A C T A P A L A E O N T O L O G I C A P O L O N I C A
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THE CLASSIFICATION AND EVOLUTION OF THE HETEROSTRACI

Abstract. — An outline classification is given of the Heterostraci, with diagnoses of the following orders and suborders: Astraspidiformes, Eriptychiiformes, Cyathaspidiformes (Cyathaspidida, Poraspidida, Ctenaspidida), Psammosteiformes (Tesseraspidida, Psammosteida), Traquairaspidiformes, Pteraspidiformes (Pteraspidida, Doryaspidida), Cardipeltiformes and Amphiaspidiformes (Amphiaspidida, Hibernaspidida, Eglonaspidida). It is shown that the various orders fall into four main evolutionary lineages — cyathaspid, psammosteid, pteraspid and amphiaspid, and these are traced from primitive tessellated forms. A tentative phylogeny is proposed and alternatives are discussed.

INTRODUCTION

Since 1858, when Huxley demonstrated that in the histological structure of their dermal bone *Cephalaspis* and *Pteraspis* were quite different from one another, it has been recognized that there were two distinct groups of ostracoderms for which Lankester (1868—70) proposed the names Osteostraci and Heterostraci respectively. Although these groups are generally considered to be related to one another, Lankester believed that "the Heterostraci are at present associated with the Osteostraci because they are found in the same beds, because they have, like *Cephalaspis*, a large head shield, and because there is nothing else with which to associate them".

In 1889, Cope united these two groups in the Ostracodermi which, together with the modern cyclostomes, he placed in the Class Agnatha, and although this proposal was at first opposed by Traquair (1899) and Woodward (1891*b*), subsequent work has shown that it was correct as both the Osteostraci and the Heterostraci were agnathous. A third group of ostracoderms — the anaspids — was first described by Traquair (1899) from Scotland, and Kiaer (1924) when describing members of this group from Norway, proposed a division of the Agnatha into two different groups, this time on the basis of the number of nasal sacs present. Those with one nasal sac — the Monorhina — included the Osteostraci, Anaspida and modern cyclostomes, while those with two sacs — the Diplorhina — included the Heterostraci and Thelodonti (the latter having been first fully described by Traquair, 1899).

In his detailed description of the cephalaspids of Spitzbergen and Great Britain, Stensiö (1927, 1932) also divided the ostracoderms into two main groups, but this time on different criteria. He used the terms Pteraspidomorphi to include the Heterostraci and the myxinoid cyclostomes, and Cephalaspidomorphi to include the Osteostraci, Anaspida and petromyzontid cyclostomes, thus suggesting a diphyletic origin for the cyclostomes.

The classifications produced by Kiaer and Stensiö are both used at the present time by different authors, although they are mutually exclusive, but the fossil evidence would appear to lend greater support to Kiaer's views. Stensiö's classification which was amplified in 1958, and accepted by Lehman (1959) and Jarvik (1960), postulates the presence in the Heterostraci of a single nasal sac comparable to that found in the myxinoid cyclostomes, thus suggesting that the Heterostraci may have been ancestral to the myxinoids. However, Kiaer's contention that the Heterostraci had double nasal sacs seems to have been accepted by the majority of workers on the Agnatha (Kiaer & Heintz, 1935; Wills, 1935; White, 1935, 1961; Obruchev, 1945, 1949; Balabai, 1948, 1956; Wängsjö, 1952; Watson, 1954; Tarlo, 1958, 1961b; Heintz, 1962).

In consequence, the Heterostraci and Thelodonti must be considered entirely separately from the other Agnatha, and it is here proposed to give an outline classification of the Heterostraci and to discuss the main features of their evolution. The Thelodonti will be discussed in a later work.

CLASSIFICATION OF THE HETEROSTRACI

The Heterostraci can be divided into different groups on the number and arrangement of the bony plates making up the carapace, and it was Traquair (1899) who first recognized that on this basis it was possible to distinguish three families[1] — the Pteraspidae, the Drepanaspidae, and the Psammosteidae. Subsequently, Kiaer (1932) divided the Heterostraci into three main suborders — the Pteraspida, the Psammosteida (syn. Drepanaspida), and the Cyathaspida, which latter he further divided into the tribes Cyathaspidei and Poraspidei. This classification was accepted by White (1935) who however emended it slightly, recognizing a fourfold division of the Heterostraci into the families Palaeaspidae (syn. Poraspidei Kiaer), Cyathaspidae (syn. Cyathaspidei Kiaer), Ptera-

[1] In Britain and America (White, 1935, 1946; Romer, 1945; Dineley, 1953; Denison, 1953, 1960) the Heterostraci have been divided into families, whilst in Scandinavia and Russia (Kiaer, 1932; Kiaer & Heintz, 1935; Obruchev, 1938, 1941; Berg, 1940, 1955; Stensiö, 1958), these divisions are usually recognized as either suborders or orders. In the present work they will be taken as orders.

spidae, and Drepanaspidae (syn. Psammosteidae) for which he gave diagnoses. (It should be noted that in these classifications Kiaer did not take into account the family Astraspidae proposed by Eastman (1917), and White also omitted this group as well as the Cardipeltidae proposed by Bryant (1933)).

In 1938, Obruchev introduced a new suborder — the Amphiaspida, with a single family — the Amphiaspidae, and in 1941 he produced a list of the divisions he recognized, and this is given below:

Order Heterostraci
Suborders: Cyathaspida
Pteraspida
Amphiaspida
Psammosteida
Families: Psammosteidae
Drepanaspidae
Weigeltaspidae?
Cardipeltidae

Romer (1945) recognized six divisions in the Heterostraci — the families Astraspidae?, Poraspidae, Cyathaspidae, Pteraspidae, Drepanaspidae, and Amphiaspidae, and then White (1946) introduced another new family which he called the Phialaspidae. Subsequently however it was recognized (White & Toombs, 1948) that *Phialaspis* Wills, 1935 was congeneric with *Traquairaspis* Kiaer, 1932, and hence it was necessary to use Kiaer's name and call the family the Traquairaspidae. Dineley (1953) proposed a further new family — the Corvaspidae, and in the same year Denison proposed a three-fold division of the family Cyathaspidae into the subfamilies Poraspinae, Ctenaspinae and Cyathaspinae.

In 1955, Berg produced a much fuller classification, together with diagnoses, his classification being as follows:

Class Pteraspides
Orders: Astraspiformes
Psammosteiformes
Families: Psammosteidae
Aspidosteidae
Cardipeltidae
Weigeltaspidae
Tesseraspidae
Orders: Pteraspiformes
Phialaspiformes
Cyathaspiformes
Suborder Cyathaspidoidei
Families: Cyathaspidae
Tolypelepidae
Diplaspidae
Traquairaspidae
Suborder Poraspidoidei

Families: Poraspidae
Americaspidae
Dinaspidae
Dictyonaspidae
Anglaspidae
Ctenaspidae
Order Amphiaspiformes

A further and more detailed classification was given by Stensiö (1958) in which he included a considerable amount of new morphological information on the cyathaspids and pteraspids, and his scheme is outlined below:

Subclass Pteraspidomorphi
Superorder Heterostraci
Orders: Astraspida
Eriptychida
Drepanaspida
Pteraspida
Traquairaspida
Cyathaspida
Corvaspida
Amphiaspida
Cardipeltida
Turiniida

In his work however, Stensiö did not discuss the eriptychiids, and there seems to be no real justification for his inclusion of the turiniids as they are thelodonts (see also Westoll, 1960). In addition, for his information on the groups other than the pteraspids and cyathaspids Stensiö was largely obliged to rely on the literature, and was consequently unable to take into account the results of current studies on them by other workers.

It is, however, now possible to amplify Stensiö's work, and the following section provides diagnoses of the main divisions now recognized within the Heterostraci, together with a short disussion of each.

DESCRIPTIONS

Order **ASTRASPIDIFORMES** Berg, 1940
(syn. Astraspida Stensiö, 1958)

Family **Astraspididae** Eastman, 1917
Type genus and species: *Astraspis desiderata* Walcott, 1892

Diagnosis. — Carapace composed of discrete polygonal tesserae produced by cyclomorial growth, ornamented by rounded crenulated tubercles. Pineal area present. Three longitudinal dorsal ridges; median

ridge extending from posterior margin to pineal area, two lateral ridges extending only two thirds of the way. Lateral margins of carapace consisting of row of strongly angulated ridge plates. Histological structure: basal aspidin lamellar layer, middle layer of spongy aspidin, external aspidin tubercles surmounted by enamel-like substance.

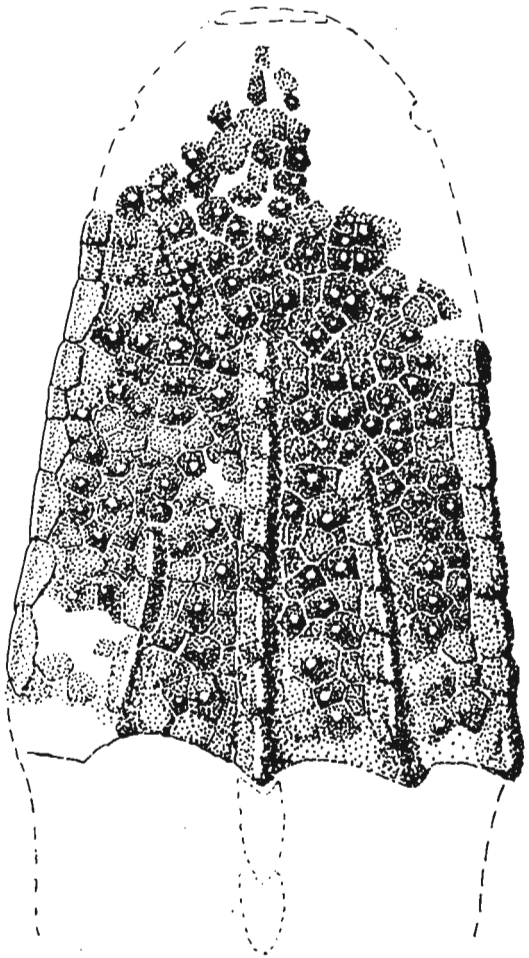

Fig. 1. — *Astraspis desiderata* Walcott, dorsal carapace composed of discrete cyclomorial tesserae and lateral ridge plates (from photograph published by Eastman, 1917, pl. 12, fig. 6).

Remarks. — *Astraspis desiderata* was originally described by Walcott (1892) on the basis of a number of fragmentary plates, although in a footnote he noted the discovery of a natural cast of an almost entire dorsal carapace. This was figured by Eastman (1917) who erected the new family Astraspidae for the reception of this form. The material was redescribed by Bryant (1936) with particular reference to its histology.

More recently, Ørvig (1958) described the new genus *Pycnaspis* belonging to this order, in which he demonstrated the presence of short dentine tubules at the junction of the enamel-like caps of the tubercles and the underlying aspidin.

Order **ERIPTYCHIIFORMES**[2]
(syn. Eriptychiida Ørvig. 1958, Eriptychida Stensiö, 1958)

Family **Eriptychiidae** nov.

Type genus and species: *Eriptychius americanus* Walcott, 1892

Diagnosis. — Carapace largely composed of discrete polygonal tesserae with elongated tubercles. Row of lateral ridge plates, one of which has deep notch forming branchial opening. Fulcral plates or scales present. Histological structure: basal lamellar and middle spongy aspidin layers surmounted by dentine tubercles.

Remarks. — *Eriptychius americanus* was originally described by Walcott (1892) and was reinvestigated by Bryant (1936) who demonstrated that it differed histologically from the contemporary *Astraspis*, while Ørvig (1958) showed the presence of the notched branchial plates. The eriptychiids are distinguished from the astraspids on the differences in the histological structure of their dermal armour. Bryant noted that the eriptychiids shared a number of close similarities with the later psammosteids, but as these are in fact common to most primitive heterostracans, it could just as well be argued that *Eriptychius* was a primitive representative of the traquairaspids or cyathaspids as of the psammosteids. For this reason it is considered best to retain the Eriptychiiformes as a separate order.

Order **CYATHASPIDIFORMES** Berg, 1940
(syn. Cyathaspida Kiaer, 1930)

Suborder **Cyathaspidida** Kiaer, 1930, emend.
(syn. Cyathaspidei Kiaer, 1930, Cyathaspidae Kiaer, 1932, emend. White, 1935, Cyathaspidoidei Berg, 1940, Cyathaspinae Zych, 1931)

Family **Cyathaspididae** Kiaer, 1932

Type genus and species: *Cyathaspis banksii* (Huxley & Salter, 1856).

Diagnosis. — Carapace composed of four major plates — dorsal, ventral and paired laterals. Dorsal plate superficially divided into four parts

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[2] Following Berg (1940, 1955) all orders are given the suffix „-iformes" in this work, for the sake of uniformity.

— anterior rostral, central and two lateral. Pineal macula present on central part. Ornamentation of longitudinal dentine ridges.

Remarks. — The genus *Cyathaspis* was erected by Lankester (1864) on a dorsal shield, which had previously been described and figured by

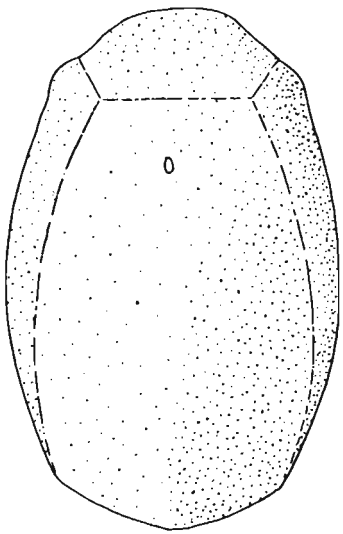

Fig. 2. — *Archegonaspis integer* (Kunth), dorsal plate showing pineal macula, and superficial division into rostral, central and lateral areas (after Kiaer, 1932, fig. 3).

Huxley & Salter (1856). This suborder includes all the earliest representatives of the Cyathaspidiformes, a number of which show traces of primitive tesserae, to a greater or lesser extent. Although the carapace is formed of four major plates, these are clearly the result of fusion of more numerous elements. The classic accounts of the cyathaspids are given by Kiaer (1932), and Kiaer & Heintz (1935), while more recently Stensiö (1958) has added considerably to our knowledge of the group. Kiaer (1932) divided the cyathaspids (*s.s.*) into the following families: Cyathaspidae, Tolypelepidae, Diplaspidae, and Traquairaspidae, but the Traquairaspidae are now known to represent a separate order, and the other families require further revision which is beyond the scope of the present paper.

Suborder **Poraspidida** new rank

(syn. Poraspidei Kiaer, 1930, Palaeaspidae White, 1935, Palaeaspinae Zych, 1931, Poraspidoidei Berg, 1940, Poraspinae Denison, 1953)

Family **Poraspididae** Kiaer, 1932

Type genus and species: *Poraspis sericea* (Lankester, 1873)

Diagnosis. — Carapace composed of four main plates — dorsal, ventral and two lateral branchials. Dorsal plate not superficially divided into

areas, although these can still be recognized from the arrangement of the ornament of longitudinal dentine ridges. Small suborbital plates and oral plates known. Squamation of large deep scales on trunk, and small scales on tail.

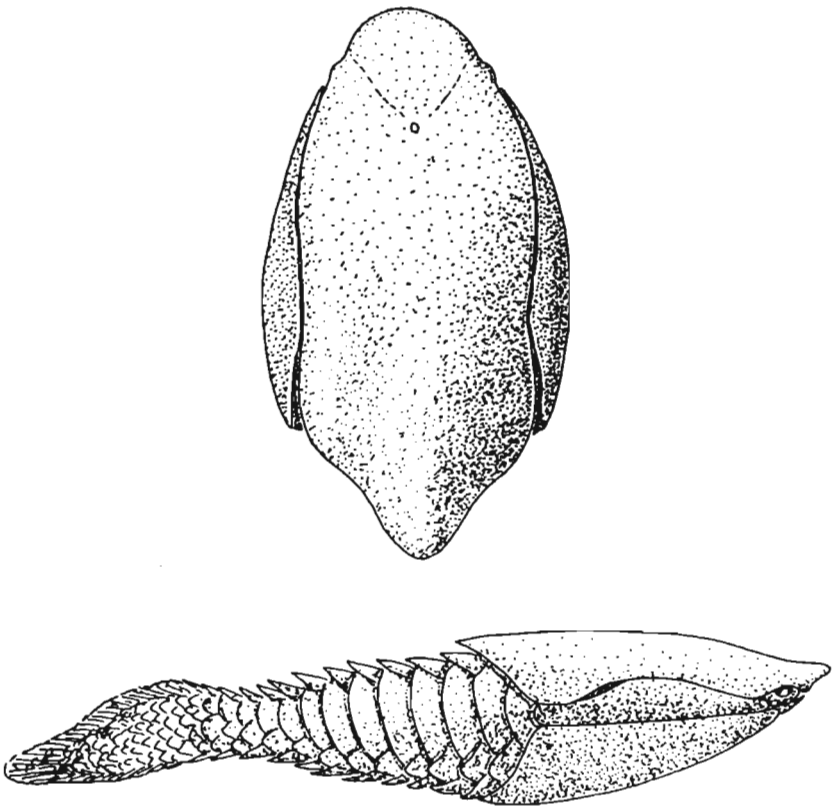

Fig. 3. — *Anglaspis heintzi* Kiaer, upper figure: dorsal carapace showing dorsal plate and paired lateral branchials; lower figure: lateral view of entire animal showing squamation and hypocercal tail (after Kiaer, 1932, fig. 11).

Remarks. — This group represents the main development of the Cyathaspidiformes which flourished during the early part of the Lower Devonian. Within this suborder there is no longer any direct evidence of the derivation of the carapace from the fusion of more numerous small units. The genera of the Poraspidida generally have a very convex ventral plate and comparatively flat dorsal plate, suggesting that these forms were nectonic rather than benthonic (see Obruchev, 1959), although some specimens of *Anglaspis* show a certain amount of abrasion of their ventral surface.

Kiaer (1932) divided the poraspids into the following families: Poraspidae, Palaeaspidae, Dinaspidae, Dictyonaspidae, Anglaspidae and Cte-

naspidae, but these are in need of a detailed revision which is beyond the scope of the present work.

Suborder **Ctenaspidida** Zych, 1931
(syn. Ctenaspinae Denison, 1953)

Family **Ctenaspididae** Kiaer, 1932

Type genus and species: *Ctenaspis dentata* Kiaer, 1930

Diagnosis. — Carapace composed of two major plates — branchio--dorsal and ventral. Oral, post-oral and suborbital plates known.

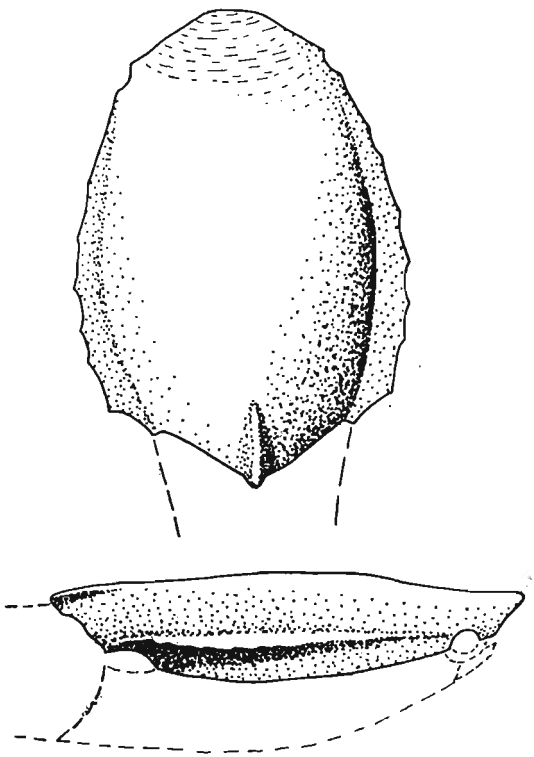

Fig. 4. — *Ctenaspis dentata* Kiaer, dorsal carapace composed of single unit, with lateral flange over branchial region; lower figure lateral view (after Stensiö, 1958, fig. 176).

Remarks. — Although *Ctenaspis* was originally described by Kiaer (1930), it was not until Stensiö (1958) recognized that the branchials were fused with the dorsal plate, that this type of carapace was known to exist in the Cyathaspidiformes. Another cyathaspid, *Allocryptaspis* from N. America with the same type of carapace, was independently described by Denison (1960). Whether or not these two genera are directly related, they nevertheless show a morphological stage which is

quite distinct from that of the normal cyathaspids. The fact that their carapace is composed of only two main plates could be used as a basis for separate ordinal status, but since their relationship to the normal cyathaspids is quite clear, it is felt that they should be retained within the order Cyathaspidiformes as a suborder. Like the poraspids the ctenaspids have a very convex ventral plate.

Order **PSAMMOSTEIFORMES** Berg, 1940
(syn. Drepanaspida Stensiö, 1958)

Suborder **Tesseraspidida** nov.

Diagnosis. — Carapace composed of independent polygonal plates or tesserae which may be fused to form discrete larger plates. In forms

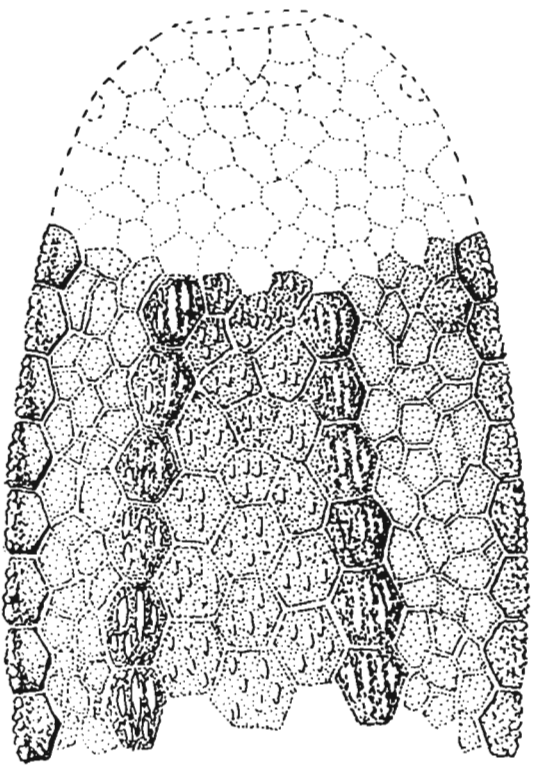

Fig. 5. — *Tesseraspis tessellata* Wills, dorsal carapace showing organization of tesserae into regions foreshadowing arrangement found in later psammosteids.

where fusion has not taken place the tesserae are differentiated into separate areas foreshadowing such plates. In all forms large areas of the carapace are still composed of discrete tesserae, and the full complement of plates found in the later psammosteids is not achieved.

Family **Tesseraspididae** Berg, 1955
Type genus and species: *Tesseraspis tessellata* Wills, 1935

Diagnosis. — Carapace composed of discrete tesserae differentiated into separate areas foreshadowing dorsal and ventral median plates, branchials and fields of tesserae of later forms. Ornamentation of crenulated dentine tubercles which vary in different parts of the carapace.

Family **Weigeltaspididae** Brotzen, 1933
Type genus and species: *Weigeltaspis alta* Brotzen, 1933

Diagnosis. — Long narrow dorsal median plate (originally erroneously described as branchial), rectangular postorbital, orbital, arched branchial plate and fields of tesserae. Rostral area composed of tesserae. Ornamentation of large crenulated, striated, well spaced dentine tubercles.

Family **Corvaspididae** Dineley, 1953
(syn. Corvaspida Stensiö, 1958)
Type genus and species: *Corvaspis kingi* Woodward, 1934

Diagnosis. — Dorsal and ventral median plates, orbital, branchial and ? post-orbital plates. Fields of tesserae. Ornamentation of short longitudinal dentine ridges generally arranged as superficial synchronomorial tesserae.

Remarks. — Wills (1935) described *Tesseraspis* and suggested that it had affinities to the psammosteids. This view has been accepted by Gross (1937), Tarlo (1957, 1961*a*), Stensiö (1958) and Ørvig (1961), although Denison (1956) claimed that it was a cephalaspid and Obruchev (1961*b*) has denied that it was a psammosteid.

The specialized heterostracan *Corvaspis* was originally described as a cyathaspid by Woodward (1934), but Dineley (1953) showed that this was not so, and created a new family Corvaspidae for its reception, which Stensiö (1958) raised to ordinal status. It was later suggested (Tarlo, 1960) that *Corvaspis* could be retained within the psammosteids. It is here included in a separate family within the Tesseraspidida, which is a major division of the Psammosteiformes.

Weigeltaspis is also here included in a separate family within the Tesseraspida. This genus was originally described by Brotzen (1933) as representing a new group of heterostracans which showed some relationship to the psammosteids, and although accepted as a psammosteid by Wills (1935), Gross (1937), Obruchev (1941), Berg (1955) and Tarlo (1957, 1961a), other authors such as Denison (1956) and Ørvig (1961) have considered that it is not possible to tell whether or not this is so.

Work now in progress however, confirms that both *Tesseraspis* and *Weigeltaspis* belong in the Psammosteiformes.

Suborder **Psammosteida** Kiaer, 1932

(syn. Psammosteidae Traquair, 1896, Drepanaspidae Traquair, 1899, emend., White, 1935)

Diagnosis. — Carapace composed of twelve main plates — dorsal and ventral median plates, rostral plate, pineal plate, paired orbitals, post-

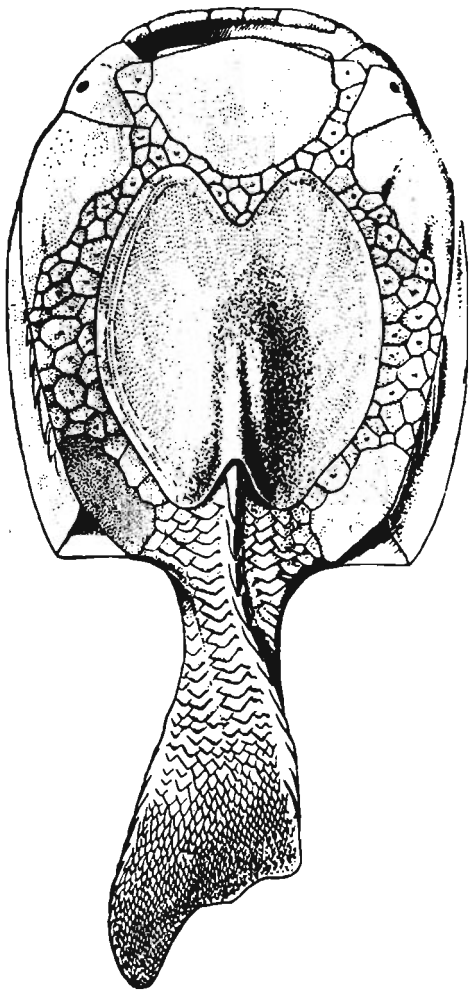

Fig. 6. — *Drepanaspis gemundenensis* Schlüter, dorsal view showing median rostral and dorsal plates, and paired orbital, post-orbital, branchial and cornual plates; note fields of tesserae separating the median plates from the laterals (after Obruchev, 1943, fig. 1).

orbitals, branchials and cornuals. Median and lateral plates separated by zones of polygonal tesserae (fields of tesserae). Oral plates with well developed oral tooth lamellae present. Ornamentation of rounded crenulated dentine tubercles.

Family **Drepanaspididae** Traquair, 1899

Type genus and species: *Drepanaspis gemundenensis* Schlüter, 1887

Diagnosis. — Branchial plates long and narrow, post-orbitals with posterior projection median to branchial plate.

Family **Psammolepididae** nov.

Type genus and species: *Psammolepis paradoxa* (Agassiz, 1845)

Diagnosis. — Branchial plates as wide as long, post-orbital plate same length as branchial, which it overlaps posteriorly. Ventral median plate generally with anterior portion showing concentric zones of growth, built up posteriorly by superficial synchronomorial tesserae. In later species entire plate covered by superficial synchronomorial tesserae.

Family **Pycnosteidae** nov.

Type genus and species: *Pycnosteus palaeformis* Preobrajenski, 1911

Diagnosis. — Branchial plate as wide as long, ventral median plate with deep persistent posterior notch. No superficial tesserae present on median plates, except in *Tartuosteus* (see Obruchev, 1961 *a*).

Family **Psammosteidae** Traquair, 1896

Type genus and species: *Psammosteus maeandrinus* Agassiz, 1845

Diagnosis. — Branchial plate short and wide, post-orbital plate long and narrow. Ventral median plate long and narrow, covered by superficial cyclomorial tesserae.

Family **Aspidosteidae** Berg, 1955

Type genus and species: *Aspidosteus heckeri* Obruchev, 1941

Diagnosis. — Branchial plates long and narrow, strongly arched from side to side. Dermal armour without dentine tubercles, but strengthened by pleromic dentine.

Remarks. — The best known genus of this group is *Drepanaspis* which was first fully described and reconstructed by Traquair (1899, 1903, 1905). The most recent reconstruction of this form has been produced by Obruchev (1943). Traquair (1896) in his study of the Scottish

psammosteids first introduced the Psammosteidae as the name of a group, which he was later (1899) able to show belonged to the Heterostraci. At the same time (1899) he introduced the Drepanaspidae which he kept separate from the Psammosteidae, but subsequent authors have used these terms synonymously, with the exception of Obruchev (1941). The valid term for the suborder is the Psammosteida, but this can be divided into five main families: the Drepanaspididae Traquair, 1899, Psammolepididae nov., Pycnosteidae nov., Psammosteidae Traquair, 1896, and Aspidosteidae Berg, 1955.

The Psammosteida show an important radiation in Middle and Upper Devonian times, and although all the plates of the carapace remain homologous, the morphological changes that take place are considerable. These changes and their significance are discussed below in the section on evolution.

Unlike most other heterostracans, those belonging to this suborder have a mouth which is situated dorsally and in consequence it might be expected that they would have distinctive oral plates. It is true that the oral plates in the Psammosteida have an extension which curves over anteriorly from the ventral surface to the dorsal, but from Heintz (1962) it is now evident that these dorsal extensions of the oral plates are homologous to the oral tooth lamellae found in the pteraspids and cyathaspids. Thus this type of oral plate appears to be a common feature of most orders of Heterostraci. In the psammosteids, which have a very wide mouth, these plates have been greatly increased in width, but their homology to those found in the pteraspids is indisputable, and they can in no way be considered to represent specialized post-oral covers as was suggested by White (1935).

Order **TRAQUAIRASPIDIFORMES**

(syn. Phialaspidae White, 1946, Phialaspiformes Berg, 1955, Traquairaspida Stensiö, 1958)

Family **Traquairaspididae** Kiaer, 1932

Type genus and species: *Traquairaspis campbelli* (Traquair, 1913)

Diagnosis. — Carapace composed of eight main plates — rostral, pineal, dorsal and ventral median plates, paired orbital and branchiocornual plates. Branchial opening completely enclosed in branchio-cornual plates.

Remarks. — Representatives of this order, of which only two species are known — *Traquairaspis campbelli* (Traquair) and *Traquairaspis symondsi* (Lankester) — were originally variously assigned to the cyathaspids and psammosteids, but White (1946) was able to demonstrate

that they represented a separate grouping of the Heterostraci for which he proposed the new family Phialaspidae. Since *Phialaspis* Wills, 1935 is a synonym of *Traquairaspis* Kiaer, 1932, the name of the order was accordingly changed to Traquairaspida by Stensiö (1958). This group in many respects is intermediate between the psammosteids and the pteraspids, and this relationship is discussed below in the section on evolution.

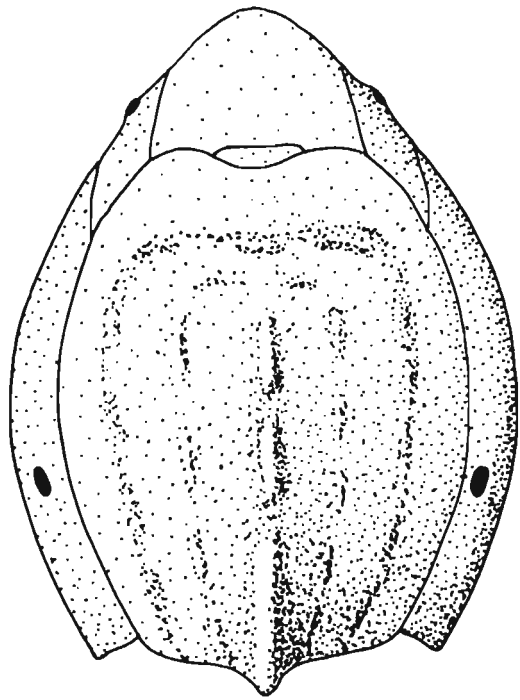

Fig. 7. — *Traquairaspis campbelli* (Traquair) — (syn. *T. pococki* (White)); dorsal carapace showing median rostral, pineal and dorsal plates, and paired orbital and composite branchio-cornual plates (after White, 1946, fig. 40).

Order **PTERASPIDIFORMES** Berg, 1940

Suborder **Pteraspidida** Kiaer, 1932, emend.

Family **Pteraspididae** Woodward, 1891

Type genus and species: *Pteraspis rostrata* (Agassiz, 1835)

Diagnosis. — Carapace composed of ten main plates — rostral, pineal, dorsal and ventral median plates, paired orbital branchial and cornual plates. Frequently with post-oral and lateral plates, together with normal oral plates.

Remarks. — The pteraspids were first described by Agassiz in 1835 under the name *Cephalaspis.* These forms were subsequently separated from typical cephalaspids and Huxley (1858) demonstrated that they were quite dissimilar in the microscopic structure of their armour.

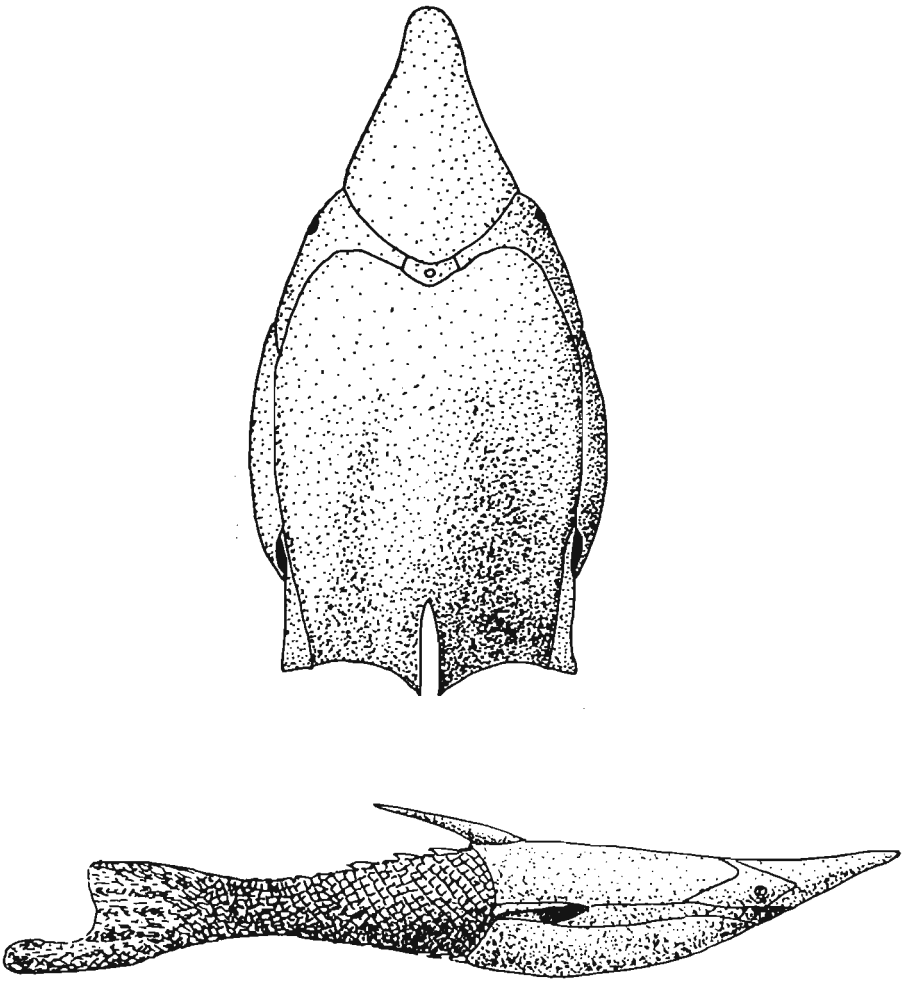

Fig. 8. — *Pteraspis rostrata* (Agassiz), dorsal view of carapace showing median rostral, pineal and dorsal plates, and paired orbital, branchial and cornual plates; lower figure: lateral view of entire animal (after White, 1935, figs. 81, 84).

The classic work on the pteraspids was carried out by Kiaer (1928) and White (1935). More recently Stensiö (1958) has considerably advanced our knowledge of this order, in consequence of which it has been necessary to revise the previous classifications used for this group (see Tarlo, 1961 *b*).

Suborder **Doryaspidida** N. Heintz

Family **Doryaspididae** N. Heintz

Type genus and species: *Doryaspis nathorsti* (Lankester, 1884)

Diagnosis (information supplied by Dr. N. Heintz). — Full pteraspid complement of plates, except that oral plates absent. Mouth dorsal with a very long narrow pseudo-rostrum, formed from one of ventral elements of carapace. Rostral plate transversely truncated anteriorly. Paired cornual plates very short and wide, forming two slender lateral projections. Ornament consisting of characteristic network of stellate ridges.

Remarks. — Lankester (1884) first described remains of this form which were characterized by their ornamentation. These were later shown by Woodward (1891 *a*) to belong to a pteraspid, and White (1935) placed this in the new genus *Doryaspis* Kiaer M. S. Further work is in progress on this form by N. Heintz, and a full description will be published in the near future. The nature of the mouth region with the development of the pseudo-rostrum possibly from a median post-oral unit or a highly specialized median oral plate, shows that *Doryaspis* clearly represents a highly specialized side-branch of the Pteraspidiformes, which warrants at least subordinal distinction. This form is likely to have been a surface feeder and not benthonic as the normal pteraspids are considered to have been, although it should be noted that even the normal pteraspids are considered by Obruchev (1959) to have been at least nectonic.

Order **CARDIPELTIFORMES**

(syn. Cardipeltida Stensiö, 1958)

Family **Cardipeltidae** Bryant, 1933

Type genus and species: *Cardipeltis wallacii* Branson & Mehl, 1931

Diagnosis. — Carapace comprises large dorso-branchial plate, together with composite branchials and tesserae. Ventral part of carapace probably composed of tesserae.

Remarks. — This unusual form was first described by Branson and Mehl (1931) as part of a cyathaspid shield, with an orbital notch at either side. These notches were re-interpreted by Bryant (1933) as branchial openings, and in the same work he proposed the new family Cardipeltidae. Obruchev (1941) described *Aspidosteus* as a member of the Cardipeltidae, which family he included in the suborder Psammosteida, and orientated the wider part of the *Cardipeltis* dorsal carapace anteriorly to bring it in line with the psammosteids. Denison (1953) showed that this orientation of *Cardipeltis* was incorrect, because of the direction of the branchial openings, and subsequently Stensiö (1958)

redescribed this form and gave a tentative reconstruction of the complete dorsal carapace, a modified version of which is shown in text-fig. 9. At the same time however, Stensiö included *Aspidosteus* in the order,

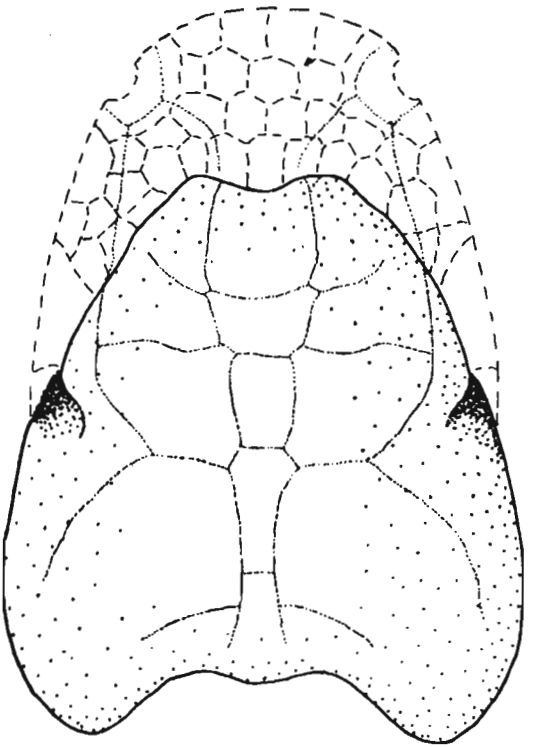

Fig. 9. — *Cardipeltis wallacii* Branson & Mehl, reconstruction of dorsal carapace showing compound dorso-branchial plate, lateral ridge plates and tesserae (modified after Stensiö, 1958, fig. 184A).

but this time orientated so that the widest part of its carapace was posterior. As already noted above, *Aspidosteus* is a psammosteid, and its resemblance to *Cardipeltis* when inverted has no bearing on the classification of either.

Order **AMPHIASPIDIFORMES** Berg, 1940

Suborder **Amphiaspidida** Obruchev, 1938

Family **Amphiaspididae** Obruchev, 1938

Type genus and species: *Amphiaspis argos* Obruchev, 1938

Diagnosis (supplied by Prof. D. Obruchev). — Head and fore-part of trunk covered by an undivided dorso-ventral armour. No branchials or cornuals have been observed. No rostrum. Orbits at the anterior margin of carapace. Mouth ventral. Ventral side flat, dorsal convex. Surface covered with small dentine tubercles.

Remarks. — *Amphiaspis* was originally described by Obruchev in the Kureyka region of N. W. Siberia. From the same fauna he described *Hibernaspis macrolepis* which although originally considered to be a cyathaspid, is now known to belong to the same group as *Amphiaspis* (Obruchev, 1959). Several other related genera are known, the names of which are listed by Obruchev (1958), but their description is still awaited.

Suborder **Hibernaspidida** Obruchev

Family **Hibernaspididae** Obruchev, 1938

Type genus and species: *Hibernaspis macrolepis* Obruchev, 1938

Diagnosis (supplied by Prof. D. Obruchev). — Flattened heterostracans with a subtriangular head and trunk armour, consisting of fused dorsal, ventral and paired branchial plates. Triangular mouth adjoining the anterior margin ventrally. Orbits dorsally near anterior margin. Surface covered with wide and flat dentine ridges, 5—8 cm.

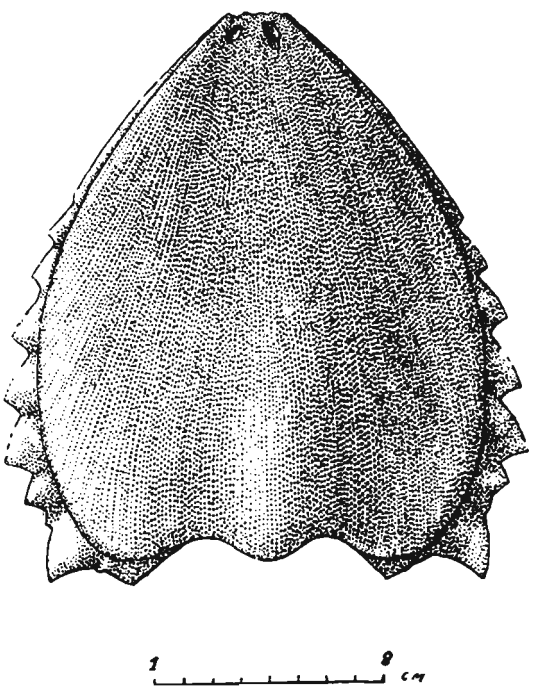

Fig. 10. — *Hibernaspis macrolepis* Obruchev, dorsal view of carapace showing anterior position of eyes and terminal mouth (after Obruchev, 1959, fig. 1).

Suborder **Eglonaspidida** nov.

Family **Eglonaspididae** nov.

Type genus and species: *Eglonaspis rostrata* Obruchev, 1959

Diagnosis. — Blind amphiaspid, with circular hole in mid-line near posterior margin of dorsal carapace into which dorsal spine may have been inserted. Mouth at end of tubular anterior extension to carapace.

Remarks. — The name of this form was listed by Obruchev (1958) and in 1959 he figured the carapace, but only with the generic name. This anomalous heterostracan, although clearly belonging to the amphiaspids in the broadest sense, is such a highly specialized form that it is considered necessary to give it at least subordinal status.

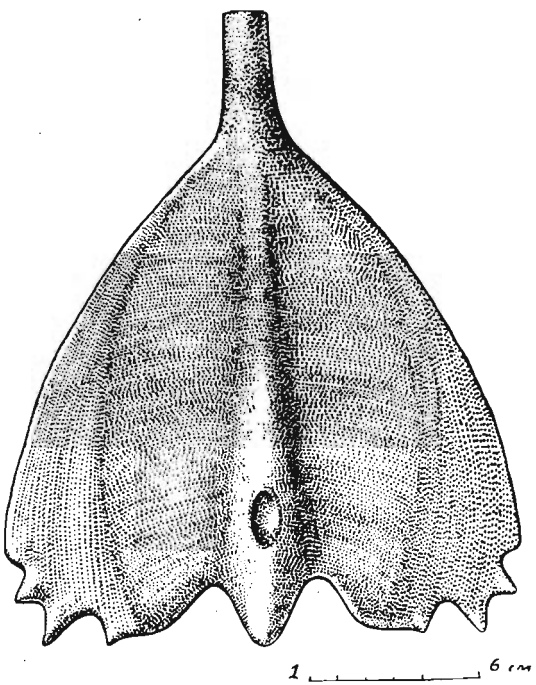

Fig. 11. — *Eglonaspis rostrata* Obruchev; dorsal view of carapace showing anterior oral extension and position of ?dorsal spine (after Obruchev, 1959, fig. 2).

EVOLUTION OF THE HETEROSTRACI

Although it is possible to divide the Heterostraci into a number of orders, suborders and families, it is less easy to establish the relationships of these groups to one another. This difficulty is in large measure due to the fact that evolutionary trends can be followed which affect

the Heterostraci as a whole (see Tarlo, 1962), and because most of the groups go through similar morphological stages at some time in their history, confusion has arisen when attempts have been made to link together forms at the same structural grade which may not necessarily be directly related.

However, from a study of the development of the armour of the carapace in the various groups it becomes possible to show the way in which these groups are related to one another, and hence to trace the main evolutionary lineages within the Heterostraci. Although, as has been shown above, eight groups are recognizable, these seem to fall into four main lines — the cyathaspid, psammosteid, pteraspid and amphiaspid lineages, and each of these will be considered separately below.

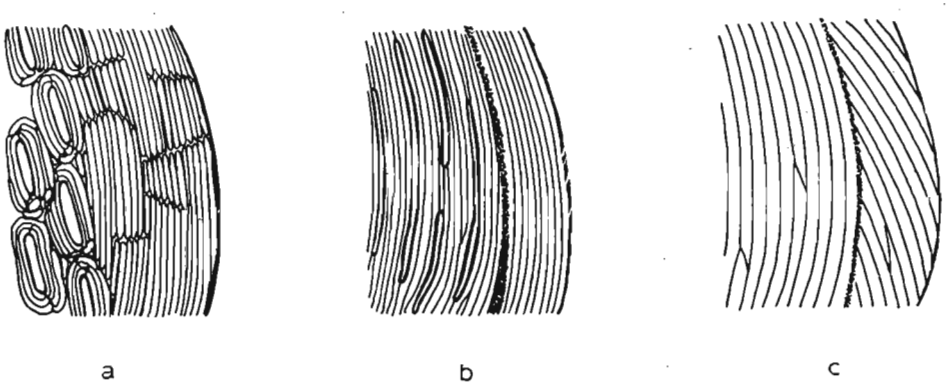

Fig. 12. — Cyathaspid lineage; diagram showing progressive elimination of tesserae: *a Tolypelepis* with cyclomorial tesserae adjoining lateral region of synchronomorial growth, *b Cyathaspis* showing isolated longitudinal „first generation" dentine ridges set in later, finer longitudinal ridges, *c Anglaspis* showing synchronomorial longitudinal ridges with differing lineation in median and lateral regions of plate.

I. *Cyathaspid Lineage*

From the type of primitive carapace found in the Ordovician forms, which was composed of discrete tesserae produced by cyclomorial growth, it is easy to envisage the production of the carapace found in the primitive cyathaspid *Tolypelepis*. In this form the dorsal plate has an ornamentation of cyclomorial tesserae, although there are no rounded tubercles present, it having instead short dentine ridges no doubt formed by the fusion of tubercles. The possession of these tesserae indicates that until the animal neared ist definitive size the carapace grew to keep pace with the growth of the animal, and it was only when it reached its definitive size that the lateral margins and the rostral area of the

dorsal plate appeared as single units (synchronomorially), and the whole dorsal area became fused together.

In the later *Cyathaspis* the main plates were again formed when the animal was fully grown, although in this case the initial dentine ridges (which in *Tolypelepis* would have been the primordia of tesserae) are much elongated suggesting the fusion of a number of shorter ridges. In addition these ridges must have remained isolated in the skin until the animal reached its definitive size, for at that time a further generation of longitudinal dentine ridges formed between the initial ones, while simultaneously the lateral margins of the main plates also appeared and became fused to the central areas. Thus in many ways *Cyathaspis* is similar in its young stage to the condition seen in *Tolypelepis*, although the production of the main part of the dermal armour is delayed until the definitive size is reached (Obruchev, 1945). As a result of the method by which the plates grow in these two genera, their dorsal plates show a superficial division into rostral, lateral and central areas.

In the poraspids, the entire plates appear as single units (synchronomorially) when the animal is fully grown, and although the ornamentation consists of longitudinal dentine ridges, these are all of one generation (Obruchev, 1945). From their alignment however it is still frequently possible to distinguish the four areas of the dorsal plate.

A more advanced stage of fusion is seen in the ctenaspids, where the carapace is composed of only two plates — one dorsal and the other ventral, the lateral margins of the dorsal plate being overturned to cover the branchial areas, thus suggesting the fusion of the branchial plates to the dorsal. *Ctenaspis* itself which is an early ctenaspid still retains some evidence of original tesserae, which in this instance are scale-like, but the much later *Allocryptaspis* is similar in its ornamentation to the poraspids.

II. *Psammosteid Lineage*

The carapace of the primitive psammosteid *Tesseraspis* is similar to the type seen in the Ordovician *Astraspis*, being composed of discrete tesserae and lateral ridge plates. *Tesseraspis* however, has thick tesserae in the median areas of its carapace ornamented by large tubercles, and separating these from the lateral ridge plates are thinner tesserae with smaller tubercles. *Tesseraspis* therefore shows the organization of the tesserae into different groups foreshadowing the later plates and fields of tesserae of the typical psammosteid carapace.

A further advance is seen in *Weigeltaspis*, where although its ornamentation is like that of *Tesseraspis*, it would nevertheless appear to

have a similar complement of plates to the well known *Drepanaspis*. However, the tesserae of the rostral area in *Weigeltaspis* are not fused to form a rostral plate, and so far a cornual plate has not been recognized. It can therefore be taken as a form intermediate between *Tesseraspis* and a typical later psammosteid such as *Drepanaspis*.

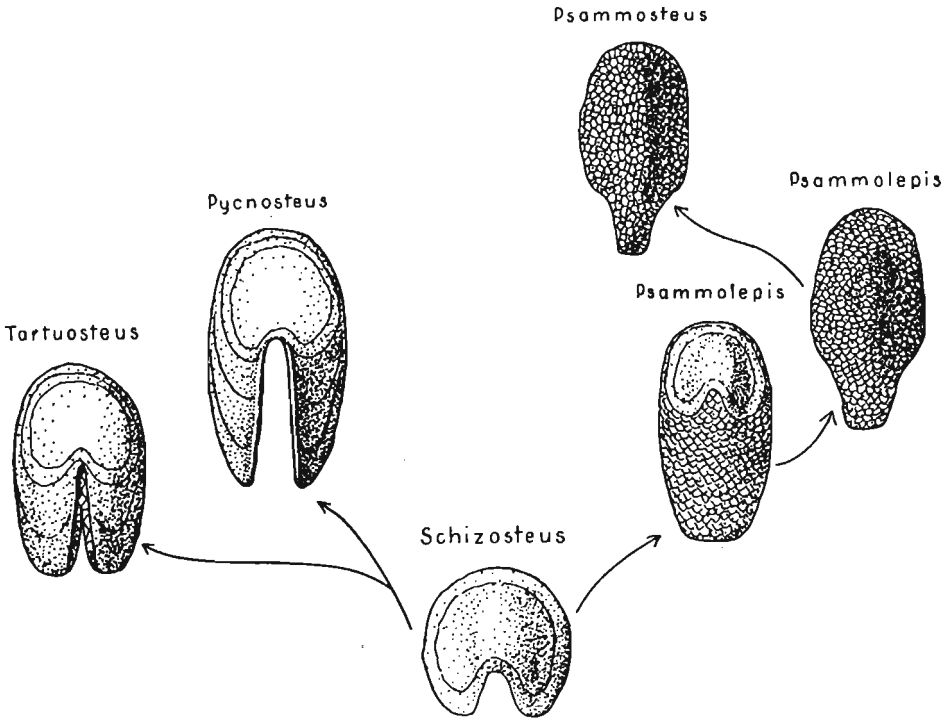

Fig. 13. — Psammosteid lineage; ventral median plates of Middle Devonian genera, illustrating the two main evolutionary lines: the pycnosteid (*Pycnosteus* and *Tartuosteus*), and the psammolepid (*Psammolepis*) which grades into the psammosteid (*Psammosteus*).

The subsequent history of the psammosteids reveals an apparent reversion of the trend towards the fusion of elements, and the persistent fields of tesserae between the main plates become progressively more important. In fact by the time the family Psammosteidae for example, is reached, the entire dorsal and ventral median plates are composed of superficial cyclomorial polygonal tesserae, overlying a bony plate.

Although *Drepanaspis* is the best known of the later psammosteids, the genus *Drepanaspis* itself is not ancestral to the Middle and Upper Devonian forms. Their ancestry is to be sought in the freshwater Polish psammosteids of Emsian age which belong to a new family and are shortly to be described.

From these Emsian forms two main lineages developed — the pycnosteids with their deeply notched ventral median plate and the psammolepids, with their long narrow median plate, these latter eventually grading into the psammosteids (*s.s.*) in which the branchial plates are very wide and short. Contemporaneous with the latest psammosteids, the aspidosteids represent a separate development, as in them there appears to be a reversion to a long narrow branchial plate. They have also lost the ornamentation of normal dentine tubercles, but have retained the ability possessed by the other psammosteids to produce pleromic dentine as a strengthening. Whereas in the other groups this is only as a direct response to abrasion, in the aspidosteids the ability has been utilized throughout the entire carapace, whether or not abrasion has occurred (see also Tarlo & Tarlo, 1961).

Obruchev (1945, 1961*b*) has suggested that the psammosteids can be derived from an advanced pteraspid such as *Protaspis*, in particular the form now renamed *Europrotaspis* by White (1961). It is true that the pattern of plates in *Europrotaspis* is similar to that in the psammosteids, except that the orbital plate of the pteraspid is equivalent to two in the psammosteids — the orbital and post-orbital. Furthermore, in *Europrotaspis* the relationship of the cornual plate to the branchial plate and its opening is comparable to the condition in *Drepanaspis*. However, there is one very important difference. The psammosteids possess fields of tesserae separating the paired lateral plates from the median ones, while no such tesserae are present in the pteraspids. Obruchev (1943, 1945) suggests that the fields of tesserae of the psammosteids are a neo-formation which developed to protect the sensory canal system in the young stages, but it seems much more likely that they are a primitive feature which has been retained, as such fields of tesserae are present in the early forms *Tesseraspis* and *Weigeltaspis*. This latter view would thus take into account the primitive nature of a carapace composed of tesserae, and would enable such forms as *Tesseraspis* and *Weigeltaspis* to be fitted into any evolutionary scheme. By treating the fields of tesserae of the later psammosteids as a neo-formation, these genera could not easily be accounted for.

III. *Pteraspid Lineage*

The fact that the main plates of pteraspids are homologous to those of the psammosteids and traquairaspids suggests that these groups are closely related to one another. However, as has been pointed out above, the pteraspids do not possess fields of tesserae. Nevertheless if the young stages of *Traquairaspis* are studied, it is evident that the traquairaspids possessed tesserae covering the sensory canal system along the sides of the median plates, although these were incorporated into the median

plates as the animal grew, and can only be recognized in the adult by a study of the pattern of the ornamentation.

This suggests that in *Traquairaspis* the typical fields of tesserae seen in the psammosteids were reduced, so that early in ontogeny they were confined to covering the sensory canals.

It is therefore quite likely that in the pteraspids the fields of tesserae were further reduced so that in the young stages the sensory canals were

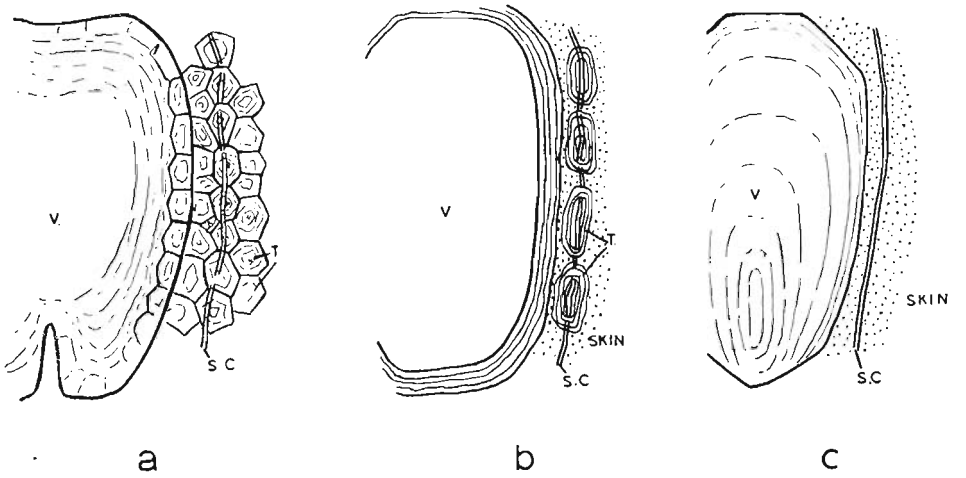

Fig. 14. — Pteraspid lineage; diagram of young stages to illustrate progressive reduction of tesserae: *a* psammosteid, *b* traquairaspid, *c* pteraspid. S. C. sensory canal, *T* tesserae, *V* ventral median plate.

completely unprotected by tesserae. These three stages which are illustrated in text-fig. 14, could perhaps be used to illustrate the appearance of fields of tesserae *de novo* from the pteraspids, but this would make it difficult to fit into the correct stratigraphic sequence the forms concerned, and it would also not be easy to explain the considerable width of the fields of tesserae in the psammosteids. In addition as was mentioned earlier, all the primitive Heterostraci have a carapace composed of tesserae, and such tesserae are unlikely to have all been lost and then produced anew. It seems more likely therefore that the pteraspids were derived from a primitive psammosteid, through a stage such as that represented by *Traquairaspis*.

Another theory for the origin of the pteraspids suggests that they were derived from an advanced cyathaspid (Bryant, 1933) as both the cyathaspids and earliest pteraspids were small animals, and the most primitive pteraspid shows in the dorsal and ventral median plates, a type of synchronomorial growth similar to that found in the cyathaspids. The mouth parts are also very similar, but this is a feature common to all heterostracans in which these elements are known.

The superficial resemblance between the two groups is therefore quite striking, and it was previously argued that the cyathaspids gave rise to the pteraspids by the subdivision of their armour. However, there is no evidence to support this theory, and in any case it would require a certain amount of concomitant fusion to produce the orbital plates of the pteraspids. Besides this, the main evolutionary trend within the Heterostraci as a whole is one in which small elements fuse to form larger units, and it seems more probable therefore that the cyathaspids and the pteraspids were both derived independently from primitive forms with tesserae.

IV. *Amphiaspid Lineage*

The amphiaspids with their carapace composed of a single unit, have been considered to be connected with the cyathaspids because of the high degree of fusion in the carapace (Stensiö, 1958). On the other hand, it has been further suggested that they could represent a side-branch of the psammosteids via the cardipeltids (Tarlo, 1960).

One of the earliest psammosteids *Kallostrakon,* has plates formed of cyclomorial tesserae, and this grades into a form such as *Corvaspis* in which the ornamentation consists mainly of synchronomorial tesserae. Within *Corvaspis* again, there are some forms in which various stages can be seen in one plate, in the gradual elimination of the tesserae by fusion (Tarlo, 1960). In this respect these plates of *Corvaspis* are similar to the large dorsal plates of *Cardipeltis,* and by postulating the fusion of the branchial and dorsal plates in *Corvaspis* to form a single unit, the cardipeltid condition could be arrived at. This may well have been the way in which the cardipeltids originated from the main psammosteid line.

From the sensory canal system in *Cardipeltis* it is evident that there were further elements of the carapace anterior to the dorso-branchial plate, and Stensiö's reconstruction of the entire carapace (1958) would seem to be largely justified. This reconstruction shows an astonishing similarity to some of the amphiaspids, except that they have the anterior plates and the ventral plate fused to the dorso-branchial, making the carapace one single unit. The amphiaspids therefore very likely represent an advanced specialized group of heterostracans in which the fusion from original tesserae has been taken as far as possible. The fact that their carapace is an apparently simple one does not necessarily imply any relationship to the cyathaspids, but instead it is considered to be a sign of the parallel development of these two lineages, as there is no other marked similarity between them. Although once again it is neces-

sary ultimately to derive all the groups from primitive forms with tesserae, in the amphiaspid lineage it is possible to recognize the earliest representative among the psammosteids. Also, as the cardipeltids form a well defined natural group, they can be distinguished from both the early psammosteids and the amphiaspids proper.

CONCLUSION

The relationships of the orders, suborders and families discussed above, are indicated in text-fig. 15 below, and as can be seen, this proposed phylogeny is divided into what are considered to be the main taxonomic units.

One of the difficulties met with when drawing up this classification has been the fact that two or more lineages often originated from a single group, but within that group it is not possible to recognize any division. Thus although the end results are quite easy to separate off as natural groups, it is difficult to know where to draw a line between the earlier forms. For example, a case could be made out for including the Ordovician eriptychiids as either primitive psammosteids, traquairaspids or even cyathaspids. However, any of these alternative procedures would obscure the fact that the eriptychiids represent a primitive structural grade from which it is possible to derive any or all of these groups.

Again, when considering the tesseraspids, the early members of this suborder are difficult to distinguish from the early cyathaspids, because they are both just on the point of diverging from a similar basal stock in which the carapace is composed essentially of tesserae. In the tesseraspids however, the fusion took a rather different path from that seen in the earliest known cyathaspids, and hence these two groups can be separated from one another on this basis. At the same time, within the tesseraspids are to be found the possible ancestors of the three other major lineages — the advanced psammosteids, pteraspids and amphiaspids, but no specific tesseraspid, with the possible exception of *Corvaspis*, can be said to lead directly to any one of them.

Any attempt to produce a viable phylogeny of the Heterostraci must take into account the earliest known forms from the Ordovician, in which the carapace is composed of numerous discrete tesserae. In addition the present phylogeny has been based on the realization that within the Heterostraci there exists an overall evolutionary trend in which small units of the dermal armour have tended to fuse to form larger units, although there is an apparent reversal of this trend in the later psammosteids.

For these reasons therefore, it is considered erroneous for the cyathaspids to be taken as the starting point from which the other groups could have been derived by a progressive subdivision of the armour, even though morphological similarities can be seen between the cyathaspids and members of other groups. In fact it has been possible to show

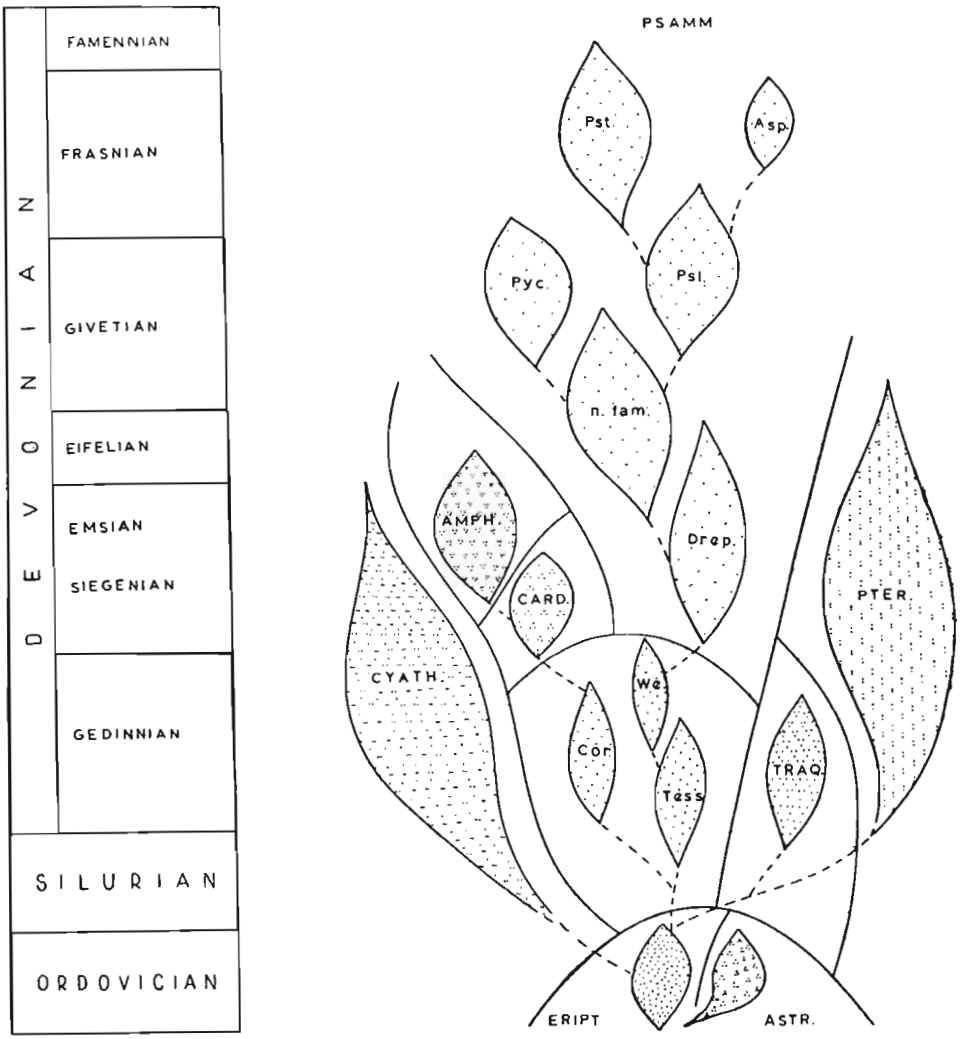

Fig. 15. — Tentative phylogeny of the Heterostraci

AMPH Amphiaspidiformes, *ASTR* Astraspidiformes, *CARD* Cardipeltiformes, *CYATH* Cyathaspidiformes, *ERIPT* Eriptychiiformes, *PSAMM* Psammosteiformes, *PTER* Pteraspidiformes, *TRAQ* Traquairaspidiformes

Asp Aspidosteidae, *Cor* Corvaspididae, *Drep* Drepanaspididae, *Psl* Psammolepididae, *Pst* Psammosteidae, *Pyc* Pycnosteidae, *Tess* Tesseraspididae. *We* Weigeltaspididae.

how the cyathaspid conditions could have been arrived at by the progressive fusion of primitive tesserae (see Obruchev, 1945).

Again, it has been demonstrated how the main psammosteid line could quite easily have been derived from the Ordovician forms, by way of such genera as *Tesseraspis* and *Weigeltaspis*. In this line it has been shown how a system of plates could have been built up gradually, while at the same time fields of tesserae were retained throughout the whole lineage. Although the fact that the main plates of the psammosteids are homologous to those found in the pteraspids, means that these two groups are closely related, it is not considered probable that the psammosteids were derived from a late pteraspid. Instead it is believed that the pteraspids may well have evolved from a group of early psammosteids, by way of a stage similar to that found in *Traquairaspis*, where reduced fields of tesserae have become incorporated into the median plates of the adult. A further reduction of such fields of tesserae would have produced the condition seen in the pteraspids, and this seems more likely than that late advanced pteraspids should suddenly have acquired fields of tesserae anew, between the main plates, and thus given rise to the psammosteids.

It has also been suggested that the cardipeltids could have been an early side-branch from the psammosteids in which there was a greater degree of fusion than in the main line, although persistent tesserae are still present in the rostral area. Finally, it is thought that the cardipeltids in turn are likely to have given rise to the amphiaspids through an even greater degree of fusion, as superficial tesserae are sometimes present in these latter forms in the rostral area, although the plate beneath them is fused to the rest of the carapace. It is thus considered more reasonable to derive the amphiaspids from the cardipeltids than from the cyathaspids, even though these latter achieved a comparable state of fusion of the carapace. The amphiaspids and cyathaspids can therefore best be understood as representing the end products of two separate lineages, in which there was a similar evolutionary trend.

Thus, when the known groups of the Heterostraci are considered in their correct stratigraphic sequence, the overall picture of their evolutionary history here outlined, seems to be less beset by problems and anomalies than many of the previous theories, although further discoveries may well require some modification of the present scheme.

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Department of Geology and Mineralogy
University Museum
Oxford, December 1961

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KLASYFIKACJA I EWOLUCJA HETEROSTRACI

Streszczenie

Autor przedstawia szkic klasyfikacji Heterostraci, wyróżniając w tej grupie osiem rzędów i dziewięć podrzędów. Poniżej podane są ich diagnozy.

Rząd **Astraspidiformes** Berg, 1940
(fig. 1)

Diagnoza. — Pancerz złożony z oddzielnych, wielokątnych płytek, czyli tesserae, powstałych wskutek przyrostu cyklomorialnego i ornamentowanych okrągłymi, krenulowanymi guzkami. Istnieje pole pinealne. Trzy podłużne grzebienie dorsalne, z których środkowy biegnący od brzegu tylnego do pola pinealnego, a dwa lateralne, rozciągające się tylko na 2/3 tej odległości. Brzegi lateralne pancerza utworzone przez rząd silnie kanciastych płytek grzebieniowych.

Budowa histologiczna: bazalna warstwa blaszkowatej aspidiny, środkowa warstwa gąbczastej aspidiny oraz zewnętrzne guzki aspidiny, pokryte substancją podobną do emalii.

Rząd **Eriptychiiformes**

Diagnoza. — Pancerz złożony w dużej mierze z wielokątnych tesserae, z wydłużonymi brodawkami. Rząd lateralnych płytek grzebieniowych, z których jedna opatrzona głębokim wcięciem, odpowiadającym otworowi skrzelowemu. Obecne też płytki fulkralne albo łuski.

Budowa histologiczna: bazalna warstwa blaszkowata; środkowe warstwy gąbczastej aspidiny pokryte dentynowymi brodawkami.

Rząd **Cyathaspidiformes** Berg, 1940
Podrząd **Cyathaspidida** Kiaer, 1930, emend.
(fig. 2)

Diagnoza. — Pancerz złożony z czterech większych płytek: dorsalnej, wentralnej i parzystych lateralnych. Płytka dorsalna podzielona zewnętrznie na cztery części: przednią rostralną, środkową i dwie lateralne. W części środkowej obecna plamka pinealna. Ornamentacja w postaci podłużnych grzebieni dentyny.

Podrząd **Poraspidida** nov.
(fig. 3)

Diagnoza. — Pancerz złożony z czterech głównych płytek: dorsalnej, wentralnej i dwóch lateralnych branchialnych. Płytka dorsalna nie podzielona zewnętrz-

nie na pola, chociaż są one jeszcze dostrzegalne w ułożeniu podłużnych grzebieni dentyny. Występują małe płytki suborbitalne i oralne. Pokrywa łuskowa złożona z dużych, grubych łusek tułowia i małych łusek ogona.

Podrząd **Ctenaspidida** Zych, 1931
(fig. 4)

Diagnoza. — Pancerz złożony z dwóch dużych płytek: branchio-dorsalnej i wentralnej. Istnieją płytki: oralna, postoralna i suborbitalna.

Rząd **Psammosteiformes** Berg, 1940
Podrząd **Tesseraspidida** nov.
(fig. 5)

Diagnoza. — Pancerz złożony z niezależnych, wielokątnych płytek (tesserae), które mogą się zrastać w większe, odrębne płytki. U form, u których nie nastąpiło zrośnięcie tesserae, są one zróżnicowane w postaci oddzielnych pól, poprzedzających zrastanie. U wszystkich form duże części pancerza złożone są jeszcze z oddzielnych tesserae i pełny komplet płytek, występujący u późniejszych Psammosteidae, nie jest zrealizowany.

Podrząd **Psammosteida** Kiaer 1932
(fig. 6)

Diagnoza. — Pancerz złożony z dwunastu głównych płytek: dorsalnej, wentralnej, rostralnej, pinealnej, parzystych orbitalnych, postorbitalnych, branchialnych i kornualnych. Płytki środkowe i lateralne oddzielone są od siebie wielokątnymi tesserae (pola tesserowe). Płytki oralne z dobrze rozwiniętymi blaszkami zębowymi. Ornamentacja utworzona przez okrągłe, krenulowane brodawki dentynowe.

Rząd **Traquairaspidiformes**
(fig. 7)

Diagnoza. — Pancerz złożony z ośmiu głównych płytek: rostralnej, pinealnej, dorsalnej i wentralnej, parzystych orbitalnych i branchio-kornualnych. Otwór skrzelowy całkowicie otoczony przez płytki branchio-kornualne.

Rząd **Pteraspidiformes** Berg, 1940
Podrząd **Pteraspidida** Kiaer, 1932, emend.
(fig. 8)

Diagnoza. — Pancerz złożony z dziesięciu głównych płytek: rostralnej, pinealnej, dorsalnej i wentralnej, parzystych orbitalnych, branchialnych i kornualnych. Często istnieją płytki postoralne i lateralne, wespół z normalnymi płytkami oralnymi.

Podrząd **Doryaspidida** N. Heintz

Diagnoza (według informacji Dr N. Heintz). — Pełny skład płytek pteraspidowych, z wyjątkiem płytek oralnych. Otwór gębowy położony dorsalnie, z bardzo długim i wąskim pseudo-rostrem, utworzonym z jednego z elementów wentralnych pancerza. Płytka rostralna poprzecznie ścięta. Parzyste płytki kornualne bardzo krótkie i szerokie, tworzące dwa słabe występy lateralne. Ornamentacja złożona z charakterystycznej siatki gwiaździstych grzebieni.

Rząd **Cardipeltiformes**

(fig. 9)

Diagnoza. — Pancerz obejmuje dużą płytkę dorso-branchialną razem ze złożonymi branchialnymi i tesserae. Wentralna strona pancerza przypuszczalnie złożona z tesserae.

Rząd **Amphiaspidiformes** Berg 1940
Podrząd **Amphiaspidida** Obruchev, 1938

Diagnoza (otrzymana od Prof. D. Obruczewa). — Głowa i przednia część tułowia pokryte przez niepodzieloną tarczę dorso-wentralną. Nie zaobserwowano żadnych płytek branchialnych i kornualnych. Brak rostrum. Orbity przy przednim brzegu pancerza. Otwór ustny wentralny. Strona wentralna płaska, dorsalna wypukła. Powierzchnia pokryta małymi guzkami dentyny.

Podrząd **Hibernaspidida** Obruchev
(fig. 10)

Diagnoza (otrzymana od Prof. D. Obruczewa). — Spłaszczone Heterostraci, z trójkątną głową i tarczą tułowiową, złożoną ze zrośniętych dorsalnych, wentralnych i parzystych branchialnych płytek. Trójkątny otwór ustny, przylegający wentralnie do przedniego brzegu. Orbity dorsalne blisko przedniego brzegu. Powierzchnia pokryta przez szerokie i płaskie grzebienie dentyny, 5—8 cm.

Podrząd **Eglonaspidida** nov.
(fig. 11)

Diagnoza. — Ślepy amfiaspid, z okrągłym otworem wzdłuż linii środkowej, w pobliżu brzegu tylnego; w otworze mógł tkwić kolec dorsalny. Otwór gębowy na końcu przedniego, rurkowatego wyrostka pancerza.

*

Opierając się na analizie morfologicznej znanych Heterostraci, autor dochodzi do wniosku, że w grupie tej można wyróżnić cztery główne linie rozwojowe: cyataspidowa, psammosteidowa, pteraspidowa i amfiaspidowa. Rozwój ewolucyjny pancerza cyataspidów został prześledzony przez stadia, wykazujące stopniową eliminację tesserae. W linii psammosteidowej prześledzono stopniowe zlewanie się tesserae w płytki, chociaż charakterystyczne dla tej linii jest zachowanie przez cały czas trwałych pól tesserae. U późniejszych psammosteidów zachodzi wyraźne odwrócenie tendencji zlewania się tesserae. Pteraspidy reprezentują boczne odgałęzienie prymitywnych psammosteidów, u których pola tesserae progresywnie redukują się poprzez stadia takie, jakie reprezentuje *Traquairaspis*. Amfiaspidy są uważane za dalsze, boczne odgałęzienia psammosteidów, poprzez kardipeltidy, u których dążność do zlewania się osiąga szczyt. Szkic filogenezy Heterostraci przedstawiono na fig. 15; w związku z tym przedyskutowane zostały różne możliwości ewolucyjne.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 253)

Astraspis desiderata Walcott, pancerz grzbietowy składający się z oddzielnych cyklomorialnych tesserae i z lateralnych grzebieniowatych płytek (z fotografii opublikowanej przez Eastmana, 1917, pl. 12. fig. 6).

Fig. 2 (p. 255)

Archegonaspis integer (Kunth), płytka dorsalna z plamką pinealną i powierzchniowym podziałem na obszary: rostralny, centralny i lateralne (wg Kiaer, 1932, fig. 3).

Fig. 3 (p. 256)

Anglaspis heintzi Kiaer, u góry: pancerz grzbietowy z płytką dorsalną i z parzystymi płytkami lateralnymi branchialnymi, u dołu: całe zwierzę widziane z boku, z widoczną łuskowatością i hipocerkalnym ogonem (wg Kiaer, 1932, fig. 11).

Fig. 4 (p. 257)

Ctenaspis dentata Kiaer, pancerz grzbietowy składający się z pojedynczego elementu, z lateralnym występem nad regionem branchialnym, u dołu: to samo, widziane z boku (wg Stensiö, 1958, fig. 176).

Fig. 5 (p. 258)

Tesseraspis tessellata Wills, pancerz grzbietowy ukazujący tesserae ułożone w regiony, zapowiadające układ występujący u późniejszych psammosteidów.

Fig. 6 (p. 260)

Drepanaspis gemundenensis Schlüter, zwierzę widziane od strony grzbietowej, z uwidocznionymi płytkami środkowymi: rostralną i dorsalną, oraz z parzystymi płytkami orbitalnymi, postorbitalnymi, branchialnymi i kornualnymi. Należy zwrócić uwagę na pola tesserae, oddzielające płytki medialne od lateralnych (wg Obruczewa, 1943, fig. 1).

Fig. 7 (p. 263)

Traquairaspis campbelli (Traquair) — (syn. *T. pococki* (White)), pancerz grzbietowy ukazujący płytki środkowe: rostralną, pinealną i dorsalną oraz parzyste płytki orbitalne i złożone branchio-kornualne (wg White, 1946, fig. 40).

Fig. 8 (p. 264)

Pteraspis rostrata (Agassiz), pancerz od strony grzbietowej, ukazujący płytki środkowe: rostralną, pinealną i dorsalną oraz parzyste płytki orbitalne, branchialne i kornualne, u dołu: całe zwierzę widziane z boku (wg White, 1935, fig. 81, 84).

Fig. 9 (p. 266)

Cardipeltis wallacii Branson & Mehl, rekonstrukcja pancerza grzbietowego, ukazująca złożoną płytkę dorso-branchialną, boczne płytki grzebieniowe oraz tesserae (zmienione, wg Stensiö, 1958, fig. 184A).

Fig. 10 (p. 267)

Hibernaspis macrolepis Obruchev, pancerz od strony grzbietowej, ukazujący położenie przednie oczu i terminalny otwór gębowy (wg Obruczewa, 1959, fig. 1).

Fig. 11 (p. 268)

Eglonaspis rostrata Obruchev, pancerz od strony grzbietowej ukazujący przednie oralne rozszerzenie oraz położenie kolca dorsalnego (?), (wg Obruczewa, 1959, fig. 2).

Fig. 12 (p. 269)

Cyathaspidowa linia rozwojowa; schemat ukazujący stopniową eliminację tesserae: *a Tolypelepis* z cyklomorialnymi tesserae, przylegającymi do lateralnego regionu, o wzroście synchronomorialnym, *b Cyathaspis* ukazujący izolowane podłużne „pierwsze pokolenie" grzebieni dentyny, ustalających się później jako delikatne podłużne grzebienie, *c Anglaspis* ukazujący synchronomorialne podłużne grzebienie o różnym poliniowaniu w środkowym i bocznych regionach płytki.

Fig. 13 (p. 271)

Psammosteidowa linia rozwojowa, wentralne płytki środkowe rodzajów środkowo-dewońskich, ilustrujące dwie główne linie ewolucyjne: pyknosteidową *(Pycnosteus* i *Tartuosteus)* i psammolepidową (*Psammolepis*), która stopniowo przechodzi w psammosteidową (*Psammosteus*).

Fig. 14 (p. 273)

Pteraspidowa linia rozwojowa; schemat młodych stadiów, ilustrujący stopniową redukcję tesserae: *a* psammosteidy, *b* traquairaspidy, *c* pteraspidy, *S.C.* kanał czuciowy, *T* tesserae, *V* wentralna płytka środkowa.

Fig. 15 (p. 276)

Przypuszczalna filogeneza Heterostraci.

Л. БЕВЕРЛИ ТАРЛО

КЛАССИФИКАЦИЯ И ЭВОЛЮЦИЯ РАЗНОЩИТКОВЫХ (HETEROSTRACI)

Резюме

Автор дает очерк классификации разнощитковых бесчелюстных, выделяя среди них восемь отрядов и девять подотрядов. Ниже приведены их диагнозы.

Отряд **Astraspidiformes** Berg, 1940
(фиг. 1)

Диагноз. — Панцырь из отдельных, многоугольных пластинок (tesserae), возникших в результате цикломориального роста и покрытых скульптурой из круглых зарубенных бугорков. Имеется пинеальное поле. Три продольные дорсальные гребени; срединный протягивающийся от заднего края до пинеального поля, боковые-же на двух третьих этого расстояния. Боковые краи панцыря состоят из ряда остроконечных гребневых пластинок.

Гистологическое строение: основной аспидиновый пластинчатый слой, средний из губчатого аспидина, наружные аспидиновые бугорки покрыты эмальеподобным веществом.

Отряд **Eriptychiiformes**

Диагноз. — Панцырь в большой части состоит из многоугольных tesserae с удлиненными бугорками. Ряд боковых гребневых пластинок, среди которых одна снабжена глубоким вырезом образующим жаберное отверстие. Присутствуют фулкральные пластинки или чешуи.

Гистологическое строение: основной пластинчатый и средний губчатый слой покрыты дентиновыми бугорками.

Отряд **Cyathaspidiformes** Berg, 1940
Подотряд **Cyathaspidida** Kiaer, 1930, emend.
(фиг. 2)

Диагноз. — Панцырь из четырех больших пластинок — спинной, брюшной и парных боковых. Спинная пластинка разделена на поверхности на четыре части: переднюю ростральную, центральную и две боковые. На центральной части имеется пинеальное пятно. Скульптура из продольных дентиновых гребней.

Подотряд **Poraspidida** nov.
(фиг. 3)

Диагноз. — Панцырь состоит из четырех главных пластинок: спинной, брюшной и двух боковых жаберных. Спинная пластинка не разделена на поверхности, хотя отдельные поля могут быть установлены на основании расположения скульптуры, состоящей из продольных дентиновых гребней. Известны маленькие суборбитальные и ротовые пластинки. Чешуи большие и толстые на туловище, маленькие на хвосте.

Подотряд **Ctenaspidida** Zych, 1931
(фиг. 4)

Диагноз. — Панцырь состоит из двух больших пластинок: бранхиодорсальной и вентральной. Известны посторальные и суборбитальные пластинки.

Отряд **Psammosteiformes** Berg, 1940

Подотряд **Tesseraspidida** nov.

(фиг. 5)

Диагноз. — Панцырь сложенный независимыми многоугольными пластинками (tesserae), которые могут соединяться образуя обособленные большие пластинки. У форм, у которых не произошло соединение, tesserae дифференцированы на отдельные поля предшествующие таким пластинкам. У всех форм большие поля панцыря все еще состоят из отдельных tesserae и полный комплект пластинок, свойственный позднейшим псаммостеидам, не приобретен.

Подотряд **Psammosteida** Kiaer, 1932

(фиг. 6)

Диагноз. — Панцырь из двенадцати главных пластинок: срединных дорсальной и вентральной, ростральной, пинеальной, парных орбитальных, посторбитальных, бранхиальных и корнуальных. Срединные и боковые пластинки разделены зонами многоугольных пластинок tesserae (поля тессеров). Оральные пластинки с хорошо развитыми оральными зубными пластинками. Скульптура состоит из округленных зарубенных бугорков.

Отряд **Traquairaspidiformes**

(фиг. 7)

Диагноз. — Панцырь из восьми главных пластинок: ростральной, пинеальной, дорсальной и вентральной срединных пластинок, парных орбитальных и бранхио-корнуальных. Жаберное отверстие целиком заключено в бранхио-корнуальной пластинке.

Отряд **Pteraspidiformes** Berg, 1940

Подотряд **Pteraspidida** Kiaer, 1932, emend.

(фиг. 8)

Диагноз. — Панцырь из десяти главных пластинок: ростральной, пинеальной, дорсальной и вентральной срединных и парных орбитальной, бранхиальной и корнуальной. Часто с посторальными и боковыми пластинками вместе с нормальными оральными.

Подотряд **Doryaspidida** N. Heintz

Диагноз (по сообщению Др. Н. Геинц). — Полный птераспидовый комлект пластинок, за исключением отсутствующих оральных. Рот на спинной стороне с очень длинным, узким ложным ростром, образованным одним из вентральных элементов панцыря. Ростральная пластинка срезана впереди. Парные корнуальные пластинки, очень короткие и широкие, образуют два слабые боковые выступы. Скульптура состоит из характерной сетки звездчатых гребней.

Отряд **Cardipeltiformes**
(фиг. 9)

Диагноз. — Панцырь содержит большую дорсо-бранхиальную пластинку, вместе со сложными бранхиальными и tesserae. Вентральная часть панцыря состоит по всей вероятности из tesserae.

Отряд **Amphiaspidiformes** Berg, 1940
Подотряд **Amphiaspidida** Obruchev, 1938

Диагноз (получен от Проф. Д. Обручева). — Голова и передняя часть туловища покрыты одним нераздельным спинно-брюшным панцырем. Не замечено никаких жаберных и корнуальных пластинок. Глазные отверстия на переднем берегу панцыря. Ротовое отверстие вентральное. Вентральная сторона плоская, дорсальная выпуклая. Поверхность покрыта мелкими дентиновыми бугорками.

Подотряд **Hibernaspidida** Obruchev
(фиг. 10)

Диагноз (получен от Проф. Д. Обручева). — Сплюснутые Heterostraci с треугольной головой и панцырем туловища, сложенным со сросшихся дорсальных, вентральных и парных бранхиальных пластинок. Треугольное ротовое отверстие примыкает от вентральной стороны к переднему краю. Глазные отверстия на дорсальной стороне, вблизи переднего края. Поверхность покрыта широкими и плоскими гребнями дентина, 5—8 см.

Подотряд **Eglonaspidida** nov.
(фиг. 11)

Диагноз. — Слепые амфиаспиды с круглым углублением в срединной линии, в поблизости заднего края спинного панцыря, в котором мог прикрепляться спинной шип. Ротовое отверстие на конце трубкообразного переднего выступа панцыря.

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Опознается четыре эволюционные линии: циатаспидовая, псаммостеидовая, птераспидовая и амфиаспидовая. Эволюционное развитие панцыря циатаспид прослежено в ряде стадии и обнаруживает постепенное соединение tesserae в пластинки, хотя эта линия отличается тем, что на протяжении всей своей исто-

рии сохраняет поля tesserae. Наоборот, позднейшим псаммостеидам свойственны изменения по направлении к соединению tesserae. Птераспиды показаны как представляющие боковую ветвь отходящую от примитивных псаммостеид, у которых поля тессеров подвергаются прогрессивной редукции через стадии соответствующие *Traquairaspis*. Амфиаспиды рассматриваются как дальнейшая боковая ветвь, отходящая от псаммостеид посредством кардипельтид, в которой стремление к соединению достигает максимум. На рисунке фиг. 15 дано начертание филогенеза разнощитковых. В связи с этим подвергнуты обсуждению разные альтернативы.