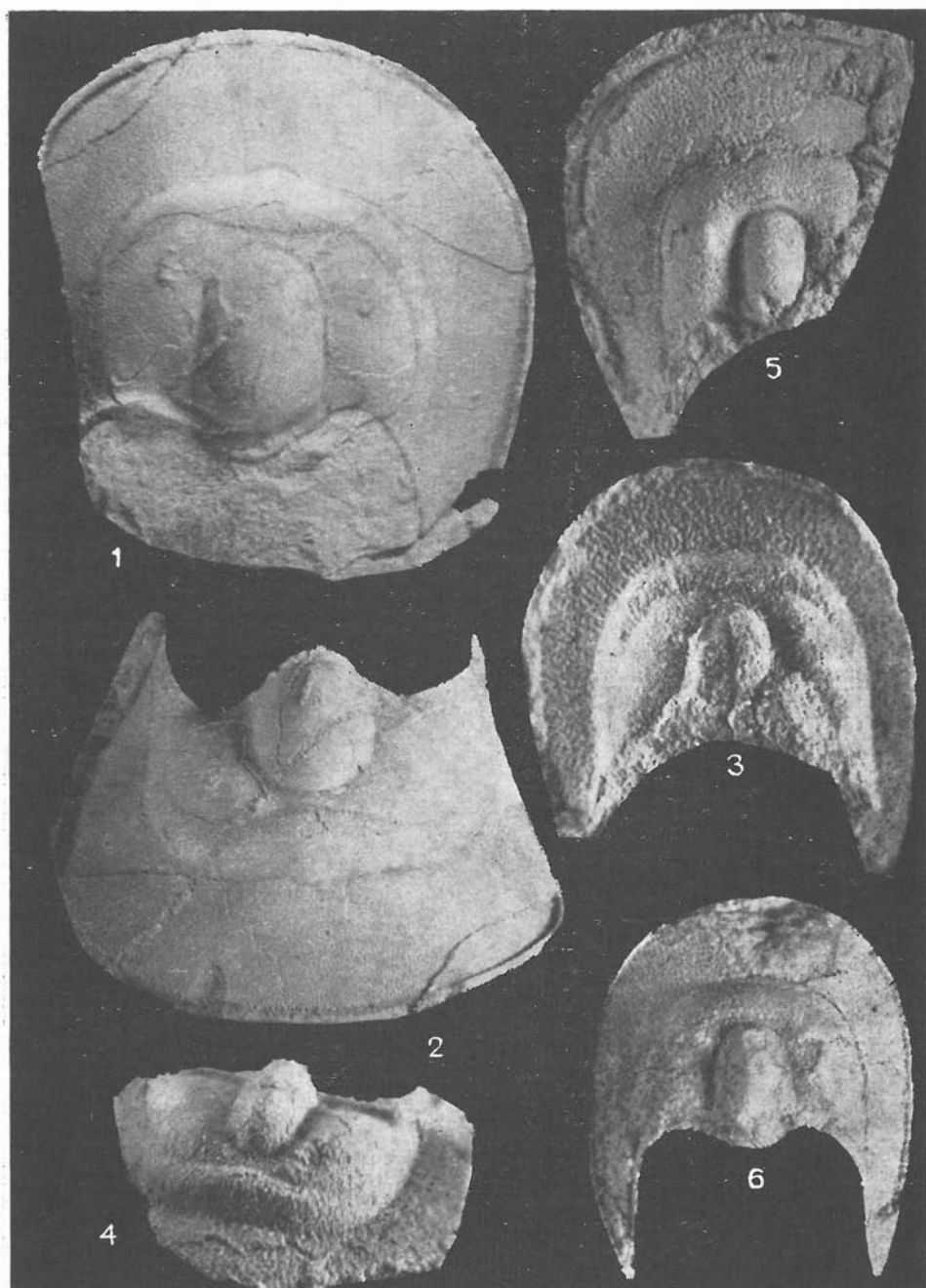
Text-fig. 6



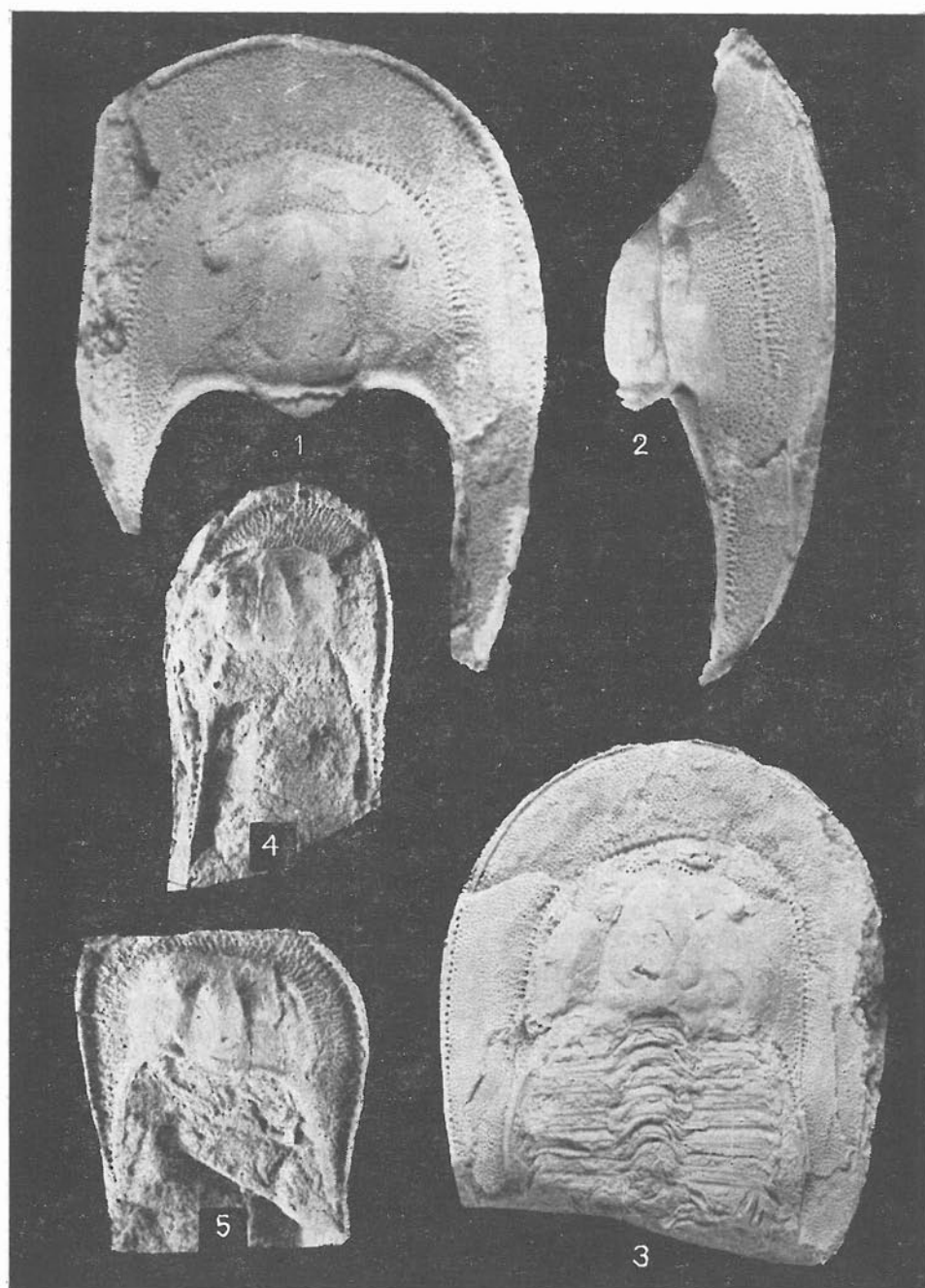
Text-fig. 7



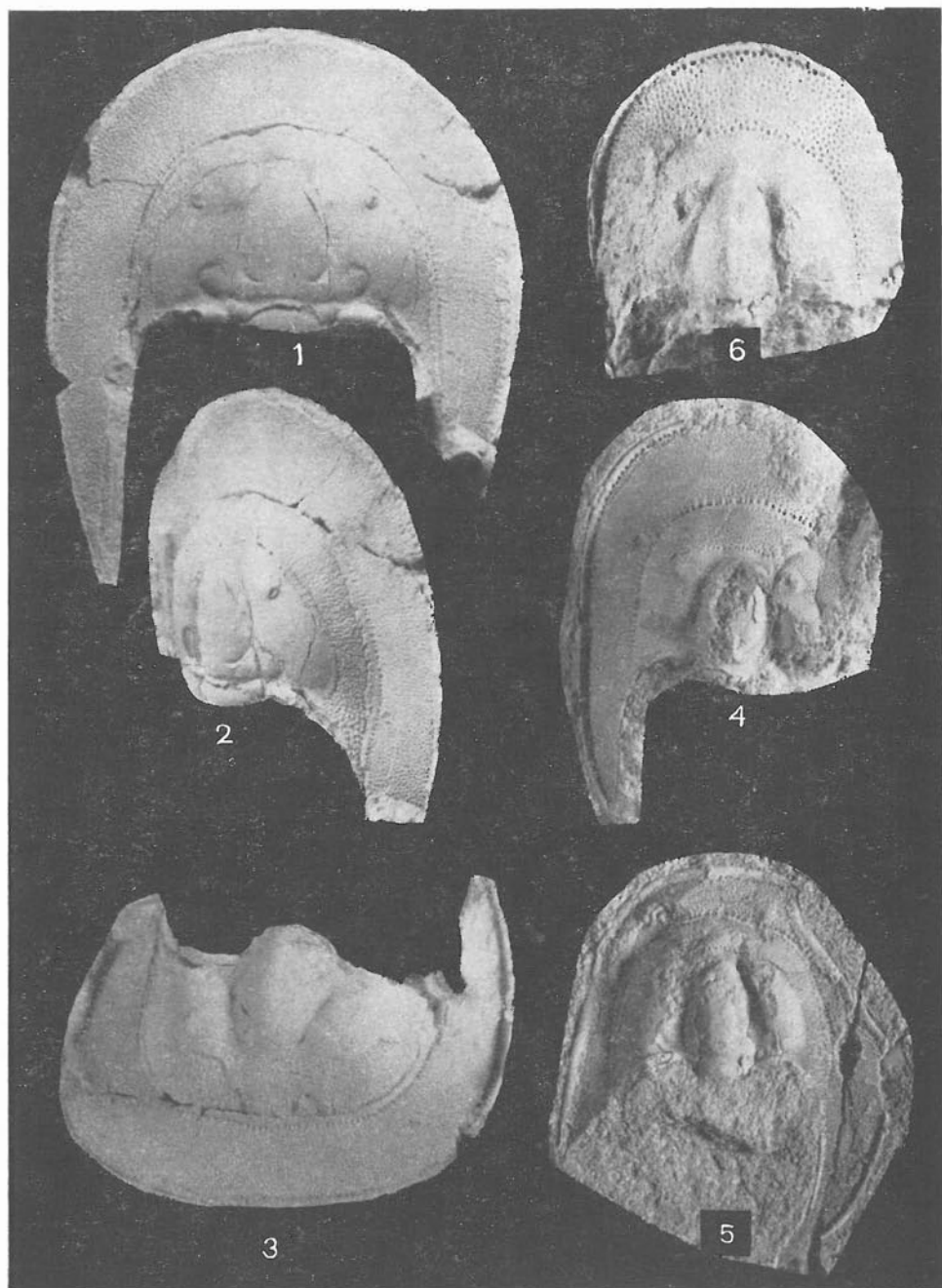
Text-fig. 8



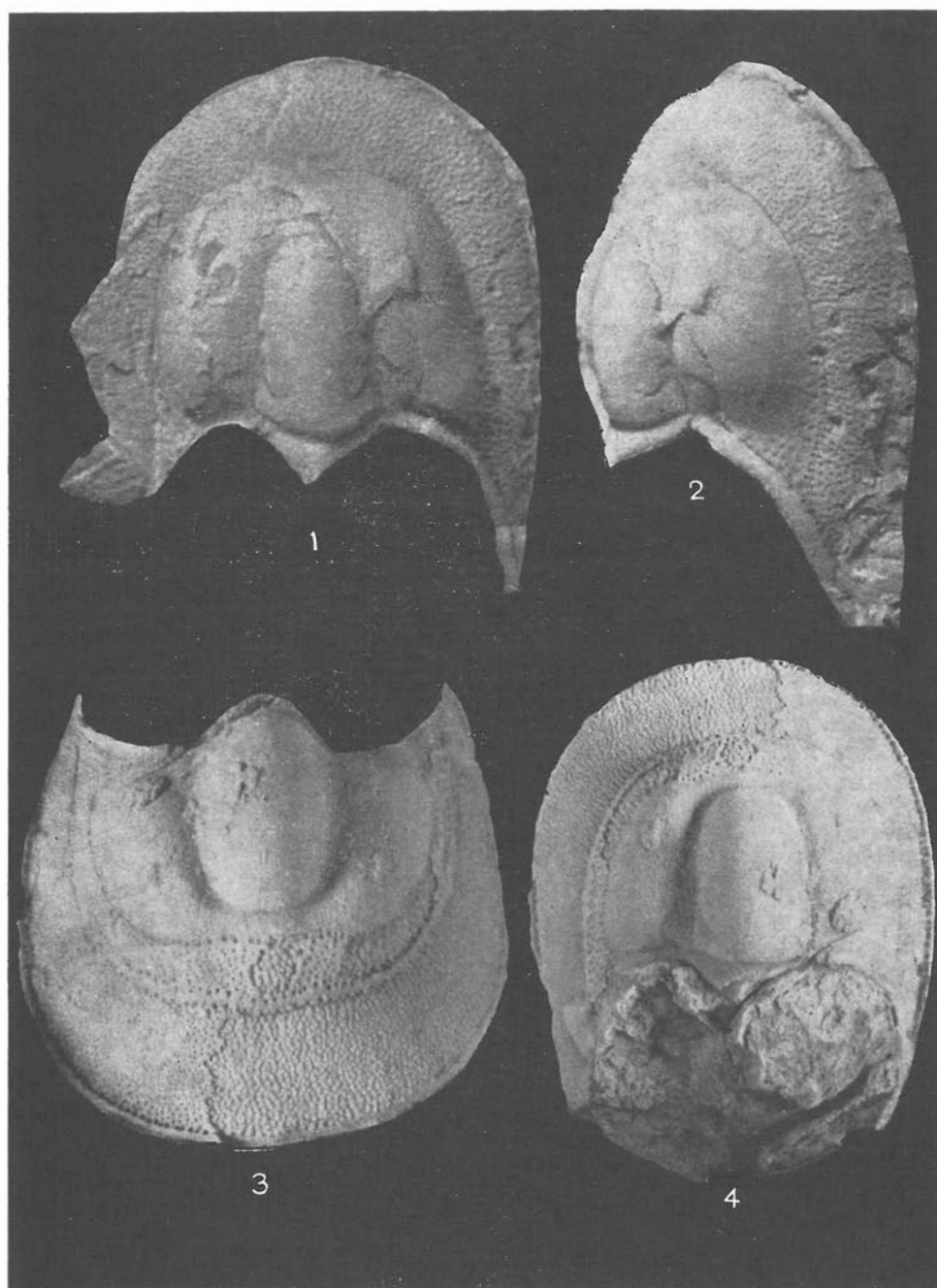
Text-fig. 9



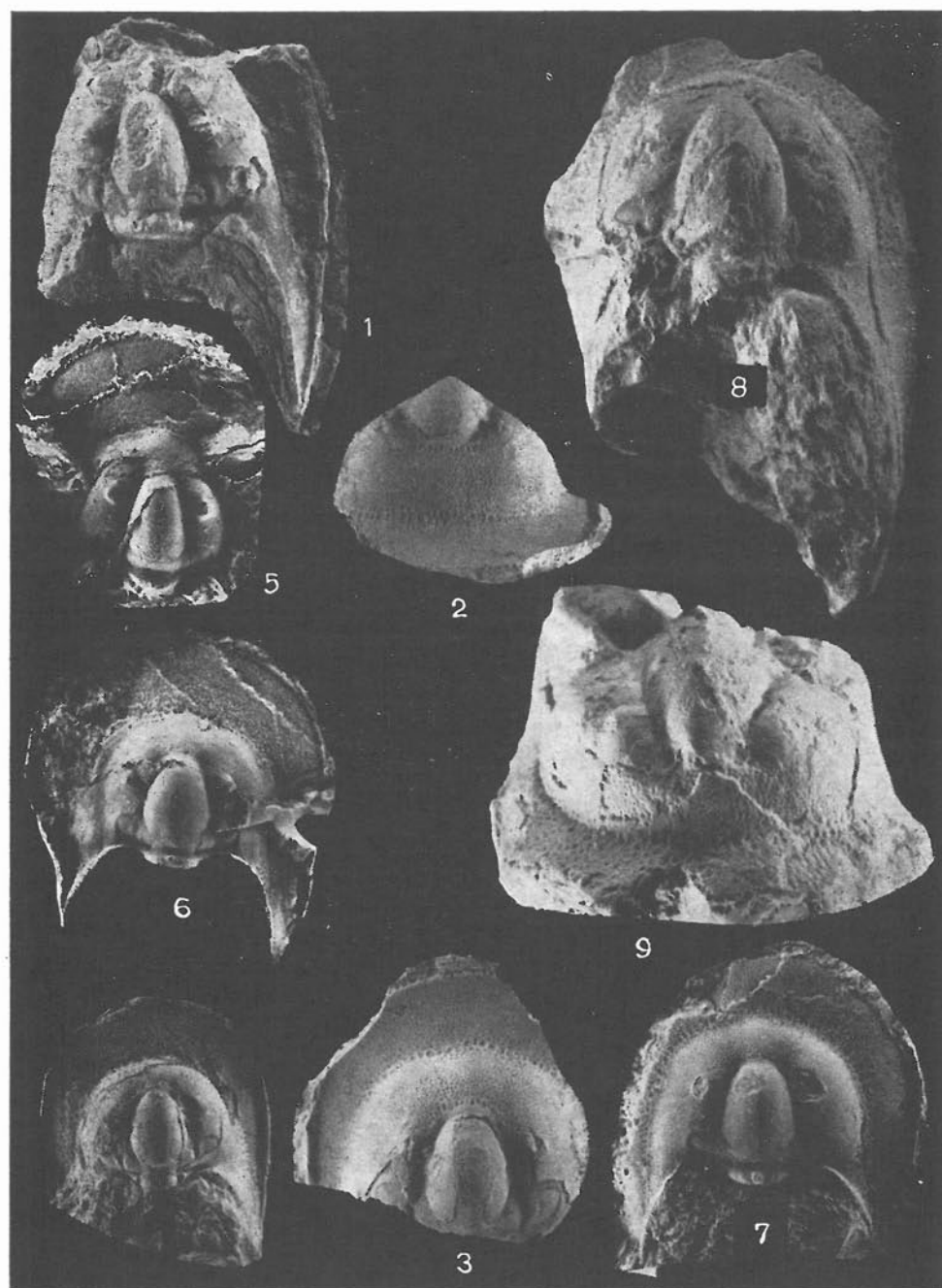
Text-fig. 10



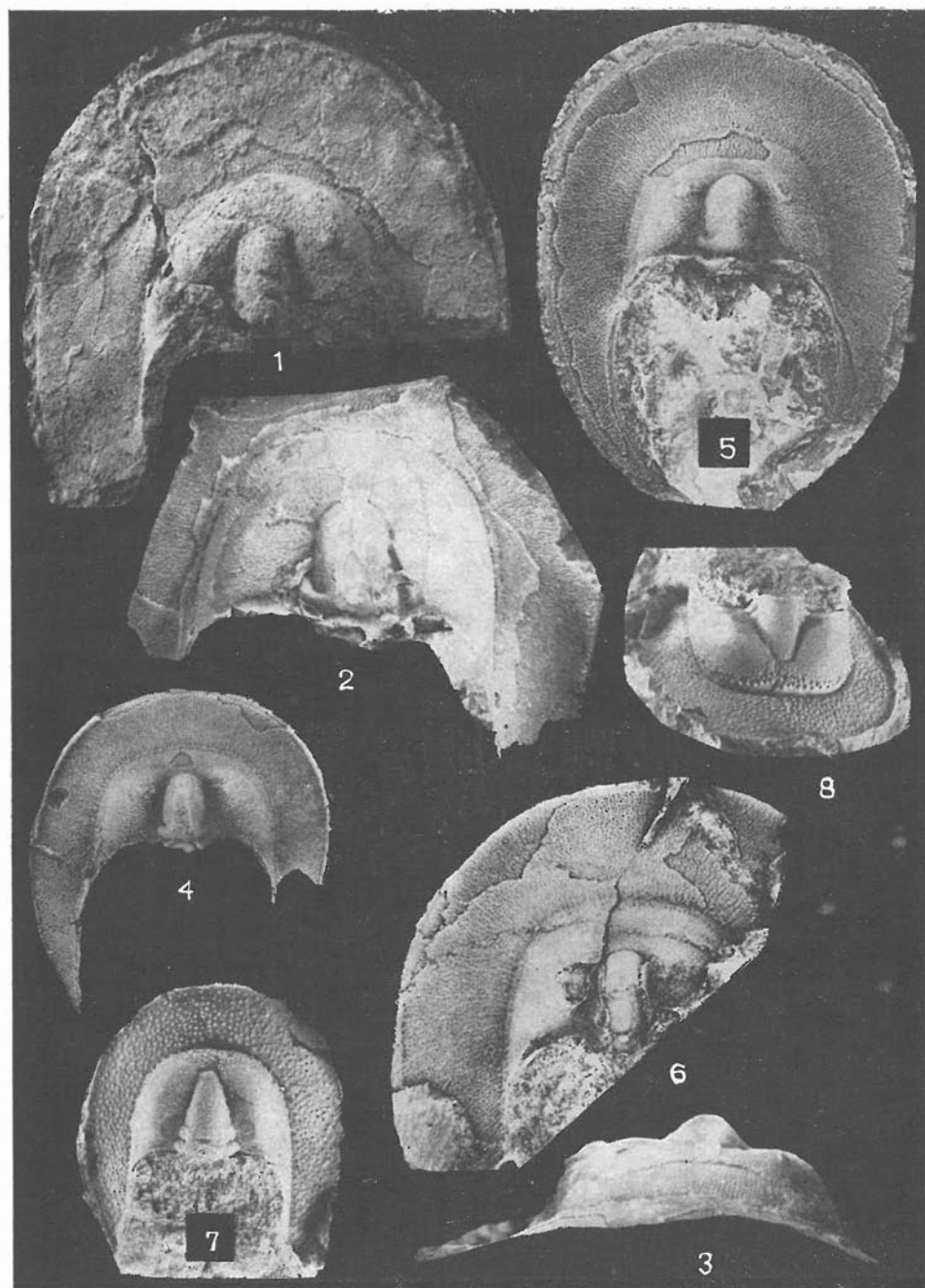
Text-fig. 11



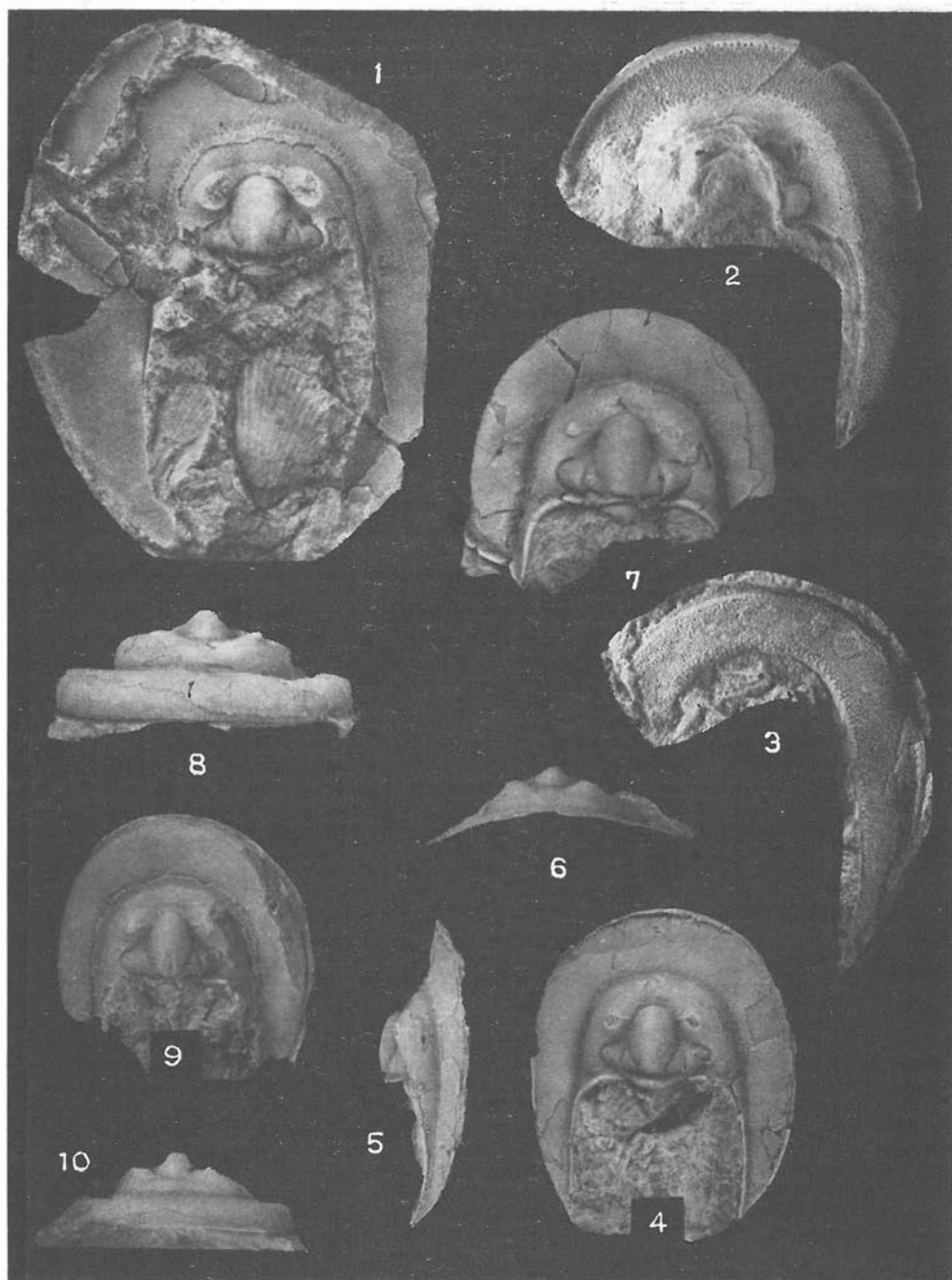
Text-fig. 12



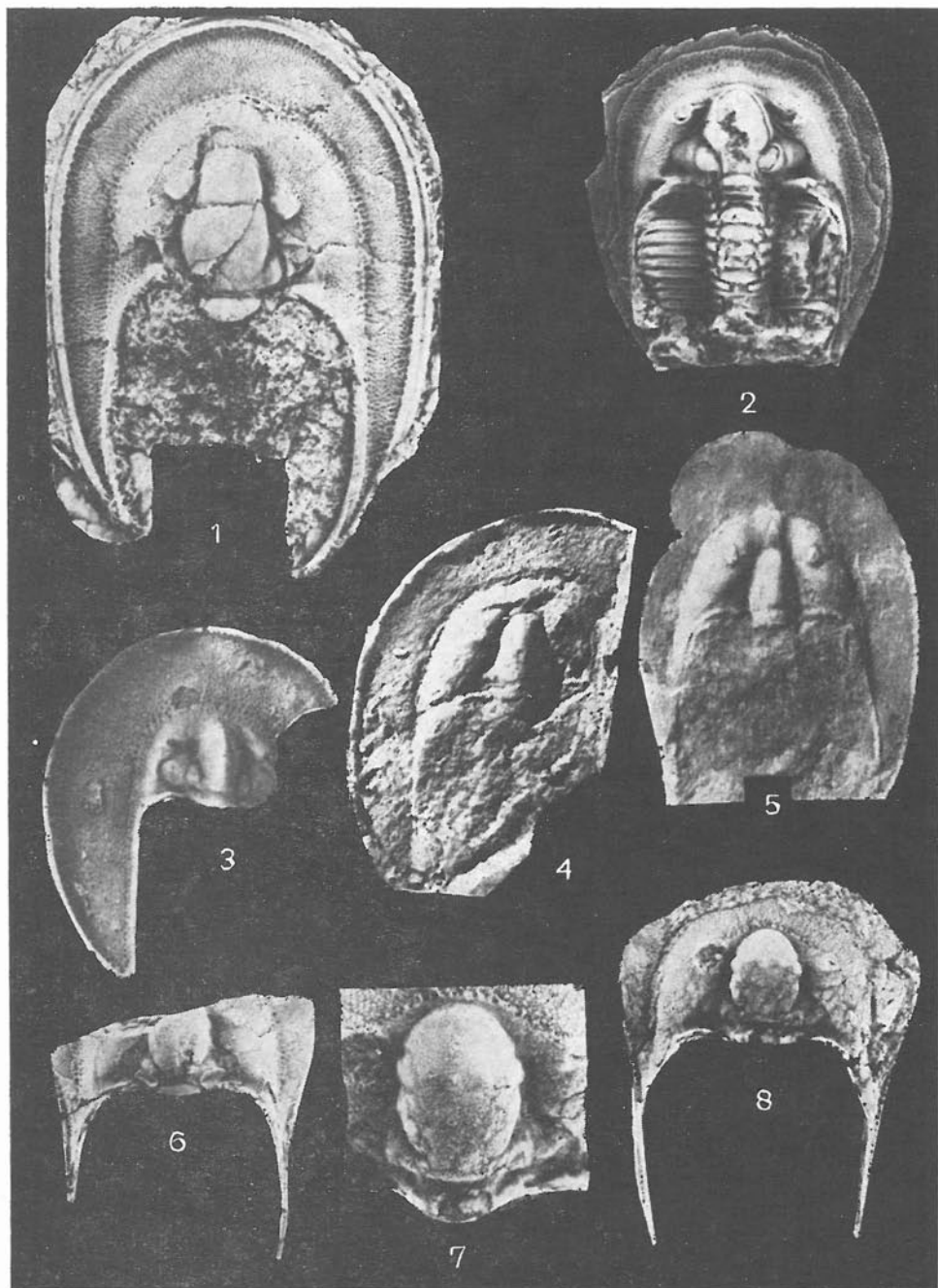
Text-fig. 13



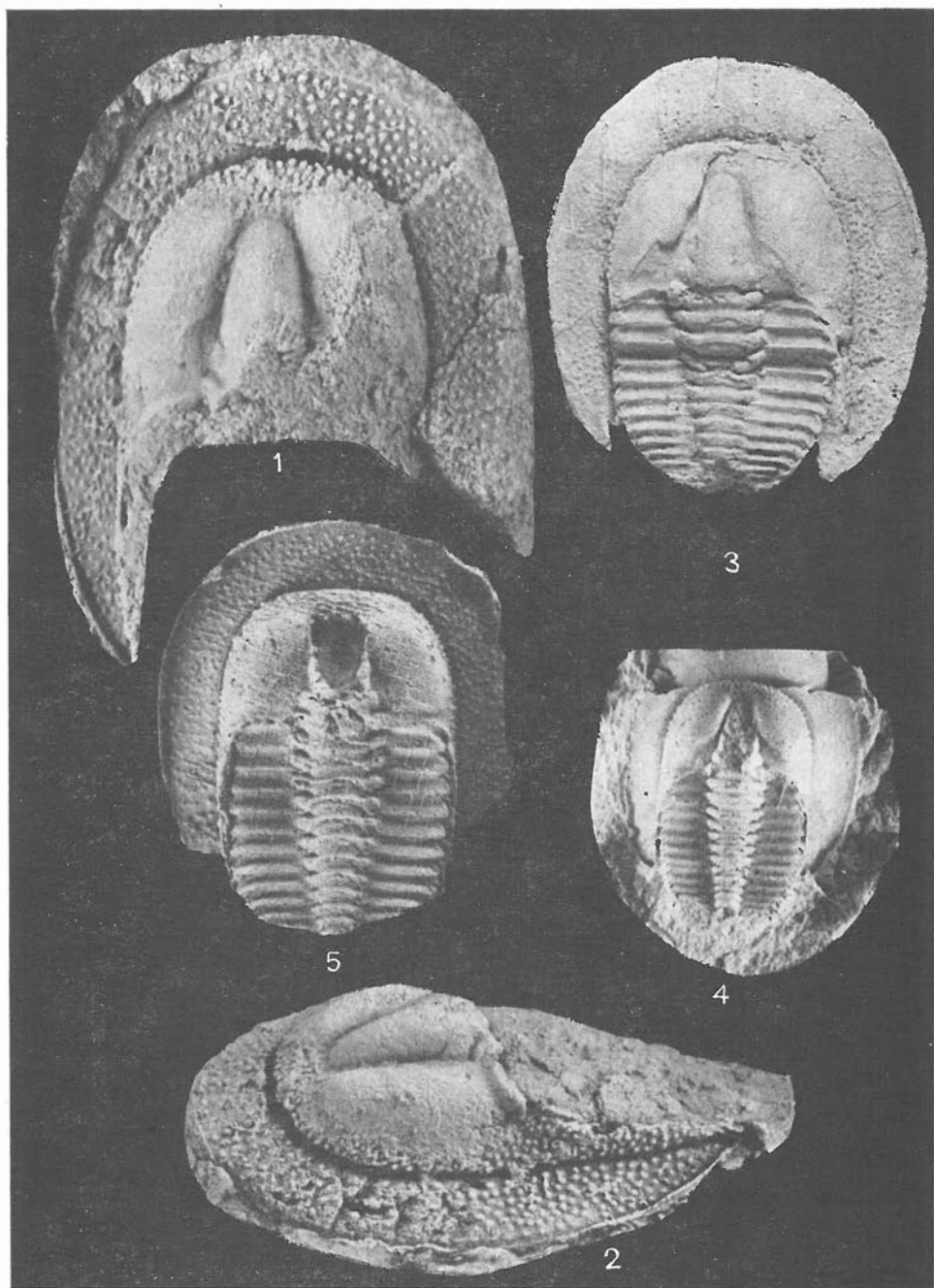
Text-fig. 14



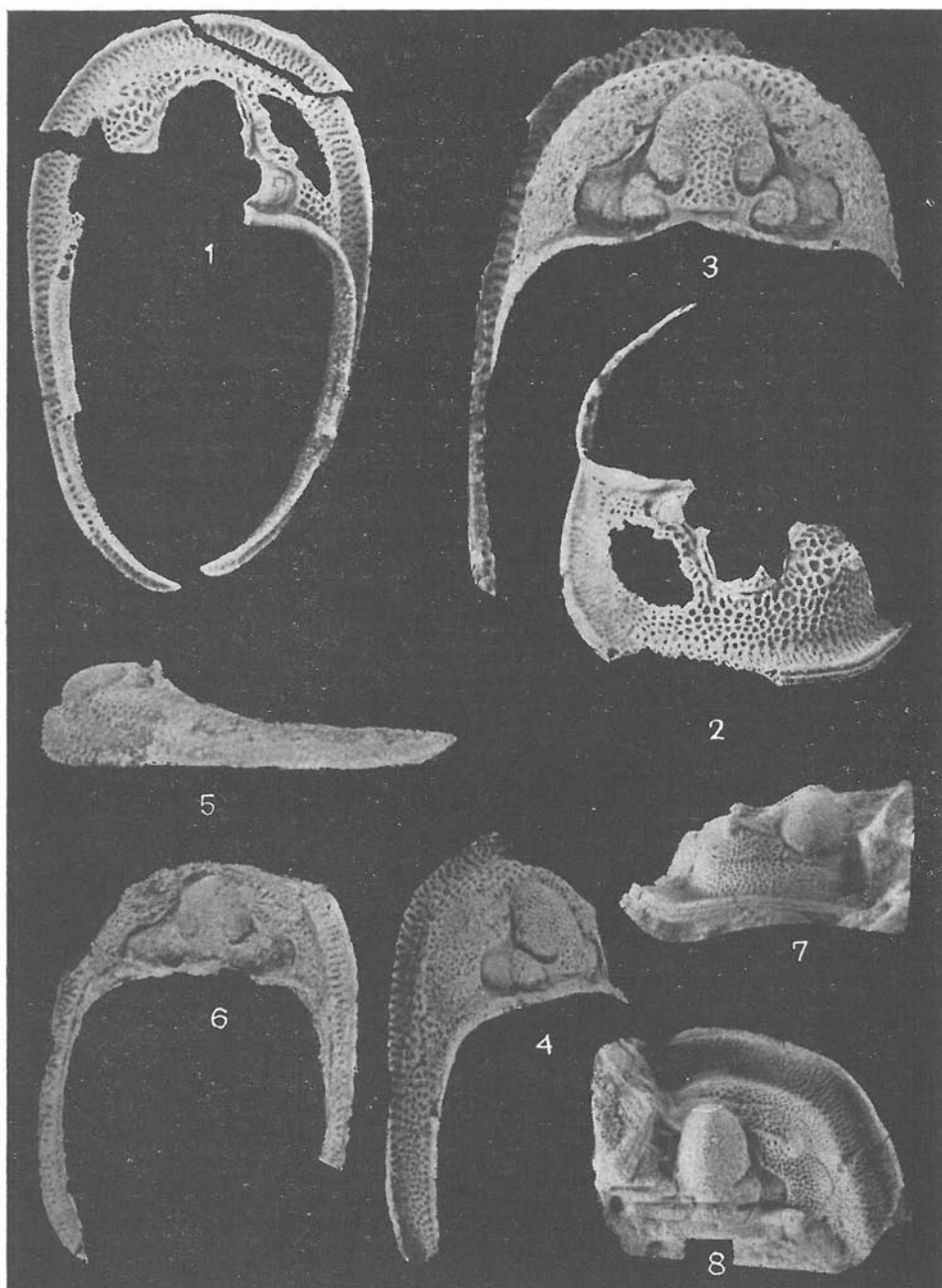
Text-fig. 15



Text-fig. 16



Text-fig. 17



EXPLANATION OF PLATES

PLATE 1

- Figs. 1—4. *Bohemoharpes (Unguloharpes) ungula ungula* (Sternberg, 1933)
Kopanina Formation; Horizon with *Prionopeltis archiaci*. Kosov hill near Beroun, central Bohemia.
1. Nearly entire exoskeleton, partly exfoliated, with a parasitic neoplasm on the brim, dorsal view. Orig. Příbyl and Vaněk, 1981, Pl. 1, fig. 1. (NM, L 18298). x2,5.
 2. Anterior view. x2,5.
 3. Negative cast of incomplete exoskeleton with hypostome "in situ". (ÚÚG, JV 543). x3,0.
 4. Enrolled exoskeleton with hypostome [negative] "in situ". (ÚÚG, JV 629). x2,5.
- Fig. 5. *Bohemoharpes (Unguloharpes) ovatus* (Bouček, 1935)
Kopanina Formation, Horizon with *Cromus beaumonti*. Koda near Beroun, Bohemia.
5. Incomplete cephalon, partly exfoliated (NM, L 18276). x2,5.
- Fig. 6. *Lioharpes (Fritchaspis) ruderalis* (Hawle et Corda, 1847)?
6. Hypostome, probably belonging to this species. Lochkov Formation. Ko-soň near Prague-Radotín. (ÚÚG, JV 874). x5,5.

PLATE 2

- Figs. 1—6. *Bohemoharpes (Unguloharpes) ungula viator* subsp. n.
Kopanina Formation, Horizon with *Cromus beaumonti*. Zadní Kopanina near Prague-Radotín, old abandoned quarry "Zmrzlíky" (Bohemia).
1. Teratological cephalon, partly exfoliated, dorsal view. Paratype. NM, L 18288). x3,0.
 2. Lateral view. x3,0.
 3. Cephalon, partly exfoliated, dorsal view. Holotype. (NM, L 15419). x2,5.
 4. Anterior view. x2,5.
 5. Lateral view. x2,5.
 6. Incomplete cephalon, partly exfoliated, dorsal view. Paratype. (NM, L 2859). x2,5.

PLATE 3

- Figs. 1—4. *Bohemoharpes (Bohemoharpes) hypsipyle* sp. n.
Lochkov Formation. Měňany near Beroun, central Bohemia.
1. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. (NM, L 18297). x3,0.
 2. Ibidem. x2,0.
 3. Anterior view. x2,0.
 4. Lateral view. x2,0.
- Figs. 5—6. *Bohemoharpes (Bohemoharpes) crassifrons* (Barrande, 1846)
Motol Member. Liteň-Formation; Testograptus testis Biozone. Kozel near Beroun (Bohemia).
5. Incomplete cephalon, internal mould, dorsal view. (NM, L 15428). x3,0.
 6. Anterodorsal view. x3,0.

PLATE 4

- Figs. 1—4. *Lioharpes (Lioharpes) venulosus venulosus* (Hawle et Corda, 1847)
Praha Formation, Koněprusy Limestone. Koněprusy near Beroun (Bohemia).
1. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18290). x1,5.
 2. Lateral view. x1,5.
 3. Anterior view. x1,5.
 4. Teratological incomplete cephalon, dorsal view. (NM, L 15423). x2,0.
- Figs. 5—6. *Lioharpes (Lioharpes) venulosus alter* subsp. n.
Praha Formation, Vinařice Limestone. Měňany near Beroun, Homolák hill (Bohemia).

5. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. (NM, L 18295). x1,5.
6. Anterior view. x1,5.

PLATE 5

- Figs. 1—4, 7. *Lioharpes (Lioharpes) sculptus* (Hawle et Corda, 1847)
 Praha Formation, Dvorce-Prokop Limestone (figs. 1—3) and Loděnice Limestone (figs. 4, 7), Damil hill near Beroun (figs. 1—3) and Klukovice near Prague, old abandoned quarry "Červený lom" (figs. 4, 7). (Bohemia).
 1. Dorsal view of incomplete cephalon with some thoracic segments, partly exfoliated. Holotype. Orig. Hawle and Corda, 1847, p. 163. (NM, 212/67). x2,0.
 2. Anterior view. x2,0.
 3. Lateral view. x2,0.
 4. Incomplete cephalon with some thoracic segments, partly exfoliated, dorsal view. (NM, L 15430). x8,0.
 7. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 15431). x5,6.
- Figs. 5—6. *Lioharpes (Lioharpes) venulosus venulosus* (Hawle et Corda, 1847)
 Praha Formation, Koněprusy Limestone. Koněprusy near Beroun, Zlatý kůň hill (Bohemia).
 5. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18283). x1,5.
 6. Anterior view. x1,5.

PLATE 6

- Figs. 1—3. *Kielania (Kielania) novaki* (Prantl et Přibyl, 1954)
 Praha Formation, Dvorce-Prokop Limestone, Prague 5-Hlubočepy (Bohemia).
 1. Incomplete cephalon, partly exfoliated, lateral view. Holotype. Orig. Prantl and Přibyl, 1954, Pl. 9, fig. 1. (NM, L 6120). Slightly retouched. x2,5.
 2. Dorsal view. x2,5.
 3. Anterior view. x2,5.
- Fig. 4. *Kielania (Kielania?) sp. n.*
 Třebotov Formation, Holyně near Prague, old abandoned quarry "Prastav" (Bohemia)
 4. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18296). x2,5.
- Figs. 5—6. *Kielania (Kielania) dorbignyana* (Barrande, 1846)
 Praha Formation, Dvorce-Prokop Limestone, Prague 5-Hlubočepy (Bohemia).
 5. Dorsal view of incomplete cephalon, partly exfoliated. (NM, L 18282). x2,5.
 6. Cephalon, partly exfoliated, dorsal view. (NM, L 18291). x5,0.

PLATE 7

- Figs. 1—3. *Kielania (Kielania) kayseri* (Novák, 1890)
 Choteč Formation, Acanthopyge Limestone. Koněprusy near Beroun, small abandoned quarry between Zlatý kůň and Zadní kobyla hill (Bohemia).
 1. Cephalon, partly exfoliated, dorsal view. (NM, L 2966). x3,0.
 2. Lateral view. x3,0.
 3. Anterior view. x3,0.
- Figs. 4—6. *Lioharpes (Fritchaspis) perneri* (Prantl et Přibyl, 1954)
 Třebotov Formation, upper layers. Holyně near Prague, old abandoned quarry "Prastav" (Bohemia).
 4. Dorsal view of cephalon, partly exfoliated. Paratype. Orig. Prantl and Přibyl, 1954, Pl. 3, fig. 10. (NM, L 6141). x4,0.
 5. Dorsal view of cephalon, partly exfoliated. Holotype. Orig. Prantl and Přibyl, 1954, Pl. 7, fig. 3. (NM, L 6140). x3,0.
 6. The same, anterior view. x3,0.

PLATE 8

- Figs. 1—2. *Bohemoharpes (Unguloharpes) ungula ungula* (Sternberg, 1833)
Kopanina Formation; Horizon with *Prionopeltis archiaci*. Kosov hill near Beroun (Bohemia).
1. Incomplete pathological cephalon with some thoracic segments, partly exfoliated, anterior view. (NM, L 2901). x2,5.
2. Dorsal view. x2,5.
- Fig. 3. *Harpes? dvorcensis* Prantl et Přibyl, 1954
Praha Formation, Dvorce-Prokop Limestone, Prague 4-Podolí (old abandoned quarry).
3. Incomplete cephalon, internal mould, dorsal view. (NM, L 15420). Slightly retouched. x4,0.
- Figs. 4—5. *Kielania (Kielania) obuti* sp. n.
Lochkov Formation, Lochkov Limestone. Kosoř near Prague-Radotín, gorge "Černá rokle" (Bohemia).
4A, 5A. Incomplete cephalon, partly exfoliated, dorsal (4A) and lateral (5A) views. Paratype. (ÚÚG, JV 2166). x2,5.
4B, 5B. Incomplete cephalon, dorsal (4B) and lateral (5B) views. Holotype. (ÚÚG, JV 2166). x2,5.

PLATE 9

- Fig. 1. *Bohemoharpes (Bohemoharpes) naumanni naumanni* (Barrande, 1852)
Motol Member, Liteň Formation; *Cyrtograptus ramosus* — *C. radians* Biozone. Loděnice near Beroun, the road (at "Černidla") from Loděnice to Bubovice (Bohemia).
1. Cephalon with some thoracic segments, partly exfoliated, dorsal view. (NM, L 15433). Slightly retouched. x3,0.
- Fig. 2. *Bohemoharpes (Unguloharpes) buphthalmus* (Bouček, 1935)
Kopanina Formation; Horizon with *Ananaspis fecunda*. Kosov hill near Beroun (Bohemia).
2. Incomplete cephalon, partly exfoliated, dorsal view. Paratype. Orig. Bouček, 1935, Pl. 1, fig. 2. (NM, 25121). Slightly retouched. x3,0.
- Fig. 3. *Harpes? dvorcensis* Prantl et Přibyl, 1954
Praha Formation, Dvorce-Prokop Limestone, Prague 4-Podolí (Dvorce) (Bohemia).
3. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. Orig. Prantl and Přibyl, 1954, Pl. 8, Fig. 5. (NM, CF 1040). Slightly retouched. x1,0.
- Fig. 4. *Kielania (Kielania) obuti* sp. n.
Lochkov Formation, Lochkov Limestone. Kosoř near Prague-Radotín, gorge "Černá rokle" (Bohemia).
4. Brim and fringe, ventral view. Paratype. (ÚÚG, JV 2165). x2,5.
- Fig. 5. *Bohemoharpes (Unguloharpes) bubovicensis* sp. n.
Přídolí Formation, lower layers. Small abandoned quarry at the road from Bubovice to Loděnice near Beroun (Bohemia).
5. Incomplete cephalon, partly exfoliated, dorsal view. Holotype. (ÚÚG JV 534). x2,0.
- Fig. 6. *Helioharpes transiens* (Barrande, 1872)
Srbsko Formation, Roblín Beds, Prague 5-Hlubočepy (Bohemia).
6. Displaced exoskeleton (counterpart), dorsal view. (ÚÚG, ICH 1941). x2,5.

PLATE 10

- Figs. 1—2. *Bohemoharpes (Bohemoharpes) ovatus* (Bouček, 1935)
Kopanina Formation; Horizon with *Cromus beaumonti*. Kosov hill near Beroun (Bohemia).
1. Cephalon, partly exfoliated, dorsal view. (NM, L 18287). x2,5.
2. Anterior view. x2,5.
- Fig. 3. *Eoharpes benignensis* (Barrande, 1872)
Dobrotivá Formation. Svatá Dobrotivá (Zaječov), western Bohemia.

3. Incomplete displaced exoskeleton of young specimen, internal mould, dorsal view. (NM, L 2833). x10,0.

Figs. 4—6. *Reticuloharpes reticulatus* (Hawle et Corda, 1847)
Suchomasty Limestone (lower layers). Koněprusy near Beroun, central Bohemia.

4. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 15429). x3,5.

5. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 18294). Slightly retouched. x2,0.

6. Incomplete cephalon, partly exfoliated, dorsal view. (NM, L 15427). x2,0.

