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PSAMMOSTEIFORMES (AGNATHA) — A REVIEW WITH DESCRIPTIONS OF NEW MATERIAL FROM THE LOWER DEVONIAN OF POLAND

I. GENERAL PART

(PSAMMOSTEIFORMES (AGNATHA) — OGÓLNY PRZEGLĄD I OPIS NOWEGO MATERIAŁU Z DOLNEGO DEWONU POLSKI
I. CZĘŚĆ OGÓLNA

BY

L. BEVERLY HALSTEAD TARLO

(WITH 32 TEXT-FIGURES AND 14 PLATES)

WARSZAWA 1964
PAŃSTWOWE WYDAWNICTWO NAUKOWE

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PREFACE

In the Summer of 1955, at the invitation of Professor **Roman Kozłowski**, and with the kind help of Professor **Zofia Kielan-Jaworowska**, I was priviledged to spend some time in the Holy Cross Mountains of central Poland, where I took part in Field Excursions directed by Dr. Z. **Kotański**. We visited various fossiliferous localities including the Placoderm Sandstone quarry at Daleszyce, where we collected numerous vertebrate fragments, and subsequently Dr. J. **Kulczycki** who was at that time concerned with the Palaeozoic vertebrates of Poland, generously agreed to allow me to describe the ostracoderms from the deposit. He and I then spent part of the 1956 field season at Daleszyce where we obtained a large collection of vertebrate remains, including new psammosteids. A further collection was made by Mr. H. **Łobanowski** and myself during the summer of 1958, not only from Daleszyce, but also from many other Lower Devonian (Emsian) localities in the Holy Cross Mountains.

The present work was originally intended to be a detailed account of the new psammosteid fauna from central Poland, but when attempting to assess the significance of this discovery by means of comparison with known material, it became evident that this alone would not suffice. It was found for example that a considerable amount of the material available had never been described, and that much already described was in need of revision. Indeed, the late Professor J. **Kiaer** had intended to produce a complete survey of the psammosteids, but unfortunately he died in 1931 with this aim unfulfilled. In consequence therefore, with the help and active encouragement of Professor R. **Kozłowski** and Professor Z. **Kielan-Jaworowska**, it was decided to undertake a complete systematic review of the psammosteids, and Part II of this work, which will appear separately, will include descriptions of 74 species of which 22 are new, 22 genera of which 6 are new, as well as 9 families of which 1 is new. Furthermore, since all known material was of necessity examined, it has also been possible in Part I of this work, to provide an account of the stratigraphical range and geographical distribution of the psammosteids, as well as a discussion on their origin and evolution.

ACKNOWLEDGEMENTS

I owe a special debt of gratitude to Professor R. **Kozłowski** and Professor Z. **Kielan-Jaworowska** of the Palaeozoological Institute, Polish Academy of Sciences and Warsaw University, for their constant help and encouragement over these last 8 years. I am also greatly indebted to the late Professor J. **Samsonowicz**, Dr. and Mrs. A. **Urbanek**, Dr. and Mrs. Z. **Kotański**, Dr. and Mrs. J. **Kulczycki**, Dr. W. **Jesionek-Szymańska**, Dr. J. **Lefeld** and Mr. H. **Łobanowski**, all of Warsaw, for their generous hospitality and assistance, and to the Polish Academy of Sciences, the Polish Ministry of Higher Education, the Percy Sladen Memorial

Fund of the British Museum (Natural History) and the British Council, for their financial support for the field work carried out in central Poland.

The present work could not have been so comprehensive without the long and stimulating discussions held with Professor D. OBRUCHEV in Moscow, and with Dr. ELGA MARK in Tallinn, to both of whom I am also deeply grateful for their warm hospitality and for allowing me the free run of their extensive collections of psammosteids. I also wish to express my thanks to Professor J. ORLOV of the Palaeontological Institute, Moscow, and Professor K. ORVIKU of the Geological Institute, Tallinn, who helped to make my visit to Russia and Estonia in 1961, a valuable and enjoyable one, and to the Academy of Sciences of U. S. S. R., the British Council and the D. S. I. R. who arranged and financed the visit. My thanks are also due to Professor W. GROSS, Dr. H. JAEGER and Dr. and Mrs. H. WERMUTH of the Humboldt University, Berlin, for their hospitality and for the provision of facilities to examine material, some of which I borrowed, in 1956 and 1958, and to the D. S. I. R. and the British Council for their financial support for these visits. I am also greatly indebted to Professor E. A. STENSIÖ, Professor E. JARVIK and Dr. and Mrs. T. ØRVIG of Stockholm, for their kind hospitality and for the invaluable discussions I had with them as well as for the material I have been allowed to describe, and to Professor P. THORSLUND of the Palaeontological Institute, Uppsala, for allowing me to examine material. My warm thanks are also due to Professor A. HEINTZ and Dr. NATASCHA HEINTZ of the Palaeontological Museum, Oslo, for their hospitality, for the discussions they had with me, and for their allowing me to examine the collections in their charge and to describe material. Once again I am grateful to the D. S. I. R. for their financial assistance for these visits.

Thanks are also due to Dr. E. I. WHITE of the British Museum (Natural History) for the provision of facilities to examine material, and to Dr. H. W. BALL, Mr. H. A. TOOMBS and Mr. P. R. GURR also of the British Museum (Natural History), for their kind assistance. I would also like to record my thanks to the following for loans of material and for the provision of facilities for studying specimens in their charge: Mr. J. D. D. SMITH (Geological Survey and Museum, London); Dr. C. L. FORBES and Dr. P. F. FRIEND (Sedgwick Museum, Cambridge); Mr. J. M. EDMONDS (University Museum, Oxford); Professor L. J. WILLS and Dr. I. STRACHAN (Geological Museum, University of Birmingham); Dr. R. M. C. EAGAR (Manchester Museum); Dr. C. D. WATERSTON (Royal Scottish Museum, Edinburgh); the late Dr. ETHEL CURRIE (Hunterian Museum, Glasgow); Miss J. I. MACDONALD, Mr. J. BRODIE and Mr. W. A. ROSS (Elgin Museum); and Dr. J. S. JACKSON (National Museum of Ireland, Dublin).

In addition I would like to express my thanks to the undermentioned: Professor D. OBRUCHEV (Palaeontological Institute, Moscow) and Dr. ELGA MARK (Geological Institute, Tallinn) for the gift of a representative collection of Baltic psammosteids; Dr. F. PRANTL (National Museum, Prague) for the cast of the holotype of *Schizosteus perneri*; Professor H. K. ERBEN and Dr. E. DEDE (University of Bonn) for the cast of the holotype of *Drepanaspis gemundenensis*; Dr. F. BROTZEN (Geological Survey Museum, Stockholm) and Dr. S. MATTHES (Halle University) for the loan of the types of *Weigeltaspis alta*; Dr. L. KOCH (University of Copenhagen) and Dr. T. ØRVIG (Swedish Museum of Natural History) for the loan of the Greenland psammosteid; Professor J. W. WELLS (Cornell University, New York) and Dr. J. S. STEPHENS (Ohio State University) for the loan of material from the Ohio Bone Bed, and Dr. R. H. DENISON (Chicago Museum of Natural History) for his very kind gift of Idaho psammosteids.

Besides the above, I also wish to acknowledge with thanks the useful discussions I have had with the following: Mr. J. R. L. ALLEN (University of Reading), Professor R. AMPRINO

(University of Bari), Professor A. J. Boucot (California Institute of Technology), Dr. J. D. Currey (University of Oxford), Professor D. L. Dineley (University of Ottawa), Professor J. Trueta (University of Oxford) and Professor T. S. Westoll (University of Newcastle).

Text-figures 2, 5, 6, 8, 10, 11, 14, 15, 17-21 and 30-32 were drawn by Miss Jennifer Middleton under my direction, and photographs for plates are by Messrs. P. R. Gurr and J. R. Mercer.

The work embodied in this monograph was carried out during the period 1955—1963, although for the first three years work on psammosteids was possible only during brief intervals. Full-time study on the group commenced in October 1958 with the award of a D. S. I. R. Senior Fellowship which was held at the British Museum (Natural History), London, by kind permission of the Director and his Keeper in Palaeontology. Subsequently the work was continued and completed jointly in the Department of Geology and Mineralogy, University of Oxford and at the Royal Dental Hospital, London, during the tenure of a Nuffield Research Fellowship, and my sincere thanks are due to Professor L. R. Wager and Professor R. B. Lucas for the hospitality of their respective Departments. Finally, I wish to record my indebtedness to my wife, without whose constant and unflagging assistance and criticism this work would never have been completed.

The following abbreviations are used:

B.M. — Department of Palaeontology, British Museum (Natural History), London, England.
B.U. — Geological Museum, University of Birmingham, England.
E.M. — Elgin Museum, Scotland.
G.I.T. — Geological Institute, Tallinn, Estonia.
G.I.U.B. — Geological Institute, University of Bonn, West Germany.
G.M.O. — Geological Museum, State University of Ohio, United States.
G.M.U.L. — Geological Museum, University of Leningrad, U. S. S. R.
G.M.U.K. — Geological Museum, University of Copenhagen, Denmark.
G-P.I.H. — Geological-Palaeontological Institute, Halle, East Germany.
G-P.M.B. — Geological-Palaeontological Museum, Humboldt University, Berlin, East Germany.
G.P.M.L. — Geological and Prospecting Museum, Leningrad, U. S. S. R.
G.S.M. — Geological Survey and Museum, London, England.
M.M. — Manchester Museum, England.
N.M.D. — National Museum of Eire, Dublin, Ireland.
N.M.P. — National Museum, Prague, Czechoslovakia.
O.U.M. — University Museum, Oxford, England.
P.I.M. — Palaeontological Institute, Moscow, U. S. S. R.
P.I.U. — Palaeontological Institute, Uppsala, Sweden.
P.M.O. — Palaeontological Museum, Oslo, Norway.
R.S. — Swedish Museum of Natural History, Stockholm, Sweden.
R.S.M. — Royal Scottish Museum, Edinburgh, Scotland.
S.M. — Sedgwick Museum, Cambridge, England.
S.M.F. — Senckenberg Museum, Frankfurt am Main, West Germany.
U.W. — Palaeozoological Institute, Polish Academy of Sciences and Warsaw University, Poland.

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London, September 1963

GENERAL PART

INTRODUCTION

The main purpose of the present work is to consider the Psammosteiformes in detail, but since they are a major order of the subclass Heterostraci, it would seem necessary to commence with a brief discussion of the Heterostraci as a whole, so that the psammosteids can be seen in perspective. It has long been recognized that the earliest vertebrates — the ostracoderms — can be divided into two main groups on the histology of their dermal armour, and for these groups LANKESTER (1868—70) proposed the names Osteostraci and Heterostraci. The latter were distinguished by the lack of bone-cell spaces in their dermal bone, but although they can still be recognized on the histology of their armour, it has recently been demonstrated that the dermal armour of heterostracan ostracoderms is not acellular. In fact their dermal bone does possess cell spaces, although these are spindle-shaped and have not previously been recognized as such (TARLO, 1963 *a*, 1964).

Since LANKESTER's time, it has been accepted that the ostracoderms belong to the Agnatha, and two further groups are now distinguished within them — the Anaspida and the Thelodonti. Nevertheless, the basic division proposed by LANKESTER is still in use, since the Osteostraci and Anaspida are linked together under the name Cephalaspidomorphi, while the Heterostraci and Thelodonti are separated from them under the name Pteraspidomorphi. However, the relationships of the various groups to one another and to the cyclostomes (living Agnatha) have been the subject of some controversy, and an excellent historical account of this matter is to be found in the work of KIAER & HEINTZ (1935). More recently various classifications of the Agnatha have been proposed, of which the two most important are those of BERG (1955) and STENSIÖ (1958). Nevertheless, a rather different classification from either of these is here accepted (see below). BERG's view that all the major groups of Agnatha are quite independent of one another is not agreed, but instead certain subclasses are grouped together. Furthermore, STENSIÖ's claim that the Heterostraci are related to the modern myxinoids is unacceptable, as has been demonstrated elsewhere (TARLO, 1961 *c*, 1962 *c*), and in consequence the Heterostraci are here classed as *Diplorhina*.

Superclass Agnatha (Ostracodermi + Cyclostomata)
    Class Cephalaspidomorphi (Monorhina)
        Subclass Osteostraci
        Subclass Anaspida
        Subclass Petromyzontia } Cyclostomata
        Subclass Myxinoidea }

Class Pteraspidomorphi (Diplorhina)
  Subclass Heterostraci
  Subclass Thelodonti

The Heterostraci as a whole, possess an armour of plates covering the head and forepart of the body, and in general these bony plates have a superficial ornamentation of tubercles or ridges of dentine. In the one known instance in which such ornamentation is absent however, the outer part of the armour is formed of spongy bone strengthened by pleromic or infilling dentine. Two nasal capsules are present, but outer nasal openings are found only occasionally, since in most cases the nostrils must have opened into the cavity of the mouth as in the living hagfish *Myxine*. The eyes are situated at the sides of the head, and were probably immoveable. There is a common exit for the branchial pouches at each side, at the posterior lateral corners of the carapace. The trunk and tail are covered by a series of bony scales which overlap distally, and may be strongly developed to form dorsal and ventral fulcral scales or a large spine posterior to the dorsal median plate. The scales are composed of the same tissues as the plates of the carapace. The tail is generally inequilobate, the lower lobe being the larger of the two, but in some forms the tail may be almost symmetrical. Lateral fins are not developed, but extensions of the carapace may well have served as an aid to maintaining stability.

The subclass Heterostraci is divided into a number of orders, as indicated below, which are characterized by possessing particular patterns of plates in their dermal armour.

- Subclass Heterostraci
  - Order Astraspidiformes
  - Order Eriptychiiformes
  - Order Cyathaspidiformes
    - Suborder Cyathaspidida
    - Suborder Poraspidida
    - Suborder Ctenaspidida
  - Order Psammosteiformes
    - Suborder Tesseraspidida
    - Suborder Psammosteida
  - Order Traquairaspidiformes
  - Order Pteraspidiformes
    - Suborder Pteraspidida
    - Suborder Doryaspidida
  - Order Cardipeltiformes
  - Order Amphiaspidiformes
    - Suborder Amphiaspidida
    - Suborder Hibernaspidida
    - Suborder Eglonaspidida

The Ordovician genera, which were first described by WALCOTT in 1892, all possess a carapace composed of a mosaic of small polygonal plates or tesserae. These are best exemplified by the order Astraspidiformes in which most of the dorsal shield is known from an associated specimen (EASTMAN, 1917; BRYANT, 1936). In this specimen lateral ridge plates can easily be recognized in addition to the pineal region and the sensory canal system. Unfortunately the other Ordovician forms which belong to the order Eriptychiiformes, are known only from isolated fragments and tesserae, but it would seem reasonable to assume that these too possessed a carapace composed of small plates of much the same type as those known in *Astraspis* (Ørvig, 1958*a*).

In the Silurian, there occur members of the order Cyathaspidiformes (Huxley & Salter, 1856; Kunth, 1872; Kiaer, 1930, 1932; Kiaer & Heintz, 1935; Wills, 1935; Denison, 1963). In these the carapace comprises four major plates — a dorsal, ventral and paired lateral branchials. However, the early representatives of the cyathaspids possessed main plates which show traces of their having been formed by the fusion of numerous smaller units (Rohon, 1893). This particular trend in the cyathaspids towards the fusion of small units into larger ones has been well documented by Obruchev (1945), beginning with the early genus *Tolypelepis*. Numerous isolated polygonal tesserae also occur in the same deposits as those in which the

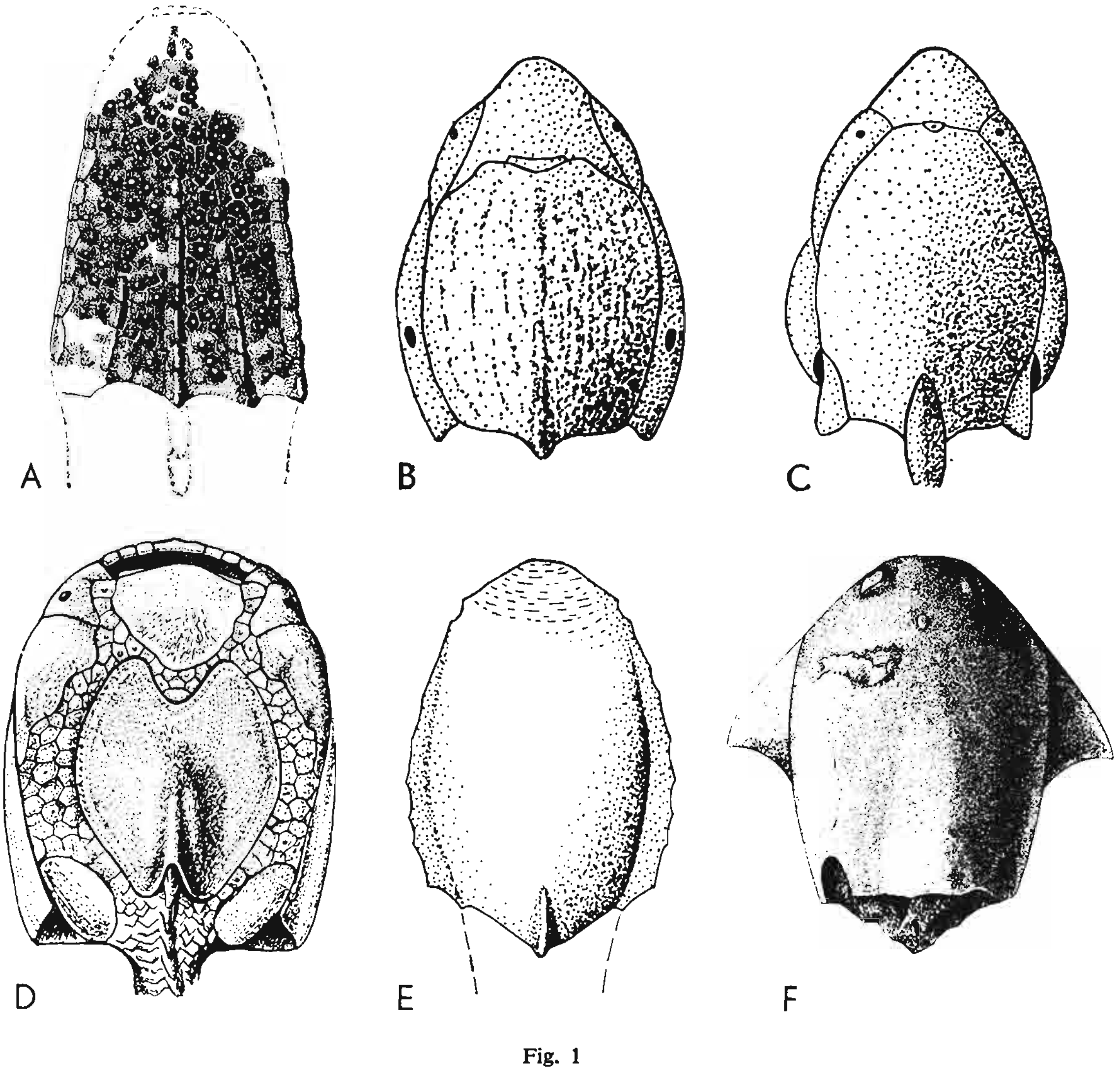

Fig. 1

Diagrams of carapace of representative heterostracans, in dorsal view (trunk and tail omitted). *A Astraspis* (from Tarlo, 1962*c*); *B Traquairaspis; C* pteraspid *Protopteraspis; D* psammosteid *Drepanaspis* (modified from Obruchev, 1943*b*); *E* cyathaspid *Ctenaspis* (from Stensiö, 1958); *F* amphiaspid *Angaraspis* (from Obruchev, 1964*a*)

Silurian cyathaspids are found, and these frequently possess an ornamentation of dentine tubercles which if found in the Devonian would be accepted as typically psammosteid. These remains were first figured by PANDER (1856) and ROHON (1893), and are here assigned to the psammosteids.

At the very top of the Silurian and in the basal Devonian is found the primitive psammosteid *Kallostrakon*, first figured by LANKESTER (1870). Also present is *Tesseraspis* a further primitive psammosteid, which was described and figured by WILLS (1935), and *Corvaspis* (WOODWARD, 1934). These as well as *Weigeltaspis* from the Lower Devonian (BROTZEN, 1933*a*) are distinguished by the fact that although their carapace is mainly composed of tesserae, these are either fused into discrete plates, or are at least organized into areas foreshadowing the plates of more advanced psammosteids. The later Psammosteiformes, the best known of which is *Drepanaspis* from the Lower Devonian (TRAQUAIR, 1903; OBRUCHEV, 1943*b*; GROSS, 1963), possess rostral, pineal, dorsal, paired orbital, post-orbital and cornual plates as well as seven oral plates on the dorsal surface, and ventral median plates on the ventral surface. Branchial plates which form part of the lateral margin extend from one surface to the other, while some part of the orbitals and post-orbitals can be seen on the ventral side. Such typical psammosteids, which continue through well into the Upper Devonian, are characterized by the possession of a zone of tesserae between the ventral and dorsal median plates and those of the lateral margins.

Again in the basal Devonian are found the Traquairaspidiformes which are closely related to, and clearly derived from the psammosteids, as evidenced by their possession of fields of tesserae in the young stages. These however are to begin with, much reduced, and they finally become incorporated into the median plates as the animals approach maturity (TARLO, 1962*c*). The traquairaspids, which were first described by LANKESTER (1868) and TRAQUAIR (1898) and were redescribed by WILLS (1935) and WHITE (1946), possess rostral, pineal, dorsal, paired orbital and fused branchio-cornual plates in addition to a basin-shaped ventral plate.

The most successful heterostracans of Lower Devonian times seem to have been the Pteraspidiformes (AGASSIZ, 1835; KIAER, 1928; WHITE, 1935; STENSIÖ, 1958; TARLO, 1961*c*), and it has been suggested (TARLO, 1962*c*) that these were also derived from the psammosteids via a traquairaspid-like form, by the reduction and final loss of the primitive tesserae seen in the young stages of this intermediate form. In the pteraspids, vestiges of tesserae still survive, but these are known only in the pre-oral region of genera such as *Loricopteraspis*. The plates present in the pteraspids are rostral, pineal, dorsal median, paired orbital, branchial and cornual, and ventral median, while as in the cyathaspids and psammosteids, oral plates also occur. In all these orders these latter are built on the same plan, exceedingly strong oral tooth lamellae being developed, and these have been illustrated in the psammosteids by TRAQUAIR (1903), STETSON (1931) and OBRUCHEV (1943*b*), in the pteraspids by KIAER (1928), STENSIÖ (1958), TARLO (1961*c*) and WHITE (1961), and in the cyathaspids by DENISON (1960) and A. HEINTZ (1962).

It is also of interest to note that in the aberrant pteraspid *Doryaspis*, the mouth is dorsal as in the psammosteids, and not ventral as in normal pteraspids. Furthermore, instead of it being bounded by normal oral plates, a long pseudo-rostrum is developed from one of the ventral elements of the carapace, producing a very long narrow snout. The posterior margin of the mouth is also bounded by the rostral plate which is sharply truncated transversely, and appears to be hinged so that it can be opened rather like a trap door. A further pteraspid genus which shows a remarkable degree of parallelism to the psammosteids is *Europrotaspis*.

This, like the psammosteids is a flat broad benthonic form, with branchial openings situated dorsally, bounded laterally by the branchial plate and medially by the cornual plate. However, in *Europrotaspis*, the cornual plate although in a similar position to that known in the psammosteids, is very much smaller. In *Gigantaspis* this reduction of the cornual plate has gone even further, since it has been completely eliminated (N. HEINTZ, 1962).

The Cardipeltiformes which are known from the upper part of the Lower Devonian of North America (BRANSON & MEHL, 1931; BRYANT, 1933; DENISON, 1953; STENSIÖ, 1958; TARLO, 1962*c*), also seem to have evolved from the psammosteids by the fusion of plates and the elimination of tesserae. In this case there is a single dorso-branchial plate, lateral ridge plates and isolated tesserae, but so far no plates are known with certainty from the ventral surface. There is every likelihood that some of the tesserae were situated anterior to the large dorso-branchial plate as postulated by STENSIÖ (1958), although DENISON (personal communication) states that from new material there seems to have been at the most only a narrow zone of tesserae in front of the dorso-branchial plate. The cardipeltid carapace however, may be on the way to the condition found in the final order in the subclass Heterostraci — the Amphiaspidiformes (OBRUCHEV, 1938, 1959, 1964*a*), which are found in the upper part of the Lower Devonian (Emsian), and the base of the Middle Devonian (Eifelian). In this order, the carapace is made up of one single unit which covers the dorsal, ventral and lateral surfaces of the animal. The cardipeltids therefore may represent a condition intermediate between primitive psammosteids such as *Corvaspis* where there are a number of separate plates in the carapace, and the amphiaspids where there can be one plate covering most of the anterior part of the body.

The cardipeltids and the amphiaspids therefore, establish the view that heterostracans with a completely fused carapace are not necessarily close relatives of the cyathaspids, but can have evolved separately. It is true that the cyathaspids show an almost comparable degree of fusion in their carapace, particularly such genera as the Lower Devonian *Ctenaspis*, in which the branchial plates have become incorporated into the dorsal plate. However, the evidence at present available suggests that the similarities between the amphiaspid and cyathaspid carapace have been achieved by different routes, although both demonstrate the end stages of an evolutionary trend towards the fusion of the plates of the dermal armour. It should be noted however that the amphiaspids are more varied than the cyathaspids, since the latter were small compact forms, while the former often reached a considerable size and many developed lateral extensions to the carapace. In addition, some amphiaspids such as *Eglonaspis* were blind and had a long anteriorly projecting tube with a terminal mouth (OBRUCHEV, 1959).

INTERNAL ANATOMY OF THE HETEROSTRACI

Despite the fact that there is a considerable amount of variation in the external appearance of the different groups of Heterostraci, many of which indicate that they must have colonized a variety of ecological niches, nevertheless they are built on much the same basic plan and form a well-defined natural grouping. As regards their internal anatomy therefore, although information is available only in certain cases, it seems reasonable to assume that the organization of the soft parts was much the same for all members of the subclass. As no soft tissues are known preserved in the Heterostraci, their disposition can only be inferred from a study of the impressions made by them on the inner surface of the plates of the dermal armour. Furthermore, these seem to be preserved only in the smaller more compact animals and in consequence are only well known in the cyathaspids and small pteraspids, although a few impressions are known in the traquairaspids and have been seen in the field in the

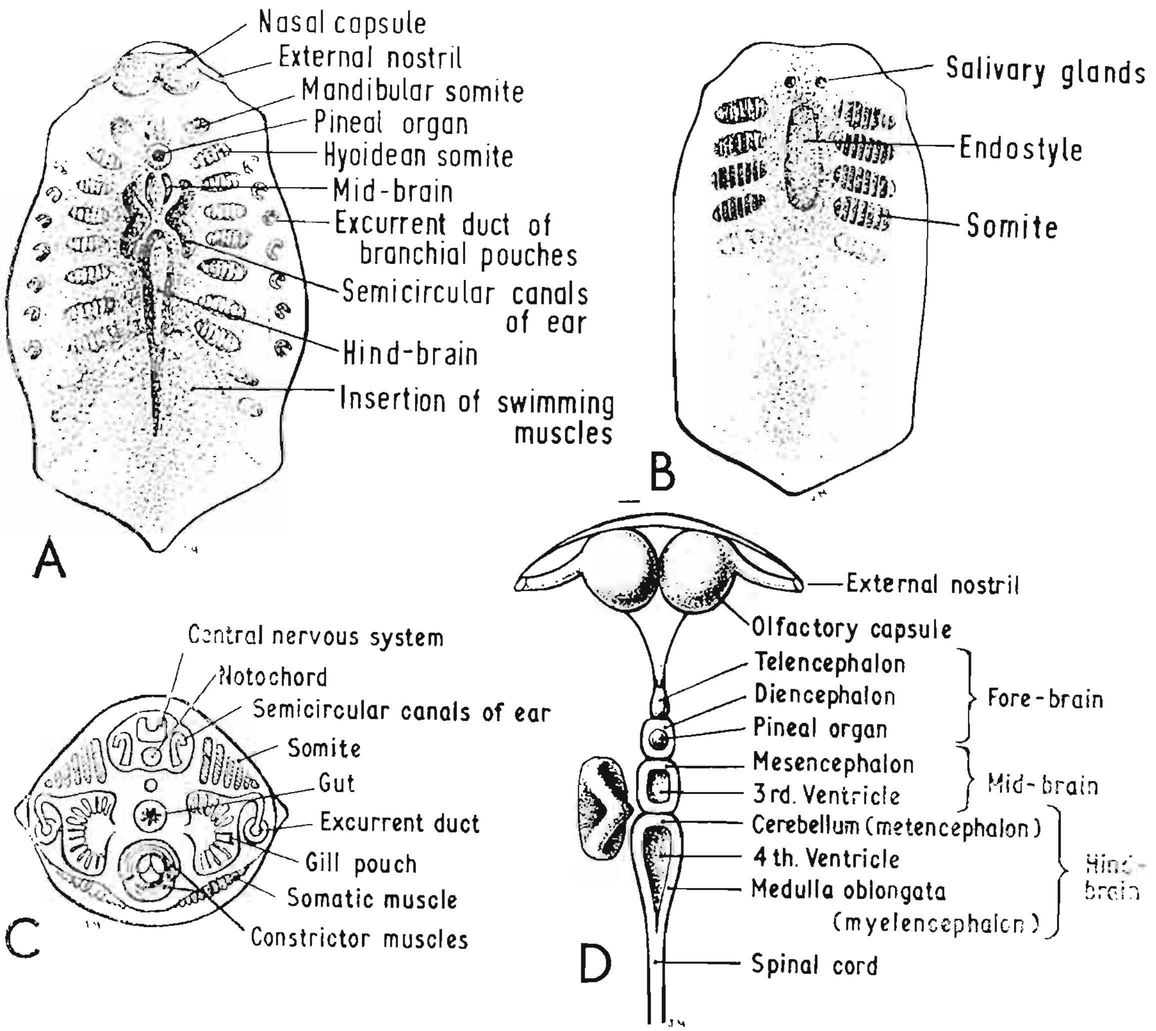

Fig. 2

A-*B* Diagrams of impressions of soft parts on internal surface of median plates of Heterostraci. *A* dorsal plate; *B* ventral plate; *C* diagrammatic cross-section of body; *D* restoration of central nervous system

psammosteid *Corvaspis*. The following account therefore is based largely on information available from the cyathaspids, although the structures are presumed to have been present in all the various heterostracan orders.

A deep pit situated midway between the orbital notches which in the cyathaspids is on the underside of the pineal macula, and in other forms is beneath the pineal plate, is obviously considered to have been made by a pineal organ (ALTH, 1874; KUNTH, 1872; WOODWARD, 1891*b*, 1898). The pair of crescent-shaped impressions on either side of, and posterior to the pineal pit are considered to have been the site of the two semi-circular canals of the auditory capsule (WOODWARD, 1891*b*), thus indicating that the Heterostraci are more primitive than the higher vertebrates which possess three such canals. A groove running longitudinally in the mid-line has been accepted by most workers to represent the position of the brain. However, there have been various restorations of the central nervous system, that of STENSIÖ (1958) being the most detailed. Recently, WHITING & TARLO (1964) have come to rather different conclusions from STENSIÖ, and consider that he was incorrect to attempt to insert the type of brain found in living cyclostomes. This has a deep flexure, which causes the hind part of the forebrain to overlie the anterior part and even project anteriorly beyond it. While it is considered perfectly reasonable to assume that the heterostracan brain is of a primitive pattern, it is considered that the contortion of the brain in living forms did not apply to the Heterostraci.

Thus, the faint depression anterior to the pineal pit thought by STENSIÖ (1958) to have been made by a single nasal sac is now considered to represent the position of the telencephalon or anterior part of the fore-brain, and the region around the pineal pit to represent the hind part of the fore-brain or thalamencephalon, or diencephalon. The impression of the mesencephalon or midbrain is thought to be that situated between the anterior pair of semi-circular canals, and was in fact so identified by KIAER & HEINTZ (1935). The marked constriction in the longitudinal groove in the mid-line in between the semi-circular canals, is believed to indicate the division between the mid and hind brain, while it is thought that the part of the groove immediately behind the constriction must be taken as the metencephalon or cerebellum, since this borders what appears to be the site of the fourth ventricle. Thus the arrangement of the central nervous system in the Heterostraci can be shown to be comparable to that known in other vertebrates, and not as STENSIÖ's restoration would make it — something unique to members of this one subclass.

The pair of round impressions towards the anterior edge of the inner surface of the dorsal shield were considered by JAEKEL (1903, 1926), KIAER & HEINTZ (1935) and WILLS (1935) to mark the position of nasal sacs, while KIAER & HEINTZ (1935) and WATSON (1954) also noted the existence of small notches at the lateral margin of the dorsal plate in front of the orbital notches, which they interpreted as nasal openings or external nostrils. Thus it would have been natural to believe the Heterostraci possessed double nasal sacs. However, STENSIÖ (1927, 1932 and 1958) has contended that the group were related to the myxinoid cyclostomes and hence had only a single nasal sac, and in consequence there has been some controversy on this question. Nevertheless, well marked grooves on either side of the month on the ventral surface of the rostrum of certain pteraspids were noted by ZYCH (1931) and have recently been described and figured by TARLO (1961*c*) as olfactory grooves, thus affording confirmation of the view that the nasal organs were paired. Furthermore GROSS (1963) figured paired nasal capsules in *Drepanaspis*, while it has also been shown that the hypothetical elements proposed by STENSIÖ (1958) to support his theory could not have existed (TARLO, 1961*c*), and that hence the Heterostraci unquestionably possessed double nasal sacs, and are not directly related to either group of living Agnatha.

On the inner surface of the ventral plate very near the anterior margin are two small pits arranged side by side which were figured by KIAER & HEINTZ (1935), while in the same position on another specimen, WILLS (1935) figured a single large pit. Although WILLS believed this to be the site of an organ or large blood vessel, it seems rather more likely that the various pits were made by salivary glands. The ventral plate also furnishes evidence of the primitive nature of the Heterostraci, since specimens figured by KIAER & HEINTZ (1935) show a longitudinal groove in the midline which TARLO & WHITING (1964) believe could only have been produced by a hypobranchial sac or endostyle. A similar although less prominent structure is found in larval lampreys, which in the adult forms the thyroid gland.

Clearly visible on either side of the midline of the dorsal plates, are a series of paired oval impressions, each of which is sub-divided longitudinally into ridges and grooves. The oval impressions were considered to have been made by a row of gill pouches (WOODWARD, 1891*b*; LERICHE, 1906; JAEKEL, 1903, 1926; KIAER, 1930, 1932; KIAER & HEINTZ, 1935; WILLS, 1935 and WATSON, 1954), while STENSIÖ (1958) thought that the longitudinal grooves had been made by gill lamellae. TARLO & WHITING (1964) however, feel that if this interpretation were correct it would mean that the Heterostraci must have been some of the most highly specialized of any vertebrates, since the musculature of this surface of the animal would have needed to have been much reduced if the gill pouches were able to make such impressions on the dorsal shield. They therefore consider that some other explanation must be sought for these impressions. Since during the ontogeny of normal vertebrates segmental muscle blocks or somites develop early on, which are always situated dorsally on either side of the notochord, then it would seem more likely that the oval impressions were made by blocks of muscle than by gill pouches. Furthermore in living cyclostomes such muscle blocks are sub-divided into longitudinally aligned sections in much the same way as the oval markings are divided in the fossils, and this would appear a more likely explanation for the impressions than that they were caused by gill lamellae. Such an explanation thus has the advantage of bringing the Heterostraci more into line with other vertebrates, while at the same time indicating the primitive nature of the subclass.

A similar series of paired oval impressions are also visible on the inner surface of the ventral plate on either side of the midline, and again these are sub-divided longitudinally. If therefore the interpretation of those on the dorsal plate are valid, then these too must have been caused by blocks of muscle. However, this creates a certain problem, since it is not normal for sufficient muscle to migrate to the ventral side of the animal to produce as strong an impression as on the dorsal side. TARLO & WHITING (1964) consider the probable explanation to be that with the development of the bony carapace encasing the entire anterior part of the body, the musculature became modified from its original locomotory function to one in which it assisted the pumping of the branchial pouches. For this purpose the muscle of the ventral side of the animal would have needed to be of some strength, since branchial pouches must have been situated on the inner side of both the dorsal and ventral muscle blocks.

The dorsal plates have a second series of paired impressions lateral to the median series, and somewhat smaller than them. These are frequently somewhat arcuate in outline, and are not divided longitudinally. Such impressions are not found on the ventral plates. These impressions have also been interpreted as having been made by gill pouches (KIAER, 1930, 1932; KIAER & HEINTZ, 1935; WILLS, 1935), but WATSON (1954) suggested that they were produced by the excurrent ducts of the individual pouches, which led at each side into the single common branchial opening at the posterior lateral margin of the dorsal carapace. This latter explanation was accepted by STENSIÖ (1958) and is no doubt the correct one, although part of the impression it likely to have been caused by the dorsal aspect of the visceral arch itself. In addition, further structures associated with these excurrent ducts made a groove on the antero-lateral part of each impression. These were interpreted correctly by STENSIÖ (1958) as being similar to structures known in the same position in the lampreys, but unfortunately he did not realize that although these structures in the lampreys had originally been thought to have been thymus glands, they are now known to be lymph nodes. Hence the grooves in the Heterostraci are now considered to have been made by lymph nodes, and not thymus glands as mentioned by STENSIÖ.

It has been suggested (SÄVE-SÖDERBERGH, 1941*b*), that the most anterior of the lateral impressions marks the excurrent duct of the first functional gill pouch, which by analogy with living vertebrates would be the hyoidean gill pouch. Hence, the paired oval impression medial and slightly anterior to it, which is situated just in front of the semi-circular canals, would mark the most posterior of the pre-otic somites, i. e. the hyoidean somite on the visceral surface of which would be the functional gill pouch. Although variously interpreted by WILLS (1935), WATSON (1954) and STENSIÖ (1958) the pair of median impressions sometimes found anterior to the hyoidean ones would seem to be best interpreted as having been made by mandibular somites not associated with gill pouches, since no paired impressions are found lateral to them. It is further suggested that a pre-mandibular somite was likely to have been present in the Heterostraci as in all other vertebrates, although no impression appears to have been made by it. This may well be due to the fact that this somite had a more ventral position than the hyoidean and mandibular somites and would therefore not necessarily have impinged on the dorsal plate. This view is supported by the fact that the impression made by the mandibular somite is considerably fainter than that made by the hyoidean one, and is often missing altogether. This suggests that there was a tendency for the somites to become more ventral in position at the anterior end of the body.

With regard to the more posterior somites, as far as can be ascertained from the fossils, these did not retain their individuality but became aligned more or less longitudinally and joined to form the main swimming muscles of the animal. As shown in STENSIÖ's restoration (1958), these seem to have been inserted on to the under surface of the dorsal plate behind the series of paired oval impressions, and their anterior limit is frequently marked by a sinuous ridge. On the other hand, the mandibular and hyoidean pre-otic somites seem to have been retained as discrete units even in the adult, a condition more primitive than that known in any living vertebrate, where the three pre-otic somites are normally transformed during development into the muscles of the eye. Although since there is no firm evidence to the contrary, there is the possibility that the premandibular somite had already migrated to the eye to form four eye muscles, it is certain that at least two of the three pre-otic somites are quite independent of the eye, and retain their primitive serial arrangement in the Heterostraci. With regard to their possession of this feature therefore, the Heterostraci are particularly noteworthy, since although it is generally accepted that the vertebrates must have passed through such a stage during the course of evolution, it is of considerable value to have preserved in the fossil record, examples of animals at that particular level of organization. The Heterostraci then, besides being some of the earliest known vertebrates, are clearly the most primitive (TARLO & WHITING, 1964).

STRATIGRAPHICAL RANGE AND GEOGRAPHICAL DISTRIBUTION OF THE HETEROSTRACI

The Heterostraci had a considerable stratigraphical range, since they extended from the Lower Ordovician through to the Upper Devonian, a period of time encompassing some 150 million years. Their remains however are comparatively rare in the Ordovician and Silurian Periods. The Ordovician forms have been placed in the orders Astraspidiformes and Eriptychiiformes (ØRVIG, 1958*a*), while in the Silurian and basal Devonian the Cyathaspidiformes predominate (Denison, 1956). A few fragments which belong to the Psammosteiformes have also been found with the cyathaspids in rocks of Silurian age. These latter flourished until the end of the Lower Devonian (Emsian) when they almost died out, although as Obruchev (1958) has pointed out, a few forms lingered on until the Middle Devonian (Eifelian). The Lower Devonian Period was also a time when the Pteraspidiformes were very successful, and in fact they were the most dominant heterostracan order from the Upper Gedinnian until the end of the Emsian (White, 1956; W. Schmidt, 1959). At that time it was believed that they became extinct, but Føyn & Heintz (1943) figured a pteraspid plate from the Middle Devonian (Givetian) of Spitzbergen, and Dineley (1955) described further similar remains from the same area.

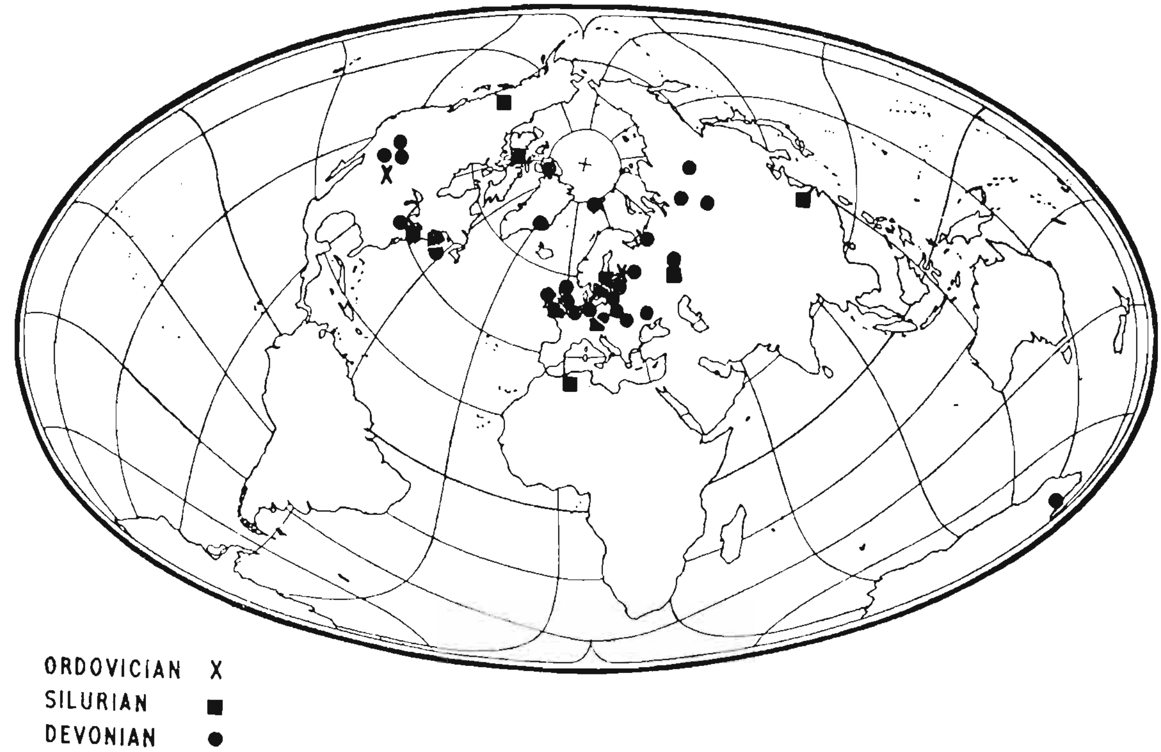

Fig. 3
Distribution of Palaeozoic Heterostraci

At the end of the Silurian, the Psammosteiformes made their first appearance. However they remained a subsidiary part of the fauna for some time, until towards the latter part of the Lower Devonian, in Siegenian and Emsian times, they began to increase in importance. Perhaps the most significant development was of a dorso-ventrally compressed form exemplified by the genus *Drepanaspis*, which successfully colonized marine lagoonal environments, while during the Emsian an isolated freshwater fauna of similar dorso-ventrally compressed psammosteids flourished in the Holy Cross Mountain region of central Poland (Tarlo, 1957). From these latter there evolved the varied psammosteid faunas centred on the Baltic Province during Middle and Upper Devonian times (Mark, 1955; Obruchev, 1958). Also in Emsian and Eifelian times a north west Siberian amphiaspid fauna flourished, spanning the Lower and Middle Devonian (Obruchev, 1958), and in fact after the end of Lower Devonian times the psammosteids alone among the fossil Agnatha can be considered to have been at all successful.

Besides possessing a long stratigraphical range, the Heterostraci are also notable for their unusually wide geographical distribution. During the Ordovician Period they occur in both North America (WALCOTT, 1892; ØRVIG, 1958*a*), and Western Russia (ROHON, 1889), while in the Silurian in addition to occurring in western Russia (Estonia, PANDER, 1856; ROHON, 1893) and North America (New Brunswick, Canada, MATTHEW, 1887, 1888); Pennsylvania, United States (CLAYPOLE, 1885, 1892); New York State, United States (BRYANT, 1926; FLOWER & WAYLAND-SMITH, 1952); Cornwallis Island, Canada (THORSTEINSSON & FORTIER, 1954) and Yukon, Canada (DENISON, 1963), they are also known in the Urals (OBRUCHEV, 1937), the Timan (KOSSOVOI & OBRUCHEV, 1962), Sweden (Gotland, LINDSTROM, 1894, 1896), Bohemia (PERNER, 1918), England (STRAW, 1927; WHITE, 1958), North Africa (Algeria, MUTVEI, 1956), and East China, Nanking (P'AN, 1961, 1962).

It was in the Lower Devonian however, that they reached their acme, and at that period they occurred in Lithuania (LIEPINS, 1959); Latvia (MARK, in litt.); Northern Siberia (BYSTROW, 1959); Kureyka-Norilsk region of North West Siberia (OBRUCHEV, 1938, 1958, 1959, 1964*a*); Podolia (Ukraine, ALTH, 1874; ZYCH, 1927, 1931); Poland (GÜRICH, 1896; TARLO, 1957, 1961*c*); Rhineland (ROEMER, 1855; SCHLÜTER, 1887; GROSS, 1933*b*, 1937, 1963); the Ardennes (LERICHE, 1906); England (AGASSIZ, 1835; LANKESTER, 1868-70; WOODWARD, 1891*b*; WHITE, 1935, 1950, 1961); Scotland (POWRIE, 1861, 1864; TRAQUAIR, 1912; WHITE, 1946, 1963; TARLO, 1960*b*); Ireland (HARPER & HARTLEY, 1938); Canada (Nova Scotia, WOODWARD, 1892; DENISON, 1955; DINELEY, 1964); United States (Utah-Wyoming, BRYANT, 1932, 1933, 1934, 1935; DENISON, 1953; Ohio, DENISON, 1960); and in Spitzbergen (LANKESTER, 1884; WOODWARD, 1891*a*; KIAER, 1928, 1930, 1932; KIAER & HEINTZ, 1935).

During the Middle Devonian the Heterostraci flourished in the Baltic Province (OBRUCHEV, 1930, 1958; GROSS, 1933*a*, 1942; MARK, 1955); Bohemia (RŮŽIČKA, 1929); United States (Ohio, WELLS, 1944*a*, *b*); in the Urals (SMIRNOV, 1948); Spitzbergen (WOODWARD, 1891*b*; FØYN & HEINTZ, 1943; DINELEY, 1955); and in Greenland (ØRVIG, 1961). In the Upper Devonian besides remaining in the Baltic Province (OBRUCHEV, 1958) the Heterostraci also became established in the Donbas (OBRUCHEV, 1958); the Timan (ROHON, 1899; OBRUCHEV, 1961); in Scotland (TRAQUAIR, 1894, 1896*b*, 1897; TARLO, 1961*a*); and in Ellesmereland (Canadian arctic, KIAER, 1915). They were also possibly in the Antarctic (WOODWARD, 1921*b*).

Due to their wide distribution throughout the northern hemisphere, members of the Heterostraci have proved of considerable value as zonal indices, particularly the pteraspids in the Lower Devonian and the psammosteids in the Middle and Upper Devonian periods. Furthermore, since the Heterostraci had a long range in time, it has been possible to trace their evolutionary history and development in some detail. This has enabled the relationships of the different orders to one another to be worked out, and in addition has allowed a number of evolutionary lines to be traced in the pteraspids and psammosteids (TARLO, 1961*c*, 1962*c*). At the same time it has become possible to follow several evolutionary trends within the Heterostraci which are applicable to the sub-class as a whole (OBRUCHEV, 1945; TARLO, 1962*d*).

HISTORY OF PREVIOUS RESEARCH

The first description and figures of psammosteid remains are due to J. J. F. W. VON PARROT, who read his «Essai sur les ossements fossiles des bords du lac de Burtneck, en Livonie» at the Imperial Academy of St. Petersburg on 27th September, 1833. According to PARROT, he first saw the specimens among other remains, at the home of Miss CAROLINE

DE BUDBERG, who had discovered them some ten years previously. He stated that he was highly pleased when «she had the kindness to make me a present of some interesting pieces which are to be found in the collection which I presented to the Academy». However, the greater part of this same collection, which at the present time is housed in the Palaeontological Institute, Moscow, was the result of the zeal of his own son WILLIAM, Pastor of Burtneck. He informed his father of fossils which had come to light after storms had swept Latvia, in particular Lake Burtneck, and had been discovered by the naturalist ULPRECHT. These PARROT was also given, and his description of the various specimens was a model of careful and painstaking work. Although he could not identify them with certainty, since he was faced with remains unlike any previously named, he came to the tentative conclusion that the armour belonged in the main to either amphibia or fish of kinds hitherto unknown. We now know that some at least of this armour formed part of the dermal covering of certain psammosteids, since fragments figured by PARROT belong to the species *Pycnosteus tuberculatus* (ROHON, 1901) and *Ganosteus stellatus* ROHON, 1901.

PARROT's account was three years in the press, not appearing until 1836, and in that same year KUTORGA published his first account of fossil vertebrates from the Dorpat region of Estonia. A second paper on the same subject appeared in 1837, and in this latter work KUTORGA figured two psammosteid fragments which clearly belong to *Pycnosteus tuberculatus* and *P. palaeformis* PREOBRAJENSKI, 1911, although he suggested that they formed part of the carapace of the chelonian *Trionyx*. Indeed, KUTORGA claimed to have identified from the same Devonian rocks remains of a mammal, crocodiles, lizards, turtles and ichthyosaurs, and in consequence propounded some rather revolutionary theories regarding the life in past geological eras. In fairness it must be admitted that some of the teeth he discovered, which are now known to belong to crossopterygians, at first glance appear rather similar to those of ichthyosaurs and crocodiles.

The next author to be concerned with psammosteids was EICHWALD, although he too misinterpreted their remains. He described specimens from the River Slawanka in 1844 and 1845, but no figures appeared until 1846. EICHWALD believed that the remains were part of the squamation of fishes, and placed them in the genera *Cheirolepis* and *Microlepis*. In fact they are fragments of psammosteid plates, and are here referred to *Pycnolepis splendens* (EICHWALD, 1844). Both AGASSIZ (1845*a*) and PANDER (1857) took EICHWALD to task for his mistake, since they considered that he should have realized that the fragments were of tubercles on the outside of bony plates. However, recent examination of the original specimens in the Geological Museum of Leningrad University indicates how easy it was for such a mistake to have been made, since the plates were very thin and the tubercles were diamond-shaped, and looked like small scales.

Also in 1844 AGASSIZ listed the names of numerous new species of Devonian vertebrates, but since these were unaccompanied by a description or any indication of which specimens were referred to, they were naturally invalid. The following year he introduced the generic name *Psammosteus* for the first time and described four species belonging to it, these being *P. maeandrinus* which is the type species of *Psammosteus*, *P. paradoxus* which is now the type species of *Psammolepis*, *P. undulata* now also referred to *Psammolepis* and *P. arenatus* which is included in the synonymy of *Psl. paradoxa*. It should also be noted that one of the fragments figured by AGASSIZ under *P. arenatus* is here referred to *Schizosteus heterolepis* (PREOBRAJENSKY, 1911). In the same work, AGASSIZ described as selachian spines under the name *Ctenacanthus serrulatus*, material which EICHWALD (1860) suggested belonged to *Psammosteus maeandrinus*, and this latter has proved to be correct. Later in 1845, there appeared a further paper by

AGASSIZ in which he described all of the same material, but this time under the names *Psammolepis paradoxus*, *Placosteus undulatus*, *Pl. arenatus*, and *Pl. maeandrinus*. Since the generic name *Psammosteus* was correctly established *Placosteus* has been taken as a junior synonym of it. Furthermore, since the material belonging to *Psammosteus paradoxus* has been shown to be generically distinct from *Psammosteus maeandrinus* (GROSS, 1933*a*), then AGASSIZ's name *Psammolepis* could be taken as being available for it, the species thus becoming *Psammolepis paradoxa*.

AGASSIZ (1845*a*) briefly discussed KUTORGA's work, but seems to have missed that of PARROT, despite the fact that it was mentioned by MURCHISON (1845). Furthermore in the Appendix of his work of 1845*a* AGASSIZ made a lengthy attack on EICHWALD from which the following is a typical extract: «...in all the descriptions of M. EICHWALD one is constantly halted by a lack of precision in the appreciation of organic characters... It would be easy for me to show that most of the genera of M. EICHWALD possess an incredible elasticity, and that in one of his Memoirs he makes, without any scruples, synonyms of such or such a genus of another author to distinguish them from a new later genus». This kind of criticism drew a spirited reply from EICHWALD (1846), as follows: «AGASSIZ described among other things the Russian fish remains sent over to him without mentioning in the least my determinations... At least he was told by me in a letter before the appearance of the third volume that the new species were already named by me... Is it perhaps that my new names attracted AGASSIZ's dislike because he himself had reserved the sole rights to the fossil fish of Russia? One would not have expected that from such a great man, therefore there must have been some other reasons, as yet unknown to me, which influenced him». Whatever the rights of AGASSIZ's case, EICHWALD's comments seem to have been well justified, at least as far as the psammosteids are concerned, since in fact AGASSIZ had made EICHWALD's species all synonyms of his own later species — the very crime of which he had accused EICHWALD! However, by great good fortune, none of the material described by these two authors happens to be conspecific, so that whatever they may have thought of each other, this had no bearing on the synonymy of the species in question.

In 1848, MCCOY described remains from Ireland under the names *Psammosteus granulatus* and *P. vermicularis*, and this material is figured for the first time in the present work. Although MCCOY's identification of this material was mentioned by later workers (PANDER, 1857; WOODWARD, 1891*b* and ROHON, 1901), it has generally been ignored, since it was thought that the fossils came from rocks of Carboniferous age, by which time it was believed all heterostracans had become extinct. This view has now been confirmed. In 1851 and 1854, MCCOY described *Steganodictyum carteri* from Lower Devonian slates of Cornwall as a polyzoan (bryozoan), although he did not figure it until 1855. It was subsequently assigned by LANKESTER (1868*a*) to the genus *Cephalaspis*, but recently it has been included in the psammosteid genus *Drepanaspis* (TARLO, 1961*c*), and is redescribed and figured in the present work.

PANDER (1856) described and figured vertebrate remains from the Upper Silurian of Estonia of which *Oniscolepis dentatus* (Syn. *O. serratus*, *O. crenulatus*, *Strosipherus indentatus*, *S. serratus*, *S. laevis*) was subsequently recognized as a psammosteid by ROHON (1893) and GROSS (1947), while *Lophosteus superbus* was assigned incorrectly to the psammosteids by EICHWALD (1860). In 1857, in a critical study of the antiarch *Asterolepis*, PANDER described a number of fragments which he assigned to *Asterolepis* in spite of the fact that he recognized that «the ground substance approaches dentine rather than genuine bone, as AGASSIZ has already quite correctly noted, contains no bone cells and the little tubercles are real tooth-like humps», and that in this respect the remains contrasted with all the other material he assigned to this genus. Hard though it may be to believe, his most telling argument was the close association of the fossils! However, this material has since been recognized as belonging to the psammosteid species *Psammosteus maeandrinus*, *Psammolepis paradoxa* and *Ganosteus stellatus*. Remains that had been recovered from erratic boulders on the north European Plain were described and figured by KADE in 1858, and these he identified as belonging to *Psammosteus maeandrinus* and *P. arenatus* (now known to be *Psammolepis paradoxa*).

In 1860, EICHWALD published further figures of the species he described in 1844, 1845 and 1846, and again rightly contended that they were different from those of AGASSIZ despite AGASSIZ's claim to the contrary. In fact all of the material described in these works by EICHWALD is now known to belong to *Pycnolepis splendens*. In the same work (1860) EICHWALD suggested correctly that AGASSIZ's *Ctenacanthus serrulatus* was the same as *Psammosteus maeandrinus*. Ten years later in 1870, LANKESTER figured two specimens which he called *Kallostrakon podura*, but he gave no description or explanation of them, and it was subsequently realized (ROHON, 1893; BYSTROW, 1955) that these belong to psammosteids. Two further specimens figured by LANKESTER in the same work, but not named, are also referable to the same genus.

There were no further important contributions on the group until 1880, when TRAUTSCHOLD described and figured the branchial plate of a psammosteid under the name *Coccosteus megalopteryx*, believing it to be a lateral spine of an arthrodire. TRAQUAIR (1890) thought it was a selachian appendage, but it was later referred to the genus *Psammosteus* by GÜRICH (1891) and WOODWARD (1891*b*). LANKESTER (1884) figured some «bony fragments» from Spitzbergen, which WOODWARD (1891*a*) subsequently recognized as being psammosteid, and which he identified as *Psammosteus arenatus*. OBRUCHEV (1964*c*) has now placed the Spitzbergen form in the species *Pycnosteus nathorsti*. In 1887, SCHLÜTER described several genera from the Lower Devonian of the Rhineland, including *Drepanaspis gemuendenensis* which he identified as a cephalaspid. TRAQUAIR (1896*a*) however, demonstrated that this genus was a relative of the heterostracan *Pteraspis*, although it should be noted that the type specimen which is figured for the first time in the present work, looks at first glance rather like a cephalaspid.

WOODWARD (1891*a*) described some material from Spitzbergen under the name *Psammosteus arenatus*, and as previously noted, included in this species some fragments described earlier by LANKESTER. The Spitzbergen *Psammosteus arenatus* however, has since been referred by OBRUCHEV (1964*c*) to *Pycnosteus nathorsti*. In 1891*b* WOODWARD listed the known psammosteid species and made a valiant attempt to bring order to the confusion of specific names. However, his unique record of *Psammosteus* from the Middle Devonian Wick Flags cannot be substantiated, and in fact TRAQUAIR (1894) when he saw the specimens considered that they were from a Russian locality. Mr H. A. TOOMBS (personal communication) provides the following explanation of WOODWARD's record; the specimens in question «were given the wrong numbers, just a clerical error when they were registered. The number should be 43453 [not 42453 as listed in WOODWARD, 1891*b*] and under this number in the Register is the entry '*Psammosteus arenatus*', Old Red Sandstone. Riga. Russia'...». WOODWARD (1891*b*) also erroneously suggested psammosteid affinities for the Middle Devonian arthrodire spines described by NEWBERRY (1875, 1889) from Ohio. ROHON (1893) revised PANDER's (1856) work on the Oesel fauna, recognizing only two species — *Oniscolepis dentata* and *O. serrata* — as valid, out of PANDER's original six. ROHON compared *Oniscolepis* with *Kallostrakon* and suggested possible psammosteid affinities for these two genera. He also discussed the histology of the psammosteid carapace, noting the presence of spindle-shaped structures which he interpreted as «fibrebundles», although he did make the point that «one can convince oneself of the presence of simple bone cells», but later in the same paper he withdrew this idea. The presence of bone cells however, has recently been demonstrated (TARLO, 1963*a*, 1964).

The first genuine record of a psammosteid from Scotland was provided by TRAQUAIR (1894) when he described and figured a dorsal median plate of *Psammosteus taylori* from the Upper Old Red Sandstone. This species has recently been shown (TARLO, 1961*a*) to be conspecific with *Psammosteus megalopteryx.*

In the following year (1895), WOODWARD gave a description of the psammosteid remains in the Geological Museum of the University of Dorpat (Tartu), which are now housed in the Geological Institute at Tallinn. He figured and described the median shield of a form he identified as *Psammosteus paradoxus,* the specimen being the original from which a papier-maché cast had been made and given to MURCHISON during his journey to Russia in the 1840's. This cast later enabled TRAQUAIR to recognize *Psammosteus* from near Elgin, and is now preserved in the British Museum (Nat. Hist.), London. Not being aware of WOODWARD's earlier work, PREOBRAJENSKY (1911) figured and described as *Dyptychosteus tessellatus,* the original specimen. This has recently been given the new name *Psammosteus markae* by TARLO (1961*a*). In the same paper of 1895, WOODWARD also described under the name *Psammosteus arenatus,* an unusual plate from the Dorpat collection in the following terms: «It looks, indeed, like one end of a keel-less boat with the maximum bendings thickened; and where it tapers towards what would be the middle of the boat, the centre of the floor is excavated by a long re-entering angle». He also noted that this same species occured in Spitzbergen. The specimen described by WOODWARD was also described by PREOBRAJENSKY (1911) who made it the type of the new genus and species *Pycnosteus palaeformis.* Since WOODWARD's reference of the plate to *Psammosteus arenatus* was incorrect, PREOBRAJENSKY's name is the valid one. The material from Spitzbergen is also referable to the same genus, although to a different species.

GÜRICH (1896) described *Psammosteus* sp. from the Lower Devonian of central Poland, but although its occurrence was mentioned by SOBOLEV (1909), KIAER (1915) and CZARNOCKI (1937), it was overlooked until 1957 when figures of the material were published for the first time by TARLO, together with a preliminary discussion of the significance of these remains. In the present work they are referred to *Guerichosteus kozlowskii* and *Hariosteus kielanae.* In 1896*a* TRAQUAIR established the heterostracan affinities of *Drepanaspis* from the Rhineland, and in the same year (1896*b*) he described and figured further remains of *Psammosteus* from Scotland. Besides a second dorsal median plate of *Psammosteus taylori* (now placed in *P. megalopteryx*) he figured a small lateral plate which he did not attempt to name, but which has since been identified as *Psammosteus falcatus* OBRUCHEV, 1947*a*, by TARLO (1961*a*). In this paper, TRAQUAIR introduced the family name Psammosteidae (frequently supposed to have been erected in 1899).

Descriptions and figures of the remains of further Scottish psammosteids were given in 1897 by TRAQUAIR. These included the external ornamentation of tubercles found on polygonal tesserae in *Psammosteus taylori* (= *P. megalopteryx*) and the ornament of the two new species *Psammosteus tesselatus* and *P. pustulatus. P. tesselatus* has recently (TARLO, 1961*a*), been referred to *Psammolepis undulata* and *P. pustulatus* is assigned to the new genus *Traquairosteus* in this work. In 1898, TRAQUAIR described *Psammosteus anglicus* from the Lower Devonian of the Welsh Borderland, but subsequently WILLS (1935) demonstrated that it was conspecific with *Cyathaspis symondsi* LANKESTER (1868), which however did not belong to either *Cyathaspis* or *Psammosteus.* Instead he showed that it was a heterostracan different from either of these, and proposed the new genus *Phialaspis* for its reception. WHITE (1946) redescribed *Phialaspis symondsi* and also a new species of the same genus, and noted the close similarity of the ornamentation to that seen in *Traquairaspis*, while GROSS (1947) showed that fragments described by BROTZEN (1934) under the names *Orthaspis plana* and *Lophaspis crenulata* were congeneric with WILLS' *Phialaspis*. Later WHITE & TOOMBS (1948) realized that *Phialaspis* should be placed in the genus *Traquairaspis* (erected by KIAER (1932) for the reception of *Cyathaspis campbelli* described by TRAQUAIR (1912)). The Traquairaspidiformes are now recognized as an order of the Heterostraci separate from the Psammosteiformes, although it has recently been demonstrated that they represent a group intermediate between the psammosteids and the pteraspids (TARLO, 1962*c*).

In 1899, ROHON described and figured psammosteid remains from the Timan, and at the same time introduced the family name Psammosteidae, not being aware of TRAQUAIR's work of 1896. The species identified by ROHON as *Psammosteus arenatus* is now known to belong to *Psammosteus praecursor* OBRUCHEV (1947*a*), but his *P. undulatus* was correctly diagnosed. ROHON's new species *Psammosteus ornatus* was tentatively assigned to the genus *Tartuosteus* by OBRUCHEV (1961), but in the present work the new genus *Rohonosteus* is proposed for its reception. The first restoration of *Drepanaspis* was produced by TRAQUAIR in 1899, but unfortunately, as was later realized, this was upside down. However, he erected the family Drepanaspidae to receive this genus and in the same work showed that the Psammosteidae were related to the Drepanaspidae and hence could also be placed within the Heterostraci. TRAQUAIR's contribution ended doubts that were prevalent regarding the affinities of the psammosteids, since before that time AGASSIZ (1845*a*) had considered them to be coelacanths, TRAUTSCHOLD (1880) had thought that they were arthrodires, WOODWARD (1891*b*, 1895) had looked upon them as armoured sharks, while even TRAQUAIR himself (1890) believed them to be the armour of elasmobranchs.

WOODWARD (1900) when reviewing TRAQUAIR's paper of the previous year, correctly took him to task for suggesting that the postero-lateral plates (branchials) were homologous to pectoral fins, and also argued correctly against his view of the elasmobranch origin of the Heterostraci. WOODWARD preferred COPE's (1889) assignation of this group to the Agnatha. Again in 1900, TRAQUAIR gave a more detailed description of *Drepanaspis*, and this time considered that the antero-lateral plates bearing a round opening were not «?orbits» as he had previously and correctly believed, but instead were sensory plates. Since the work of TRAQUAIR there have been many attempts to restore *Drepanaspis*, but the only significant difference between the later versions and that of TRAQUAIR is the addition of small polygonal plates between the «mental» (rostral) and «median ventral» (dorsal) plates. Later in 1900 in his Presidential Address to the Zoological Section of the British Association, TRAQUAIR discussed the evolution of the Heterostraci, and postulated a general trend towards the fusion of small elements in the carapace to form a mosaic of small plates, and later patterns of large plates. In this concept TRAQUAIR anticipated many of the more recent contributions on the subject of evolutionary trends in the development of dermal armour (OBRUCHEV, 1945; STENSIÖ, 1958; TARLO, 1960*b*, 1962*d*) although for some years STENSIÖ (1927, 1932), WHITE (1935), STENSIÖ & HOLMGREN (1936), HEINTZ (1938) and others, believed the opposite view to be correct.

When reviewing knowledge of the psammosteids up to that date, ROHON (1901) discussed their histological structure and introduced the generic name *Ganosteus* for the two new species *G. stellatus* and *G. tuberculatus*. Later, *G. tuberculatus* was transferred to the genus *Pycnosteus* by OBRUCHEV (1940). In the following year (1902) TRAQUAIR published further details on *Drepanaspis* and in 1903 he wrote his major work on the genus. This was discussed by innumerable authors, including KEMNA (1903, 1904), BRIDGE (1904), EASTMAN (1904), ABEL (1909, 1912, 1919, 1920, 1924), DOLLO (1909), GOODRICH (1909), and KOKEN (1911). These authors all agreed in the main with TRAQUAIR's observations and conclusions. Only DEAN (1904) pointed out that in fact TRAQUAIR had figured *Drepanaspis* upside down. TRAQUAIR (1905) defended his orientation of this animal at considerable length, but in spite of this, later work supported DEAN's view. Nevertheless, as late as 1931 a figure of *Drepanaspis* was still being reproduced in the reversed position by WELLS, HUXLEY & WELLS.

The histology of *Psammosteus* was briefly mentioned by GOODRICH (1908) who figured a fragment of the dermal armour of this genus together with a section of *Pycnosteus palaeformis*. In 1911 WOODWARD made a major contribution to the study of the psammosteids with his description of the first associated *Psammosteus* carapace. This belonged to *Psammosteus taylori (= P. megalopteryx)* and although the figure was incomplete, it assisted OBRUCHEV (1947*a*) in his attempted restoration of the ventral surface of *Psammosteus praecursor*. A re-examination of WOODWARD's original specimen has resulted in a further attempt at a restoration (TARLO, 1961*a*) and a corrected version is provided in the present work, together with figures of the actual carapace. It should be noted that in his work of 1911, WOODWARD tentatively suggested that the branchial plates might have been moveable, a view of some importance when considering the evolution of moveable appendages.

As has already been mentioned, PREOBRAJENSKY described in 1911, the material in the Dorpat University Museum, without being aware of WOODWARD's previous account of this material (a fact pointed out by EASTMAN in 1917). PREOBRAJENSKY provided excellent figures of the material, particularly of *Pycnosteus palaeformis* and also erected the new species *Psammosteus imperfectus*. However, an examination of the type material, now housed in Tallinn, demonstrates that this species is identical to *Pycnosteus palaeformis* (previously suggested by GROSS, 1940*b*). Further, PREOBRAJENSKY's new species *Psammosteus heterolepis* was transferred to the genus *Psammolepis* by GROSS (1933*a*), but was later placed in the genus *Schizosteus* by OBRUCHEV (1940). In addition, as mentioned above, PREOBRAJENSKY's *Dyptychosteus tessellatus* is a species of *Psammosteus*, and since the name *Psammosteus tesselatus* had already been used for a different species by TRAQUAIR (1897), the new name *Psammosteus markae* has been proposed (TARLO, 1961*a*).

In 1915, KIAER described two new psammosteids from the Upper Devonian of Ellesmere Land in the Canadian Arctic. These he named *Psammosteus arcticus* and *P. complicatus*. In the present work the material assigned to *P. arcticus* is referred to *Psammolepis arctica* and the new species *Psammosteus kiaeri*, while *P. complicatus* is placed in the new genus *Rohonosteus*. KIAER discussed in some detail the question of the confusion of the dorsal and ventral sides of *Drepanaspis*, and was able to show conclusively that DEAN's interpretation was the correct one. KIAER also achieved the distinction of making the only known microscopic sections of *Drepanaspis* (normally the material of this genus is found pyritized and cannot be sectioned satisfactorily, see BYSTROW, 1959). In consequence KIAER was able to demonstrate the similarity of the microstructure of *Drepanaspis* to that of *Psammosteus*. Also in 1915 DOSS described and figured as *Psammosteus arenatus*, the dorsal median plate of what has subsequently been identified by GROSS (1933*a*) as *Psammolepis undulata*. Then in 1917, EASTMAN pointed out that PREOBRAJENSKY had described the same material in the Dorpat Museum as that previously figured and described by WOODWARD in 1895.

STENSIÖ (1918) introduced the name *Psammosteus spinosus* as a further species of *Psammosteus* from the Middle Devonian of Spitzbergen, but since he gave no figures or description, this name is a *nomen nudum*. In any case however, *P. spinosus* and *P. arenatus* although listed separately by GROSS (1950), are both the same species, and as has been shown by OBRUCHEV

(1964*c*), belong to *Pycnosteus nathorsti*. The genus *Drepanaspis* was briefly discussed by WOODWARD (1921*a*), and in this work he recognized branchial openings for the first time and also considered that the mouth in this genus was situated ventrally, in consequence of which in his restoration he joined the oral plates on to the rostral plates, and in this aspect of his work was followed by STENSIÖ (1927). In his next paper (1921*b*), WOODWARD described and figured isolated denticles from the Upper Devonian of the Antarctic, and suggested elasmobranch or ostracoderm affinities for them. GROSS (1950) thought they might be psammosteid, and in fact a recent re-examination of the specimens indicates that they represent a heterostracan, and since all other groups were extinct by the Upper Devonian, presumably a psammosteid. As mentioned above, in 1927, STENSIÖ also discussed *Drepanaspis* and in the main he followed WOODWARD's (1921*a*) interpretation. In addition he discussed the histology of the bone-like material of the dermal armour of heterostracans, and concluded that the absence of cell spaces was a secondary feature, and that in fact the tissue was true bone in which such cells must have been present in the early part of development, but had then been lost. Recently it has been shown (TARLO, 1963*a*, 1964) that in fact the tissue is not acellular, and is not secondarily specialized but is instead a primitive one. Further work was carried out on *Drepanaspis* by KIAER (1928) and this time he postulated a terminal mouth for this animal, while PATTEN (1929) said that the mouth was dorsal and also stated that a pineal plate was present.

Also in 1929, RŮŽIČKA described a psammosteid from the Middle Devonian (Eifelian) of Bohemia under the name *Psammosteus (Ganosteus) perneri*, but this material is here referred to the genus *Schizosteus*. In the following year GROSS provided the first detailed account of the histology of the psammosteids, and described in particular what he called «massiv-spongiosa» and «wucherdentin» (termed pleromic and eruptive dentine respectively by TARLO & TARLO, 1961). At the same time GROSS introduced the term «aspidin» for the bone-like tissue of the dermal armour, and also re-described the species *Psammosteus paradoxus*, complete branchial and ventral plates of this form being figured in this work for the first time. He considered that the dorsal part of its carapace must have been very steeply arched, while the ventral was much less so. In the same paper GROSS described the new species *Psammosteus heteraster*. In 1931, STETSON demonstrated that the mouth of *Drepanaspis* was actually on the dorsal surface of the animal. Moreover, he added further details to the existing description of the mouth plates and the anterior ventral plates of the carapace (see GROSS, 1963), and his figure of the rostral region shows that small plates are present between the rostral and dorsal plates. His restoration gave the animal a symmetrical tail, and although this may be the case in certain specimens, generally the lower lobe is somewhat larger than the upper.

HEINTZ (1932) pointed out that the ventral surface of the carapace in *Psammosteus paradoxus* was more convex than the dorsal surface — the reverse of the view put forward by GROSS (1930) — but the specimen of a dorsal shield on which he based this assumption was not described until 1957. In this same work (1932), HEINTZ also sketched part of the associated carapace previously described by WOODWARD (1911), but unfortunately he incorrectly identified the lateral plates as cornuals. PATTEN made a further contribution in the same year, by providing a restoration of *Drepanaspis* which showed that the rostral and dorsal plates were separated by a pineal plate surrounded by small tesserae. He also showed splayed-out oral plates and small olfactory notches. Since the restoration was merely a figure in a popular article published posthumously, it has been difficult to confirm. However, a pineal plate is also known in the contemporaneous *Guerichosteus* and in the later *Psammolepis* and *Psammosteus*, and very recently GROSS (1963) has described such plates in *Drepanaspis*, which are highly variable. With regard to the oral plates, it is considered unlikely that these were so widely spaced, and so far olfactory notches as figured by PATTEN have not been confirmed. PATTEN also made the tail a normal heterocercal one, which was a retrograde step, since it had been known even by such early authors on *Drepanaspis* as TRAQUAIR that the longer lobe of the tail pertained to the surface containing the majority of the plates, i. e. what is now known to be the dorsal surface.

A further major contribution on the psammosteids was made by GROSS (1933*a*) in which work he restored the generic name *Psammolepis* separating it from *Psammosteus* itself. He also erected the following new species: *Psammolepis gigantea* (assigned by OBRUCHEV (1961) to the genus *Tartuosteus* of which it is now the type species), and *Psl. striata* (placed by OBRUCHEV (1940) in the genus *Schizosteus*). In addition GROSS described *Psammolepis paradoxa*, *Psl. heteraster*, *Psl. undulata*, *Psl. heterolepis* (now referred to *Schizosteus*), *Psammolepis imperfecta* (now referred to *Pycnosteus palaeformis*), *Pycnosteus palaeformis*, *Psammosteus maeandrinus* (assigned to the new species *P. falcatus* by OBRUCHEV (1947*a*)), *P. megalopteryx*, *P. ? serrulatus (= P. maeandrinus)*, and *Ganosteus tuberculatus* (remains given this name by GROSS have been referred to *G. stellatus* and *Pycnosteus tuberculatus* by OBRUCHEV (1940)). Later in the same year, GROSS (1933*b*) described the new species *Drepanaspis schrieli* from the Lower Devonian of the Rhineland, and this species was also mentioned by GROSS (1933*c*) and SCHMIDT (1933). In the same year OBRUCHEV described and figured a new psammosteid from the Upper Devonian of the Leningrad region under the name *Karelosteus weberi*, and BROTZEN described the new genus and species *Weigeltaspis alta* from the Lower Devonian of Podolia (now Ukraine). He erected the new family Weigeltaspidae for its reception, and considered that it was closely related to the psammosteids. It should be noted that although WHITE (1935) considered *Weigeltaspis* to be an arthrodire, he later (1946) recognized its heterostracan nature. Further, the plate originally thought by BROTZEN to be a branchial, is now known to be the median dorsal plate (TARLO, 1962*c*). WOODWARD also in 1933 described *Psammosteus* from the Lower Devonian of Little Missenden, England, but this material, as suggested by DENISON (1956), can now be seen to be a fragment of an acanthodian spine.

In 1934, WOODWARD described the new form *Corvaspis kingi* as a cyathaspid, and subsequently DINELEY (1953) erected the new family Corvaspidae for its reception. More recently however, this genus has been assigned to the psammosteids (TARLO, 1960*b*). Again in 1934 BROTZEN described and figured a psammosteid under the name *Lophosteus mutabilis* which is here referred to the genus *Tesseraspis*. In the following year GROSS (1935) published a further study of the microstructure of the dermal armour of the psammosteids, while WILLS (1935) described and figured *Tesseraspis tessellata* from the «Downtonian» of Shropshire, England. He suggested that this genus was closely related to the psammosteids, and in this view has been followed by subsequent authors (e. g. ØRVIG, 1961; TARLO, 1962*c*) although DENISON (1956) considered the form to be that of a cephalaspid, while OBRUCHEV (in TARLO, 1961*a*) did not agree that it was a psammosteid.

A detailed study of the Ordovician genera *Astraspis* and *Eriptychius* was given by BRYANT in 1936, which showed that these genera can be distinguished on their histology. He concluded that they were closely related to the psammosteids, but were primitive forms. In the present study as well as in previous works (TARLO, 1960*a*, 1961*a*, 1962*c*), it has been shown that the psammosteids could have developed from forms with a carapace like those known in *Astraspis* and *Eriptychius* by retaining some of the tesserae, although most of these fused to form the large plates found in the later genera. Also in 1936, OBRUCHEV gave a brief description of *Aspidophorus heckeri* from the Upper Devonian of the Leningrad region, but since this generic name was preoccupied he later (1941) gave a fuller description under the name *Aspidosteus* *heckeri*. Unfortunately although this name has been used in the literature it too is invalid, since WHITLEY (1940) had already introduced the valid name *Obruchevia* for the form in question. In 1937, GROSS erected the new species *Drepanaspis lipperti*, while in 1938 HEINTZ produced a restoration of *Drepanaspis* in which he brought the oral plates closer together than in the restoration of PATTEN (1932).

OBRUCHEV (1940) erected the new genus *Schizosteus* with the type species *S. asatkini*, and at the same time assigned *Psammolepis striata* to this genus and tentatively included all EICHWALD's psammosteid material in *S. splendens*. He also incorrectly placed PREOBRAJENSKY's *P. imperfectus* tentatively in *Schizosteus*, but as mentioned earlier this material is conspecific with *Pycnosteus palaeformis*. In the same work, OBRUCHEV transferred *Ganosteus tuberculatus* to the genus *Pycnosteus*. In the following year OBRUCHEV described the late Devonian *Aspidosteus heckeri (= Obruchevia heckeri)* in which the armour possessed no superficial dentine tubercles. Instead as he showed, the outer part of the normally middle layer of aspidin-bone was infilled with a type of secondary dentine. This strengthening has been discussed by BYSTROW (1955) and TARLO & TARLO (1961), the latter authors terming it pleromic dentine. Originally, as shown above, OBRUCHEV (1936) named the form *Aspidophorus heckeri*, but WHITLEY (1940) recognizing *Aspidophorus* was already preoccupied, proposed the new name *Obruchevia*, which name is valid despite the fact that OBRUCHEV (1941) gave a fuller description under the name *Aspidosteus*. At first this genus was assigned to the Cardipeltidae which OBRUCHEV included in the psammosteids. When he did this, he orientated the wider part of the median plate of *Cardipeltis* anteriorly so that it conformed to the median plate of *Obruchevia [Aspidosteus]* and the normal psammosteids. DENISON (1953) however, showed that the orientation of the median plate in *Cardipeltis* should be with the broad end posterior. This resulted in STENSIÖ (1958) orientating the median plate of *Obruchevia [Aspidosteus]* with its wider part as the posterior one. In point of fact, *Obruchevia [Aspidosteus]* is a psammosteid and the wider part of its plate should be anterior, while *Cardipeltis*, to which it is not closely related, has its wider end posterior (see TARLO, 1962*c*).

GROSS (1942) described a branchial plate as belonging to *Schizosteus* (?) n. sp. but this can now be assigned to the genus *Yoglinia*. He also corrected the information on *Psammosteus maeandrinus* and *P. serrulatus* given in his work of 1933 with information provided by OBRUCHEV, while at the same time he figured two branchial plates using the names *Psammosteus grossi* and *P. falcatus* provided by OBRUCHEV. These two latter species however, were not validated until OBRUCHEV's paper of 1947*a* appeared (see also TARLO, 1961*a*). In the following year (1943*a*) OBRUCHEV described the new form *Yoglinia bergi* as a pteraspid, although it was later recognized to be a psammosteid (MARK, 1955; TARLO, 1957; OBRUCHEV, 1958). Later in the same year (1943*b*), OBRUCHEV produced a new restoration of the Lower Devonian *Drepanaspis* which is by far the most satisfactory of all attempts. The occasional presence of a pineal plate is not indicated, but apart from this and GROSS's (1963) correction of the details of the oral region it is unlikely that there will be any important modifications to it. STENSIÖ (1958) suggested that there was a soft rostrum in *Drepanaspis*, and in consequence that the mouth would have been situated ventrally rather than dorsally, but as has been pointed out (TARLO, 1961*a*) there is neither evidence nor need for such a structure. In the following year (1944), OBRUCHEV attempted a restoration of *Psammolepis* based on dorsal, ventral and branchial plates only. Although subsequent discoveries made by Dr. ELGA MARK show that the entire complement of plates normally found in the psammosteids is actually present in this genus, the overall shape of the body as depicted by OBRUCHEV is still to be preferred to that seen in the restoration of MARK (1958). Also in 1944, WELLS described and figured some small psammosteid fragments from the Middle Devonian beds of Ohio. These are referred in the present work to *Schizosteus wellsi*, and appear to be comparable to material from Idaho sent to the author by Dr. R. H. DENISON, and figured in the present work with his kind permission.

In his paper on the evolution of the Agnatha, OBRUCHEV (1945) discussed the derivation of the later psammosteids from the *Drepanaspis* condition and also suggested the possible derivation of the group from the advanced pteraspids. This latter view has been contested by TARLO (1961*a*, 1962*c*). Furthermore in the same work OBRUCHEV illustrated the branchials of *Psammosteus megalopteryx* showing various degrees of abrasion. Later (1947*a*) OBRUCHEV produced the first attempt at a restoration of *Psammosteus* itself, based on WOODWARD's (1911) description and figures and on the ventral median plate and branchial of *P. praecursor*. Unfortunately the median plate is incorrectly orientated, since the narrow «neck» should be placed posteriorly (see TARLO, 1961*a*, 1962*c*). In his paper OBRUCHEV in addition gave diagnoses and figures of the following species of *Psammosteus*: *P. maeandrinus*, *P. praecursor* n. sp., *P. megalopteryx*, *P. falcatus* n. sp., and *P. grossi* n. sp. In the same year (1947*b*) OBRUCHEV published an account of Russian psammosteids in the Atlas of Guide Fossils..., in which excellent figures were given of the following species, in particular of their ornamentation: *Schizosteus striatus*, *Psammolepis paradoxa*, *Ganosteus stellatus*, *Pycnosteus palaeformis*, *Pycnosteus tuberculatus*, *Psammosteus maeandrinus* and *Psammosteus megalopteryx*. He also figured for the first time the distinctive elongated branchial tesserae which are characteristic of *Psammosteus*. Although published in 1947, this Atlas was not available outside the Soviet Union until 1956, having until then been considered as classified material. GROSS (1947) redescribed *Strosipherus indentatus (= Oniscolepis dentata)*, first figured by PANDER (1856), as a primitive psammosteid related to *Tesseraspis*.

A redescription of *Corvaspis* was given by DINELEY in 1953, and the new species *C. graticulata* was erected by him. He showed that this genus could no longer be assigned to the cyathaspids, but although he noted its similarity to the psammosteids instead of including it in that group, he erected the new family Corvaspidae for its reception. However, as indicated above, the genus *Corvaspis* is now assigned to the psammosteids (TARLO, 1960*b*). In 1955, BERG in his Classification of Fishes erected the families Aspidosteidae and Tesseraspidae to include members of the genera *Aspidosteus* (= *Obruchevia)* and *Tesseraspis* respectively. In the same year too, MARK published an abbreviated account of a thesis on the psammosteids of Estonia. In this work numerous new species were described and the evolution and stratigraphical range of the group was considered. Unfortunately since it is not an official publication, this important work has no standing for the purpose of zoological nomenclature, although it has been quoted by several authors (OBRUCHEV, 1958, 1961; TARLO, 1961*a*). Again in 1955, BYSTROW gave a detailed account of the microstructure of the psammosteids, including the genera *Kallostrakon*, *Corvaspis*, *Psammolepis* and *Aspidosteus (= Obruchevia)*. He discussed what is now called pleromic and eruptive dentine (see TARLO & TARLO, 1961) and the nature of the cells — aspidinoblasts — which produced aspidin.

In the following year (1956) BYSTROW published further figures of histological sections of psammosteid dermal armour, in a work on fossil saprophytic fungi. Also in 1956 MARK described the genus *Pycnosteus* and the species *Pyc. palaeformis* and *Pyc. tuberculatus* and erected the new species *Pyc. pauli*. However, she still retained *Pyc. imperfectus* as an independent species although it is now known that it is conspecific with *Pyc. palaeformis*. HEINTZ (1957) gave a detailed description of the dorsal shield of *Psammolepis paradoxa* and at the same time figured MARK's restoration of the genus. This showed for the first time the full complement of plates in *Psammolepis* — the same as already known in *Drepanaspis*, although the proportions of the plates were rather different. Also in 1957 TARLO briefly described and figured Lower Devonian psammosteids from central Poland, and the two forms figured in that work are here referred to *Guerichosteus kozlowskii* and *Hariosteus kielanae*.

In an article on Devonian sandstones of Estonia, MARK (1958) figured specimens of *Pycnosteus* and a more life-like restoration of *Psammolepis* which had been drawn for her by Professor BYSTROW, based on her original restoration. This figure has since been reproduced by ROMER (1959) and TARLO (1962*b*). In the same year, STENSIÖ (1958) discussed the psammosteids, and since he was not at that time aware of MARK's work or her restoration, he believed that no rostral, orbital, post-orbital or cornual plates were present in psammosteids later than *Drepanaspis* (i. e. the psammosteids found in the Middle and Upper Devonian). Instead he considered that these plates had either become fused to other plates and had lost their separate identity, or else had been broken down into small tesserae to become indistinguishable. Naturally MARK's work makes such theories unnecessary.

BYSTROW (1959) described a fragment of a Lower Devonian psammosteid from Siberia, and in the same year LIEPINS described a fragment from the Lower Devonian of Latvia. In the following year TARLO discussed the genus *Corvaspis* and assigned it to the psammosteids, while in 1961 *(a)* he redescribed the psammosteids from Scotland and assigned them to species already known in the Baltic province. These were *Psammosteus megalopteryx* (formerly *P. taylori*), *Psammolepis undulata* (formerly *P. tesselatus*), *Psammosteus falcatus* (formerly *Psammosteus* sp.). In addition he redescribed *Psammosteus pustulatus* which is known only from Scotland, and proposed the new name *P. markae* for *Psammosteus tessellatus* (PREOBRAJENSKY). At the same time he attempted the first complete restoration of the carapace of *Psammosteus*, based on the associated carapace originally described by WOODWARD in 1911, and described and figured part of the sensory canal system. Also in 1961, ØRVIG described and figured the new genus and species *Psephaspis williamsi* from the Lower Devonian of Utah, U.S.A., and in this work he discussed the early genera *Tesseraspis* and *Weigeltaspis*. He concluded that the former was a psammosteid, but that the latter was of uncertain affinities. However, TARLO (1961*a*, 1962*c*) showed that in fact *Weigeltaspis* belonged to the psammosteids. ØRVIG also figured a psammosteid fragment from the Lower Devonian of Podolia (Ukraine), and recorded a *Psammolepis* fragment from Greenland. These remains are here referred to *Tesseraspis orvigi* and *Psammolepis groenlandica* respectively.

In the same year (1961) OBRUCHEV finally erected the genus *Tartuosteus*, which name had been appearing in the literature since 1943, but had never been validated. This genus was for the reception of *Psl. gigantea*, and OBRUCHEV's work included a description of the complete sensory canal system in the dorsal median plate of *Tartuosteus*. He also tentatively assigned *Psammosteus ornatus* from the Timan to *Tartuosteus*, but in the present work this species is made the type of the new genus *Rohonosteus*. In 1962 TARLO discussed the classification of the psammosteids and their evolution, and showed in particular that separate lineages can be recognized from a study of the ventral median plates. In this work the new families Psammolepididae and Pycnosteidae were erected.

GROSS (1963) gave a detailed account of the morphology of *Drepanaspis*, based on much new material, and showed that the oral plates were quite distinct from the plates of the anterior margin on the ventral surface of the carapace. He also figured several pineal plates, and the impressions of paired nasal capsules on a rostral plate. GROSS in addition produced a new restoration of the genus with an almost symmetrical tail, and with the branchial plates produced laterally, in contrast to the section given by TARLO (1961*a*) where these plates are downturned.

GROSS also refigured the immature specimen previously described by KUTSCHER (1933) with its pteraspid-like appearance, and agreed with OBRUCHEV (1943*b*, 1945) that the psammosteids could have been derived from the pteraspids, a view strongly opposed in the present work. TARLO (1963*a*, 1964) discussed the nature of aspidin, showing that it possessed simple spindle-shaped bone cells and that there was a gradual evolution of the organization of the matrix to the condition found in bone. Together with B. J. TARLO (1963, 1964) he also discussed the significance of eruptive dentine. OBRUCHEV (1964*b*) described and figured the branchial plates of *Obruchevia [Aspidosteus]* and contrary to expectation these proved to be long and narrow and markedly bent from side to side, resembling sleigh runners. This confirmed that the genus represents a sidebranch of the later psammosteids quite separate from the main psammosteid (s. s.) lineage. In a further work (1964*c*) OBRUCHEV gave a comprehensive description of the Middle Devonian psammosteid from Spitzbergen previously identified by WOODWARD (1891*a*) as *Psammosteus arenatus*, and assigned it to the new species *Pycnosteus nathorsti*. In 1964 OBRUCHEV & MARK published their account of the Middle and Upper Devonian psammosteids from the Baltic region, and much of the new material they described has been incorporated into the present work with their kind permission.

CLASSIFICATION OF THE PSAMMOSTEIDS

The first formal designation of the psammosteids as a separate group was made by TRAQUAIR (1896*b*), when he introduced the family name Psammosteidae, although at the time the affinities of the group were not known. Subsequently (1899) TRAQUAIR established that the Psammosteidae belonged to the Heterostraci, and at the same time introduced a further family within this grouping, — the Drepanaspidae. Later still it was generally accepted that the Psammosteidae and Drepanaspidae were synonymous although certain text books, such as BRIDGE (1904) and GOODRICH (1909) still followed TRAQUAIR and listed the two families separately. KOKEN (1911) and KIAER (1915) used the collective term Psammosteidae, while STENSIÖ (1927) used Drepanaspidae for them. KIAER later (1932) raised this group of the Heterostraci to the rank of suborder and employed the term Psammosteida, while BERG (1940) raised them still further, making the Psammosteiformes an order with the families Psammosteidae (syn. Drepanaspidae), Weigeltaspidae (a name introduced by BROTZEN, 1933*a*), and Cardipeltidae (introduced by BRYANT, 1933, as a major division within the Heterostraci). In 1941, OBRUCHEV retained the Psammosteida as a suborder and recognized four families within it: the Psammosteidae, Drepanaspidae, ?Weigeltaspidae and Cardipeltidae. (The Cardipeltiformes are now taken to be a separate order within the Heterostraci (DENISON, 1953; STENSIÖ, 1958; TARLO, 1962*c*)).

DINELEY (1953) introduced the family Corvaspidae as an independent group within the Heterostraci and STENSIÖ (1958) raised it to ordinal status with the name Corvaspida, but TARLO (1960*b*) suggested that *Corvaspis* belonged to the psammosteids, and later (1962*c*) placed the family Corvaspididae within the Psammosteiformes. BERG (1955) still retained his order Psammosteiformes with the families Psammosteidae, Weigeltaspidae and Cardipeltidae, but also included within it the new family Aspidosteidae and tentatively the family Tesseraspidae although he thought it might perhaps deserve independent ordinal status. STENSIÖ (1958) considered that the psammosteids belonged to the order Drepanaspida, and also recognized an important division between *Tesseraspis* on the one hand, and the «post Downtonian»

Drepanaspida on the other, based on the type of carapace found. However, TARLO (1962*c*) used BERG's Psammosteiformes and divided it into two sub-orders: the Tesseraspidida, to which were assigned the families Tesseraspididae, Weigeltaspididae and Corvaspididae, and the Psammosteida, in which were placed the families Psammosteidae, Aspidosteidae and Drepanaspididae as well as the new families Psammolepididae and Pycnosteidae. In the present work a further new family is proposed — the Guerichosteidae, and the new name Obrucheviidae is introduced to replace Aspidosteidae.

When considering the morphology of the carapace, it is quite clear that the psammosteids fall into two well defined groups, and this is reflected in the present classification. On the one hand there are the forms divided off as the Psammosteida, in which the carapace is composed of a set pattern of fairly large plates and in which there is a mosaic of small tesserae separating the median plates from those of the lateral margins. On the other hand are those forms grouped as Tesseraspidida, which mark the morphological stages between the primitive unspecialized tessellated carapace, and the later full complement of plates. Professor OBRUCHEV considers that only the forms in the sub-order Psammosteida can strictly be taken as psammosteids, but in the present work it is considered that the forms approaching the condition found in the members of the Psammosteida can with all justification be included in the same overall grouping. Hence these are brought within the order Psammosteiformes, but are separated off as the sub-order Tesseraspidida.

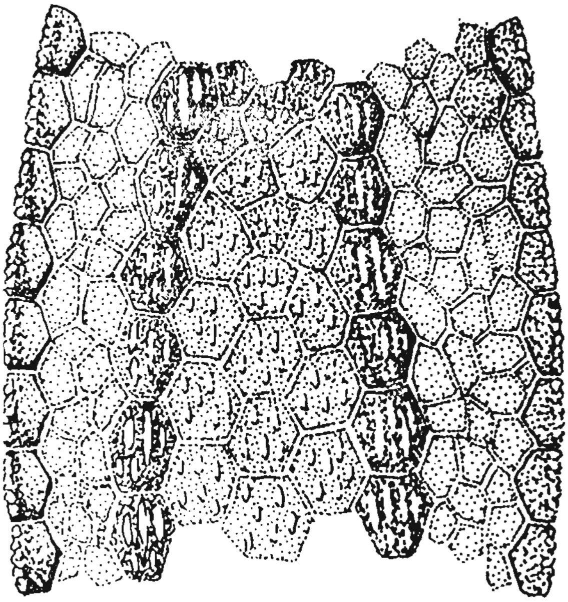

Fig. 4

Tesseraspis tessellata WILLS — part of dorsal carapace showing organization of tesserae into regions (after TARLO, 1962*c*)

The greatest difficulty to be overcome when discussing the members of the Tesseraspidida, is the fact that as yet no complete carapace is known for any member of the group, which could serve as a point of reference for the various families within this sub-order. The nearest approach is in the genus *Tesseraspis* in which WILLS (1935) described various parts of the carapace, showing that groups of different types of discrete tesserae were found in natural association. From his described material and further specimens collected by him, it is possible to give some indication of the relationships of the different types of tesserae to one another (see Text- fig. 4). What is already clear in *Tesseraspis* is that even though the entire carapace is composed of separate tesserae (and it is for that reason placed in the family Tesseraspididae) these are already differentiated and organized into areas foreshadowing the discrete plates seen in later forms. In the median areas of both the dorsal and ventral surfaces the tesserae are thick and possess an ornamentation of large tubercles, and on the ventral side there are two parallel rows of gently arched tesserae bordering the median area. Between these and the sharply angulated tesserae of the lateral margin there are fields of thin tesserae ornamented by small tubercles, and in some specimens such fields of tesserae are also present on the dorsal surface. Unfortunately due to the rarity of associated areas, it is not possible to state how far the differentiation and organization into areas has gone, and if for example precursors of cornual, or rostral plates were present. Nevertheless, what is perfectly clear is that between the differentiated groups of tesserae of the lateral margin and those of the median areas, there are well defined fields of tesserae. Since these are also present in the carapace of the more advanced forms which possess discrete plates, then such fields of tesserae can be taken as characteristic of the order Psammosteiformes as a whole.

A further stage in the development of plates is seen in *Kallostrakon*. Here also, different types of tesserae are known although they have not been found in natural association, but even more important is the fact that on occasions fully formed discrete plates have been discovered. These show evidence on their external surface that they were formed during development by the fusion together of smaller elements, and hence illustrate the way in which the plates known in the advanced psammosteids came to be evolved. *Kallostrakon* is closely related to *Corvaspis* in which again distinct plates are known, these also having been formed by the fusion of separate tesserae. In *Corvaspis* a variety of plates have been recognized, including large orbitals, branchials, and median plates. In addition, fields of tesserae are presumed to have existed although none are actually known, since medium plates are frequently found in which single tesserae have become incorporated into the margins. *Corvaspis* clearly represents a stage further towards the typical psammosteid condition, and is placed in the family Corvaspididae. It should perhaps be noted however that in the details of its ornament (discussed in a later section) *Corvaspis* is becoming specialized towards the condition found in *Cardipeltis*, and instead of leading directly to the later psammosteids is already beginning to branch off from the main line.

A later genus, *Weigeltaspis*, first described by BROTZEN (1933*a*) seems to have been derived from a form close to *Tesseraspis*, since its ornamentation is much the same as that of some of the tesserae in that form. Well developed dorsal median plates are known as well as orbital, post-orbital and branchial plates, but so far cornual and rostral plates have not been recognized. The plates of *Weigeltaspis* do not show a superficial division into tesserae as is the case in *Corvaspis* and *Kallostrakon*, and it seems, as far as present knowledge goes, to be the closest to the later typical psammosteids. For this reason it is placed in the family Weigeltaspididae. One feature of some of the species of *Weigeltaspis*, particularly *W. heintzi*, is that the ornamentation is very similar to that of *Traquairaspis symondsi*, and as noted by ØRVIG (1961) there is some suggestion of a relationship between these genera. As argued elsewhere however (TARLO, 1962*c*), *Traquairaspis* is not included in the psammosteids, but is considered to represent a sidebranch from the primitive Psammosteiformes. It probably evolved from a form like *Tesseraspis*, but one in which fusion and consequent elimination of tesserae had commenced, since in *Traquairaspis* tesserae are present only in the young stages, and then become incorporated into the main plates as the animal approaches its definitive size. *Weigeltaspis* is also probably derived from a form fairly close to *Tesseraspis*, but one which continued on the main psammosteid line.

Thus, although perhaps since only parts of the carapace are known, it could be considered unsatisfactory to group these three families with the Psammosteida in the order Psammosteiformes, nevertheless there is strong justification for this policy. It is true that the Tesseraspidida could be set on one side and considered entirely separately from the typical psammosteids, but these latter must ultimately be derived from forms in which the entire carapace was tessellated. Hence the families Tesseraspididae, Corvaspididae and Weigeltaspididae, can be taken to represent morphological stages which link the members of the Psammosteida with primitive forms, of the same structural grade as *Astraspis* and *Eriptychius* from the Ordovician.

The Psammosteida are best exemplified by *Drepanaspis* from the Lower Devonian (Siegenian-Emsian) and the contemporary *Guerichosteus*, and include all later members of the order Psammosteiformes. As already mentioned the Psammosteida all possess a definite pattern of plates as well as fields of tesserae, and although it can be modified in various ways, the basic arrangement of these plates is the same for all members of the sub-order. *Drepanaspis*, the most detailed and extensive study of which is due to Gross (1963), is the only psammosteid in which the entire carapace, trunk and tail are known (Traquair, 1903; Obruchev, 1943*b*), and in consequence it has come to be used as a standard with which to compare all other members of the group. Its overall outline is like that of a stool-ball or table tennis bat, and in section it is compressed dorso-ventrally. Its carapace is fairly square, with rounded antero-lateral margins and it has a rather short trunk and a deep almost equilobate tail. The carapace is very flat, with an overall dorsal convexity, but the ventral plate is slightly more convex than the dorsal plate, although this view is contested by Gross (1963) (see Text-fig. 5).

Drepanaspis possesses on the dorsal surface oral plates, a rostral plate, pineal plate and dorsal median plate, while at the lateral margins are paired lateral marginal, orbital, post-orbital, branchial and cornual plates, these latter being separated from those in the mid-line by fields of small tesserae. Present on the ventral surface is a ventral median plate, besides extensions of the branchial plates and the margins of the lateral marginal, post-orbital and orbital plates. On both surfaces the fields of tesserae posterior to the median plates grade into the squamation of the hind part of the trunk and tail. Large fulcral scales form a ridge in the mid-line of both the dorsal and ventral sides of the trunk, and are extended into short spines. The tail is almost equilobate, the lower lobe however being the longer of the two. The mouth is situated dorsally, and oral tooth lamellae which are dorsal extensions of the oral plates form the anterior margin of the mouth, the posterior margin being formed by the rostral plate. The oral plates themselves form the floor of the anterior part of the mouth. They are not visible on the ventral surface of the carapace (Gross, 1963).

The rostral plate is somewhat arcuate in outline where it borders the mouth, and in front of it are two pairs of small pre-rostral plates. The sides of the rostral plate are roughly parallel and they then converge gently to form a rounded posterior angle. Separating the rostral plate from the dorsal median plate is a zone of tesserae. Within this zone a fairly large pineal plate which is variable in shape, is sometimes found situated in the mid-line in the re-entrant angle at the anterior margin of the dorsal median plate. This latter plate is a wide oval shape, with a broad re-entrant angle at its anterior margin and a lesser one at the posterior margin. In the posterior median part of the plate there is a gentle ridge which is confluent with the dorsal ridge of fulcral scales. At the antero-lateral margin of the carapace there is a triangular orbital plate with the orbit facing laterally and slightly dorsally. In front of this plate is a small lateral marginal plate which almost reaches the antero-lateral margin of the rostral plate. The slight gap between these plates at the margin of the mouth may well be an olfactory notch, since it is situated to the side of the paired nasal sacs figured by GROSS (1963). Abutting the straight posterior margin of the orbital plate is a fairly long, roughly triangular plate with a straight anterior margin — the post-orbital — which also forms part of the lateral margin. Occasionally these two plates may be partially fused to one another (GROSS, 1963). The median border of the post-orbital plate is irregular and tapers posteriorly and its postero-lateral border adjoins the antero-median border of the branchial plate. The lateral marginal, orbital and post-orbital plates curve gently round the lateral margin so that they are partly visible on the ventral surface. The branchial plate appears on the dorsal surface as a long narrow plate forming the main part of the lateral border of the carapace. Posteriorly it delimits the branchial opening, and against its postero-median edge is situated the roughly oval or oblong cornual plate which bounds the branchial opening postero-laterally. At the lateral border the branchial plate turns at a sharp angle and on the ventral surface is produced

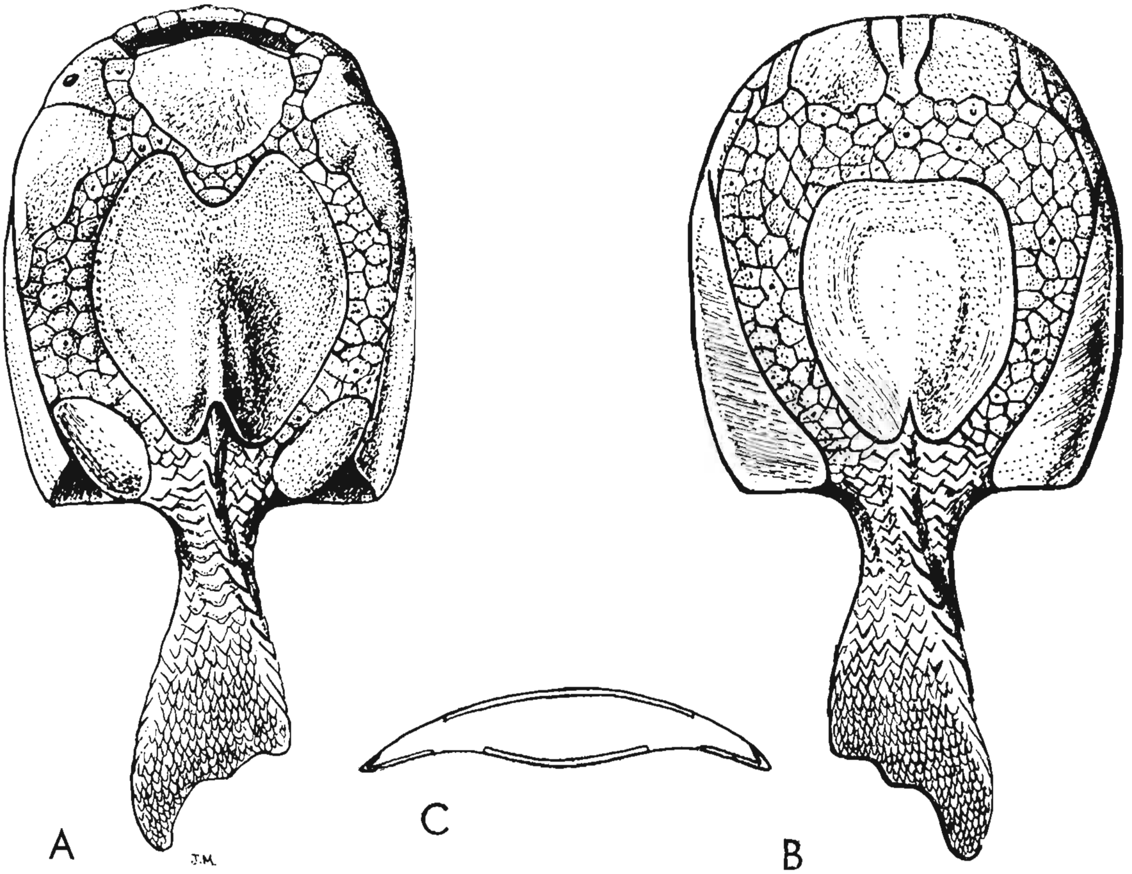

Fig. 5

Drepanaspis gemuendenensis SCHLÜTER — *A* restoration, in dorsal view; *B* in ventral view (modified from OBRUCHEV, 1943*b*); *C* diagrammatic cross-section (from TARLO, 1961*a*) into a well marked postero-median flange which forms the ventral margin of the branchial opening. Between these plates of the lateral margin and the median plate is a zone of tesserae continuous with that separating the rostral and ventral median plates.

On the ventral surface, most of the anterior margin of the shield is formed by five main plates. The median plate («median tesserae») is Y-shaped and is bounded on either side by a pair of large, broad, almost square plates («complex plates») and laterally by a pair of small, slightly sigmoidal plates («median marginal plates»). On their visceral (dorsal) surface are situated seven oral plates with very strong oral tooth lamellae which form the anterior margin of the dorsally situated mouth. Closely associated with the most lateral of the oral plates are a median and a lateral marginal plate which latter, as already mentioned, extends on to the dorsal surface. There is a wide zone of tesserae separating the most anterior ventral plates from the ventral median plate and also the ventral median plate from those forming the lateral margins. The ventral plate itself is roughly oval in outline, but is truncated transversely both anteriorly and posteriorly although the anterior margin of the plate is wider than the posterior margin. At this latter margin there is a narrow, deep re-entrant angle or posterior notch. This feature however, is very variable, and is not always present. In OBRUCHEV's restoration (1943*b*) it is filled in by a small lancet-shaped anal plate, the existence of which has not yet been confirmed. Behind the ventral plate there are again median ridged fulcral scales, and tesserae which grade into the squamation.

The type of dermal armour seen in *Drepanaspis*, which belongs to the family Drepanaspididae, demonstrates the basic plan of the carapace in all the families within the Psammosteida, these being distinguished from one another only on the varying proportions of the different plates. In the family Guerichosteidae which includes the genera *Guerichosteus*, *Hariosteus*, and *Schizosteus*, the main difference from the drepanaspids lies in the fact that the carapace as a whole is less quadrangular, since the branchial plates are somewhat wider and their lateral parts are solid and free, and are drawn out into sheets which project laterally from the body, and are downturned. The limb of the branchial plate on the ventral surface is also more expanded medially in its posterior part, and the impression is given that the dorsal limb of the plate has fused to the lateral part of the ventral limb and this latter has then grown further medially. As it happens the branchial plate of *Guerichosteus* was not produced in this way, as can be seen from a series of growth stages. To begin with the branchial plate is like that known in *Drepanaspis* and as it develops there is a progressive thickening or infilling of calcified tissue at the angle at the lateral margin of the carapace. By the time the adult is reached the solid part of the plate extends as far medially as the median edge of its dorsal limb. In *Guerichosteus* the dorsal and ventral limbs of the branchial plates are still at a considerable angle to one another, but in the later *Schizosteus* they have become more nearly parallel, while the freely projecting margin of the plate is both thinner and more laterally extensive. As far as the ventral median plates are concerned, in both *Guerichosteus* and *Schizosteus* these are characterized by a well developed, fairly wide, open posterior notch.

In *Guerichosteus* a lozenge or diamond-shaped pineal plate is known in which the major axis is transverse, as well as isolated oral plates which appear narrower than those known in *Drepanaspis*. In *Guerichosteus* also, the cornual plates seem to be square rather than oval or oblong. In the young stages of *Schizosteus* the ventral median plate is slightly convex like that of the adult *Drepanaspis*, but in the adult *Schizosteus* the lateral and anterior parts of the plate become more steeply inclined, so that the plate finally takes on the shape of a shallow bowl. In its convexity the ventral median plate of *Guerichosteus* is closer to that known in *Drepanaspis*, although in its open posterior notch it is similar to that of *Schizosteus*. In addition, the deepening of the ventral plate in the guerichosteids together with the downturning of the extended branchial plates produces a deeper carapace than that seen in *Drepanaspis*. From within the guerichosteids two major lineages developed — the pycnosteids and the psammolepids. In the Pycnosteidae the branchial plate is somewhat wider and shorter than in *Schizosteus*, with very thin lateral extensions which are downturned. In consequence the carapace has become wider posteriorly and the postero-lateral corners have become more drawn out. With the shortening of the branchial plate there is a concomitant and compensatory increase in the length of the post-orbital plate. In the latest species of *Pycnosteus* the branchial plate has become shorter and wider and the anterior margin concave, with even wear on both dorsal and ventral surfaces.

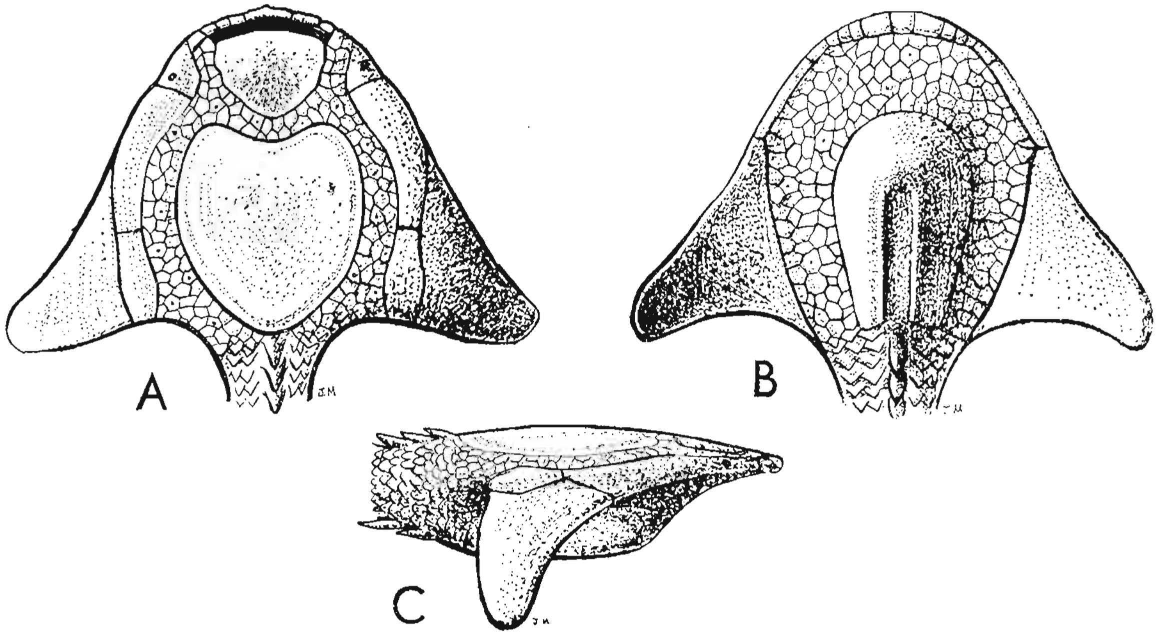

Fig. 6

Pycnosteus tuberculatus (Rohon) — *A* restoration, in dorsal view; *B* in ventral view; *C* in lateral view

In *Ganosteus* the branchial plates are comparable to those in the early members of *Pycnosteus*, although in the later species the postero-lateral corner is drawn out distally into a posteriorly directed spine. In *Ganosteus* also, the cornual plates seem to be similar to those in *Guerichosteus*, being more or less square in outline, although one very large specimen seems to have a large anterior extension which has grown on to it. The Pycnosteidae are characterized by a deep ventral plate which can be compared with a keel-less rowing boat, with its wider end anterior (Text-fig. 6). This plate has a long, persistent posterior notch (Preobrajensky, 1911), which can be secondarily infilled with tesserae as in *Tartuosteus* (Obruchev, 1961). The plate in the young stage was small and round with a wide posterior notch, but since during development the main areas of growth were the two postero-lateral projections on either side of the notch, this resulted in the plate appearing to have separate prongs on either side of a very exaggerated long notch. The plate as a whole is flat in its median part, but has very steep lateral sides and a sharply inclined anterior margin. *Pycnolepis* appears in its ventral medium plate to represent a stage intermediate between *Schizosteus* and a typical *Pycnosteus*, but since it is quite obviously well on the way to the typical pycnosteid condition, it is here included in the Pycnosteidae.

In *Pycnosteus* and *Ganosteus* the posterior notch remains wide, and particularly in *Pycnosteus* itself the part of the plate bordering the notch is downturned to form two solid runners which in the later species of *Pycnosteus* may be several centimetres below the main level of the plate (Text-fig. 7). These must have been used by the animal for gliding along the substratum.

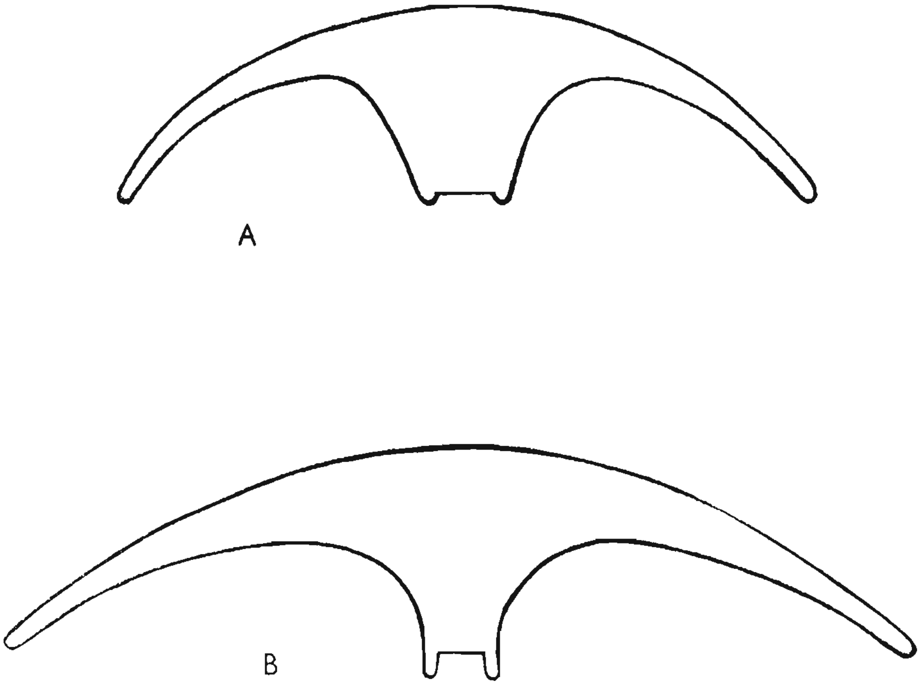

Fig. 7
Diagrammatic cross-sections of carapace — *A Pycnosteus palaeformis* PREOBRAJENSKY; *B Pycnosteus tuberculatus* (ROHON); (from MARK, 1956)

In *Tartuosteus*, the general shape of the ventral median plate is as in *Pycnosteus*, but the long posterior notch is very much narrower and becomes gradually infilled with secondary tesserae. Within this genus are found the largest of all heterostracans, since the branchial plates can measure 58 cm across, and the ventral median plates can be as long as 45 cm, suggesting a probable overall length of some 160 cm. Sometimes identified as belonging to *Tartuosteus* is *Yoglinia*, which is known only from branchial plates and a few fragments. The branchial plates are extremely short and wide and their distal extremities are frequently upturned; in the character of these plates this genus seems close to the much later *Psammosteus* itself, but since the fragments of plates are very similar in appearance to those known in *Tartuosteus* with which they can easily be confused, in the present work *Yoglinia* is tentatively placed in the Pycnosteidae.

In the Psammolepididae the branchial plate is again wider and shorter than in *Schizosteus*, and may also be gently arched from side to side. In this group too the post-orbital plate has lengthened, and it has now become roughly as long as the branchial plate. The post-orbital is now more or less oval in outline, and since its lateral edge is overturned it forms an important part of the margin of the carapace. In addition the two plates are no longer in the same plane on the dorsal surface, since the post-orbital plate appears to sit on the anterior part of the branchial plate at a marked angle, thus increasing the overall curvature of the dorsal carapace.

The full complement of plates found in *Drepanaspis* is also known in *Psammolepis* (HEINTZ, 1957), and a pineal plate is present of much the same shape as that known in *Guerichosteus*. In the young stage the ventral median plate of *Psammolepis* is circular with a broad shallow posterior notch similar to that known in *Schizosteus asatkini*, and as the animal grows the plate increases in size by the addition of scale-like tesserae. These first fill in the notch and then extend posteriorly to form a long narrow plate, which is usually oval or oblong (Text-fig. 8). In the most advanced species of *Psammolepis* — *Psl. undulata* — the young *Schizosteus*-like stage is no longer visible, the entire plate being formed of superficial scale-like tesserae. This young stage in fact becomes progressively smaller when the species of *Psammolepis* are traced through time, as it is most marked in the earliest forms. When considering the dorsal median plate, exactly the same trend can be followed. In the early members of *Psammolepis* the initial growth area is more or less circular with a broad shallow excavation at the anterior margin, and as the animals grow the area comes to be relatively small compared with the plate as a whole, and tends to occupy a more anterior position. In the earlier species of *Psammolepis* this initial growth area comes to be situated in the adult just anterior to the centre of the plate, while in the later species the area becomes progressively smaller and comes to

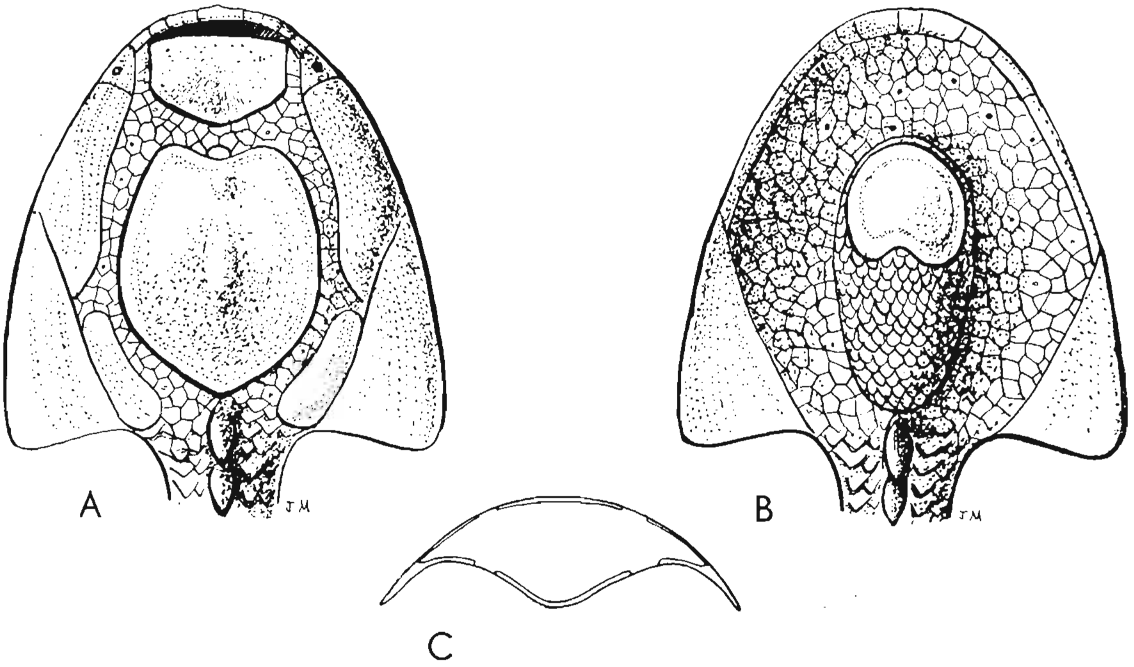

Fig. 8

A Psammolepis venyukovi OBRUCHEV — restoration, in dorsal view (after MARK, 1958); *B Psammolepis paradoxa* (AGASSIZ) — restoration, in ventral view; *C* diagrammatic cross-section (from TARLO, 1961*a*) lie closer and closer to the anterior margin. In the latest species — *Psl. undulata* — the stage is reached where there is no sign at all of the initial growth area, the entire plate being covered in superficial tesserae.

The family Psammosteidae which seem to have originated from the Psammolepididae are characterized by the extreme width and shortness of their branchial plates. From *Guerichosteus* through the psammolepids to the members of the Psammosteidae, there is a gradual shortening and widening of these plates, so that by the time *Psammosteus* itself is reached they are just solid arcuate plates forming the postero-lateral corners of the carapace. Unlike the branchial plates of the forms already considered, the greater part of the branchial plates of *Psammosteus* are enclosed within the carapace, only the distal tips projecting free. The ventral surface of the proximal part of the plate is generally covered with characteristically elongated tesserae (Obruchev, 1947*b*), but the proximal part of the dorsal surface seems to have been covered by soft tissue. The free distal tip was subjected to a considerable amount of wear, and since in many examples this wear has produced two facets more or less at right angles to one another, this indicates that the plates must have been capable of a certain degree of movement (Text-fig. 9). In this respect therefore, the psammosteids seem to have been the only heterostracans to develop, albeit in a rudimentary manner, some sort of moveable paired appendages. With the shortening of the branchial plate there was a compensatory increase in the length of the post-orbital plate, and this came to take up the major part of the lateral margin.

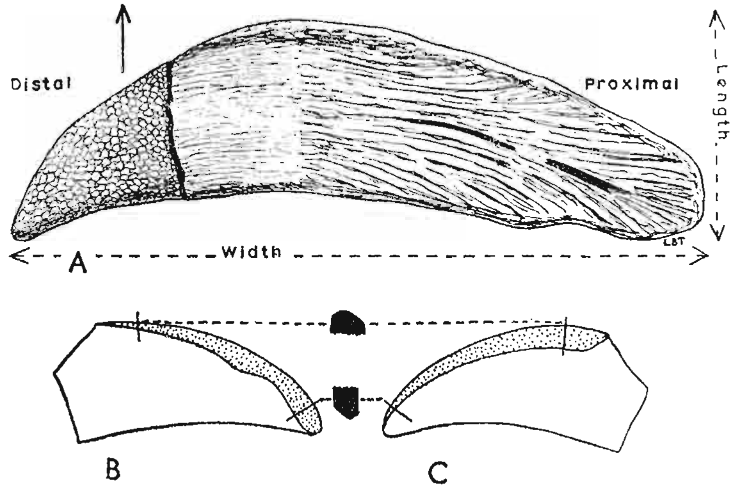

Fig. 9

A-C Psammosteus megalopteryx (Trautschold) — *A* branchial plate (R.S.M., 1904.2.10, Whitemire); × 1; *B-C* distal tip of branchial plate showing zones of abrasion on two adjacent surfaces (P. I. M. Colln., Stolbovo), × 0·75; *B* ventral view; *C* dorsal view

The ventral median plates are elongated and flat in their median region, but then curve gently upwards at the sides, so that as with the pycnosteids and psammolepids there must have been a concavity between the lateral margins of the carapace and the main part of the ventral median plate. The ventral plate in the earliest species, *Psammosteus praecursor*, is rather flask-shaped with the wide end anterior (Text-fig. 10*D*), and in this respect is similar to the ventral median plate in *Psammolepis undulata.* Also as in this last species of *Psammolepis*, in the ventral plate of *Psammosteus* there is no evidence of an initial growth area like that seen in *Schizosteus* and the other species of *Psammolepis*, and in consequence no posterior notch developed. With regard to the dorsal median plate in *Psammosteus* although it is only completely known in one species, *Psammosteus megalopteryx*, it is clear that it was extremely variable in shape. In some instances the plate is almost flat, long and narrow, while in others it is very strongly convex from side to side. In this latter case although at first glance this is contrary to the situation found in the psammolepids and pycnosteids which have a more or less flat dorsal plate, nevertheless the overall convexity of the dorsal surface of the carapace remains much the same as in those two groups. In the pycnosteids and psammolepids it is the great laterally projecting branchial sheets which give the entire carapace its dorsal convexity, but in the case of *Psammosteus* since the branchial plates are reduced in length and only their distal tips are free, the overall convexity is provided by the dorsal median plate. Furthermore, although the overall shape of the carapace of *Psammosteus* is comparable to that of earlier families, the animal is now more compact (Text-fig. 10).

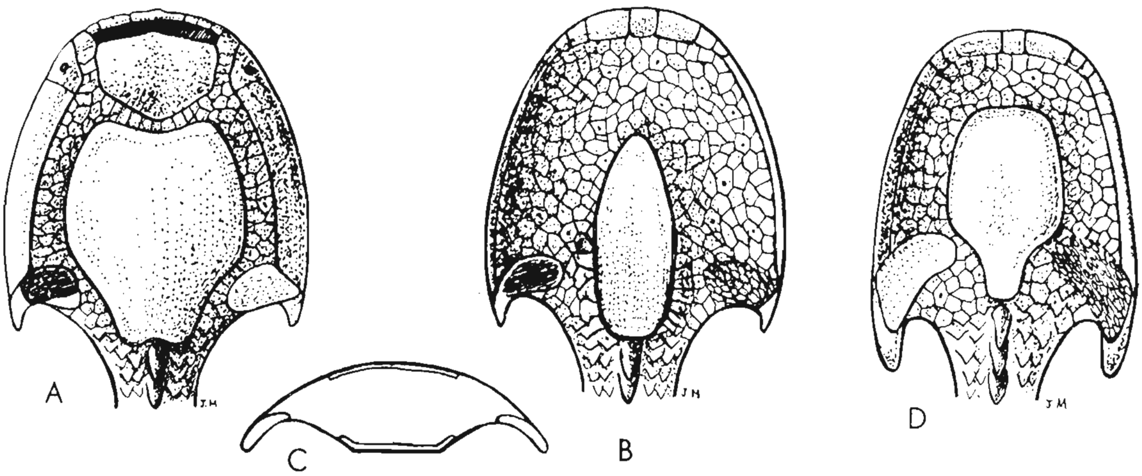

Fig. 10

A-C Psammosteus megalopteryx (TRAUTSCHOLD) — *A* restoration, in dorsal view; *B* in ventral view; *C* diagrammatic cross-section (modified from TARLO, 1961*a*); *D Psammosteus praecursor* OBRUCHEV — restoration, in ventral view (modified from OBRUCHEV, 1947*a*)

The genera *Rohonosteus*, *Karelosteus* and *Crenosteus* which are known only from branchial plates are also included within the family Psammosteidae for convenience. This is because their branchials although intermediate in shape between those in *Psammolepis* and *Psammosteus* (OBRUCHEV, 1933*a*, 1961) are nevertheless evidently well on the way to the typical *Psammosteus* condition.

The final family to be considered under the Psammosteida is the family Obrucheviidae [Aspidosteidae]. This group is known from dorsal median plates notable for their large size and thickness, and also for the fact that the outer surface of the armour has no ornamentation of dentine tubercles such as are present in all other psammosteids. Instead the aspidin of the plate has been strengthened by an infilling of pleromic dentine (OBRUCHEV, 1941; TARLO & TARLO, 1961) and the outer surface is sculptured with pits and grooves. The only other plates known are branchial plates and these are very long and are bent at right angles from side to side, so that in life the animal must have moved over the substratum on two runners formed by the free lateral margins of the vertical halves of the plates (OBRUCHEV, 1964*b*). These branchial plates are remarkable for being so thin compared with the massive thickness of the dorsal plate, and also for reversing the trend in the other psammosteid families towards the development of shorter, wider branchial plates. Assigned to the same family is the genus *Traquairosteus* in which the ornamentation of tubercles has been reduced to isolated pustules and in which there seems to be an incipient development of pleromic dentine. (It should be noted that in the restoration (Text-fig. 11) of *Obruchevia [Aspidosteus]* a deep basin-shaped ventral median plate has been inserted in conformity with the ventral plate of other psammosteids, as well as the full complement of dorsal plates. However, these are purely hypothetical).

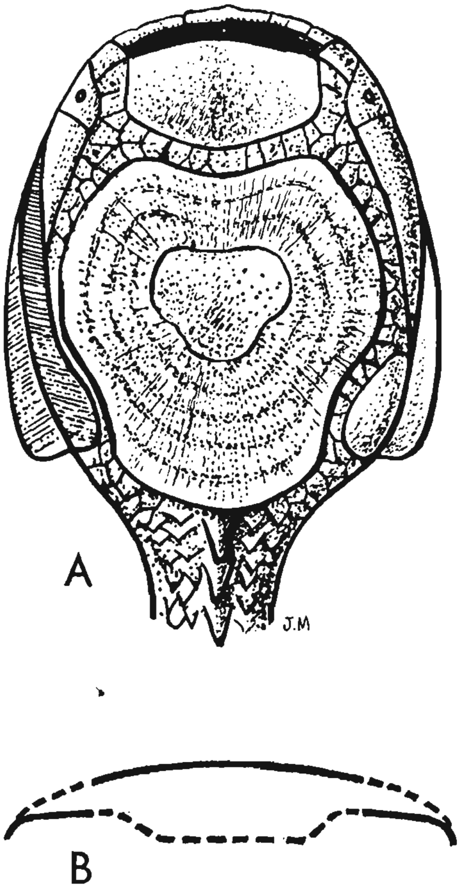

Fig. 11
Obruchevia [Aspidosteus] heckeri OBRUCHEV — *A* restoration, in dorsal view; *B* diagrammatic cross-section

SENSORY CANAL SYSTEM

The carapace in the Heterostraci is characterized by the possession of a complex sensory canal or lateral line system, such as is common to the majority of primitive vertebrates. In general in the Heterostraci this system consists of a series of closed canals which open to

Table 1
AVAILABLE MATERIAL OF IMPORTANT SPECIES

Genera and species	*D*	*V*	*Br.*	*PO*	*O*	*C*	*R*	*Pi.*	*Or.*
Tesseraspididae									
Tesseraspis tessellata WILLS	×	×	×						
Tesseraspis toombsi n. sp.		×	×						
Corvaspididae									
Corvaspis kingi WOODWARD	×		×		×			?	
Weigeltaspididae									
Weigeltaspis alta BROTZEN	×								
Weigeltaspis godmani n. sp.	×	×	×	×					
Weigeltaspis heintzi n. sp.	×	×	×						
Drepanaspididae									
Drepanaspis gemuendenensis SCHLÜTER	×	×	×	×	×	×	×	×	×
Drepanaspis lipperti GROSS	×		×	×					
Guerichosteidae									
Guerichosteus kozlowskii n. sp.	×	×	×	×		×	×	×	×
Hariosteus kielanae n. sp.	×		×	×					
Schizosteus heterolepis (PREOBR.)			×	×	×				
Schizosteus striatus (GROSS)	×	×	×	×			×		
Schizosteus asatkini OBRUCHEV	×	×	×						
Pycnosteidae									
Pycnolepis splendens (EICHWALD)	×	×	×				×		
Pycnosteus palaeformis PREOBR.		×	×						
Pycnosteus pauli MARK	×	×	×						
Pycnosteus tuberculatus (ROHON)	×	×	×		×				
Pycnosteus nathorsti OBRUCHEV	×	×	×						
Ganosteus stellatus ROHON		×	×			×			
Ganosteus artus MARK		×	×						
Tartuosteus giganteus (GROSS)	×	×	×						
Tartuosteus maximus MARK	×	×	×	×					
Psammolepididae									
Psammolepis paradoxa (AGASSIZ)	×	×	×		×				
Psammolepis venyukovi OBRUCHEV	×		×	×			×		
Psammolepis undulata (AGASSIZ)	×	×	×						
Psammolepis proia MARK		×	×			×			
Psammolepis abavica MARK	×	×	×					×	
Psammolepis alata OBRUCHEV	×	×	×						
Psammosteidae									
Psammosteus megalopteryx (TRAUTSCH.)	×	×	×	×		×	×	×	
Psammosteus praecursor OBRUCHEV		×	×						
Psammosteus markae TARLO	×								
Obrucheviidae									
Obruchevia heckeri (OBRUCHEV)	×		×						

The following species are known from branchial plates, but no other main plates: *Drepanaspis schrieli* GROSS, *Schizosteus toriensis* MARK, *Schizosteus perneri* (RŮŽIČKA), *Ganosteus obtusus* MARK, *Tartuosteus luhai* MARK, *Yoglinia bergi* OBRUCHEV, *Psammolepis aerata* OBRUCHEV, *Psammosteus maeandrinus* AGASSIZ, *Psammosteus falcatus* OBRUCHEV, *Psammosteus grossi* OBRUCHEV, *Psammosteus pectinatus* OBRUCHEV, *Psammosteus tchernovi* OBRUCHEV, *Psammosteus livonicus* OBRUCHEV, *Psammosteus kiaeri* n. sp., *Crenosteus levis* (OBRUCHEV), *Rohonosteus ornatus* (ROHON), *Rohonosteus complicatus* (KIAER), *Karelosteus weberi* OBRUCHEV.

D dorsal median, *V* ventral median, *Br.* branchial, *PO* post-orbital, *O* orbital, *C* cornual, *R* rostral, *Pi.* pineal, *Or.* oral the surface by means of small pores. These are usually located between tubercles, but may pierce the ornament. The canals can also occasionally be situated in grooves on the external surface of the plate. This latter situation is found in *Astraspis* and *Amphiaspis* as well as probably in *Guerichosteus kozlowskii*. In the majority of heterostracans the system of canals runs just below the layer of ornament and in consequence is known only where this ornament has been worn off, or where the canals have been filled in with sediment posthumously and stand out as ridges when the bony material is lost. It is however also possible to see the canals if the specimen is immersed in oil of aniseed, since this makes the dentine and aspidin transparent.

Although it was recognized by WOODWARD (1887) that sensory canals existed in *Pteraspis*, the homology of such canals with those of other vertebrates was not fully discussed until 1926 when STENSIÖ compared them with the pattern found in living cyclostomes. Later, SÄVE-SÖDERBERGH (1941*b*) showed that the system in the Heterostraci could be compared directly with that of primitive jawed vertebrates and in fact contrasted it with the system known in the cyclostomes. HOLMGREN (1942) pointed out that the heterostracan system was primitive and that both the cephalaspid and cyclostome patterns could be derived from it; while STENSIÖ (1958) demonstrated the close similarity of the sensory canal system in the Heterostraci to that in the gnathostomes. It is evident that the heterostracan pattern is very primitive and can be considered a possible precursor of the sensory canal system of both the cephalaspids and cyclostomes as well as the early gnathostomes.

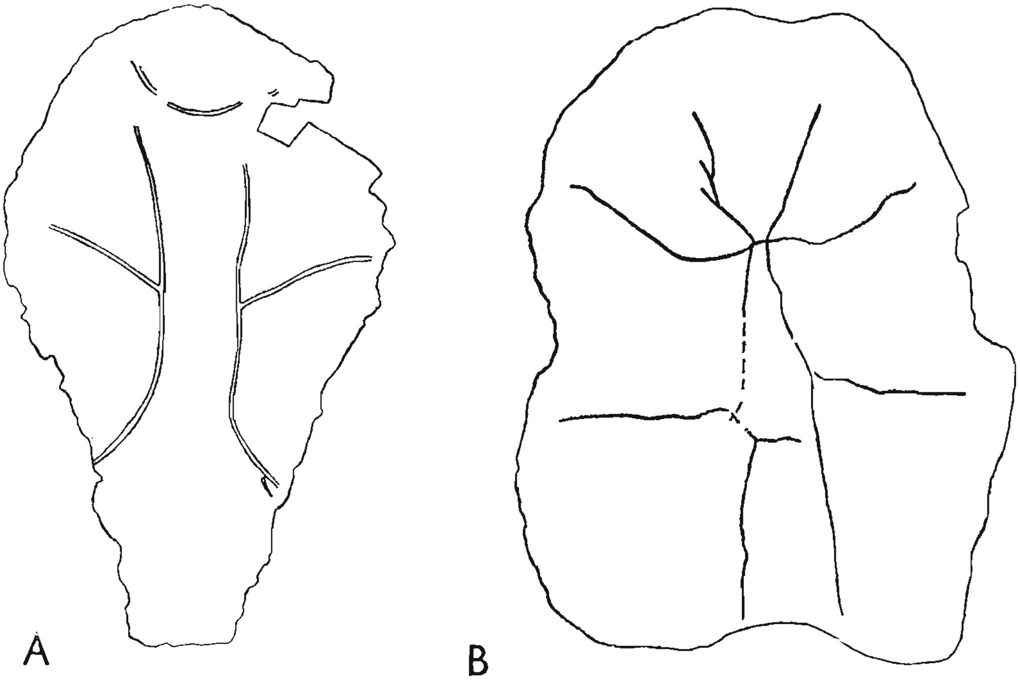

Fig. 12

Sensory canal system. *A Psammolepis undulata* (AGASSIZ) — ventral median plate (G.I.T., 247); *B Tartuosteus giganteus* (GROSS) — dorsal median plate (G.I.T., 152)

With regard to the system present in the psammosteids, unfortunately parts of it only are preserved in occasional dorsal and ventral median plates, but these are sufficient to show that the pattern is consistent with that of normal heterostracans. Short sections of a canal system were figured by WILLS (1935) in a fragment of the primitive psammosteid *Tesseraspis*, where tubercles had been broken off to reveal them. These however were not recognized as part of a sensory canal system until ØRVIG (1961). In *Corvaspis*, WOODWARD (1934) showed that there were rows of sensory pores in the median plates, while TARLO (1960*b*) illustrated ground fragments in which segments of canals were visible. Previously, GROSS (1933*c*, 1963) figured a dorsal median plate of *Drepanaspis* with what he suggested was a sensory canal system, and OBRUCHEV (1940) figured similar striations on a dorsal median plate of *Schizosteus*. In both cases however, it seems unlikely that the markings represent part of a sensory canal system, and it is suggested that they are merely a result of the method of growth of the plates. However, a complete sensory canal system in a dorsal median plate has recently been figured for the first time (OBRUCHEV, 1961). This plate (152 G.I.T.) which belongs to *Tartuosteus giganteus*, shows two median longitudinal canals diverging slightly posteriorly, with two pairs of lateral branches, and a pair of antero-laterally directed branches. A composite pattern of the system in the dorsal median plate of *Psammosteus megalopteryx* was provided by TARLO (1961*a*), who figured two fragments. In the larger fragment (1960. 9, R.S.M.) there are two longitudinal median canals with connecting transverse commissures as well as a pair of lateral branches, the left one of which bifurcates. Unfortunately the lateral branches were made symmetrical, but since it is now known that in the psammosteids the canal patterns can be markedly asymmetrical, this does not seem to have been justified. Furthermore in the smaller upper fragment figured (1894. 169. 3, R.S.M.), the longitudinal canal should have been lateral rather than median, since a further fragment has now been found which adjoins it and forms part of the margin of the plate.

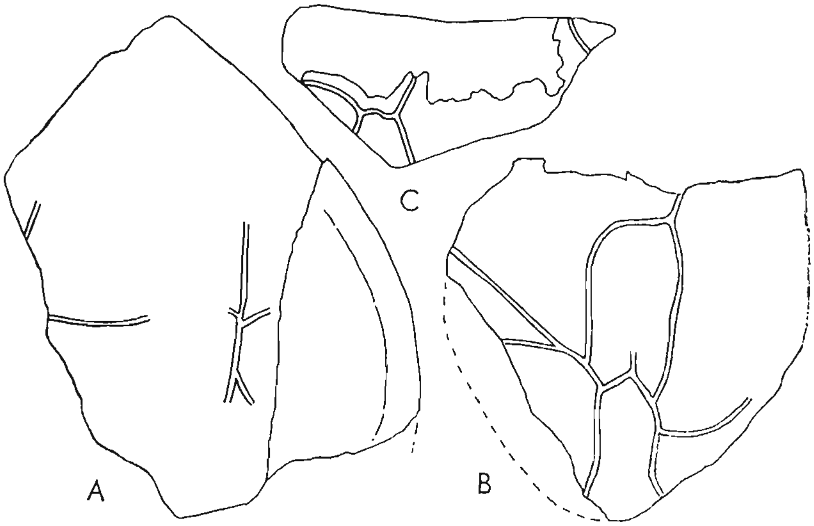

Fig. 13

Sensory canal system. *A-C Psammosteus megalopteryx* (TRAUTSCHOLD) — fragments of median plates, *A* (R.S.M., 1894.169.3); *B* (R.S.M., 1960.9); *C* (P.I.M., 220/201); all × 0·5

The pattern of sensory canals is also now known in a ventral median plate, this time belonging to *Psammolepis undulata* (247, G.I.T.). From the shape of the plate there appears little doubt that it is a ventral median plate, and the absence of transverse commissures in the mid-line of the canal system would seem to confirm this. It is true that the arcuate canal near the anterior margin has a faint resemblance to the pineal canal of the dorsal surface of the carapace, but it is sufficiently distinct not to be confused with it. Moreover, a similar arcuate canal to that found in this ventral plate is also known in the ventral plates of other heterostracan groups.

ORNAMENTATION AND GROWTH OF DERMAL ARMOUR

(Pls. I-V; Pl. XIII, figs. 1-2; Pl. XIV)

The plates making up the dermal armour of the psammosteids generally bear a superficial ornamentation of dentine tubercles surmounting a much thicker layer of spongy aspidinbone. The tubercles themselves which vary considerably in size and shape are found arranged in complex patterns. Sometimes they are rounded and crenulated, while at other times they are star or lozenge-shaped. Furthermore they can be widely separated, packed closely together, or even fused into long or short ridges which again can show much diversity. The ornamentation which is virtually specifically distinct, provides in consequence the chief means of identifying the different psammosteids, and it is particularly valuable as an aid to diagnosis since only a fragment of the armour is needed for the purpose. However, this method must be used with caution since the arrangement of the tubercles can vary considerably from one part of the carapace to another, and this has often led in the past, to different plates of one species being described under various names. In fact the form of the tubercles often depends on the shape of the plate on which they are situated, and on the manner in which it has grown, this being particularly true where the tubercles are packed closely together. For example, tubercles which when scattered over a dorsal plate may be fairly round, can often take on a different appearance on a branchial plate. Here, if they are packed closely together, they tend to become fan-shaped, since the plate is wider at one end than the other and the tubercles are squashed distally to fit the outline of the plate. In fulcral scales, round tubercles similarly become fan-shaped in the mid-line, while these are often flanked by tubercles pushed into a naviculate shape. In superficial tesserae on the other hand, such as are known in *Psammosteus*, where the tubercles are arranged concentrically, they tend to become somewhat arcuate in outline (Text-fig. 14*A*). However, with close study, the relationship between these different sets of tubercles becomes fairly obvious.

Although the tubercles are often rounded and finely crenulated at their margins, when they are found widely separated there is more possibility of variation, and a whole number of different shapes are known. For example in *Weigeltaspis* the tubercles appear in outline rather like oak leaves, with raised veining converging on to a median ridge (Text-fig. 14*C*), while in *Ganosteus* the tubercles have sharply pointed crowns with very long, strongly bifurcated radial ribs. These latter give the appearance of flying buttresses and they often turn at the foot of the tubercles to continue across the intervening floor (Text-fig. 14*B*). Situated between the main tubercles are very much smaller star-shaped ones. In *Rohonosteus* the tubercles are more closely packed and are frequently lozenge or diamond-shaped, while in *Crenosteus* a number of tubercles are found fused together to form flat strips with short comb-like crenulations. A further feature which occurs sporadically is the development of accessory tubercles between the main ornamentation. This has already been mentioned in *Ganosteus stellatus*, but it is also well seen in *Pycnosteus tuberculatus*, *Psammolepis undulata*, *Psl. venyukovi* and in the genus *Hariosteus*. It is of interest to note that this phenomenon frequently seems to arise among the end members of particular lineages.

The various species of *Psammosteus* are mainly distinguished from one another on the differences in the ornamentation of their branchial plates. For example *P. falcatus* and *P. grossi* have transverse ridges of fused tubercles with very long, bifurcating crenulations drawn out proximally, although those of *P. grossi* are considerably coarser than those of *P. falcatus* and so could not be confused with them, while in *P. tchernovi* the tubercles are quite different, being single, shaped like ridge tiles, and packed closely together. In some forms the tubercles are drawn out into longitudinal strips as in *P. maeandrinus*, or even into long ridges. The most striking example of this type of ornamentation is found in *Yoglinia* where the dentine ridges run along the main axis of the plate and initially led to this form being identified as a pteraspid. It should be noted however, that the situation is more complicated in the more advanced psammosteids *(s. l.)* since the median plates are generally characterized by an ornamentation of superficial tesserae which may be scale-like in appearance in such genera as *Psammolepis* and *Tartuosteus* or merely polygonal as in *Psammosteus* itself, while the plates of the lateral margin do not possess such tesserae but merely show concentric zones of growth. Nevertheless the ornamentation is still characteristic.

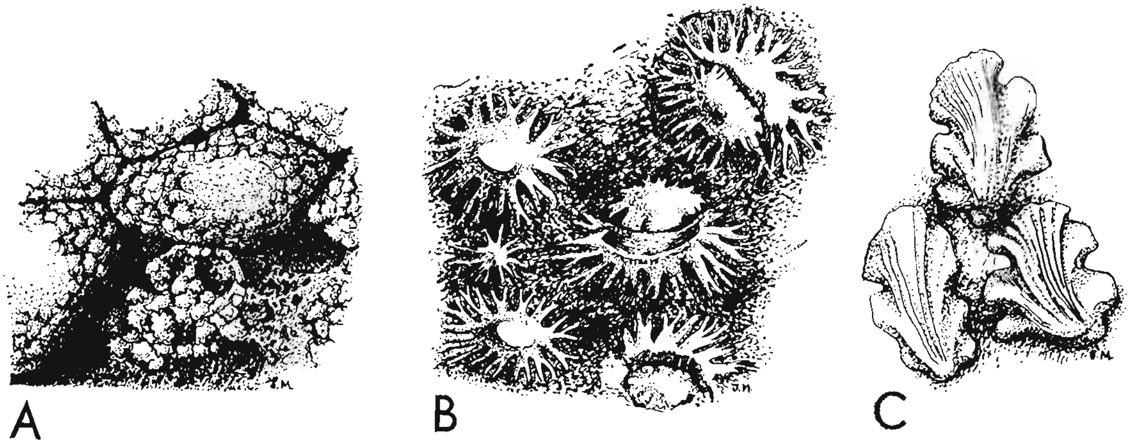

Fig. 14

Ornamentation of selected psammosteids. *A Psammosteus megalopteryx* (Trautschold)—superficial polygonal cyclomorial tesserae showing cavity due to loss of tessera healed by secondary tubercles lining its floor and walls (P.I.M., 220/246); *B Ganosteus stellatus* Rohon — large well separated tubercles with resorption cavities with secondary tubercles situated in them (G.I.T., 174); *C Weigeltaspis alta* Brotzen — three isolated oak-leaf tubercles (R.S., C 1728)

Apart from its value as an aid to identification, the external ornamentation is also of great importance when considering the way in which the plates of the dermal armour have developed. Except where they are worn or broken, or in rare cases where there is some resorption (see Tarlo & Tarlo, 1961), after they have been formed, the tubercles retain their size and shape throughout the life of the animal. Thus each area of ornamentation, once having become calcified, is preserved as a permanent record of the stage of growth reached at that point by the plate in question. The recognition of this fact led Ørvig and Stensiö to develop a new theory on the growth of scales and dermal elements in the early vertebrates, and this was outlined by Ørvig in 1951. A more detailed account of this — the lepidomorial theory — has recently been provided by Stensiö (1961, 1962), and it has also been discussed by Tarlo & Tarlo (1962).

In 1958, STENSIÖ applied the lepidomorial theory to a study of the dermal armour of the Heterostraci, and in doing so recognized that two basic types of growth occurred in the plates. The first type, called cyclomorial growth, is one in which there is to begin with, a central tubercle or primordium, around which new tubercles or units are added on one at a time concentrically. Such a type of growth is well seen in the Ordovician genus *Astraspis* where the carapace is composed of a number of small cyclomorial plates or tesserae ornamented by well spaced rounded tubercles. The central tubercle of each tessera is fairly large and around it smaller tubercles were added on successively as the tessera grew to keep pace with the growth of the animal. Cyclomorial growth is also found in the carapace of the pteraspids, where from a primordium, large plates are built up by the addition of concentric rings of dentine ridges. The second basic type of growth is termed synchronomorial, and in this case tesserae or plates are formed as single complete units, all the tubercles or ridges of the ornament appearing at one and the same time. Moreover, TARLO (1960*b*) was able to show how synchronomorial plates themselves could have developed from cyclomorial tesserae such as those known in *Astraspis*, by the fusion and consequent elimination of such tesserae. In this way it was demonstrated that the types of growth used by STENSIÖ as major criteria for separating the various orders within the Heterostraci, could in fact be derived from one another. Subsequently TARLO (1962*d*) was able to show that the evolutionary trend towards the development of plates of the carapace by the fusion of tesserae could be followed separately in most of the heterostracan orders (see also TRAQUAIR, 1899; OBRUCHEV, 1945), although in the later psammosteids this trend was apparently reversed.

From the condition seen in such primitive heterostracans as *Astraspis*, where the complete carapace is formed of cyclomorial tesserae there was therefore a tendency during the course of evolution, for such a type of carapace to give way to one in which there was an organized system of large plates such as are well seen in the amphiaspids and cyathaspids. Since to begin with the plates were formed synchronomorially, i. e. as complete units, they could not have appeared until the animals were more or less fully grown, although on occasions they could be enlarged to some degree by the addition of cyclomorial areas of growth at their margins. This is well seen in the median plates of *Corvaspis* (TARLO, 1960*b*). The result of possessing this synchronomorial type of dermal armour was that for the greater part of their lives the animals concerned were unprotected, and in addition their shape had to be compact since any large extensions to the body would have been unsupported in the young stages.

The synchronomorial carapace was however improved upon, for in the traquairaspids the synchronomorial plate appeared when the animal was half grown, and then increased in size cyclomorially until the definitive size was reached. In this way the synchronomorial plate formed a primordium around which cyclomorial growth was possible. In later forms the primordium was achieved earlier and earlier in ontogeny, until by the time the pteraspids and later psammosteids were reached, the bulk of the plate was formed cyclomorially, and the animals were able to produce important anterior and lateral extensions to the carapace. These took the form of long snouts and branchial or cornual plates and were built up gradually as the animal itself grew. The development of such projections by the later pteraspids and psammosteids no doubt enabled them to compete successfully with the more advanced jawed vertebrates, after the less adaptable heterostracans became extinct.

Once the significance of the ornamentation of the dermal armour is understood therefore, an analysis of it enables the growth stages of the carapace to be mapped, thus revealing the manner in which the plates and hence the carapace as a whole developed. It is also now possible to trace the way in which one form developed from another, and to demonstrate relationships which were not previously apparent. Such an analysis has already been made in outline for the Heterostraci as a whole (TARLO, 1962*d*), but it is here proposed to examine the Psammosteiformes in greater detail.

When discussing the ornamentation and growth of the dermal armour in the Psammosteiformes, it is useful to take as the starting point the condition found in *Astraspis* from the Ordovician, although it is not considered that this form was necessarily ancestral to the group. It is merely that the type of carapace well preserved in *Astraspis* is likely to have been the primitive arrangement common to all the earliest heterostracans, from which the Psammosteiformes must have been derived. In *Astraspis* the carapace is composed of a large number of small discrete polygonal tesserae, these plates bearing an ornamentation consisting of one large round crenulated tubercle surrounded by concentric rows of smaller similar tubercles. It is evident that during the early stages of ontogeny single tubercles were present in the skin, and as this latter grew in extent, the tubercles formed primordia around which successive zones of tubercles grew cyclomorially forming tesserae. Such tesserae would have additional tubercles added on to them until the animal reached its definitive size, and in this way a complete carapace would have been maintained throughout life. Presumably calcification of the soft tissue at the base of the tubercles occurred gradually from the centre of the tessera outwards, immediately after the separate tubercles became calcified, and since the edges of the individual tesserae would always abut on several others, this would produce the typical polygonal shape.

In *Tesseraspis*, the first true member of the Psammosteiformes, the carapace is again formed of independent tesserae, but these appear to have been produced partly synchronomorially, although the frequent occurrence of small secondary tubercles between the main tubercles suggests that the tesserae were formed in several stages. First to appear all at the same time would have been the large tubercles of the ornament, then smaller secondary tubercles would have occurred between them and finally the soft tissue at the base of all the tubercles would have calcified to form complete tesserae, all these being completed at much the same time. Nevertheless, there is a certain amount of cyclomorial growth around the edge of each tessera, suggesting that some additional growth took place. In *Tesseraspis*, although the tesserae are still discrete, they are already differentiated and grouped into areas foreshadowing the plates of later forms, and in addition, they are unusual since the tesserae belonging to various parts of the carapace are ornamented rather differently. In the median areas of the carapace the tesserae are fairly thick and the tubercles appear as large, rather low bosses between which smaller similar rounded tubercles occur together with fine stellate ridges. On the thinner tesserae found between the median areas and the ridge-shaped tesserae forming the lateral borders of the carapace, the tubercles are much smaller and are irregular, often having the appearance in outline of miniature ginger-bread men. The lateral tesserae are shaped like the ridge tiles of a roof, and these have very strong, oval, bulbous tubercles at their apex, with similar tubercles becoming smaller away from it.

In the roughly contemporaneous genus *Kallostrakon*, the carapace is also formed of tesserae, but these are quite clearly produced by cyclomorial .growth. However, the ornamentation in this instance is not of rounded tubercles, but instead consists of short dentine ridges, presumably the result of fusion or coalescence of several tubercles. In each tessera there is a central longitudinal ridge or primordium on either side of which successive ridges are added on until growth is complete. Sometimes the ridge is oval in outline and this is surrounded by smaller oval ridges or tubercles. Although the tesserae of *Kallostrakon* are generally found isolated, some larger plates are known in which the ornamentation shows quite clearly that they were initially composed of a number of independent tesserae, but that they had become fused together and to a plate which had formed below them. The cyathaspid *Tolypelepis* shows a remarkable degree of parallelism in this respect, as it also exhibits this stage in the transformation from a tesselated carapace to one with discrete plates.

The genus *Corvaspis*, which is probably a direct descendent of *Kallostrakon*, has a more advanced system of plates, but these are again ornamented by dentine ridges. The plates also show signs of having been formed by the fusion of numerous polygonal tesserae, although there is a significant difference in the two genera, since in *Corvaspis* the tesserae appear to have been formed synchronomorially and not cyclomorially as in *Kallostrakon*. Furthermore, the ornamentation of the carapace is of particular importance to any study of the growth of the dermal armour, since within a single species it is possible to find examples of median plates in which a series of stages can be traced leading up to the complete elimination of tesserae, or traces of former tesserae (Text-fig. 15).

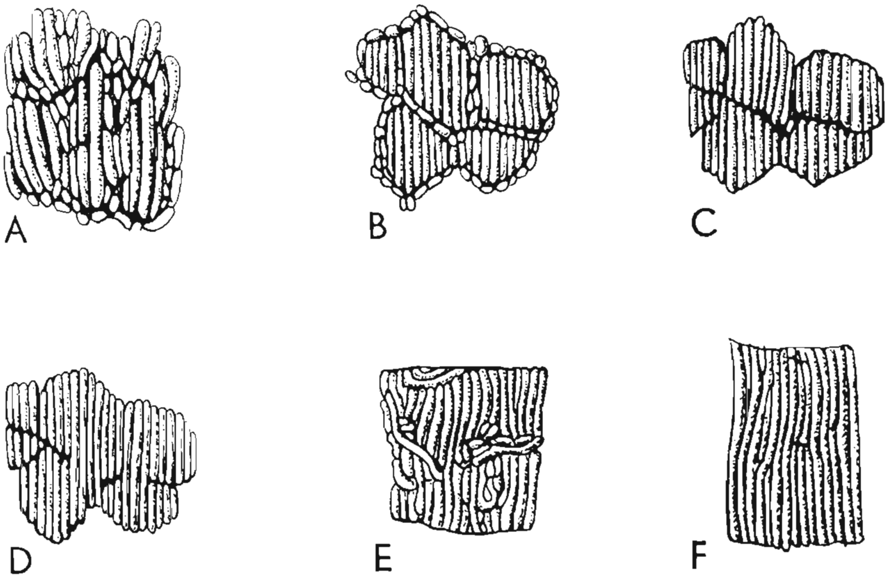

Fig. 15

Diagram illustrating progressive fusion and elimination of tesserae. *A Kallostrakon macanuffi* n. sp. — cyclomorial tesserae; *B-F Corvaspis kingi* WOODWARD — *B* synchronomorial tesserae, separated by narrow zones of cyclomorial growth; *C* synchronomorial tesserae separated by fine grooves; *D* partially fused synchronomorial tesserae; *E* synchronomorial unit with occasional irregularities indicating former presence of tesserae; *F* synchronomorial unit with no indication of tesserae

In the posterior part of most of the median plates, synchronomorial tesserae are found grading into the squamation of the hinder part of the trunk of the animal. These tesserae are polygonal in outline, and are ornamented by more or less parallel rows of short dentine ridges aligned longitudinally. The tesserae must have appeared as units prior to the complete growth of the individual since narrow zones of round, flat tubercles mark an area of cyclomorial growth around them, and separate them from one another. The bulk of the plate however, is ornamented by similar polygonal tesserae which are separated from each other by a narrow groove only, and these no doubt all formed at the same time when the animal was fully grown, no further growth being possible in that region. Examples are also found where the individual tesserae arose with some of their dentine ridges confluent with those of adjoining tesserae, while more rarely there are specimens in which the dentine ridges are more or less continuous along the entire length of the plate. In this latter case the only evidence of former polygonal tesserae lies in the short transverse grooves visible near the lateral margins of the plate, and in small irregularities in the alignment of the ridges. In all specimens of large plates in *Corvaspis* the plate as a whole although mainly formed as one unit is nevertheless bordered by a narrow zone of cyclomorial growth in which rows of small rounded tubercles are arranged concentrically. Thus it seems apparent that the main plates must have been acquired some short while prior to the achievement by the animal of its definitive size, and that growth continued around the border of the plate until the growth of the animal was complete.

Isolated synchronomorial tesserae ornamented with longitudinal dentine ridges are also found in *Corvaspis* and since on occasions they became incorporated into the cyclomorial margins of large plates, it seems highly likely that fields of such tesserae existed between the main plates of the carapace — a feature characteristic of all Psammosteiformes in which large plates have been developed. In addition in *Corvaspis* some isolated tesserae are known in which the ornamentation is of concentric zones of tubercles, the growth in this case being cyclomorial, but it is not known with certainty to which part of the carapace such tesserae belong. Cyclomorial growth also took place in the orbital plates around the orbit, and in branchial and other plates around the openings of sensory pores.

In *Weigeltaspis* the ornamentation consists of large irregular well separated tubercles, and as in *Corvaspis* the main plates appear to have been formed as synchronomorial units. However, this time the plate has a much wider border of cyclomorial growth around it, suggesting that the synchronomorial unit was acquired earlier in ontogeny than was the case in *Corvaspis*, and in consequence the animal had a protective armour during its young stage. Thus the condition found in the later psammosteids is being approached, in which most of the growth of the plate takes place cyclomorially around a small primordium. This primordium is achieved earlier and earlier in ontogeny until it becomes possible for the carapace to be gradually increased in size as the animal grows. In this way the animal has an armour throughout most of its life, and also as mentioned earlier large projections can be produced, since as a plate is gradually built up below the ornamentation these projections are supported during their development.

It is possible to see therefore that the general shape of the carapace depends to a large extent on the type of growth that has occurred, and that a study of the ornamentation provides the evidence necessary for a full understanding of this growth. In the forms where the carapace is composed of small discrete tesserae the animal must be compact in shape and there is also a restriction on size, since at no time is there a rigid exoskeleton. Similar limits on both shape and size are also imposed on the forms that develop their plates synchronomorially, since these animals are unarmoured until they are almost mature. However, once the main development of the plates is by cyclomorial growth it becomes possible to evolve such specializations as long snouts and cornual and branchial plates which project beyond the normal body of the animal. Thus by tracing the development of the plates of the carapace through members of the suborder Tesseraspidida, it becomes possible to understand how an organized system of plates could be built up in which the main growth was cyclomorial. The animals could thus not only be armoured throughout life, but could reach a considerable size and also develop anterior and lateral projections which served not only as aids to the maintenance of stability, but in addition enabled the animals concerned to become specialized for different modes of life.

In the members of the suborder Psammosteida the plates are all produced largely by cyclomorial growth, and possibly due to their ability to vary the shape of the carapace, these animals were highly successful and experienced a considerable radiation in Middle and Upper Devonian times. However, as will be shown below, the evolutionary history of the later psammosteids reveals an apparent reversion of the trend towards the fusion of small elements into large units, and tesserae begin to reappear on the median plates. This time however, they become fused to an underlying plate which grows concentrically. The evolutionary trend is reversed to such an extent that by the time the family Psammosteidae is reached, the entire dorsal and ventral median plates are covered by superficial cyclomorial polygonal tesserae.

In *Drepanaspis*, a typical early member of the Psammosteida, the median plates show concentric zones of growth although these are not always easily discernible, and the ornament consists of small stellate tubercles. These are arranged in rows on the bulk of the plate, although towards the margins some tesserae, which generally appear to have been produced cyclomorially, take their place. In the guerichosteids, the median plates are characterized by well developed growth rings in which the rows of rounded crenulated tubercles are far easier to see than in *Drepanaspis*. These rings of tubercles are best seen in *Guerichosteus* itself and also in the drepanaspid *Psephaspis*, whilst in *Hariosteus* not only are these concentric rings well marked, but they are also organized into graduated zones, bands of larger tubercles gradually giving way to smaller ones. As mentioned above, the genus *Hariosteus* is also characterized by the development of small accessory tubercles between the normal ones, this phenomenon being very constant, since they are found in all the plates and scales of this genus.

A specimen which may prove to belong to *Psephaspis* has kindly been given to the author by Dr. DENISON, and this shows not only concentric rings of tubercles, but in addition at the lateral margins of the plate large irregular polygonal areas which are marked off from the main plate. They appear to be large synchronomorial units which have been added on at the margins of the plate. Similar irregular tesserae at the margins of some median plates are also known in *Pycnolepis* and in *Schizosteus*, a further guerichosteid, where they form a narrow zone around the plates. These do not appear to have been part of the fields of tesserae between the main plates which have become incorporated into the median plates, such as happens more or less accidently in *Corvaspis*. Instead this is a method of allowing for a large measure of growth after the initial plate is formed, and not just the very small amount found in *Corvaspis*. In the guerichosteids the plates of the lateral margin develop only by normal growth — i. e. more or less concentric rings of tubercles being added on. These can thus grow to meet the animal's needs, and it is in this family that lateral extensions to the carapace first develop.

By the time the psammolepids appear, the lateral extensions which still grow cyclomorially, have become great bony sheets. Furthermore, although the early part of the development of the median plates, both dorsal and ventral, is by means of the successive addition of concentric rings of tubercles, i. e. normal cyclomorial growth, around these there is now a very wide zone of scale-like synchronomorial tesserae. These are superficial to the plate to which they are fused, and are added on concentrically, so that there is now a zone of continuous cyclomorial growth, which occurs by the addition of synchronomorial units instead of just tubercles. However, even further growth between the polygonal units is possible, since towards the edges of the plate, each synchronomorial tessera has a narrow zone of cyclomorial growth around it, where individual tubercles are added on concentrically. In such advanced species as *Psammolepis venyukovi* the initial central cyclomorial area of growth is very small indeed (Text-fig. 16), and in *Psammolepis undulata* it has completely disappeared, the dorsal median plates being ornamented solely by concentrically arranged scale-like tesserae which give indications of a certain degree of cyclomorial growth. At first glance these appear to have been formed synchronomorially like the tesserae at the edge of the plates in the early psammolepids, but when examined in more detail it can be seen that although they may have appeared almost simultaneously, there is a tendency for the tubercles to be arranged concentrically, suggesting that there was a time lag, however short, between the appearance of the tubercles towards the centre of each tessera, and those more marginally placed.

The ventral median plate of *Psammolepis* is long and narrow, and has grown by the addition of superficial tesserae along the posterior margin of the concentric growth stage

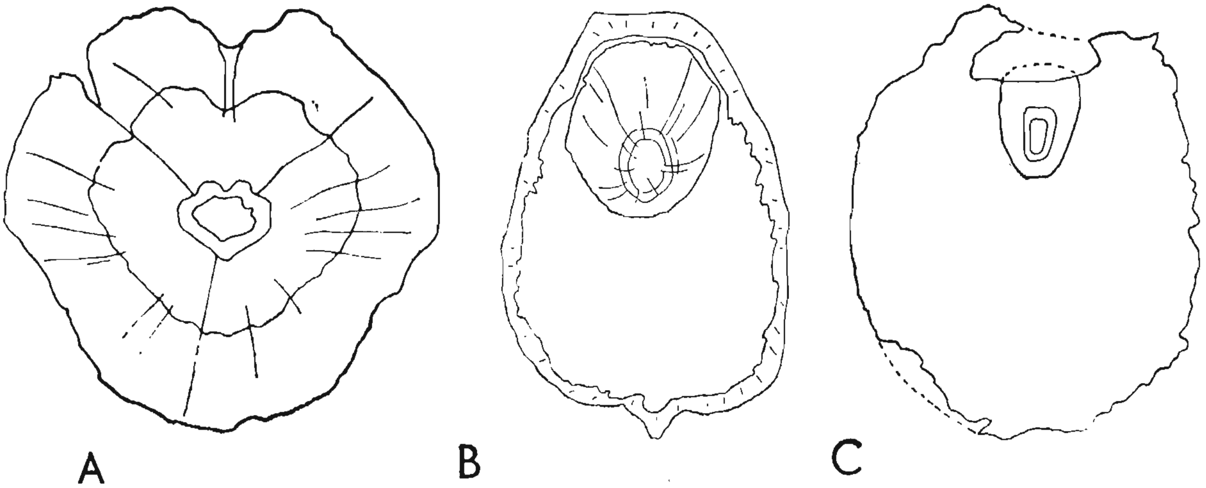

Fig. 16

Diagrams of dorsal median plates showing gradual shift of initial growth centre towards anterior margin, with progressive increase of zone of superficial tesserae. *A Pycnolepis splendens* (EICHWALD) — no superficial tesserae present (G.I.T., 426); *B Tartuosteus giganteus* (GROSS) — anterior area of cyclomorial growth surrounded by large region of superficial tesserae (G.I.T., 151); *C Psammolepis venyukovi* OBRUCHEV — small area of cyclomorial growth at anterior margin (G.I.T., 236)

seen early in ontogeny. The main plate, whether dorsal or ventral, is formed on the visceral surface of the superficial tesserae, which then become fused to it. This is evidenced by the fact that at the margins of the plate the tesserae are almost always missing, indicating that they had not yet become fused to the plate lying beneath them and were therefore easily lost after death.

In the pycnosteids the growth of the plates is generally similar to that known in the guerichosteids. In *Pycnosteus* and *Ganosteus* there is no evidence however of the median plates growing by the addition of superficial tesserae, the entire growth being by the addition of concentric rows of tubercles. This may well be due to the fact that the ventral median plate has a long persistent posterior notch, and it would not be feasible to add tesserae to this part of the plate, since they would produce a very irregular margin to the notch. In *Tartuosteus* however, the notch is secondarily filled in with lozenge-shaped tesserae. These tend to be at a different level from that of the cyclomorial plate, so that when the ventral surface became worn, these infilling tesserae were still preserved. However, the main plate formed beneath both the cyclomorial plate and the infilling tesserae, and these all fused to it. In the dorsal plate of *Tartuosteus* however the situation is similar to that seen in *Psammolepis*, where there is a central area of concentric tubercles and around this a very broad band of superficial scale-like tesserae (Text-fig. 16).

The plates of the lateral margin in *Psammosteus* are also formed by normal cyclomorial growth, with the tubercles arranged more or less concentrically. But the median plates in this genus are formed of cyclomorial tesserae in which there is a central tubercle often larger than the others, around which further tubercles are arranged in well marked rings. These superficial tesserae which are also arranged concentrically, are best seen on dorsal median plates, and are in fact thin polygonal plates very similar to the cyclomorial tesserae known in *Astraspis,* and to those forming the fields of tesserae in the members of the Psammosteida. Previously (TARLO, 1961 *a*) it was suggested that tesserae were not developed on the ventral median plates in *Psammosteus*, but the author's recognition of two fragments of *Psammosteus megalopteryx* from Russia as parts of a ventral median plate shows that typical tesserae were developed there, and that in this respect the ventral medium plates do not differ from the dorsal ones.

Median plates of *Psammosteus* are often found in which some of the tesserae have been lost, these plates having a characteristic honeycomb pattern on their surface, and GROSS (1935) believed that such a loss of tesserae at the edges of plates was evidence of the break up of large plates into a mosaic of small thin tesserae. It seems more likely however, that the tesserae merely formed separately somewhat earlier than the underlying plate, and that they fused to it later, complete fusion only taking place when the animal reached maturity. The tesserae seem to have first fused to the main plate at the underside of their margins, and then probably fused together. In this way a slight cavity would have been produced beneath each tessera which presumably became filled later by the further growth of aspidin-bone which fused the tesserae firmly to the main plate. This plate beneath the tesserae seems to have grown concentrically since on its undersurface well marked growth rings are visible. However, these are not evident on the outer surface of the plate as they do not correspond to rings of tesserae. In the earlier genera such as *Psammolepis,* it seems that as superficial tesserae developed they became fused individually to the concentrically growing plate beneath them, but as shown above, in *Psammosteus* the tesserae all seem to have appeared before complete fusion occurred.

Thus, as has been demonstrated, there was an evolutionary trend in which to begin with cyclomorial tesserae became synchronomorial tesserae. These then fused into larger plates which were achieved earlier and earlier during development so that further growth could take place around them to keep pace with the growth of the animal. Once such an organized system of plates had been built up tesserae were then produced again as a secondary feature, although this time they were superimposed on concentrically growing plates. The redevelopment of such tesserae in the dorsal and ventral median plates, first by synchronomorial and then by cyclomorial growth, is a clear instance of the reversal of an evolutionary trend, and goes completely counter to «DOLLO's Law» of the irreversibility of evolution. This ability of the psammosteids to recall secondarily elements which were possessed earlier in their evolutionary history is therefore of some general significance. In addition it appears to have conferred greater flexibility on the median plates in their growing stages, particularly in the genus *Psammosteus.*

To be best fitted for any particular environment, a carapace is likely to require a particular profile, and a median plate which in the early stages is composed of separate cyclomorial tesserae is well able to adapt to any change in the shape of the body. It would not be made rigid until the plate growing beneath the tesserae became calcified, and this need not occur until the bulk of the tesserae had appeared. In this way any required curvature could be achieved. (It should be noted that this does not apply to plates of the lateral and anterior margins which would need to grow cyclomorially in order to support any extensions to the body). Such a flexibility in the median plates would explain the remarkable difference in thickness and in curvature seen in different specimens of dorsal median plate in *Psammosteus megalopteryx*. The dorsal median plate in the forms from Scotland are generally very thick and convex (TARLO, 1961*a*), while those known from Russia have a thin flat dorsal plate (OBRUCHEV, 1947*b*). Furthermore, the fact that the sediments containing these fossils were laid down under somewhat different conditions in the two regions, tends to confirm that the differences noted are due to environmental factors, and that the secondary development of tesserae was of some value in the life of the animals concerned.

HISTOLOGY OF DERMAL ARMOUR

(Pls. VI-XII; Pl. XIII, figs. 3-6)

It has been recognized since the middle of the last century, that the plates of psammosteid dermal armour are generally sufficiently well preserved to enable a detailed study to be undertaken of their microscopic structure and the first account of such a study was provided by AGASSIZ (1845*a*). He described plates of *Psammosteus (= Psammolepis)* which he had sectioned, as possessing three layers, and stated that the thick middle layer consisted of a great many winding canals between which there was a hard homogenous substance. Since it contained no bone cells he believed it to be closer to the tissue termed dentine by OWEN (1840-5) than to bone. PANDER (1857) also drew attention to the absence of bone cells in the tissue, although he considered that the remains of *Psammosteus* represented scales of the placoderm *Asterolepis*. In addition PANDER noted that external to the tissue in question there was a layer of small tubercles which were composed of dentine. He was also the first to make the incorrect suggestion, in which he has been followed by many subsequent authors, that on top of the tubercles was an homogenous, structureless layer of parallel lamellae which appeared much like the enamel of OWEN. In well preserved specimens, however, this layer can be seen to be one in which the dentine tubules rebranch finely.

GÜRICH (1891) also mentioned that no bone cells were present in the middle layer of the plates, but he did note that there were fine fibrous tubes running out radially from the vascular canals into the intervening tissue. Two years later, ROHON (1893) in his description of the Upper Silurian vertebrate remains from Oesel, Estonia, also briefly discussed the histology of psammosteid dermal plates. Unlike previous authors, and indeed all subsequent ones up to the present time, he made the observation that in well preserved specimens «one can convince oneself of the presence of simple bone cells» which have a spindle form and show almost no cell processes. However, later in the same paper and in 1901, ROHON considered that his previous interpretation was incorrect, being based on certain optical effects caused by bitumen, and he also thought that the tubes noted by GÜRICH were not actually present, being again merely an optical illusion caused by the same substance. However, as will be discussed below, the structures described by GÜRICH and ROHON appear on re-examination to be genuine, and it is perhaps a pity that ROHON having made such an important observation, should later have abandoned it.

As long ago as 1858, HUXLEY when discussing the microstructure of the armour of *Pteraspis* had mentioned that it possessed no bone cells, and had been followed in this by LANKESTER (1868). However it was not realized at the time that there was any affinity between *Pteraspis* and the psammosteids, despite the fact that when LANKESTER introduced the term

Heterostraci for *Pteraspis* and its relatives, the diagnosis for the group began «scutae materia sine lacunis osseis». In fact, it was not until 1899 that TRAQUAIR demonstrated that because of the similarity of the histology of the dermal armour of *Pteraspis* and *Psammosteus*, this latter genus should also be included in the Heterostraci. In this same paper, TRAQUAIR noted that the inner layer of the plates of *Psammosteus* was formed of a «dense laminated substance, perforated by vessels, the middle layer being thick and showing a close network of vascular canals». Since as he was the first to point out, the substance between these canals showed numerous minute tubules, TRAQUAIR considered that this supported AGASSIZ's view that the tissue was more related to dentine than to bone.

PREOBRAJENSKY (1911) briefly discussed the histology of the psammosteid *Pycnosteus*, while although KIAER (1915) did not add much to previous descriptions of the microstructure of psammosteid dermal plates, nevertheless he produced the only known sections of the plates of *Drepanaspis*. Perhaps even more important, he provided three-dimensional block diagrams showing the mutual relationships of the three main layers of tissue in psammosteid plates. In 1927, STENSIÖ briefly discussed the nature of heterostracan dermal armour, in particular that of the pteraspids, and considered that the absence of cell spaces was a secondary feature. He believed that the aspidin was true bone which had come to lose its cells during the course of evolution, and in this has been followed by later authors including ØRVIG (1951). Nevertheless, as will be argued below, cell spaces do exist in aspidin, although it is agreed that aspidin is the primitive tissue giving rise to modern bone.

A much fuller account of the histology of psammosteid dermal plates was however provided by GROSS (1930, 1935) and in the earlier of these two works he first used the name aspidin for the tissue making up the thick middle layer and the basal layer of the plates. Unfortunately in 1935, GROSS described coarse fibres in aspidin as SHARPEY's fibres and was followed in his identification by BYSTROW (1955) and ØRVIG (1958). As will be argued below however, SHARPEY's fibres could not have existed in such a position. In 1941, when discussing *Obruchevia [Aspidosteus]* OBRUCHEV considered that the very fine canals in the aspidin had once housed the processes of osteoblasts which had themselves atrophied after producing the tissue, but BYSTROW (1955) merely thought that they marked the site of former bundles of collagen fibres. Later still, GROSS (1961) returned to the subject of this tissue, discussing in particular the question of resorption, which will be dealt with fully in the following section.

More recently (MOSS, 1961; TARLO & MERCER, 1961, 1964) it has been realized that not only can ground sections be made of the exoskeleton of the psammosteids, but in addition, since organic matter is still preserved in the fossils it is possible to decalcify them and section them on an ordinary microtome. In this way normal histological staining techniques can be employed, and a more detailed study of psammosteid and similar armour can be carried out. Moreover, demineralized sections have now been examined under the electron microscope and by X-ray and electron diffraction techniques, thus providing new information on the composition of the tissues concerned (ISAACS, LITTLE, CURREY & TARLO, 1963). It is now evident for example that tubular collagen — a constituent of modern bone and dentine — is present in both the aspidin and dentine of psammosteid armour, and furthermore that the dentine tubules in the tubercles are lined with a cellulose-like polysaccharide. This is also known lining the tubules of human dentine as well as forming a layer around osteocytes and their processes in both modern and fossil palaeoniscid bone (NEVES & TARLO, 1964).

Although there has been some controversy regarding the detailed structure of the tissues making up the various layers of the dermal armour, it is generally accepted that there are three main layers. These are a basal lamellar layer of aspidin, a much thicker layer of spongy aspidin surmounting this basal layer, and superficial to the aspidin, a layer of dentine tubercles, and it is here proposed to discuss the histology of these various tissues in some detail. At the same time, since they were produced largely by accretion, the different stages of development of these hard tissues within a given specimen can be followed quite easily, and thus some idea can be provided of the way in which they came to be produced.

ASPIDIN

Although the tissue forming the basal lamellar layer and the much thicker middle layer of the dermal plates was first described by AGASSIZ as long ago as 1845, and since that time has been discussed by various authors, it was not until 1930 when the first really detailed account of it was published by GROSS, that this tissue was given the name aspidin. Aspidin varies somewhat in appearance not only in the different layers of the plate, but also from species to species, but in the thick middle layer it is generally rather spongy, looking something like cancellous bone. It is made up of a three-dimensional scaffolding of intercrossing and connecting calcified trabeculae of varying thickness and shape, which partially surround intercommunicating vascular spaces. Apposited on all surfaces of the trabeculae are lamellae of the same substance, arranged in successive layers, which form concentric zones around the vascular spaces, comparable to the osteones in bone. For these zones GROSS (1961) introduced the term aspidones. The innermost portion of the trabeculae is composed of an homogenous calcified tissue in which, under high magnification, certain structures are clearly visible. These, which were first noted by LANKESTER (1868—70) and ROHON (1893), appear spindle-shaped and seem to form a fairly random three-dimensional network, although none of them are actually in contact with one another at their extremities. Within the aspidones, as GÜRICH (1891) pointed out, similar, but elongated spindle-shaped structures are often visible cutting through the lamellae, more or less at right angles to the concentric layers, and apparently radiating from the vascular spaces.

Under cross nicols (polarized light), dark and light banding is easy to make out in the lamellae of aspidin, where it was first observed by GROSS (1930). In modern bone such banding is also known under the same conditions, and is interpreted as marking the alignment of crystallites. These in bone are laid down parallel to the initial collagen fibrils (MCLEAN & URIST, 1961), and the light and dark rings are produced because the fibrils are arranged in alternate layers — one set longitudinally and the next more or less circularly. It seems reasonable to suppose therefore, as did GROSS (1930), that the banding in the aspidin is also due to initial collagen fibrils having been laid down alternatively in successive layers, with the crystallites aligned parallel to them.

The basal lamellar layer of the plate is also composed of aspidin, but here as GROSS (1930) observed, it is made up of very thin virtually horizontal lamellae. Through these pass roughly vertical vascular canals linking the higher layers of the plate with what must have been the underlying soft tissue. The lamellae are much like those found in the thick middle layer, although they appear to contain fewer structures, possessing merely occasional spindle-shaped ones. Under crossed nicols (polarized light) very thin light and dark bands can sometimes be seen, indicating the same arrangement of fibrils and crystallites as outlined above. The banding, however, is not so pronounced as in similar basal tissue in other groups of vertebrates, or as found in the middle layer of the plates. Indeed the bands are frequently absent all together, and this led GROSS (1930) to conclude that the basal layer was essentially different from that known in the dermal bone of other primitive vertebrates.

As mentioned in the introduction to this section, in his work of 1893, ROHON observed that the spindle-shaped structures could conceivably be simple bone cells with a spindle form but almost no cell processes. However, he firmly retracted this view in 1901, while GROSS (1935) identified as fibres of SHARFEY both the spindle-shaped structures and the elongated structures described by GÜRICH (1891). Nevertheless, the initial organic matrix of the aspidin on which calcification later took place, was likely to have been produced by cells like osteoblasts which BYSTROW (1955) has called aspidinoblasts. In modern connective tissue the cells which are primarily concerned with producing collagen fibres, are fibroblasts, and these in their growing stage are invariably spindle-shaped, as also frequently are osteoblasts (KNESE, 1964). It is quite likely therefore that the cells responsible for the development of the matrix of the aspidin were spindle-shaped aspidinoblasts. There is some controversy as to whether fibroblasts of connective tissue do actually develop into normal osteoblasts at the present day, but since spindle-shaped spaces are preserved within the hard tissue of the aspidin, there is every reason to suppose that a cell of fibroblast shape was responsible for the initial development of hard tissues in the vertebrates. In this connection it should be mentioned that in some recent fish bone the normal osteocytes are also spindle-shaped and have no branching cell processes (R. AMPRINO, personal communication).

Numerous authors including AGASSIZ (1845*a*), PANDER (1857), HUXLEY (1858), LANKESTER (1868), TRAQUAIR (1899), ROHON (1901), STENSIÖ (1927), GROSS (1930, 1935), ØRVIG (1958*b*) and BYSTROW (1955) all believed that the armour of the psammosteids, or at least of heterostracans as a whole, was characterized by the absence of cells, and in addition MOSS (1961) could offer no explanation for the spindle-shaped «light staining areas» in his decalcified sections of aspidin. Nevertheless it is quite clear that the spindle-shaped structures visible within the trabeculae of the tissue aspidin can best be explained as spaces marking the site of former cells, to which the name aspidinocytes has been applied (TARLO, 1963*a*). These must have been concerned in the formation of the organic matrix before calcification took place, and must then have become trapped in the hard tissue even before the calcification actually occurred. Once this had happened, however, the aspidinocytes would have been cut off from their supply of nutriment, and would in consequence have tended to atrophy, leaving spindle-shaped spaces to mark their former position (Text-fig. 17). It should be noted, however, that as Professor R. AMPRINO (personal communication) has pointed out «... osteocytes enclosed in lacunae which do not communicate directly or through anastomoses with other cell processes with the vascular cavities are not necessarily bound to die. Some may do so, but the permeability of calcified bone matrix is such that a rapid diffusion of fluids may take place from the vessels towards the cells. This is shown by the extremely rapid uptake of radioisotopes by bone intercellular matrix and also by the persistence of presumably living cells in the bone of teleosteans which bear spindle-shaped osteocytes, and of living cementocytes in the tooth cementum of various animals».

Around the initial calcified trabeculae which appeared within what must have been soft vascularized tissue, successive lamellae of further organic matrix were laid down and then calcified, so that the vascular spaces became progressively infilled with layers of hard tissue, and aspidones took shape. This time however, although a few of the cells producing the matrix became trapped, most of them managed to produce cytoplasmic extensions at one end, so retaining for a while a link with their source of nutriment (TARLO, 1963*a*, 1964). Such cells, thus became drawn out and aligned normal to the apposited lamellae, rather like cells found in a comparable situation in the scales of primitive bony fish (GOODRICH, 1913) or like cementocytes (H. J. J. BLACKWOOD, personal communication). It was these elongated spindle-shaped aspidinocytes that were observed, although not identified by GÜRICH (1891), while these structures as well as the spindle-shaped cells within the trabeculae were identified by GROSS (1935, 1947) as fibres of SHARPEY. In this GROSS was followed by BYSTROW (1955) and ØRVIG (1958*a*), but this interpretation is not here considered correct, since SHARPEY's fibres are not found as components of internal basic systems, being instead a means of anchoring one tissue to another.

A further set of structures is also visible running through the lamellae, at right angles to them. These are very fine tubes and were noted by GROSS (1930). OBRUCHEV (1941) suggested when discussing *Obruchevia [Aspidosteus]* that these tubules are the canaliculi which housed cell processes of retreating aspidinoblasts, but BYSTROW (1955) considered that they were exactly the same as structures already known in psammosteids, and must have marked the former position of bundles of collagen fibres. Nevertheless, as has already been shown, collagen fibrils were aligned in alternate layers, and since the fine tubules run straight through the lamellae they could not have marked the position of such fibrils. OBRUCHEV's interpretation is therefore considered to be the correct one. This view is supported by the fact that a few spindle-shaped cell spaces are found at the junction of the lamellae, lying parallel to them. Presumably the fine tubules housed the cell processes of such aspidinoblasts, which must have acted very much like odontoblasts, moving back through the tissue as it became calcified, leaving behind in the lamellae fine tubules to mark the line of retreat of their cytoplasmic processes. Most of the aspidinoblasts seem to have managed to retain contact with the vascular

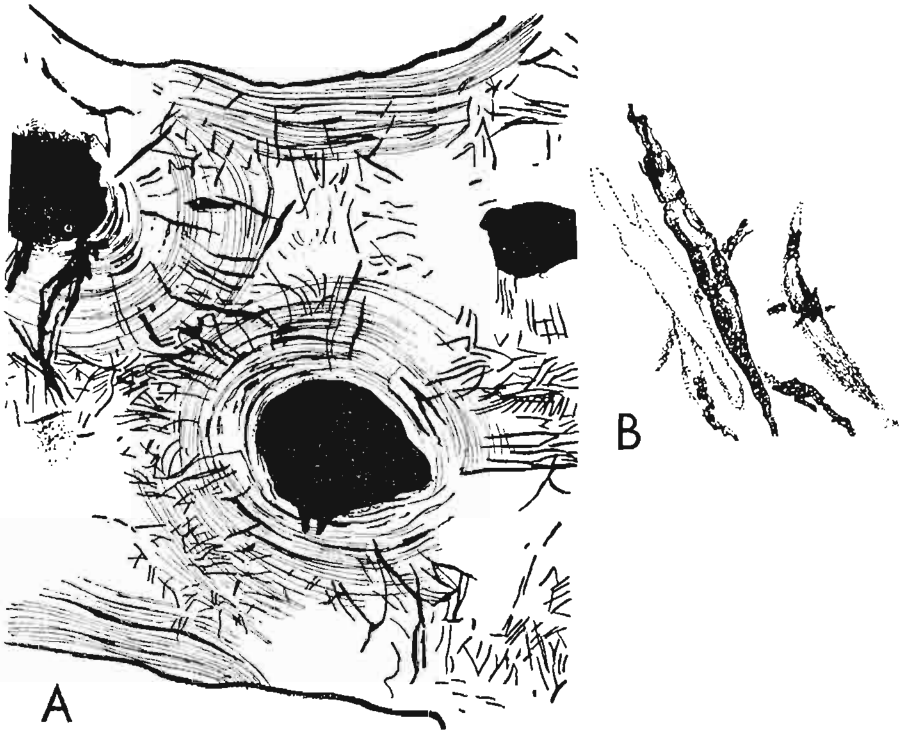

Fig. 17

Psammosteus megalopteryx (TRAUTSCHOLD) — *A* vertical section of aspidin showing random arrangement of aspidinocytes in trabeculae, and parallel alignment in concentric lamellae of aspidones, × 120; *B* detail of individual aspidinocyte spaces, × 400 (S.M., H. 4813c) space to which they retreated, but a few obviously became trapped between the successive layers (TARLO, 1963*a*, 1964).

It is most important that the different types of structure present in the tissue aspidin be recognized, since, owing to the fact that they are variously developed in the different species, they have in the past often been confused with each other, as well as misinterpreted. In *Tesseraspis* and *Weigeltaspis* for example, although fairly normal spindle-shaped aspidinocyte spaces are present in the trabeculae as a network, the situation is rather different at the margins of the plates. These are obviously regions of active growth, and here the spindle-shaped spaces are very densely packed, and are often drawn out parallel to the basal layer of the plate, i. e. in the direction of growth. These very abundant elongated spindle-shaped spaces are also common at the growing edges of plates of later forms, and may well represent not only the site of former cells, but also may mark the path of such cells. As aspidinoblasts they may well have moved back towards the vascular tissue at the margins of the plate as new aspidin matrix was laid down, in order to retain contact for some period with their source of nutriment. Occasionally these elongated spaces cut right through the trabeculae already present, and indicate that the tissue was capable of being secondarily resorbed and re-organized to some extent.

The aspidin in these early forms is largely made up of trabeculae, but in addition rings of a homogenous substance can be seen apposited against them, encircling vascular spaces. These however do not show the division into layers seen in later forms, although occasional faint rings can be made out. Moreover, the substance is virtually structureless, being more or less clear. In *Tesseraspis* and *Weigeltaspis*, the basal lamellar aspidin layer does not show the alternate light and dark banding under polarized light seen in later forms, suggesting that a stage had not yet been reached where the fibrils were arranged in alternate layers. Well marked narrow banding is not apparent either in the lamellae of the spongy aspidin when viewed under polarized light, although in this case a very faint broad banding can be seen, indicating the beginning of the differentiation of fibrils into alternately arranged layers.

In the later *Psammolepis venyukovi* there are much thicker trabeculae than in *Tesseraspis*, and within these there is an irregular network of spindle-shaped cell spaces. Occasionally such spaces are elongated as in *Tesseraspis* and *Weigeltaspis*, and these are aligned parallel to the basal layer. In *Psammolepis venyukovi* too, clear and virtually structureless lamellae are present around the vascular spaces. In *Tartuosteus maximus* the trabeculae are fairly normal, but the lamellae now show the alternate light and dark banding under polarized light. This indicates that the stage had at last been reached where the laying down of the initial collagen matrix was more highly organized, with the alternate fibrillar pattern typical of bone. Within the lamellae of this form, structures are now apparent, and these take the form of faint canaliculi. In addition between the lamellae small, elongated oval cell spaces can often be found, aligned parallel to the lamellae. These may well have been the site of former aspidinoblasts which moved back towards the vascular tissue as the lamellae were laid down, but then became trapped between one layer and the next.

Psammosteus megalopteryx provides the best example of the three-dimensional network of spindle-shaped spaces within initial trabeculae. Apposited against these to form aspidones around vascular spaces, are very thin lamellae with elongated spindle-shaped spaces running through them at right angles to the layers. In this form the light and dark banding is clearly seen in both the lamellae of the aspidones and in the basal lamellar layer, showing that a further stage had been reached in the organization of aspidin in the plates of the armour. In *Ganosteus stellatus*, there are very narrow trabeculae in which no structures can be discerned, and these are surrounded by aspidones in which the lamellae are thin and numerous. Through these lamellae pass very fine canaliculi which appear to radiate from the central vascular spaces. These canaliculi most probably marked the path of the cell processes of the aspidinoblasts which formed the lamellae, although in this instance none of the cells appear to have been trapped. Here then is an example of a variety of aspidin which is analogous to the tissue seen in the tubercles of the Ordovician *Astraspis*. This was considered by ØRVIG (1951) to be dentine, and then aspidin (1958*a*). Much the same type of aspidin is seen in *Obruchevia [Aspidosteus]*, in which OBRUCHEV (1941) first suggested that the canaliculi had been made by cell processes. Something similar is found in *Traquairosteus*, but in this latter form which appeared a little before *Obruchevia [Aspidosteus]*, aspidinocyte spaces are present in the trabeculae, unlike the situation in *Obruchevia [Aspidosteus]* or *Ganosteus stellatus*.

Resorption and remodelling

Despite the fact that it has generally been believed that remodelling of calcified tissue (i. e. resorption followed by regrowth) is a property characteristic only of true bone, it can now be demonstrated with certainty in the tissue aspidin. GROSS (1935) realized that in order that the plates of the psammosteid carapace could increase in thickness it would have been necessary for resorption to have occurred to allow for the necessary reorganization of the tissue. He contended that resorption was not possible in the upper part of the middle layer — generally termed the reticular layer — which lay just below the dentine tubercles, since the aspidin in that region appeared much denser, with smaller vascular spaces, than it was in the lower levels of the middle layer. However, although he was unable to find evidence of resorption having occurred, he believed that not only must the basal layer have been thickened by the addition of new layers from underneath, but also that the spongy layer must have increased from inside by growing in areas resorbed out of the basal layer. Furthermore, it has long been recognized that in many heterostracan groups, including the traquairaspids and pteraspids, in which large cancellae are found in the middle layer of aspidin, parts of the dermal armour fuse together during development, and the middle layer later forms a single continuous sheet of tissue. Since the original fusion of the middle layers of separate units must have taken place at the edges of plates or tesserae where no large cancellae are present, their subsequent formation throughout such areas when fused, indicates that resorption and reorganization of the tissue must have occurred. However, as with GROSS's suggestion, until recently no evidence has been produced that demonstrates how or where such resorption and regrowth took place.

Very clear examples of resorption and regrowth can however be demonstrated in aspidin. For example, a close examination of the upper part of the spongy aspidin in *Ganosteus stellatus* shows that in many instances the lamellae of the aspidones have been cut right through by resorption, presumably by cells like osteoclasts, which have been termed aspidinoclasts (TARLO, 1963*a*). In this way the mesh-work of aspidones was probably opened up to form larger vascular spaces. Moreover, at the very top of the middle aspidin layer there often appears to be a gap between this layer and the overlying dentine tubercles. Presumably this gap represents the main area of new growth in the plate, since within it small isolated areas of compact aspidin can occasionally be discerned. No doubt these joined up eventually to form a new layer of spongy aspidin on top of the original layer, thus producing the required growth in thickness of the plate as a whole. It seems evident therefore, that contrary to GROSS's suggestion, growth took place above and in the more superficial layer of the spongy aspidin, immediately below the dentine tubercles and not at the base of the spongy tissue. In fact this is consistent with HOLMGREN's Principle of Delamination recently elaborated by JARVIK (1959).

The clearest examples of the growth of new aspidin are found where a second generation of dentine tubercles has appeared on top of the old surface of the plate, and a layer of soft tissue has presumably intervened between the two sets of tubercles. The gap to be filled by soft tissue seems to have been made wider on occasions by the resorption of part of the underlying tubercles. Trabeculae of aspidin can be seen which are more or less vertical struts of hard tissue, and these are generally parallel or sub-parallel and tend to reach from the base of the overlying tubercles to the top of those lying beneath them. These trabeculae presumably mark the first stage in the development of aspidin. Next, concentric lamellae seem to have been apposited against the scaffolding of trabeculae forming aspidones with a central lumen of residual vascular tissue. It is of interest to note here that the manner in which the aspidin commences to form appears very similar to the situation in modern laminar bone. In that tissue too initial struts or trabeculae are formed more or less parallel to one another, and these are then enlarged in area by the apposition of further layers of calcified tissue. This is demonstrated in the recent reinvestigations of laminar bone by LACROIX (1960) and CURREY (1960).

The next stage visible in the plates of *Ganosteus stellatus* is one in which the initial meshwork of trabeculae and aspidones is filled in with further calcified deposits. In this way a very dense tissue is produced with only small vascular spaces. The final stage, also seen in plates of *Ganosteus stellatus* is where this dense tissue is opened up by means of selective resorption to produce large cancellae with fairly thin walls of aspidin but very much enlarged vascular spaces. Not only would this have the effect of lightening the plate, but in addition it would release the constituents of the resorbed calcified tissue to be used in the superficial portion of the plate for the production of further amounts of dense aspidin. This in turn would then be opened up later to produce the more typical wide-meshed tissue, and the cycle would be repeated until the plate had reached its definitive depth.

Resorption of aspidin of the type mentioned above, in which the walls between the vascular spaces of aspidones are broken down and the vascular areas are consequently enlarged is clearly seen in *Ganosteus stellatus* when the tissue is viewed under polarized light (crossed nicols). The light and dark banding of the lamellae is very sharp, and clean breaks in the walls stand out clearly. Narrow channels appear to have first been cut straight through the originally continuous concentric banding, and then the remainder of the cut wall seems to have been progressively «eaten» away by the aspidinoclasts (Text-fig. 18). Occasional examples are also visible where after resorption new aspidin has been laid down across the old aspidones, forming secondary aspidones. This could perhaps be considered as an approach to the secondary osteone condition in bone, where haversian systems are produced within resorbed areas of previously formed tissue. The new vascular channels cut through the lamellae seem to occur most frequently in the denser part of the aspidin at the top of the middle spongy layer of the plates, generally known as the reticular layer, and since dense tissue of this type seems to be found invariably in this position, there is good reason to postulate the process of opening up of the tissue as already outlined. Once such a postulation is accepted, then care must be taken when identifying the isolated tesserae of cyathaspids and psammosteids. In the past the relative size of the cancellae in the plates has been used as a diagnostic character, but this is no longer acceptable, since it may well prove to be the case that in many forms large cancellae are merely a sign of the tissue having been remodelled.

From evidence supplied by GROSS (1961) it appears that in plates of young individuals, all the trabeculae of the aspidin are very thin, while vascular spaces are small although numerous. Presumably during the development of the animal the tissue goes through a cycle of progressive changes rather like those seen in the development of the aspidin in the plates of more mature individuals. A small plate belonging to *Tesseraspis* appears to bear out this conception, since towards the middle of the plate there is an area of small mesh aspidin similar to that described in a young form by GROSS (1961), while around it the tissue has become more like the dense aspidin found in the upper parts of the middle layer of *Ganosteus stellatus*. Further, in *Tesseraspis* a region of even denser aspidin with abundant spindle-shaped spaces is seen at the margins of the plate, suggesting a region of very active growth. This plate seems to represent a stage in development in which the thickening of the initially formed trabeculae had begun, but had not yet reached the central portion of the aspidin. At the same time zones of very dense new aspidin were being added on at the margins which gradually became somewhat opened out to form the outermost part of the fairly dense region of the plate. This developmental picture also fits in well with the views expressed earlier in the section on ornamentation and growth of dermal armour. To begin with the tesserae of *Tesseraspis* were formed synchronomorially, i. e. the initial thin-meshed aspidin was produced all at one time, and then the tissue began to be thickened from the outside in towards the centre. Simultaneous to this secondary thickening, the tesserae were increased in area cyclomorially by the growth of new very dense aspidin around the margins of the initial synchronomorial unit. This very dense tissue then, by selective resorption and regrowth became like the secondarily thickened aspidin. Since in more mature plates of *Tesseraspis* the aspidin meshwork is a more open one, no doubt the fairly dense aspidin would later have been opened out in the way described in *Ganosteus stellatus*.

Fig. 18

Ganosteus stellatus ROHON — vertical section of upper part of spongy aspidin showing areas of resorption cutting into and through lamellae of aspidones (U.W., D 63), × 75

Origin of bone

Although various authors had already described it, STENSIÖ (1927) was the first to discuss in detail the nature of the tissue making up the bulk of heterostracan dermal armour, and in particular its relationship to bone. He believed, like previous authors, that cells or cell spaces were absent from the armour of adult forms, but thought that «cells originally must have formed the basement and middle layers of the carapace of the Pteraspidae and have been enclosed between the lamellae of these layers, though they became reduced in very young larvae». He went on to suggest that «everything seems to indicate that the absence of cell spaces in the shields of adult pteraspids is a secondary feature, and thus that the Pteraspidae in this respect are more specialized than the Osteostraci [cephalaspids]». He further stated that «it is clear that, if the ontogenetical development of them was as I have assumed here, the hard tissue that constitutes the middle and basal layers of the carapace of the Pteraspidae is in fact true bone».

GROSS (1935), although he did not comment directly on STENSIÖ's view, appears to be in agreement with it, while ØRVIG (1951) also followed STENSIÖ by believing that the absence of cell spaces in aspidin was secondary. ØRVIG stated that «the presence of cells (cell spaces) in bone tissue is, in all probability, a primitive character», and indicated therefore that he believed that aspidin was derived from bone by the secondary loss of cells. However, the fact that aspidin appears first in time makes it likely that it is a more primitive tissue than the later appearing bone, rather than a specialized derivative of it. But even more important is the fact that although aspidin has always been considered to be an acellular tissue, as has been demonstrated above, it does in fact contain various structures which although they have generally been misunderstood in the past, can best be interpreted as marking the site of former cells and cell processes. Furthermore, if the evolution of aspidin is traced from the condition found in early forms, it can be seen that the arrangement of the collagen fibrils of the organic matrix progressively approaches the condition found in modern bone (TARLO, 1963*a*, 1964). In both bone and the more advanced aspidin, the fibrils are laid down in alternate layers, producing characteristic black and white banding under polarized light. Besides this, aspidin is built up on much the same plan as lamellar bone, since in both cases when new tissue is formed initial struts or trabeculae appear, against which concentric lamellae are apposited. Moreover, aspidin, again like bone was capable of resorption and remodelling, and secondary aspidones were produced on occasions much like secondary osteones in bone.

In fact, there is only one main feature by which bone and aspidin can be distinguished from one another. That is on the general absence of stellate cell lacunae with canaliculi in the lamellae of the aspidin. However, there is not the sharp distinction between the two tissues in this respect that was previously thought to be the case. As has been demonstrated, in many instances aspidinoblasts did retain contact with their supply of nutriment for considerable periods, although they could not do this throughout the life of the animal. Since the tissue was permeated by vascular spaces, new aspidinoblasts and aspidinocytes could be produced as required, from the cells within the vascular tissue.

Thus, since it is virtually indistinguishable from bone in many respects, and since it comes before bone in time, it is here suggested that the primitive calcified tissue aspidin was the precursor of true bone. It is believed that during the evolution of this latter tissue the cells managed to maintain contact with one another and thence the vascular supply by means of intercommunicating processes, and that canaliculi formed around such processes as calcification occurred.

DENTINE

PANDER (1857) was the first to note that the tubercles forming the outermost layer of psammosteid armour were composed of the same tissue as that described by OWEN (1840-5) in the teeth of higher vertebrates, and called by him dentine. Subsequently PANDER's views were confirmed by various authors including ROHON (1893, 1901), who described incremental lines in the tissue, and PREOBRAJENSKY (1911), but it was not until 1930 that GROSS carried out a detailed examination of the dentine in the psammosteids. He demonstrated that the tubules in this tissue possessed lateral and terminal branches, although as he noted later (1935) these tended to vary in appearance in different genera and species. He stated also (1930) that the outermost layer of the dentine appears different from the rest of the dentine under polarized light (crossed nicols). A number of authors including PANDER (1857), ROHON (1893, 1901), BROTZEN (1933*a*) and WILLS (1935) had suggested that there was a further type of hard tissue surmounting the dentine of the tubercles, which had an enamel-like appearance, and this outer layer is often illustrated as a clear band. GROSS's observation therefore would seem to support such an idea. However, in well preserved specimens it can be seen in ordinary light that the region is merely one in which the terminal branches of the dentine tubules re-branch very finely (TARLO, 1960*b*), and is quite definitely part of the dentine. The difference in appearance under polarized light may well be due to the different alignment of the crystallites in this outer layer (W. J. SCHMIDT, 1959).

More recently (MOSS, 1961; TARLO & MERCER, 1961, 1964) it has been shown that it is possible to decalcify and stain thin sections of the dermal armour so that they can be studied with the aid of modern histological techniques. Using such decalcified sections together with the normal ground sections, direct comparisons have recently been made between the dentine of psammosteid tubercles and this tissue in the teeth of man. The dentine tubercles are obviously tooth-like structures, since each has a central pulp cavity which can be either simple or complex, which is directly connected to the vascular spaces of the underlying aspidin. Around the pulp, which often ramifies, there is a thick shell of dentine with its characteristic tubules appearing to radiate towards the periphery. It has been demonstrated (TARLO, 1962*b*) that the dentine of these tubercles is in general virtually indistinguishable from the same tissue in human teeth. In both cases it appears to have the same mineralogical composition, a similar arrangement of dentine tubules with lateral and terminal branches and it seems to have been laid down in much the same way, as evidenced by the presence of incremental lines. It should be noted however that in the psammosteids the tubules are generally somewhat coarser than they are in man, and less closely packed, and there are fewer side-branches. Furthermore, as already pointed out, the tubercles do not possess an enamel cap like human teeth, and in consequence the dentine was exposed at the surface.

Besides having been decalcified and stained in the normal way, psammosteid tubercles have also been examined by electron microscopy (ISAACS, LITTLE, CURREY & TARLO, 1963) and it has been discovered that the tubules are lined with a membrane of a cellulose-like substance such as is found lining the tubules of modern dentine. Evidently this membrane is also much like that found forming a layer around the cell processes of osteocytes in human bone and also the cells and cell processes in fossil palaeoniscid bone (NEVES & TARLO, 1964). Furthermore, it may be due to the considerable powers of survival of this cellulose-like substance that dentine tubules retain their form in decalcified sections. From recent histological and electron-diffraction and X-ray diffraction studies (ISAACS et al., 1963) it is also clear that the organic matrix of the dentine in psammosteid armour is still surviving, and that it has virtually the same composition as has modern bone and dentine. Thus it is quite evident that there is a close similarity between the dentine of the tubercles and that found in human teeth, and presumably the tissue was formed in much the same way in both instances. The organic matrix must have been laid down by odontoblasts around their anterior processes, and as calcification occurred the cells must have moved back so that eventually they retreated to the margin of the pulp cavity, leaving channels or tubules in the calcified tissue to mark the line of retreat of their processes. This process must have been carried out in stages, so that the tissue was apposited in successive layers which are indicated by the incremental lines.

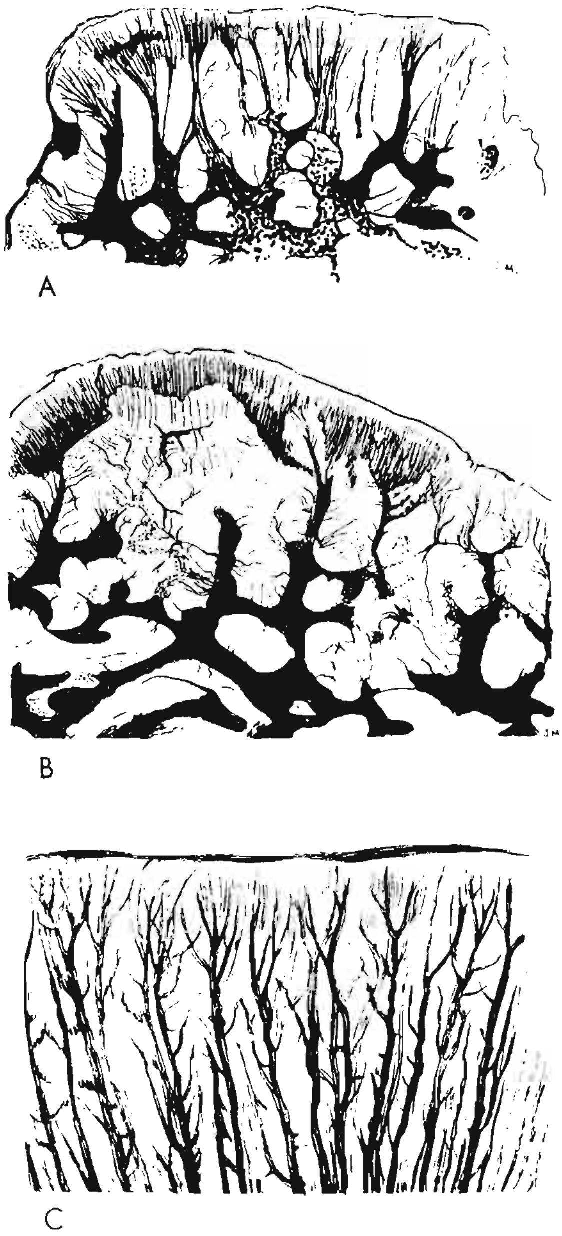

Fig. 19

A-C Vertical sections of dentine tubercles. *A Tesseraspis tessellata* WILLS — showing anastomosing pulp cavities (U.W D 64), × 75; *B Weigeltaspis godmani* n. sp. — showing complex pulp cavity with dentine tubules radiating from all surfaces of pulp canals (U.W., D 65), × 75; *C Tartuosteus maximus* MARK — detail of dentine tubules showing fine lateral and terminal branches (U.W., D 66), × 200

Although *Eriptychius* from the Ordovician is not a psammosteid, nevertheless, as previously mentioned, it may well have been from a form similar to it that the psammosteids originated. It is of interest to note therefore that the tubercles of *Eriptychius* are built on much the same basic plan as those already described, and are composed of the same type of dentine. In this form the pulp is a complex one, with irregular branches, although these do not extend far into the tubercles themselves. From the branches of the pulp, broad tubules extend to the exterior, appearing in vertical section more or less parallel. Near the pulp the tubules are very coarse, and in fact it is often difficult to tell whether they are in fact direct extensions of the pulp itself or merely extremely thick tubules. They are well separated and become somewhat less coarse as they near the periphery, where they re-branch into finer tubules. In the early psammosteid *Tesseraspis*, tube-like extensions of the pulp cavity quite clearly ramify through the bulk of the tubercles, with cross connections forming an anastomosing network (Text-fig. 19*A*). From these pulp canals, fairly fine dentine tubules radiate, and then break up into fine terminal branches towards the exterior. In this form since the canals form a three dimensional network, in vertical section the tubules radiating from them appear to run in any and every direction.

In *Kallostrakon* and *Corvaspis*, broad extensions of the pulp finger into the dentine, and from the ends of these fingerings dentine tubules radiate towards the periphery where they re-branch into minute terminal tufts. Occasionally in *Corvaspis*, examples are found where a few of the dentine tubules quite clearly extend right into branches of the pulp cavity, although retaining their separate identity. In *Weigeltaspis* there is again, as in *Tesseraspis*, a network of anastomosing pulp canals throughout the dentine, with the tubules running towards them whatever their direction (Text-fig. 19*B*). *Weigeltaspis* in addition, shows tufts of dentine tubules at the distal ends of the canals. These two genera demonstrate an arrangement in which the dentine is very closely associated with the vascular supply, in a way reminiscent of aspidin, and is not yet organized as a solid tissue around a more clearly demarked and more simple pulp cavity. Thus there seem to be varieties of dentine present in the early psammosteids, further examples of which existed in other groups (see ØRVIG, 1958*b*; GROSS, 1961), and are also known at the present time.

In *Guerichosteus*, a more typical psammosteid, dentine rather like that seen in the outer part of the tubercles in *Tesseraspis* and *Weigeltaspis* appears to have continued through, except that the pulp cavity has become somewhat simplified, and the tubules are now parallel to one another and extend to the base of the tubercle as in *Eriptychius*. From the condition seen in *Guerichosteus* there appears to be little change in the later psammosteids, although as a general rule the dentine tubules have become somewhat more closely packed and have more lateral branches, while they now radiate from a very broad pulp cavity (Text-fig. 19*C*). On occasions however the tubules can be seen to converge towards one of several foci in the broad pulp, no doubt the last traces of the earlier complex pulp cavities with their corresponding groups of tubules (TARLO, in STENSIÖ, 1962).

In sections of *Ganosteus stellatus* there is an interesting phenomenon which may throw some light on the relationship between dentine and aspidin. In this form the dentine sometimes abuts directly against the aspidin, with no intervening pulp and where this occurs, generally at the margins of the tubercle, the dentine grades imperceptibly into the aspidin, the tubules of the dentine merely becoming less and less in number until they disappear altogether. Under polarized light (crossed nicols) however it can be seen that there is a very sharp distinction between the dentine and aspidin, suggesting a different alignment of the crystallites and hence collagen fibrils in the two tissues.

Eruptive dentine

In the psammosteids, as in the Heterostraci as a whole, since the dentine formed the outermost layer of the armour, it was in direct contact with the environment and in consequence behaved much like skin in other forms. In particular it was capable of healing when damaged in any way. When a break occurred in the ornament, perhaps due to the bite of a predator, or through tesserae being lost before they became fused to the underlying aspidin, then epidermal tissue from between the adjoining tubercles must have grown across the gap. This tissue would then have set off the production of secondary tubercles to fill the damaged area or seal off any bitten edges. Examples of this type of healing by the formation of secondary dentine, are fairly common. In dorsal plates of *Corvaspis* scars can be seen filling in original cracks, bites have been sealed off in the branchial plates of *Psammolepis venyukovi* (Tarlo, in Ager, 1963), and in a dorsal plate of *Psammosteus megalopteryx*, rather small secondary tubercles are visible lining the floor and walls of the cavity left when a tessera was lost (see Text-fig. 14*A*).

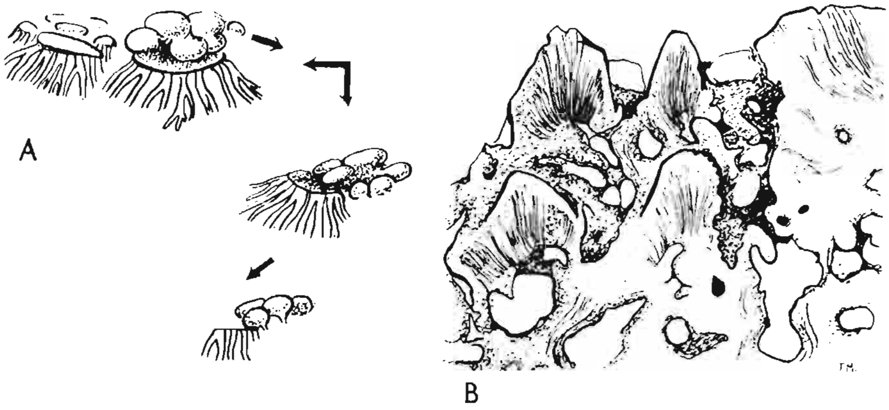

Fig. 20

Ganosteus stellatus Rohon — eruptive dentine. *A* part of branchial plate showing abraded tubercle surmounted by secondary globular tubercles (P.I.M.), × 3; *B* vertical section of tubercles with underlying earlier generation exhibiting resorption at summit (lower right tubercle) (U.W., D 67), × 75

Furthermore, in 1961 Gross figured in section the scale of the early heterostracan *Traquairaspis* from an area of the carapace which was subject to continual abrasion (Text-fig. 22*A*). This too showed the formation of secondary dentine, since it pictured a row of second generation dentine tubercles which had formed on top of the old original layer of tubercles. This type of secondary dentine was called «wucherdentin» by Gross (1930) and eruptive dentine by Tarlo & Tarlo (1961). It should be noted that when Gross figured this section (1961), he believed that he was figuring an example of resorption in the heterostracans, since he thought that the summits of the underlying tubercles had been resorbed. However, it is quite clear from his figure that the underlying tubercles had in fact been worn down, since they presented a smooth curved plane at their summits, parallel to the curve of the plate as a whole. This could obviously not have been produced by resorption, since such a process invariably produces an irregular outline, or a concavity such as was recorded in their first account of resorption in the psammosteids by Tarlo & Tarlo (1961).

Thus it would seem from Gross's figure, that when the original surface of the scale in

Traquairaspis became worn, this stimulated the epidermis to spread over the worn area and set off the production of a second generation of dentine tubercles. This type of healing or protective mechanism may well also have occurred in early psammosteids, although so far no clear examples have been recorded. Examples are known however in the psammosteids where eruptive dentine has been formed in areas where there was intermittent abrasion. On the distal ends of some branchial plates of *Ganosteus stellatus* globules of eruptive dentine are visible on top of the old surfaces of the plates (Text-fig. 20*A*), while GROSS (1930) figured something similar in *Psammolepis paradoxa*. In other psammosteids, «blisters» of eruptive dentine have been described by GROSS (1935), HEINTZ (1957), STENSIÖ (1958), ØRVIG (1961), and TARLO & TARLO (1964) in which the secondary tubercles are clustered together in patches. These «blisters» are scattered sparingly over the original layer of tubercles which form a continuous sheet below them. This time the eruptive dentine appears to have been formed in areas of the carapace where no abrasion occurs, whether continual or intermittent. ROHON (1893, 1901) and WILLS (1935) also noted two sets of tubercles on psammosteid plates, but they believed that the underlying tubercles were the secondary ones, and were being produced as a replacement for those overlying them. However, as GROSS (1930) realized, the overlying tubercles were the secondary ones, and this is confirmed by the fact that in the cornual plate of *Ganosteus stellatus*, small new tubercles are found lying in craters resorbed out of the sides and summits of the older, generally larger tubercles (see TARLO & TARLO, 1961, TARLO & TARLO, 1964, and Text-figure 14*B* which is published by kind permission of Dr. ELGA MARK).

GROSS (1935) suggested that the formation of eruptive dentine was due to a pathological condition or injury, while ØRVIG (1961) disagreed, since he considered that the formation of «blisters» was the «normal result of the growth by consecutive generations of dentine units deposited on top of each other, which is surely the common property of the dermal elements in the early Agnathi and fishes». However, although it is true that early forms possessed the ability to produce second generation tubercles on top of first generation ones (e. g. JARVIK, 1959, figured the condition in *Eriptychius* from the Ordovician), nevertheless to begin with there is no doubt that the secondary tubercles were produced as a response to some external irritant. This could take the form of abrasion, however slight, or in areas where no such abrasion occurs it may well have been of chemical origin. However, what is likely is that once the epidermal tissue acquired the ability to induce the production of successive generations of dentine tubercles as a response to some sort of irritation, during the course of evolution this type of replication became utilized as a normal method of replacing tubercles and other dermal units (BYSTROW, 1939). For example WHITE (1952) figured the carapace of an arthrodire in which there was a second layer of tubercles completely covering the original layer of worn tubercles. A further development is seen in the dipnoans, where bones of the skull can be gradually replaced by the formation of partially overlapping units on top of the original ones, producing the characteristic WESTOLL lines (BYSTROW, 1942).

With the evolution of jaws, and the change of function from tubercle to tooth, this same method was used by the higher vertebrates as a way of replacing teeth (see TARLO & TARLO, 1963, 1964) although it should be noted that often more successive generations of teeth are produced than are actually required. For example, many of the generations of teeth are never functional at all in sharks, and much the same situation is seen in the psammosteid *Schizosteus wellsi*, where up to five sets of tubercles are visible in the armour, one on top of the other. In such instances it would appear therefore, that the new units were produced merely because the epidermal tissue had the property of inducing the formation of successive generations of skeletal structures.

The system of tubercle replacement in the ostracoderms in which the new generations appeared on top of the older ones might at first sight appear to be the reverse of that known in teeth at the present day, where the second and further generations erupt from below, usually either into the same socket as a tooth that is shed, or alongside it. In fact however, this is not so, as can be demonstrated from a study of the embryological development of human teeth. Early in ontogeny the germ of the permanent tooth lies above and to the side of the germ of the milk tooth — the same spatial arrangement as seen in ostracoderm tubercles — and it is only later that the relative positions of these teeth change so that eventually the permanent tooth comes to lie beneath the milk tooth.

Pleromic dentine

In Middle and Upper Devonian psammosteids, in areas of the carapace which were subjected to continual abrasion, such as down the centre of the ventral plate and along the edges of downturned lateral plates, a further type of secondary dentine developed, called pleromic or infilling dentine by TARLO & TARLO (1961). It would appear that with the commencement of abrasion on the summits of the tubercles, the small areas of epidermis still remaining between the tubercles were stimulated to initiate the production of odontoblasts, and these in turn proceeded to lay down dentine in the vascular spaces between the tubercles (see KIAER, 1915). As the abrasion continued, the odontoblasts must have moved down gradually into the anastomosing spaces of the spongy aspidin, where they replaced the normal soft connective tissue with pleromic dentine or as GROSS (1930, 1935) termed it, massive spongiosa. This secondary dentine, unlike the normal dentine of the tubercles, contains only a few tubules, with few and poorly developed lateral branches. The tubules however are very long and wind their way through the hard tissue. When they pass through a narrow channel leading from one space to another they tend to converge, diverging once again as the spaces open out (Text-fig. 21). From the numerous specimens examined, it seems that this process was very efficient, since the infilling kept pace with the abrasion of the outer surface of the carapace, so that there was always a certain minimum thickness of solid tissue to protect the animal in vulnerable areas. This strengthening by pleromic dentine therefore, had much the same

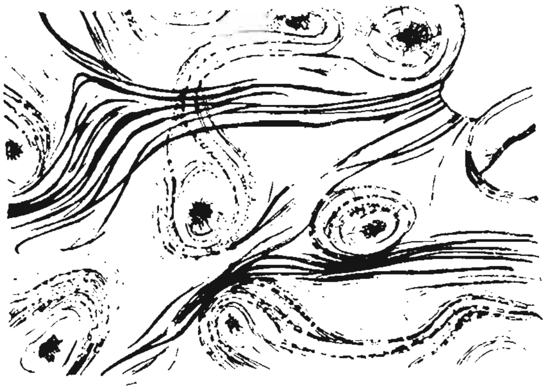

Fig. 21

Tartuosteus maximus MARK — section of branchial plate showing pleromic dentine infilling spongy aspidin (U.W., D 68), × 120 effect as the hardening and thickening that occurs in skin where there is continual abrasion, such as on the soles of the feet, and in patches on the palms of the hands in manual workers.

Secondary dentine in human teeth also shows relatively fewer tubules than are seen in normal human dentine, and its formation also appears to be initiated either by attrition or by the removal of part of the normal dentine in some other way. However, secondary dentine in human teeth is normally laid down only inside the pulp cavity by odontoblasts which originate in the pulp, whereas in the psammosteids pleromic dentine was thought only to develop between the tubercles, from where it spread into the vascular spaces of the aspidin and thence sometimes into the pulp cavities themselves. It can now be demonstrated however, that although partial infilling of the pulp cavities of the tubercles did take place by means of odontoblasts moving into them from the vascular spaces of the aspidin, in some cases secondary dentine was formed immediately below the original dentine of the tubercle, almost exactly as secondary dentine is laid down in human teeth. Pleromic dentine however, developed prior to normal secondary dentine in tubercles, as is evidenced by the fact that initial wear on the surface of the carapace first stimulated dentine production between the tubercles.

It was only some time after pleromic dentine had first spread across the floor of the pulp cavity that normal secondary dentine was produced at the periphery of the pulp. This is evident from the fact that the more or less vertical tubules of the secondary dentine turn as they near the base of the pulp, to run above but parallel to the horizontal tubules of the pleromic dentine as these pass across the pulp cavity.

The formation of pleromic dentine was a rather late development in the geological history of the psammosteids, since as already outlined, in the earliest forms severely abraded areas were probably healed by blisters of epidermis forming over the areas, within which new tubercles of eruptive dentine were produced. This must have meant however, that during the period when the new growth was taking place, it was essential for the animals to undergo a period of immobility, for any normal movement would have been likely to damage the blisters and disrupt the reparative process. However, with the development of pleromic dentine this problem no longer arose, since the armour could be strengthened from below as it was worn at the surface.

Although at first glance it might appear that there could be little connection between eruptive and pleromic dentine, nevertheless specimens observed by GROSS (1930) and BYSTROW (1955) have enabled a picture to be built up of the way the pleromic dentine of the later forms could have evolved from the condition found in the more primitive psammosteids.

GROSS (1930, 1935) noted that in *Psammolepis paradoxa*, besides secondary tubercles forming, where wear had occurred a new tissue was also produced in the affected areas. It seems that a layer of unorganized dentine was now present sandwiched between the old and new sets of tubercles. In this tissue parallel lines of long winding tubules were visible, threaded through the tissue in a more or less horizontal direction. The tubules did not penetrate the original surface of the plate, but instead the tissue merely formed a solid layer above the old tubercles (Text-fig. 22*B*). However, in 1955, BYSTROW published figures of the same form showing the tubules of the same type of secondary dentine continuing down the narrow vascular channels between the tubercles of the old surface, and into the vascular network of the underlying aspidin (Text-fig. 22*C*). Thus it is clear that the tissue which first formed beneath the eruptive dentine layer and then continued through the original surface of the plate was the same tissue as the pleromic dentine which is seen in later forms filling in the vascular spaces of the aspidin. Evidently in these last mentioned forms secondary tubercles were no longer produced, pleromic dentine being the only method used to counteract continual abrasion of the carapace. This would have been advantageous since it obviated the need for a period of enforced inactivity during the production of a second layer of tubercles on top of the original worn ones. One advanced form — *Obruchevia [Aspidosteus]* — even went so far as to produce a complete carapace strengthened by pleromic dentine, in which no tubercles were developed at all (Obruchev, 1941). In this way therefore it eliminated the possibility of harm due to the loss of tubercles such as sometimes occurred in earlier forms. It is true that many parts of the carapace were strengthened that could hardly have been subjected to serious abrasion, but nevertheless in this way it produced an armour that could be continually thickened from within, wherever the need arose.

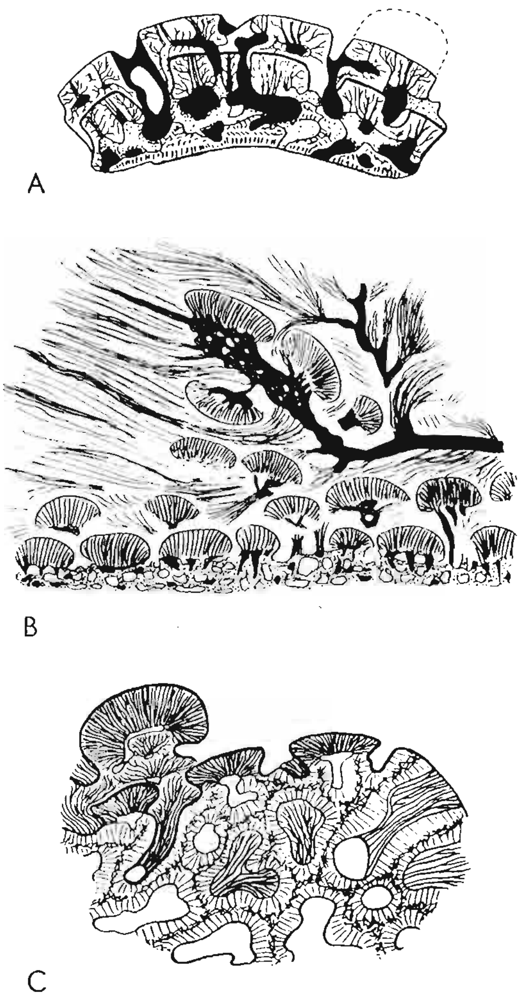

Fig. 22

A-C Diagrams illustrating possible origin of pleromic dentine. *A Traquairaspis* sp. — vertical section of scale showing abraded surface surmounted by second generation tubercles which have also been subjected to abrasion (from Gross, 1961); *B Psammolepis paradoxa* (Agassiz) — vertical section showing mass of randomly arranged eruptive dentine surmounting old surface of ornamentation (from Gross, 1930); *C Psammolepis paradoxa* (Agassiz) — section showing tubercles of eruptive dentine surmounting first generation tubercles, with dentine tubules of second generation tubercles penetrating underlying vascular spaces of spongy aspidin, to form pleromic dentine (from Bystrow, 1955)

A condition approaching that seen in ***Obruchevia [Aspidosteus]*** is also known in ***Traquairosteus***. Here isolated tubercles surmount well-spaced pustules composed of aspidin, and in section it can be observed that the dentine tubules of the tubercles often penetrate the aspidin of the pustules. Thus by the further reduction and then complete elimination of dentine tubercles it is easy to envisage how the condition found in ***Obruchevia [Aspidosteus]*** could have been arrived at.

Relationship between dentine and aspidin

There is obviously a very close relationship in the Heterostraci, between the dentine of the tubercles and the underlying aspidin, since in the Ordovician *Eriptychius* these tissues seem to possess exactly the same matrix, and both appear to consist of an acellular calcified substance which was apposited in successive layers. Under polarized light (crossed nicols) for instance, there is no change in appearance from one tissue to another in this form, indicating that the initial collagen fibrils and hence the crystallites must have had the same arrangement in both. The only difference is that the tubercles possess coarse tubules marking the course of the processes of the cells producing the substance, while the underlying tissue has no such structures, indicating that the cell processes as well as the cells must have retreated before calcification took place. Both tissues seem to have been acellular at this stage, although very occasional spindle-shaped spaces can be seen in the aspidin of *Eriptychius* showing that the trapping of cells in the tissue was possible.

It may well be therefore that dentine and aspidin are merely two varieties of the same basic primitive calcified tissue — perhaps a very primitive aspidin — which became differentiated according to its position in the external covering of the animal concerned. This is borne out by the fact that there has been some controversy regarding the tubercles of the contemporaneous *Astraspis*, which have in the past been thought to have been composed of aspidin, but which also bear very strong resemblances to tubercles made of dentine. For example BRYANT (1936) noted that the tissue «contains neither cell spaces nor dentine tubules and consequently is neither bone nor dentine», although he went on to state that it was «everywhere penetrated by a system of minute sub-parallel fibres resembling the fibres of SHARPEY», while ØRVIG (1951) interpreted these latter structures as fine dentine tubules. Later however, (1958*a*), he retracted this idea, and ,considered that they represented SHARPEY'S fibres in normal aspidin. Nevertheless it is evident that the structures cannot be fibres of SHARPEY, since as argued in the section on aspidin, these would not be found in such a position. Instead, the striae are more likely to have marked the former site of the processes of cells forming the tissue, much as normal dentine tubules indicate the presence at some time of processes of odontoblasts. However, the tubules in *Astraspis* tubercles are very much finer, more uneven, and more closely packed than are dentine tubules, and are very close to the fine canaliculi known in some types of aspidin. In consequence the substance forming the tubercles in *Astraspis* can only be considered as a tissue with strong affinities to both dentine and aspidin. Since however, the aspidin underlying the tubercles in *Astraspis* has only a very few such canaliculi, this indicates that the calcified tissue in the tubercles is probably nearer to dentine than to aspidin itself.

In the psammosteids, the dentine continues through basically unchanged from the condition in *Eriptychius*, although as mentioned earlier, the dentine tubules become less coarse, and can have a different arrangement of their lateral and terminal branches. However, under polarized light (crossed nicols) there seems to be a gradual change in the alignment of the fibrils and crystallites in the aspidin. In the primitive psammosteids from the Lower Devonian such as *Tesseraspis*, the lamellae of the aspidin can be seen to be divided up into a few broad zones appearing as different shades of grey, showing that unlike the position in the aspidin of *Eriptychius*, the collagen fibrils and crystallites must have been laid down slightly differently in adjacent groups of lamellae. Thus for the first time, there is a division under polarized light between the aspidin and the dentine of the overlying tubercles. In the more advanced genera typified by *Ganosteus* and *Psammosteus*, the lamellae of the aspidin are approaching the condition found in bone, where the collagen fibrils and crystallites of adjacent layers are arranged quite differently from one another, so producing the characteristic narrow black and white banding under polarized light. Thus, although as GROSS (1961) pointed out in ordinary light the dentine tubercles often appear to grade imperceptibly into the underlying aspidin, there is now a very sharp difference between the two tissues under crossed nicols. This is particularly striking in specimens of *Ganosteus stellatus*, where on occasions some of the dentine is without tubules and looks like aspidin, and where dentine tubules sometimes continue through into the aspidin itself.

As demonstrated above, there was more than one variety of dentine within the early psammosteids, and there is no reason why there should not have been further development of the basic tissue in other groups. This would explain the nature of the substance forming the tubercles of the cephalaspids, which ØRVIG (1958*b*) suggested was derived from bone, and called meso-dentine, and which still appears to survive as osteo-dentine in living vertebrates. In any case it has now been demonstrated that bone is not the basic calcified tissue from which all others have evolved, and thus there is no need to try to derive meso-dentine from it. Instead it is here suggested that hard tissues in the vertebrates can best be understood as having originated from a very primitive type of aspidin. This seems to have been formed by the repeated laying down in the skin of successive laminae of a calcified substance, and may well have begun as a phosphate store (PAUTARD, 1962; TARLO, 1963*b*, 1964; WESTOLL, 1963). The development of the aspidin can be traced towards a more advanced condition which approaches that of true bone, while at the same time it is easy to envisage the way in which the various types of dentine could also have differentiated from the original basic tissue.

STRATIGRAPHICAL RANGE AND GEOGRAPHICAL DISTRIBUTION OF THE PSAMMOSTEIDS

Psammosteids have been recorded from sediments ranging from the Ludlovian to the Famennian. They will be dealt with under successive Stages and within each Stage they will be considered under separate Provinces. Where appropriate a discussion will be given on any stratigraphical problems involved.

SILURIAN: LUDLOVIAN (INCLUDING DOWNTONIAN)

Yukon, Canada

DENISON (1963) described a new fauna of cyathaspids from the Upper Silurian of the Beaver River area, south eastern Yukon. Included within the fauna were a number of heterostracan fragments of which type *D* may well be referable to the psammosteids. DENISON compared this to the specimen figured by ØRVIG (1961), here referred to *Tesseraspis orvigi*, and it seems reasonable to refer DENISON's type *D* to the same genus. In the descriptive part of this work, DENISON's material is referred to *Tesseraspis denisoni*. The fauna from the Yukon so far described includes the following forms: cyathaspids *Vernonaspis*, *Ptomaspis*, *Dikenaspis*, *Ariaspis* and *Homalaspidella*, the traquairaspid *Traquairaspis angusta* and the psammosteid *Tesseraspis denisoni*. The exact age of the fauna is determined by the graptolites that are found both above and below the ostracoderm horizon. Below there occur graptolites from Upper Llandovery to the lowest Wenlock. Above the ostracoderms occurs *Monograptus dubius* which ranges from Upper Wenlock to Middle Ludlow. The ostracoderm fauna therefore may belong either to the Wenlock or even extend as high as the Middle Ludlow. According to DENISON however, from a consideration of the vertebrates, the age is either late Silurian or early Devonian. In conjunction with the invertebrate evidence therefore he suggests that the fauna is either Lower or Middle Ludlow. For this reason the fauna is here considered under the Ludlovian.

Island of Oesel, Estonia

A vertebrate fauna including heterostracans which have been assigned tentatively to the psammosteids by a number of different authors was first described by PANDER (1856) from beds now placed in the K. 4 horizon. Within this fauna PANDER recognized the following species: *Strosipherus indentatus*, *S. serratus*, *S. laevis*, *Lophosteus superbus*, *Tolypelepis undulatus*, *Oniscolepis magnus*, *O. dentatus*, *O. serratus*, *O. crenulatus*. EICHWALD (1860) suggested that *Lophosteus superbus* was probably a psammosteid, and was followed in this by WOODWARD (1891*b*). ROHON (1893) figured part of an acanthodian spine under this name and also a section which seems to be cephalaspid in nature, while GROSS (1947) suggested that PANDER's *Lophosteus* might belong to the cephalaspid *Dartmuthia*.

ROHON (1893) revised the fauna and showed that *Oniscolepis magnus* should be included in *Tolypelepis undulata*, and he recognized as valid species *Oniscolepis dentata* and *O. serrata*. He included within the synonymy of this latter species *O. crenulatus*, *Strosipherus indentatus*, *S. serratus* and *S. laevis*. At the same time he noted that the histological structure of the two species *O. dentata* and *O. serrata* was comparable to that found in the psammosteids. Subsequently, GROSS (1950) listed *Strosipherus indentatus* and *Oniscolepis* sp. and OBRUCHEV (1958) also listed *Strosipherus indentatus* from the K. 4 horizon, although GROSS (1961) recognized that in fact the valid name was *Oniscolepis dentata*, since, following ROHON (1893), this species has priority over *Strosipherus indentatus*. At the same time it seems likely that *O. serrata* should also be included in *Oniscolepis dentata*, thus as far as present knowledge goes, only one species can be recognized. The variations of ornament that are known seem to fall within the normal range of a single species, and until more material is described, it seems safer to refer the psammosteid material to *Oniscolepis dentata* only.

According to OBRUCHEV (1958) the fauna of the K. 4 horizon includes the cyathaspid *Tolypelepis undulata*, the psammosteid *Strosipherus indentatus* (= *Oniscolepis dentata*), the thelodont *Thelodus* and the acanthodians *Nostolepis*, *Gomphodus* and *Onchus*.

The stratigraphy of the beds has been discussed by HOPPE (1931) and according to AALOE, MARK, MANNIL, MUURISEPP & ORVIKU (1958, 1960) the K. 4 horizon is placed in the Upper Ludlow.

Beyrichienkalk, European Plain

A fauna similar to that known from Oesel occurs in erratic boulders of Beyrichienkalk along the southern shores of the Baltic, stretching from Lithuania and reaching as far west as Holland. This horizon has been located in situ in borings at Leba in northern Poland. GROSS (1947) showed that two horizons were represented in this deposit. One seems to be uppermost Ludlow, and the other basal Devonian, but both will be dealt with here. BROTZEN (1934) described heterostracan remains under *Orthaspis plana* and *Lophaspis crenulata*, but these are now known to belong to the genus *Traquairaspis* and are included in *Traquairaspis plana* (BROTZEN). BROTZEN also described under *Lophosteus mutabilis* remains which as GROSS (1947) pointed out had nothing to do with this genus. Although GROSS suggested that the remains were identical to *Lophaspis crenulata*, and *Strosipherus*, it seems likely that BROTZEN may well have figured a new psammosteid species which can be tentatively referred to *Tesseraspis* — i. e. *T. mutabilis* (BROTZEN). GROSS (1947) also described remains from these rocks including *Orthaspis plana* (BROTZEN) (now known to equal *Traquairaspis*), and *Strosipherus indentatus* (since referred to *Oniscolepis*). He thought that *Strosipherus* might be the same as *Tesseraspis*, but he kept this material separate for the sake of clarity. As mentioned earlier, in view of ROHON's (1893) work, the name *Oniscolepis dentata* should have been employed for this form, and in fact subsequently GROSS (1961) used the correct generic name *Oniscolepis* although he did not feel justified in giving a specific name to the remains he described. In the same work, as well as *Oniscolepis* sp. indet. GROSS described *Traquairaspis* sp. indet., *Anglaspis*

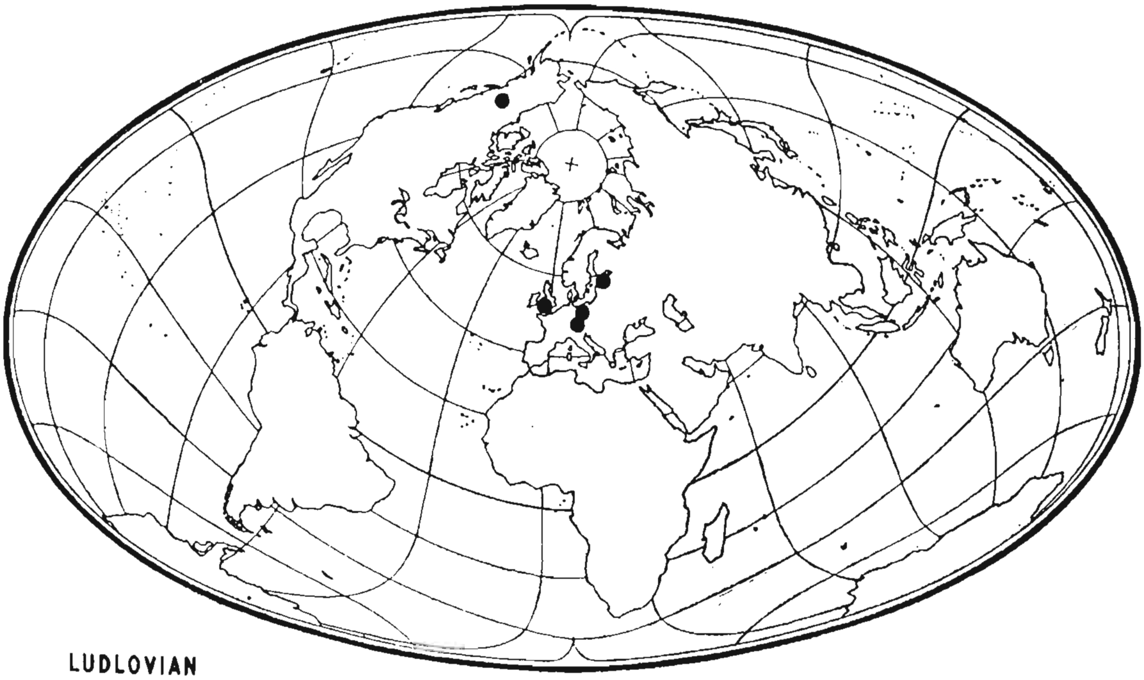

Fig. 23

Distribution of psammosteids during Upper Silurian, Ludlovian (including Downtonian) times sp. indet., and *Corvaspis* sp. indet. It should be noted that the specimens in his figure 10 named *Oniscolepis* sp. indet. appear very similar to examples of *Tesseraspis tessellata* and also *Kallostrakon macanuffi*.

As well as the heterostracans listed, the fauna also contains the thelodonts *Thelodus* and *Lanarkia*, the cephalaspids *Dartmuthia* and *Zenaspis*? sp. indet., and the acanthodians *Gomphodus*, *Poracanthodes*, *Nostolepis*, *Onchus*, *Climatius*, *Plectrodus*, *Protodus*, and *Chelomodus*.

BROTZEN considered that the material he described was of Lower Devonian age, and although this was denied by GROSS (1947) it is now clear from the further work of GROSS (1961) that BROTZEN's fauna was from the basal Devonian (Lower Dittonian), and from GROSS's contribution of 1961 the heterostracan fauna with the primitive psammosteids is characteristic of the *Traquairaspis-Protopteraspis* zones of the Anglo-Welsh Province. Since the primitive psammosteids as well as *Traquairaspis* are also found in the underlying Ludlovian however, as GROSS showed in 1947, two horizons are represented, but at least the psammosteids seem to occur both in the Silurian and the Devonian.

Bohemia

From the Prague region of Bohemia, PERNER (1918) recorded a variety of genera from the Upper Ludlovian, but unfortunately none of these remains were figured, and most of the generic names he used seem unlikely. GROSS (1950) mentioned that in 1942 he was able to examine the material briefly and he noted that there were psammosteid remains comparable to *Oniscolepis* and *Orthaspis (= Traquairaspis)* from Oesel and the Beyrichienkalk, *Tesseraspis* and *Phialaspis (= Traquairaspis)* from the English «Downtonian», and *Weigeltaspis (? = Traquairaspis)* from the Podolian «Upper Silurian». It seems evident that in the Bohemian deposits there are represented primitive psammosteids comparable to *Oniscolepis* and *Tesseraspis*, and at the same time early examples of *Traquairaspis* seem to be present. Although these latter are normally taken to indicate the base of the Devonian, the discovery of a Ludlovian species of *Traquairaspis* from the Yukon (DENISON, 1963) indicates that its occurrence does not necessarily indicate a Devonian age.

According to GROSS, as well as the psammosteids, there also occur acanthodian scales, similar to *Nostolepis*, spines of *Machaeracanthus* and the primitive arthrodire *Radotina kosoriensis* GROSS. The horizon from which these remains come is the *eγ* which is equivalent to the Upper Ludlow. In the Prague region there is a continuous marine succession from the Silurian to the Devonian, which has recently been re-examined by CHLUPAČ (1953), and it is evident that the Silurian extends much higher than the Ludlow Bone Bed of the Anglo-Welsh Province. Thus the Upper Ludlow of Bohemia extends into the Downtonian of Anglo-Wales as defined at the present time. The question of the Siluro-Devonian boundary is discussed below.

Anglo-Wales

ROHON (1893) recorded *Oniscolepis* from the Ludlow Bone Bed, although unfortunately to date this has not been confirmed. LANKESTER (1870) described remains under the name *Kallostrakon podura* from Ledbury and a further species *K. macanuffi* can now also be recognized in his material. Material now referred to *K. macanuffi* has in the past been named *Oniscolepis*, *Tolypaspis*, and *Tolypelepis* (WHITE, 1946, 1950), and also *Corvaspis* (WOODWARD, 1934). CLARKE (1955) figured a fragment of the same species from Herefordshire, which he identified as a heterostracan, Dineley (1951) recorded *Kallostrakon* from the Holdgate Sandstone, and Allen & Tarlo (1963) recorded this same genus from the Lower Red Downton formation.

With the exception of Rohon (1893) who compared *Kallostrakon* with *Oniscolepis*, little attention was paid to *Kallostrakon* material until Bystrow (1955) confirmed its psammosteid affinities. Although in the future it may turn out that *Kallostrakon* is closely related to *Oniscolepis*, it seems preferable with the present state of our knowledge to keep these two genera separate.

Occurring with *Kallostrakon* are the cephalaspids *Didymaspis*, *Thyestes*, *Hemicyclaspis*, and *Sclerodus*, as well as thelodonts and the acanthodians *Ischnacanthus*, *Onychodus*, and *Onchus*.

The deposits in which this fauna occurs are found in the Downton Series, and as is discussed in the following section, this Series is included within the Silurian, and represents the uppermost Ludlovian.

SILURO-DEVONIAN BOUNDARY

The classic area of the Siluro-Devonian trannsitio is in the Welsh Borderland of Great Britain, where one passes up from marine Ludlovian into the continental freshwater Lower Old Red Sandstone. In recent times, the Siluro-Devonian boundary has been taken at the base of the Ludlow Bone Bed (White, 1950, following Stamp, 1920). As noted by Allen & Tarlo (1963) this bone bed is only one of many, and it seems to be better known than the others merely because it has had greater publicity. Although there is a sudden diminution of the invertebrate shelly faunas of the Upper Ludlow flags at the Ludlow Bone Bed, the lower part of the overlying Downton Castle Sandstone Group possesses a shelly fauna which although reduced, contains forms also present in the underlying marine Ludlow. This indicates that there is no faunal break at the Ludlow Bone Bed. It is merely that there is a littoral facies representing the regression and renewed transgression of the sea at that point. As the invertebrate faunas gradually disappear as one goes higher in the Downtonian, it is not possible to recognize any marked change from Silurian to Devonian conditions in the Welsh Borderland as far as such faunas are concerned (Straw, 1962). However, when one takes the vertebrate faunas into account, there is a sharp break between the faunas of the Downtonian (as recently defined by Allen & Tarlo, 1963) and those of the Dittonian. Those of the Downtonian seem to consist of forms still surviving from the underlying Silurian, while in the basal Dittonian there is present a different fauna typical of the Lower Devonian.

King (1925, 1934) placed the Downtonian-Dittonian boundary high up in the pteraspid-bearing sequence, which is now recognized as being the point where *Protopteraspis leathensis* is replaced by *Pteraspis crouchi*. Later, White & Toombs (1948) proposed a revision of this boundary to a position where *Traquairaspis* was replaced by *Protopteraspis leathensis*. (See also discussion by Säve-Söderbergh, 1941*a*). Since however, numerous examples are now known in which *Traquairaspis* and *Protopteraspis* are found together (Dineley, 1951; Dineley & Gossage, 1959; Ball & Dineley, 1961) it is evident that such a faunal boundary cannot be sustained. Allen & Tarlo (1963) therefore have proposed that the boundary should be taken where the *Traquairaspis-Protopteraspis* fauna first appears, and this would agree with the procedure also taken by Dineley (1951). This coincides with the major introduction of fluviatile and other freshwater deposits in the region.

Therefore at least on the evidence of the vertebrates it seems reasonable to draw a faunal boundary between the recently defined Dittonian and Downtonian, where the *Traquairaspis*-

Protopteraspis fauna first appears. A boundary in this position is also recognizable in other regions such as Novia Scotia (Canada), Podolia (Ukraine) and Spitzbergen. In these areas it is quite impossible to effect a Downtonian-Dittonian boundary as defined by WHITE & TOOMBS (1948) or BALL & DINELEY (1961), since although the incoming of the whole fauna can be readily correlated, it is not possible to recognize the minor zones that have been worked out in Anglo-Wales.

In effecting divisions between systems, it is preferable to take faunal events which have wide application, and in this respect the Ludlow Bone Bed is entirely unsatisfactory, since it merely marks a local facies change. What seems more useful is to consider the successions of Bohemia and Thuringia (southern part of E. Germany) where there is a complete marine sequence from the Silurian into the Devonian (CHLUPAČ, 1953; JAEGER, 1959, 1962). In this area it is evident that the Siluro-Devonian boundary is taken at a horizon higher than the possible equivalent of the Ludlow Bone Bed, since several graptolite zones can be recognized higher than the highest graptolite of the Anglo-Welsh Province, *Monograptus leintwardinensis*, which occurs in the lower part of the Upper Ludlow. BOUCOT (personal communication) considers «that the zone of *leintwardinensis* should be extended to the end of the Ludlow, not because it occurs in the Whitcliffe Beds in Shropshire, but because we infer that if those beds did contain graptolites they would be of about that zone. Incidentally JAEGER feels that *leintwardinensis* is just a local facies of the zone of *tumescens* which as you can see leaves 6-8 graptolite zones well above the Whitcliffian still unaccounted for and of course put into the Devonian». Whether or not it is justifiable to give *leintwardinensis* such a long hypothetical range in the Anglo-Welsh region, it would certainly appear that the graptolite bearing sequence in Bohemia extends higher stratigraphically than the level of the Ludlow Bone Bed. Therefore it seems reasonable to follow the Czech and German workers and consider the main graptolite bearing sequence as Silurian, and to include it in the Ludlovian (CHLUPAČ, 1953; JAEGER, 1959, 1962; HORNY, 1962).

With regard to the Anglo-Welsh region, this means that the Silurian must be extended higher than the Ludlow Bone Bed, and in view of the change in the vertebrate faunas already outlined, there would appear to be some justification for including the recently defined Downtonian as part of the Silurian, a proposal supported by Dr H. JAEGER (personal communication).

This procedure was once followed by the Geological Survey of Great Britain (e. g. POCOCK & WHITEHEAD, 1948) although EDMUNDS & OAKLEY (1948) also of the Geological Survey did not commit themselves on this point.

Originally when LAPWORTH (1879—80) introduced the term Downtonian, and subsequently when it was used by GEIKIE (1882) and KOZŁOWSKI (1929), it was taken to include both the Upper Ludlow (i. e. up to the Ludlow Bone Bed), the Ludlow Bone Bed itself, and the overlying beds as far as and including the lower part of the Red Downton Formation (Ledbury Shales). The first revision of the Downtonian was by KING & LEWIS (1917) who extended it upwards to include several further hundred feet of red marls. KING (1925, 1934) further extended the Downtonian to take in part of the Lower Old Red Sandstone cornstones (i. e. conglomerates). However, the general practice of the Geological Survey and all recent workers has been to consider the Downtonian as representing the rocks extending from the Ludlow Bone Bed up to the Lower Old Red Sandstone, but leaving out the Upper Ludlow. BOUCOT (1963) introduced the new stage name Skalian which he interposed between the basal Devonian (Gedinnian) and the Upper Silurian (Ludlovian). His Skalian was equivalent to the lower part of the Downtonian of KING (1934), WHITE (1950) and WHITE & TOOMBS (1948) — the so-called *Hemicyclaspis* zone — which is the same as the Downtonian as defined by ALLEN & TARLO (1963). BOUCOT places his Skalian in the Devonian, and he takes the zone *Monograptus leintwardinensis* as marking the top of the Ludlovian, because he has extended its range theoretically up to the Ludlow Bone Bed. This means that the upper part of the Bohemian Ludlovian must also become Skalian. The introduction of this term for a new Stage is most unfortunate in view of the fact that the «étage de Skała» was defined very differently by KOZŁOWSKI (1929) when he revised the stratigraphy of the Podolian Siluro-Devonian rocks. He correlated the Skała with the Middle Ludlow, the overlying Borszczów with the Upper Ludlow, and the Czortków with the Passage Beds (i. e. Downtonian). However, Czortków can now be correlated with the Dittonian of the Anglo-Welsh Province, but even so the Skała can still only be equivalent to Middle or at the highest the Upper Ludlow of the Welsh Borderland, and in no sense can it be correlated with the Downtonian as understood by BOUCOT. In view of the confusion that would be produced by employing BOUCOT's Skalian, since it has already been used for rocks of a different age, it is here suggested that it should only be retained in the sense of KOZŁOWSKI. Nevertheless the problem still remains as to the name to be given to the beds equivalent to the English Downtonian. According to the Czech and German workers, these are simply placed in the Ludlovian. This would entail a slight revision of the Ludlovian as generally accepted in the Anglo-Welsh region (see HOLLAND, LAWSON & WALMSLEY, 1959, 1963), but when it is borne in mind that as already mentioned the term Downtonian when first introduced was for the Upper Ludlow and the overlying beds as high as and including the Ledbury Marls (i. e. Red Downton Formation), and in addition MURCHISON (1839, 1854) included within the Upper Ludlow Rock both the Ludlow Bone Bed, Downton Castle Sandstone Group and the Tilestone Formation, then there is clearly historical precedence for such a procedure. By retaining the Downtonian in the Silurian and including it in the Ludlovian Stage the whole stratigraphic framework of the Silurian of the Anglo-Welsh area is brought closer to that already established in central Europe. At the same time the need for any new Stage name is obviated.

DEVONIAN: GEDINNIAN (INCLUDING DITTONIAN)

Anglo-Welsh Region

Vertebrate remains were described by AGASSIZ (1835) and by numerous subsequent authors, the major contributions being due to LANKESTER (1868—70), STENSIÖ (1932), WHITE (1935) and WILLS (1935). Although it was recognized even at the time of LANKESTER that there were two distinct main vertebrate faunas, it was not until the time of KING (1925, 1934) that a detailed succession of faunas was established which was capable of being applied over a wide area. Subsequently WHITE & TOOMBS (1948), WHITE (1950*a*) and BALL & DINELEY (1961) produced a more detailed zonal scheme based largely on the heterostracans, which has since been found applicable throughout Western Europe (WHITE, 1956; SCHMIDT, 1959). The faunas consist of heterostracans, cephalaspids, thelodonts, acanthodians, and arthrodires, and the most recent faunal lists are to be found in BALL & DINELEY (1961) and WHITE (1961). Within this Province the entire Gedinnian sequence appears to be represented and two major zones can be recognized — the Lower Gedinnian *Traquairaspis-Protopteraspis* zone, and the Upper Gedinnian *Pteraspis crouchi* zone. The Lower Gedinnian is further sub-divided into three horizons — the lowest is typified by *Traquairaspis campbelli* (syn. *T. pococki*) and with it are associated the primitive psammosteids *Tesseraspis tessellata* (first described by Wills (1935)) and *Kallostrakon macanuffi* (here described). These two forms were first noted from this horizon by White (1946), although *K. macanuffi* was recorded at the time as *Tolypelepis (Tolypaspis)*, and since then as *Oniscolepis* sp. by Ball & Dineley (1952) and *Kallostrakon* sp. by White (1961). The succeeding zone is typified by *Traquairaspis symondsi*, and in this zone the characteristic assemblage consists of this species together with the primitive psammosteids *Tesseraspis tessellata* and *Corvaspis kingi* (first described by Woodward (1934) and redescribed by Dineley (1953) and Tarlo (1960*b*)), and also includes the cyathaspid *Anglaspis macculloughi*. Besides occurring in the Welsh Borderland, *Tesseraspis tessellata* is found in London together with *Corvaspis kingi* and *Traquairaspis symondsi*. *Tesseraspis toombsi* occurs on the Isle of Skokholm off the Pembrokeshire coast where Mr. H. A. Toombs discovered a partly articulated carapace (see in Systematic Part). It should be noted that although *Corvaspis kingi* seems to be a direct descendent of *Kallostrakon macanuffi*, there also occurs together with *Tesseraspis tessellata* and *Traquairaspis symondsi*, a further representative of *Kallostrakon* — *K. alleni* here described. In the next zone, *Protopteraspis leathensis* is the index fossil, and with it are found both *Tesseraspis* and *Corvaspis*, although these genera are rare. These three zones form the *Psammosteus* Limestones Group, and as has been shown by White (1956) and Schmidt (1959) they are equivalent to the Lower Gedinnian of the Ardennes sequence.

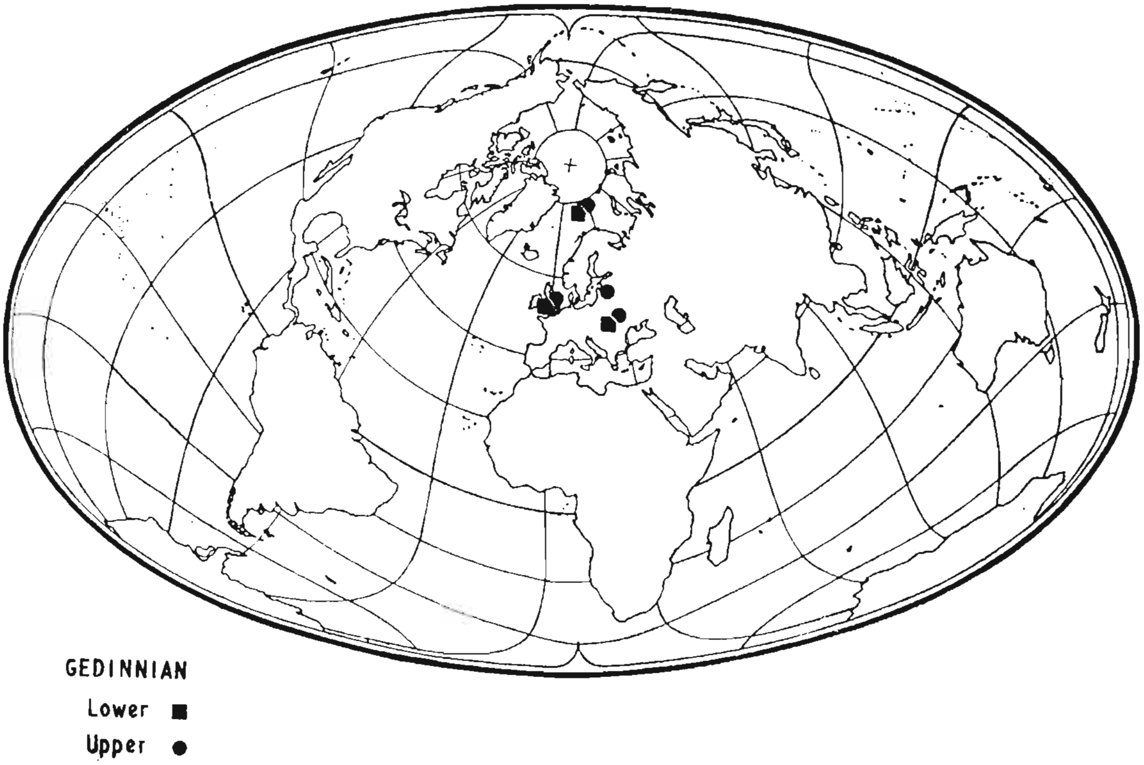

Fig. 24

Distribution of psammosteids during Lower Devonian, Gedinnian times

The whole of the Upper Gedinnian is included in the *Pteraspis crouchi* zone in which this species is found together with *Pteraspis rostrata* and also cephalaspids. Very rarely *Cor-*

vaspis kingi is present (DINELEY, 1953; BALL & DINELEY, 1961). In this zone the psammosteid *Weigeltaspis godmani* appears which is here described, although this form was first recorded from the region by WHITE (1935). The recording of *Tesseraspis* in this zone (BALL & DINELEY, 1961; WHITE, 1961) is due to the mis-identification of tesserae of *Weigeltaspis godmani*, and in fact *Tesseraspis* does not actually occur. The top of the zone marks the end of the Gedinnian, although the Ditton Group of which it is the lower part also includes some of the zone of *Althaspis leachi*, which is of Lower Siegenian age. Thus the Ditton Group of this Province which follows the *Psammosteus* Limestones Group, spans the equivalent of more than one marine stage.

The main faunal division in the Gedinnian is between the *Traquairaspis-Protopteraspis* zone and the *Pteraspis crouchi* zone, and this faunal break can be recognized in other Provinces, and is thus of considerable value when correlating over a wide area. This break also approximates to KING's (1925, 1934) original Downtonian-Dittonian boundary, which is used in this sense by SÄVE-SÖDERBERGH (1941*a*). With the revision of this boundary by WHITE & TOOMBS (1948) and WHITE (1950*a*), a certain amount of confusion has arisen. However, as noted above, ALLEN & TARLO (1963) have now produced a further revision showing that the boundary is best taken as coinciding with a major faunal and lithological break which can be recognized in other Provinces, which is not the case with the boundary now employed by BALL & DINELEY (1961) and WHITE (1961). Since therefore it is now evident that the vertebrate sequence can be accurately related to the marine sequence of Western Europe, it is possible and desirable to use the standard marine stages, thus obviating the need for such terms as Downtonian and Dittonian.

Podolia, Ukraine

A vertebrate fauna was first described by ALTH (1874), which consisted mainly of pteraspids but included a single cyathaspid. Further descriptions of this fauna were due to ZYCH (1927, 1931) and BROTZEN (1933*b*, 1936), but psammosteid remains were not recorded. However, BROTZEN (1933*a*) described *Weigeltaspis alta* which he considered to be related to the psammosteids, a view which has since been confirmed (TARLO, 1961*a*).

As in the Anglo-Welsh region, the Lower Devonian sediments can be divided into a series of zones or horizons which are characterized by their contained vertebrates. Both ZYCH (1927) and BROTZEN (1936) recognized the same set of horizons, and within the Gedinnian there are two main faunal groupings. The lower group — the Czortków — covers the *Traquairaspis-Protopteraspis* zone, and the overlying *Podolaspis lerichei* zone, which is equivalent to the *Pteraspis crouchi* zone in Western Europe. In the Czortków stage BROTZEN (1936) and SAMSONOWICZ (1950) recorded *Weigeltaspis* sp., but there seems every likelihood that these are references to fragments of *Traquairaspis plana* which is closely related to if not conspecific with *T. symondsi*. The primitive psammosteid *Corvaspis* was recorded from this horizon by STENSIÖ (1944), and his identification was confirmed by DINELEY (1953), and STENSIÖ (1958) figured a fragment of this genus which seems to be conspecific with the English *C. kingi*. Also from the same horizon, is the further psammosteid *Tesseraspis orvigi* which was first described and figured by ØRVIG (1961). From the *Podolaspis lerichei* zone BROTZEN (1933*a*) described the primitive psammosteid *Weigeltaspis*, and this seems to be a characteristic genus for the Upper Gedinnian.

From the vertebrate faunas it seems evident that both the Lower and Upper Gedinnian are represented in Podolia. BROTZEN (1936) took the *Podolaspis lerichei* zone as stage 1 of the

Old Red Sandstone, while SAMSONOWICZ (1950) took the *Podolaspis lerichei* zone as comprising the whole of the Gedinnian. However, from the vertebrate faunas, it is quite clear that this zone represents only the Upper Gedinnian, while the Czortków and Übergangsschichten together must represent the Lower Gedinnian. These beds were placed by BROTZEN and SAMSONOWICZ in the Downtonian, this term being used in the sense employed by KOZŁOWSKI (1929) and in the present work, i. e. pre-Devonian, and not in the sense of KING (1925, 1934) and WHITE (1950). However, although their meaning of Downtonian was correct, BROTZEN and SAMSONOWICZ were actually dealing with a Dittonian fauna, i. e. a truly Gedinnian Devonian fauna.

Spitzbergen

The Gedinnian vertebrates of Spitzbergen are dominated by cyathaspids which have been described by KIAER (1930, 1932), and KIAER & HEINTZ (1935). These come from the Red Bay Series in which two divisions are recognized — the lower Fraenkelryggen division and the upper Ben Nevis division (FØYN & HEINTZ, 1943; WINSNES et al., 1960; FRIEND, 1961). The Fraenkelryggen division contains the *Traquairaspis-Protopteraspis* fauna thus equating it with the Lower Gedinnian, and within this division a number of vertebrate bearing horizons can be recognized, although it is impossible to effect detailed correlations with other areas. The lowest horizon has been called the *Psammosteus* horizon, but the common species in fact belongs to *Traquairaspis* and is close to *T. symondsi.* The second horizon, which is called the *Corvaspis* horizon was discovered by HEINTZ in 1928, and the species was recognized as *C. kingi* by HEINTZ (in KIAER & HEINTZ ,1935), and DINELEY (1953). It should be noted however, that prior to this, Professor KIAER had given JAEKEL a fragment of this species which JAEKEL (1927) figured but did not name.

In the overlying Ben Nevis division the *Traquairaspis-Protopteraspis* fauna is no longer present, but a species of *Corvaspis* occurs in the lower part which seems to be different from that in the Fraenkelryggen division. The species from the Ben Nevis division was described by DINELEY (1953) under the name *C. graticulata.* Also in this upper division *Weigeltaspis heintzi* occurs, and this form which is here described was first recorded by ØRVIG (1961). The main feature of the Ben Nevis division is the absence of pteraspids which are normally important, with the exception of the primitive *Protopteraspis,* and the high proportion instead of advanced cephalaspids which unfortunately are not of great stratigraphical value. However, the presence of *Weigeltaspis* which is characteristic of the Upper Gedinnian, confirms that the Ben Nevis division is equivalent to the *Pteraspis crouchi* zone of the Welsh Borderland.

Latvian S.S.R.

LIEPINS (1959) described some fragmentary remains including tubercles which may well belong to *Weigeltaspis*, and they are here tentatively assigned to that genus. They were found together with a pteraspid which seems to be closely related to *Pteraspis crouchi*, and in consequence it is likely that Upper Gedinnian sediments are preserved in Latvia.

Correlation

Although within each Province different vertebrates are of considerable stratigraphical value, nevertheless when effecting correlations between widely separated regions there are certain genera which are of particular use. For instance, *Traquairaspis* which is frequently associated with *Protopteraspis* is characteristic of the Lower Gedinnian, although it should be remembered that a primitive species of *Traquairaspis* occurs in the Upper Silurian of the Yukon. Furthermore, primitive psammosteids such as *Corvaspis* and *Weigeltaspis* provide direct evidence of a faunal link between the three Provinces of Spitzbergen, Podolia and Anglo-Wales. In all these Provinces the same major division between Lower and Upper Gedinnian faunas can be readily recognized, and this enables an effective correlation to be made. It should be noted however, that it is not possible to employ the finer zonal scheme used for example in Anglo-Wales in other parts, for even though there was obviously an amount of faunal interchange, it is evident that these Provinces were sufficiently separated for their faunas to have developed their own distinctive features.

The same division between Lower and Upper Gedinnian has recently been recognized in Nova Scotia (DINELEY, 1963), although as yet psammosteids have not been recorded from that region, but in view of their ubiquitous distribution they can be confidently expected. At the same time, similar faunas to those discussed above seem to be present in the Canadian Arctic and in northern Siberia, and as previously suggested (TARLO, 1962*a*) it is likely that the Gedinnian faunas originated in a centre in the Arctic from where they colonised different Provinces, since when these latter are plotted on a globe they appear to radiate from such a common source.

DEVONIAN: SIEGENIAN-EMSIAN

Rhineland

Vertebrate remains have been described from the Rhineland Lower Devonian by numerous authors, and have been listed by GROSS (1950) and KUHN (1961). Since the vertebrates are found in a marine sequence, and as they form only a subsidiary part of the fauna, they are not of great importance stratigraphically. However, their preservation is normally extremely good and often complete animals are found, and they are thus of considerable importance for an understanding of many groups of Lower Devonian vertebrates. With regard to the heterostracans, the most frequently occurring species is *Rhinopteraspis cornubica* (syn. *R. dunensis*). Less frequently found are species of the psammosteid *Drepanaspis*, and the best known vertebrate remains come from the Hunsrückschiefer, which covers the upper part of the Siegenian and the lower part of the Emsian. From these rocks SCHLÜTER (1887) first described *Drepanaspis gemuendenensis* which was later redescribed by TRAQUAIR (1903) from complete carapaces. GROSS (1933*b*, 1933*c*) described the species *Drepanaspis schrieli* from the Upper Siegenian of Overath and also recorded it from the Wihéries of Belgium which are also of Siegenian age, and in addition he noted that it had been recorded from Gemünd in the Eifel. H. SCHMIDT (1933) too, recorded this species but this time from the Taunusquarzit which again is of Siegenian age. Also occurring in the Taunusquarzit are remains of a further species of *Drepanaspis*, *D. jaegeri*, which is here described. *Drepanaspis jaegeri* also occurs in the Effelsbürger Schichten (in the upper part of the Herdorfer Schichten), which seems to be near the top of the Siegenian. From the overlying Hunsrückschiefer, *Drepanaspis gemuendenensis* was described by SCHLÜTER (1887), TRAQUAIR (1903, 1905), KIAER (1915) and GROSS (1933*b*, 1933*c*, 1963). These remains therefore appear to be mainly from the uppermost Siegenian, but they may also be from the lower Emsian. GROSS (1937) described a further species *Drepanaspis lipperti* from the Klerfer Schichten, which is of Emsian age, and is either from the very top of the Lower Emsian or the lower part of the Middle Emsian. Associated with the various heterostracans mentioned above is a very large and varied fauna of arthrodires, together with acanthodians and very rare cephalaspids, and since it is a marine fauna in contrast to the majority of Lower Devonian vertebrate faunas, and the material is exceptionally well preserved, it is of particular importance. Also of interest is the fact that occurring with the four *Drepanaspis* species noted above, is the pteraspid *Rhinopteraspis cornubica*, the zonal index of the last important pteraspid zone of the Lower Devonian of Western Europe (WHITE, 1956; SCHMIDT, 1959). Unfortunately, however, this species has a considerable range, since it extends from Middle Siegenian to Upper Emsian.

South West England

PEACH (1847, 1848) described and figured fish remains from the Dartmouth Slates of this region which were later figured and described by McCOY (1851, 1854, 1855) who considered them to be polyzoan, and named them *Steganodictyum cornubicum* and *S. carteri*. The former species is now *Rhinopteraspis cornubica* (syn. *R. dunensis*) and *S. carteri* is now known to belong to the genus *Drepanaspis* (see TARLO, 1961 *c*). *Drepanaspis carteri* was previously identified as *Cephalaspis* (LANKESTER, 1868) because of its tubercular ornamentation, and WOODWARD (1901) also described the tuberculated cornua of a cephalaspid under this name. Later, DENISON (1956) recorded *Drepanaspis* from the Dartmouth Slates, again basing his identification on the tubercular ornamentation of the plates, although in this instance his specimens consisted entirely of arthrodire remains. In addition, HENDRIKS (in SIMPSON, 1951) recorded *Drepanaspis* from the Dartmouth Slates. *Drepanaspis carteri* is frequently found, but is much less common than *Rhinopteraspis cornubica*, and caution has to be exercised to avoid confusing it with both cephalaspid and arthrodire remains. Also present in the Dartmouth Slates, is a further species of *Drepanaspis*, *D. edwardsi*, which is here described. In the overlying Meadfoot Beds, DINELEY (1961) mentions a species of *Drepanaspis* having been identified, together with *Rhinopteraspis cornubica*. A small fragment of *Drepanaspis* is known, probably the one referred to by DINELEY, which appears to be indistinguishable from *D. schrieli*. This suggests an uppermost Siegenian age for the Meadfoot Beds, and confirms SIMPSON's (1951) view that the Dartmouth Slates are entirely within the Siegenian.

The vertebrate fauna of the Dartmouth Slates seems to have much in common with that of the Rhineland succession. There are many different types of arthrodire present, together with acanthodians, rare cephalaspids and pteraspids as well as *Drepanaspis*. WHITE (1956) noted that among the pteraspids *Althaspis leachi* which characterizes the Lower Siegenian, as well as *R. cornubica* (syn. *R. dunensis*) and *Europrotaspis* are found. The succession, which like that of the Rhineland is a marine one, seems to be somewhat older however, this being further confirmed by the presence of *Drepanaspis schrieli* at the top of the South West England vertebrate bearing beds, since it is found in the lower part of such beds in the Rhineland.

Poland

In the Holy Cross (Święty Krzyż) Mountains of central Poland, there is a thick sandstone sequence with an essentially marine facies — the Łysogóry, and a further freshwater facies — the Kielce facies. This latter is generally termed the Placoderm Sandstone, and a vertebrate fauna was described from it by GÜRICH (1896) which consisted of acanthodians, arthrodires, and psammosteids. Although this fauna was briefly mentioned by SOBOLEV (1909), KIAER (1915) and CZARNOCKI (1937), there were no further descriptions until the preliminary description of the psammosteids by TARLO (1957), a description of the crossopterygian *Porolepis* by KULCZYCKI (1960) and one of the pteraspid *Rhinopteraspis* by TARLO (1961 *c*). Of the psammosteids, four distinct kinds were recognized: Type A, here referred to *Guerichosteus kozlowskii*; type B, referred to *Hariosteus kielanae*; type C, which is now known to be an arthrodire and type D here named *Guerichosteus lefeldi*. Besides these three psammosteid species, the following have since been recognized within the fauna, and are described here for the first time: *Guerichosteus kotanskii*, *G. kulczyckii*, and *Hariosteus lobanowskii*.

Since *Rhinopteraspis cornubica* occurs in the Placoderm Sandstone (Tarlo, 1958, 1961 *c*), it is possible to correlate the fauna with the beds of the Western European succession containing *Rhinopteraspis cornubica*. But as noted above, the range of this species is rather long. However, in the Łysogóry facies there is a marine sequence within which fragmentary vertebrate remains are found (Tarlo, 1958), which seem to indicate the presence of the same fauna as occurs in the Placoderm Sandstone. The marine fauna shows that there was a complete development of the Emsian, and therefore the vertebrate fauna of the Placoderm Sandstone of the Kielce facies can be assigned with confidence to the Emsian. At the moment however, it is not possible to say whether this is Lower, Middle or Upper Emsian. Gürich (1896) considered the Placoderm Sandstone to be of Middle Emsian age, while Sobolev thought that it was diachronous and probably included the basal part of the Middle Devonian as well as the upper part of the Lower Devonian (i. e. Emsian). Czarnocki (1937) noted that in the Lower Emsian Barcza beds there occurred acanthodian remains which are also found in the Placoderm Sandstone. He also noted that the fauna of the Bieliny conglomerates of the Kielce facies contained a molluscan fauna which seems to be Upper Emsian. In view of this, there seems every likelihood that the Placoderm Sandstone represents the greater part of the Emsian,

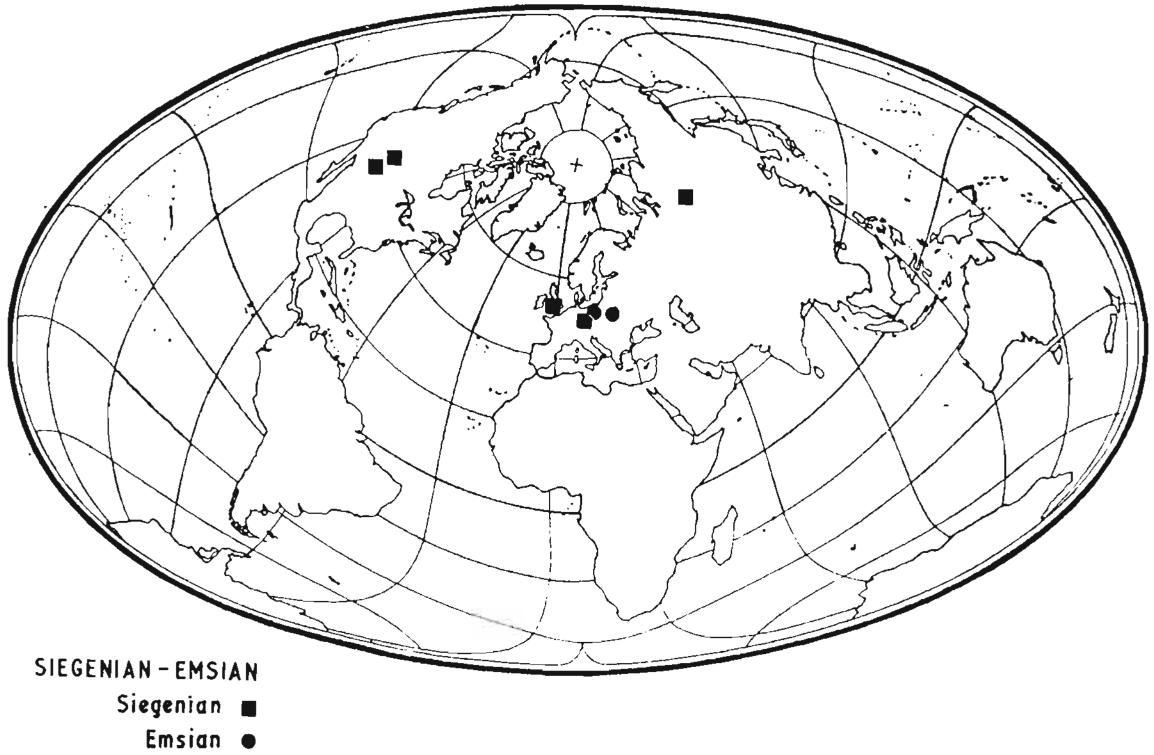

Fig. 25

Distribution of psammosteids during Lower Devonian, Siegenian-Emsian times but it is very difficult to work out a detailed stratigraphy of these beds because of the sporadic occurrence of fossils.

The Polish vertebrate fauna seems to be of a somewhat later age than the main Rhineland fauna, and in contrast to the Rhineland fauna, it appears to be mainly a freshwater fauna. With regard to the psammosteids, these seem in the main to represent a later group than those in the Rhineland which already show morphological features foreshadowing those of the advanced psammosteids of the Middle Devonian.

Northern Siberia

BYSTROW (1959) described heterostracan remains from Lower Devonian deposits from the left tributary of the river Nizhni Viluikan in northern Siberia. These were found together with *Porolepis*. The heterostracans included *Sanidaspis sibirica* and *Gunaspis orientalis* which seem to be related to the Amphiaspidiformes first described by OBRUCHEV (1938). BYSTROW also described fragments which he identified as *Drepanaspis* sp. which consisted of small isolated tesserae. From his figure these do not appear to be referable to any known species of *Drepanaspis*, and the section seems quite different from the sections of *Drepanaspis* figured by KIAER (1915) or from those of the contemporary *Guerichosteus* figured in the present work. There seems little doubt that the material belongs to a psammosteid however, and perhaps the nearest form to which it can be easily compared is *Psephaspis williamsi* described by ØRVIG (1961) from the upper part of the Lower Devonian of Utah. For the moment therefore the material discussed by BYSTROW is assigned to *Psephaspis bystrowi* in the descriptive part of the present work, and the age of the beds in which the remains described by BYSTROW (1959) occur are considered to be Siegenian.

Utah, U.S.A.

Remains of *Psephaspis williamsi* were first described by ØRVIG (1961) from the Lower Devonian Water Canyon formation of Utah, and besides scales and second generation tesserae, he recorded part of a dorsal plate. Associated with this species he recorded fragments of arthrodires, acanthodians and crossopterygians. The fauna is reminiscent of that of central Poland, and the genus *Psephaspis* shows some similarities to *Guerichosteus*. Although ØRVIG notes that *Psephaspis* and its associated vertebrates appear to be younger than the Water Canyon formation fauna described by DENISON (1952, 1953, 1958) which is clearly of Siegenian age, nevertheless it seems likely that *Psephaspis* is also of the same age although it may belong to the lowest Emsian.

Idaho, U.S.A.

A fragment, which seems to be part of a dorsal median plate of *Psephaspis* and is probably referable to *P. williamsi* was found by Dr. DENISON, and is described under this species in the descriptive part of this work. This material comes from beds near the top of the Lower Devonian.

Correlation

In the Siegenian and Emsian stages it is difficult in general to effect correlations based on vertebrates alone. In Europe however, although this is still true, since the main faunas occur in marine sediments there is little difficulty in establishing the age of the rocks. Unlike the situation in the Gedinnian, where there appears to have been radiation from an Arctic centre, with fairly free faunal interchange, during Siegenian and Emsian times the main faunas appear to have been concentrated in Europe. The locale of the chief centre in which they flourished seems to have moved gradually from South West England to the Rhineland and thence into central Poland, where the psammosteids reached their acme in Lower Devonian times. The occasional occurrences in northern Siberia, Utah and Idaho suggest that the picture was not quite as simple as this, and that there was some migration by way of the sea to other Provinces.

DEVONIAN: EIFELIAN-GIVETIAN

Bohemia

The only psammosteid known from the Eifelian stage in Europe was described by RŮŽIČKA (1929) as *Psammosteus perneri*, which is here referred to *Schizosteus*. This specimen comes from the Choteč Limestone, — upper part Gg_3 of the Hlubočepy Limestones of the Prague region of Bohemia (CHLUPAČ, 1959; PRANTL, personal communication).

Ohio, U.S.A.

WELLS (1944*a*, 1944*b*) described a vertebrate fauna from bone beds of Eifelian age consisting mainly of acanthodians and crossopterygians together with very few heterostracan remains. These latter he referred to drepanaspids, i. e. psammosteids. This designation is accepted and the material is here referred to *Schizosteus wellsi*. The value of this particular record of psammosteids is that it indicates a wide distribution of these forms in Eifelian times despite the fact that they are extremely scarce in rocks belonging to this Stage.

Idaho, U.S.A.

A fragment of a psammosteid median plate probably from beds at the base of the Middle Devonian kindly sent to the author by Dr. DENISON, seems to belong to a form closely related to *Schizosteus wellsi*. This new information thus extends the distribution of Eifelian psammosteids in N. America.

Baltic Province

The Old Red Sandstone facies in the Baltic region occur in Latvia, Estonia and the Leningrad region of Russia. Although in the 1930's these regions were studied separately, they in fact form a continuous belt of sediments. For this reason they are here taken as one Province, without reference to the boundaries of the separate Republics. Vertebrate remains have been described and figured from this region since the time of PARROT (1836), by KUTORGA (1837), AGASSIZ (1845*a*), EICHWALD (1844, 1845, 1846), PANDER (1857), ROHON (1901) and numerous subsequent authors, chief of whom are GROSS (1930, 1933*a*, 1942), OBRUCHEV (1941, 1943*a*, 1947*b*, 1961) and MARK (1955, 1956). In the Baltic Middle and Upper Devonian sediments the main sequence is zoned on the vertebrate remains, the most important zonal indices being psammosteids and antiarchs. The stratigraphy of this region has been dealt with by GROSS (1933*a*, 1934, 1940*a*, 1942), OBRUCHEV (1933*b*, 1951, 1953, 1958) and MARK (1955). The Middle Devonian sequence seems to be confined to the Givetian and three main horizons

Table 2

CORRELATION OF LOWER DEVONIAN PSAMMOSTEID FAUNAS

STAGES	ZONES	SPITZBERGEN			PODOLIA		ANGLO-WALES		RHINELAND	POLAND
EMSIAN	*Rhinopteraspis cornubica* zone								*Drepanaspis lipperti*	***Guerichosteus kozlowskii*** ***Guerichosteus kotanskii*** ***Guerichosteus kulczyckii*** ***Guerichosteus lefeldi*** ***Hariosteus kielanae*** ***Hariosteus lobanowskii***
SIEGENIAN								*Drepanaspis schrieli* *Drepanaspis carteri* *Drepanaspis edwardsi*	***Drepanaspis gemuendenensis*** ***Drepanaspis schrieli*** ***Drepanaspis jaegeri***	
	***Althaspis leachi* zone**									
GEDINNIAN	*Pteraspis crouchi* zone	RED BAY SERIES	BEN NEVIS	*Weigeltaspis heintzi* *Corvaspis graticulata*	BROTZEN'S STAGE I	***Weigeltaspis alta*** ***Weigeltaspis brotzen***	DITTON GROUP	*Weigeltaspis godmani* *Corvaspis kingi*		
	Protopteraspis-Traquairaspis zone		FRAENKELRYGGEN	*Corvaspis kingi*	CZORTKÓW	*Corvaspis kingi* *Tesseraspis orvigi*	*PSAMMOSTEUS* LST. GROUP	*Corvaspis kingi* *Tesseraspis tessellata* *Tesseraspis toombsi* *Kallostrakon alleni* *Kallostrakon macanuffi*		

are recognized. These are the Pernau which is the lowest, followed by the Narowa and finally the Tartu which is now sub-divided into a lower part — the Arukula, and an upper — the Burtnicki. The main faunal lists are given by GROSS (1942, 1950) and OBRUCHEV (1958).

The Pernau horizon is the zone of *Schizosteus heterolepis*, this particular species having been described by PREOBRAJENSKY (1911), although there is every likelihood that AGASSIZ (1845*a*) figured a fragment of it under the name *Psammosteus arenatus*. Also occurring with the index fossil is *Schizosteus toriensis* which was described by MARK (1964), as well as acanthodians, arthrodires, antiarchs (of which *Byssacanthus crenulatus* is a further zonal index), crossopterygians and dipnoans. The Narowa horizon is the zone of *Schizosteus striatus*, a species described by GROSS (1933*a*). The further species *Pycnolepis splendens* also occurs at this horizon, and this form was originally described by EICHWALD (1844, 1845, 1846, 1860). The main faunas are similar to those in the underlying Pernau, although the antiarch index fossil in this case is *Pterichthys concatinatus*. The succeeding horizon, the Arukula which forms the lower part of the Tartu has for its zonal index *Pycnosteus palaeformis*, a fragment of which was first figured by KUTORGA (1837), although it was PREOBRAJENSKY (1911) who first fully figured and described this species and named it. (It should be noted however that WOODWARD (1895) unknown to PREOBRAJENSKY had already examined and described the same material, referring it to *Psammosteus arenatus*). This species in fact only occurs in the lower part of the Arukula, being succeeded by *Pycnosteus pauli* described by MARK (1956). Also in the lower part of the Arukula, there occurs *Ganosteus artus* described by MARK (1964) while in the mid part of the Arukula is found the unique holotype of *Ganosteus obtusus* also described by MARK (1964). In the upper part of the Arukula *Ganosteus stellatus* appears, which was first figured by PARROT (1836), and then by PANDER (1857) although it was not named until ROHON (1901) described further material. Occurring throughout the Arukula is *Tartuosteus giganteus*, a form originally described by GROSS (1933*a*), while in the mid part of the horizon there occurs *Tartuosteus luhai* described by MARK (1964). In addition the primitive *Psammolepis proia* described by MARK (1964) is found in the lower part of the Arukula, as also is the latest species of *Schizosteus* — *S. asatkini* described by OBRUCHEV (1940). The rest of the vertebrate fauna is comparable to that known in the earlier horizons except that the antiarch zone index is *Asterolepis estonica*, while actinopterygians now occur.

The Burtnicki horizon which is the upper part of the Tartu is the zone of *Pycnosteus tuberculatus*, first figured by PARROT (1836) and then by KUTORGA (1837), but again this was not properly described or named until the time of ROHON (1901). *Ganosteus stellatus* which appeared at the top of the Arukula now becomes much more prominent, and the advanced *Tartuosteus maximus* described by MARK (1964) also characterizes the Burtnicki. *Yoglinia bergi* described by OBRUCHEV (1943*a*) is also characteristic of this horizon, and a few indeterminable fragments of *Psammolepis* are known with it. The associated fauna consists of acanthodians, arthrodires, and antiarchs, the index fossil of which is *Asterolepis dellei*, while crossopterygians and dipnoans are also present.

For the continental Givetian this sequence is the standard succession against which successions in other Provinces are correlated, and in this work the Soviet authors are followed, the Burtnicki being taken as the uppermost horizon of the Middle Devonian. The question of the boundary between the Middle and Upper Devonian has however been much discussed and will be dealt with more fully below (p. 86).

In view of the importance of the psammosteids in Middle Devonian stratigraphy, the ranges of the different species are given in the accompanying Table 3.

Table 3

STRATIGRAPHICAL RANGE OF MIDDLE DEVONIAN (GIVETIAN) PSAMMOSTEIDS FROM THE BALTIC

Species	GIVETIAN							
	a^1		D. m. 3 (a^2)					
	D. m. 1	D. m. 2						
			Tartu					
	Pernau	Narowa	Arukula			Burtnicki		
Schizosteus heterolepis . . .	▬							
Schizosteus toriensis	▬							
Schizosteus striatus.	. . . .	▬						
Schizosteus asatkini	. . . .	. . . .	▬					
Pycnolepis splendens	. . . .	▬						
Pycnosteus palaeformis . . .	. . . .	. . . .	▬					
Pycnosteus pauli	. . . .	. . . .	. . .	▬				
Pycnosteus tuberculatus . . .	. . . .	. . . .	. . .	. . .	. . .	▬	▬	▬
Ganosteus artus	. . . .	. . . .	▬	▬				
Ganosteus obtusus	. . . .	. . . .	. . .	▬				
Ganosteus stellatus	. . . .	. . . .	. . .	▬	▬	▬		▬
Tartuosteus giganteus. . . .	. . . .	. . . .	▬	▬	▬			
Tartuosteus luhai.	. . . .	. . . .	. . .	▬				
Tartuosteus maximus	. . . .	. . . .	. . .	. . .	■ ■ ▬	▬		
Yoglinia bergi	. . . .	. . . .	. . .	. . .	. . .	▬		
Psammolepis proia	. . . .	. . . .	▬	▬				
Psammolepis sp.	. . . .	. . . .	. . .	. . .	. . .	▬		

Urals

The only psammosteid remains known from the Urals were described by SMIRNOV (1948) and these consist of two fragments which unquestionably belong to *Ganosteus stellatus*. This indicates a Tartu age and probably the Burtnicki horizon, and shows that at the end of Middle Devonian times part of the Baltic fauna had spread eastwards.

Spitzbergen

Psammosteids are known from two formations — the Wijde Bay Series and the Mimersdalen Series, and since the Wijde Bay is generally considered to be somewhat older than the Mimersdalen, it will therefore be dealt with first. HEINTZ (1937) first recorded psammosteids from this Series which were further noted by Føyn & Heintz (1943) and Dineley (1955). Winsnes et al. (1960) identified these remains as belonging to *Psammolepis*, and Tarlo (in Friend, 1961) suggested that they were in fact conspecific with those previously described from the Mimersdalen. They are therefore here assigned to the species *Pycnosteus nathorsti* Obruchev. A further species has now also been recognized in these remains which is here described under *Pycnosteus obruchevi*. In the Mimersdalen Series, psammosteids are known from the Fiskekløfta horizon which is near the top of the series. They were first described and figured by Lankester (1884) as bony fragments, and later assigned by Woodward (1891*a*) to *Psammosteus arenatus*. Stensiö (1918) recognized *Psammosteus arenatus* and a further species *P. spinosus* which however remained a *nomen nudum*, but as in fact Stensiö subsequently recognized (in Nilsson, 1941), only a single species was present. Since Woodward (1891*a*) had identified the species as *Psammosteus arenatus*, Heintz (1937) placed it in the species *Psammolepis undulata*, probably because Gross had suggested (1933*a*) that the *Psammolepis arenatus* of Doss (1915) in fact belonged to *Psammolepis undulata*. But Nilsson (1941) placed the Spitzbergen species into *Psammolepis paradoxa* since Gross (1933*a*) had shown that the original *P. arenatus* belonged to this species. However, the Spitzbergen species has now been assigned in this work to *Pycnosteus nathorsti*.

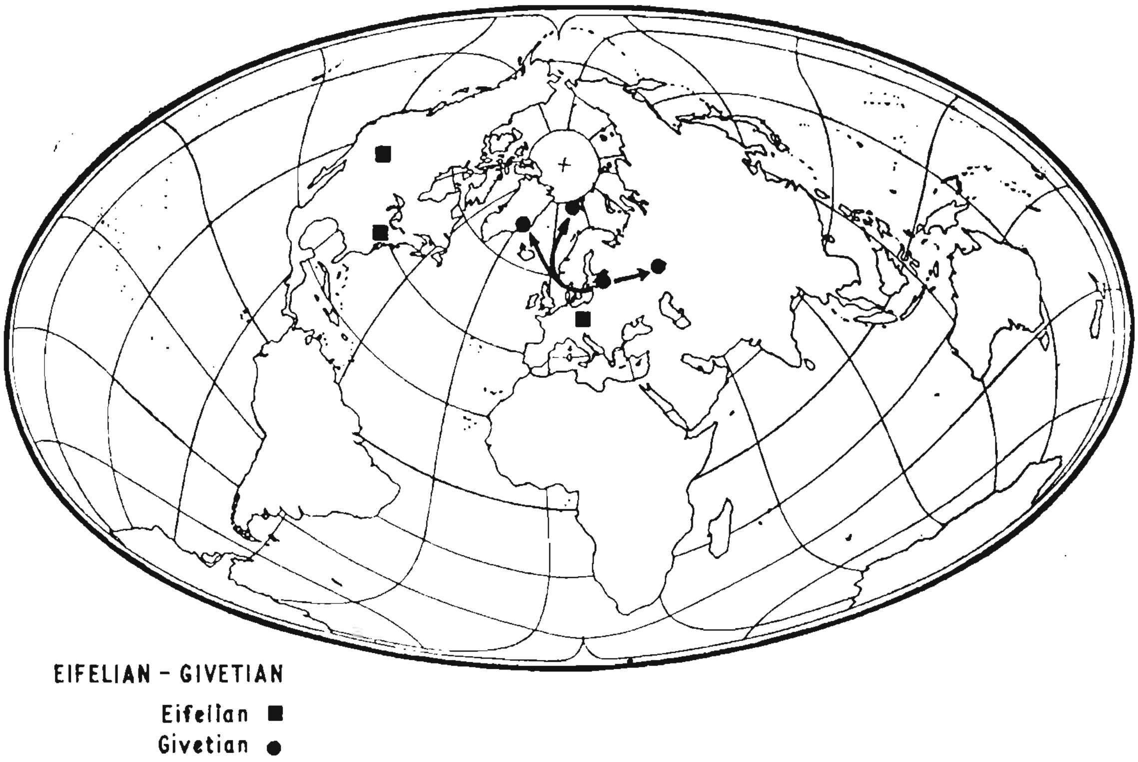

Fig. 26
Distribution of psammosteids during Middle Devonian, Eifelian-Givetian times

In the Wijde Bay Series associated with the psammosteids are primitive antiarchs, arthrodires and crossopterygians. In the Mimersdalen the antiarch *Asterolepis skabra* occurs which is the index fossil for this series, as well as arthrodires, elasmobranchs and crossopterygians. The fish faunas suggest that the Mimersdalen Series is somewhat younger than the Wijde Bay Series. HEINTZ (1937) correlates the Wijde Bay Series with the Pernau, Narowa and Tartu horizons of the Baltic, and the Mimersdalen with the overlying Gauja and Amata horizons (these latter here referred to the Upper Devonian). WESTOLL (1951) correlates the Wijde Bay with the Narowa, Tartu and Gauja horizons and takes the Fiskekløfta formation of the Mimersdalen as equivalent to the upper part of the Wijde Bay, while FRIEND (1961) equates the Fiskekløfta with the Nairn Sandstones of Scotland. This is equivalent to the Amata horizon of the Baltic with its zonal index of *Psammolepsis undulata* (see TARLO, 1961*a*). Although the psammosteid *Pycnosteus nathorsti* has certain characters in common with the Baltic *Pycnolepis splendens* from the Narowa, it is clearly a species of *Pycnosteus* which characterizes the Tartu. Also, *Pycnosteus obruchevi* which is found together with *P. nathorsti*, shows similarities to *Pycnosteus tuberculatus* which characterizes the Burtnicki horizon. It seems evident therefore, that the Wijde Bay and Mimersdalen Series are likely to be together equivalent to the Tartu, although the equivalents of the uppermost part of the Narowa may also be present. This correlation thus agrees somewhat more closely with that put forward by WESTOLL (1951).

Greenland

A single fragment of a psammosteid has been recorded by ØRVIG (1961) and JARVIK (1961) who noted its similarity to *Psammolepis*. This specimen is here described under the name *Psammolepis groenlandica*, and seems to be closely related to *Psammolepis proia* from the Tartu horizon of the Baltic and would suggest a possible correlation with this horizon. The specimen comes from the Series with *Asterolepis save-soderberghi* which is equated by STENSIÖ and SÄVE-SÖDERBERGH (1938) with the Gauja horizon of the Baltic. On the other hand WESTOLL (1951) correlates the whole of the East Greenland Middle Devonian with the Pernau and Narowa horizons. However, as GROSS (1950) has pointed out, the Middle Old Red Sandstone of East Greenland appears to be equivalent to the Wijde Bay Series of Spitzbergen, and this seems to confirm the fact that at least the Greenland *Asterolepis* Series can be broadly correlated with the Tartu of the Baltic.

Correlation

In the Eifelian, psammosteids are known only from Bohemia and North America, but in the succeeding Givetian there is evidence of a considerable radiation of psammosteids which although not adequately represented in the Eifelian, seem to be directly derived from the Emsian faunas of Poland. During Givetian times the psammosteids flourished in the Baltic Province where they seem to have undergone considerable evolutionary change, and in this region they form the basis of the zonal stratigraphical scheme. The Baltic in fact seems to have formed the centre from which waves of migration spread into other provinces. At the beginning of Tartu times, elements of the fauna seem to have reached both Spitzbergen and Greenland, and in Spitzbergen the form which became established there appears to have flourished for a considerable time, virtually unchanged. This is in contrast to the situation in the Baltic, where the psammosteids underwent rapid evolution. Since there were only sporadic periods of migration from the Baltic, it is only possible to use the psammosteids for correlation in a very broad way, as in such provinces as Spitzbergen and Greenland the detailed zonal scheme of the Baltic just does not apply.

GIVETIAN-FRASNIAN BOUNDARY

The correlation of the Continental facies of the Devonian with the standard marine sequence, and the consequent recognition of the boundary between the Givetian and Frasnian in the former facies can only be properly achieved in the Baltic Province. OBRUCHEV (1931) took the boundary to be between the Snetogor and Amata horizons, although later (1933*b*) he drew the boundary between the Gauja and Amata horizons. Nevertheless, in spite of this revision, GROSS (1933*a*, 1934, 1940*a*, 1942) still took the Snetogor as the lowest horizon of the Frasnian, perhaps because this is a particularly useful horizon, as a lower Frasnian invertebrate marine fauna is found together with vertebrates, including *Psammosteus maeandrinus*, the zonal index. The boundary in this position has been accepted by GROSS (1950), WESTOLL (1951) and TARLO (1961*a*). However, with the recent re-examination by OBRUCHEV and his co-workers of some of the type sections which were originally described by HECKER, OBRUCHEV & PHILIPPOVA (1935), it is evident that the boundary must now be taken at a lower level.

OBRUCHEV (1951) gave a detailed analysis of the problem and concluded that the boundary must now lie between the Tartu and Gauja horizons, a view which he reiterated in 1953. Since that time this new boundary has been accepted by all Soviet geologists (OBRUCHEV, 1958; AALOE et al. 1958, 1960). This view would seem to be supported by the fact that in the Shchigry Beds which are basal Frasnian, *Asterolepis radiata* occurs which is a zonal index for the Amata Beds. Thus clearly the Amata Beds must now be included in the Frasnian. The reasons for including the Gauja with the Amata seem to be that it is hardly possible to distinguish the vertebrate faunas from these two horizons, and furthermore, according to OBRUCHEV (in TARLO, 1961*a*) the Gauja Beds appear to be developed only in the Baltic, there seeming to be no equivalents of them elsewhere. In view of recent work in the Soviet Union on this question, the arguments against accepting this revision put forward by TARLO (1961*a*) cannot now be sustained.

DEVONIAN: FRASNIAN-FAMENNIAN

Baltic Province

Psammosteid remains from horizons now included in the Upper Devonian have been described by AGASSIZ (1845*a*), PANDER (1857), TRAUTSCHOLD (1880), PREOBRAJENSKY (1911), GROSS (1930, 1933*a*, 1942), and OBRUCHEV (1933*a*, 1941, 1944, 1945, 1947*a*, 1947*b*). The main stratigraphical accounts are due to OBRUCHEV (1931, 1932, 1933*b*, 1935) and GROSS (1933*a*, 1934, 1940*a*, 1942). The Upper Devonian sequence is divided into a number of horizons including both continental and marine facies. It is only the former however with which the present section is concerned. It should also be noted that although at the base of the Fammenian the psammosteids become extinct, up to that time they form important zonal indices.

There are five major horizons in the continental facies. The first is the Gauja, the zone of *Psammolepis paradoxa* which is succeeded by the Amata, with *Psammolepis undulata* as its zonal index. These two horizons were previously placed in the Middle Devonian, but as shown above are now accepted as Frasnian. The overlying horizon is the Snetogor which, as well as containing marine fossils has for its index *Psammosteus maeandrinus*. The next vertebrate horizon is the Shelon-Ilmen, which is characterized by *Psammosteus megalopteryx*, while finally there is the Upper Frasnian e Horizon with *Psammosteus falcatus*.

The Gauja horizon also contains *Ganosteus stellatus* which still survives from the underlying Givetian Burtnicki horizon, and in addition probably *Tartuosteus maximus*. The most characteristic psammosteid of this horizon is however *Psammolepis paradoxa* the index fossil. This was first described by AGASSIZ (1845*a*) and subsequently by GROSS (1930, 1933*a*) and HEINTZ (1957). *Psammolepis venyukovi, Psl. alata* first fully described by OBRUCHEV (1964) and *Psl. abavica* by MARK (1964) are also present. The species *Psammolepis heteraster* described by GROSS (1933*a*) from this horizon seems to be intermediate between *Psl. paradoxa* and *Psl. undulata* from the overlying Amata horizon, and in the present work is tentatively included in the synonymy of this latter species. The Gauja horizon also has as its index fossil the antiarch *Asterolepis ornata*, besides which acanthodians, arthrodires and crossopterygians are present together with dipnoans. The Amata horizon is notable for its great variety of psammosteid forms. The zonal index is *Psammolepis undulata* first described by AGASSIZ (1845*a*) and subsequently by GROSS (1933*a*), and at this horizon there appears the first example of *Psammosteus* itself. This was first described by PREOBRAJENSKY (1911) as *Dyptychosteus tessellatus* but was later renamed *P. markae* by TARLO (1961*a*). Closely related to *P. markae*, if not conspecific with it, is *Psammosteus praecursor* described by OBRUCHEV (1947*a*). Also known at this horizon are *Psammosteus livonicus, P. asper, P. levis* (here referred to the genus *Crenosteus*) and *Psammolepis aerata*. All these were described by OBRUCHEV (1964). In the same work he described *Psammosteus cuneatus* which seems to be a pathological specimen of a species close to *Psammosteus megalopteryx*, as well as *Psammolepis connectens* which may well be related to either *Psl. undulata* or *Psammosteus praecursor/markae*. The antiarch which characterizes this horizon is *Asterolepis radiata*, with which primitive examples of *Bothriolepis*, acanthodians, arthrodires and crossopterygians also occur.

In the Snetogor horizon only *Psammosteus maeandrinus* first described by AGASSIZ (1845*a*) and then by PANDER (1857), GROSS (1933*a*) and OBRUCHEV (1947*a*, *b*) is known among the psammosteids, and the characteristic antiarchs are *Bothriolepis cellulosa* and *B. panderi*. Also present are acanthodians, arthrodires, crossopterygians, dipnoans and actinopterygians. In the Shelon-Ilmen Stage there occurs *Psammosteus megalopteryx* described by TRAUTSCHOLD (1880), GROSS (1933*a*) and OBRUCHEV (1945) which is comparatively abundant, together with *Psammosteus pectinatus* described by OBRUCHEV (1964). Occurring with these are numerous arthrodires and crossopterygians as well as the antiarch *Bothriolepis panderi*. The next important vertebrate horizon is the e Horizon with the zone fossil *Psammosteus falcatus* described by OBRUCHEV (1947*a*). Also present are the psammosteids *Obruchevia [Aspidosteus] heckeri* described by OBRUCHEV (1936, 1941), *Karelosteus weberi* described by him (1933*a*) and *Psammosteus grossi* again described by OBRUCHEV (1947*a*), which last is the only psammosteid which continues through into the base of the Famennian. The fauna of Horizon e includes acanthodians, arthrodires, the antiarchs *Bothriolepis maxima, B. curonica* and *B. spinosa*, as well as crossopterygians and dipnoans. The Frasnian succession is characterized not only by continental vertebrate bearing horizons, but also by a series of marine incursions, some of which also contain a few vertebrate remains. Nevertheless the sequence of continental vertebrate faunas is of considerable importance for correlating since here too the Baltic provides the standard faunal sequence with which the vertebrate bearing sequences of other Provinces can be compared. Although the vertebrates continue through the Famennian, since they do not contain psammosteids the higher horizons are not considered in the present work.

In the accompanying Table, the Baltic succession is given, showing the main vertebrate-bearing horizons with their contained psammosteids, as well as the interpolated marine horizons.

Table 4

STRATIGRAPHICAL RANGE OF UPPER DEVONIAN (FRASNIAN) PSAMMOSTEIDS FROM THE BALTIC

Species	FRASNIAN						
	a^3	a^4	b^1	b^{2-4}	c	d	e
	Gauja	Amata	Snetogor	Pskov-Tchudov	Shelon-Ilmen	Buregi	
Ganosteus stellatus	▬						
Tartuosteus maximus?	▬						
Psammolepis abavica	▬						
Psammolepis paradoxa	▬						
Psammolepis venyukovi	▬						
Psammolepis alata	▬						
Psammolepis undulata	▬	▬					
Psammolepis aerata		▬					
Crenosteus levis		▬					
Psammosteus praecursor		▬					
Psammosteus markae		▬					
Psammosteus asper		▬					
Psammosteus livonicus		▬					
Psammosteus maeandrinus			▬	Marine		Marine	
Psammosteus megalopteryx					▬		
Psammosteus pectinatus					▬		
Psammosteus falcatus							▬
Psammosteus grossi							▬
Karelosteus weberi							▬
Obruchevia heckeri							▬

Timan

An important vertebrate fauna was described by ROHON (1899) from the Timan, which included *Asterolepis radiata* a zonal index of the Amata horizon. Also present were a number of psammosteids including *Psammolepis undulata*, *Psammosteus praecursor* (described by ROHON under the name *Psammosteus arenatus*), and *Rohonosteus ornatus* (included in *Psammosteus* by ROHON and tentatively referred to *Tartuosteus* by OBRUCHEV (1961)). In addition *Psammosteus tchernovi* was present, which was described by OBRUCHEV (1964). The fauna described by ROHON can be directly correlated with the Amata horizon of the main Baltic sequence, since it contains some of the same species. Also from the Timan TICHOMIROV (1948) recorded the presence of *Psammosteus falcatus*, showing that it is also in part equivalent to the Baltic Horizon c. The Timan is sufficiently close to the main Baltic Province for the zones established there to be still distinct, and since the psammosteids of both the Amata and c Horizons are present in the Province, this indicates the spread of Baltic faunas into the Timan region on at least two separate occasions.

Donbas

Recently discovered in the Donbas are a number of psammosteid remains which the author has recently examined in Moscow through the courtesy of Professor Obruchev. This material seems to be referable to *Psammolepis undulata*, and indicates a correlation with the Amata horizon of the Baltic as well as the southern spread of psammosteid faunas at this period.

Scotland

Psammosteids are known from the Upper Old Red Sandstone of Scotland, from where they were first described by Traquair (1894, 1896*b*, 1897) and subsequently by Woodward (1911) and Tarlo (1961*a*). The faunal list is given by Read & Macgregor (1948). Traquair (1896*b*) recognized three main zones. The lowest is the Nairn Sandstones containing *Asterolepis maxima* as well as the psammosteid *Psammolepis undulata*, originally described by Traquair (1897) as *Psammosteus tesselatus*. The next main zone he recognized was the Alves and Scaat Craig Beds which contain *Bothriolepis major*, but he noted that at the localities Boghole and Whitemire there occurred a mixture of both the typical Alves and Nairn faunas. Present in the Whitemire Beds and the overlying Alves Beds is *Psammosteus megalopteryx* which was originally described by Traquair (1894) as *P. taylori*, but was recognized as belonging to *P. megalopteryx* by Tarlo (1961*a*). In the Scaat Craig Beds *Psammosteus falcatus* occurs, which was originally identified by Traquair (1896*b*) as *Psammosteus* sp., as well as *Traquairosteus pustulatus*, described by Traquair (1897) as *Psammosteus pustulatus*. The third zone — the Rosebrae Beds does not contain psammosteids, and will therefore not be dealt with here.

Westoll (1937, 1951) correlated the Nairn Sandstones with the upper part of the Gauja horizon and the Amata horizon of the Baltic and the Whitemire Beds with the Snetogor, the Alves and Scaat being considered equivalent to the remainder of the psammosteid-bearing horizons of the Baltic. Obruchev (1951, 1958) correlated the Nairn Sandstones only with the Gauja, and the overlying Whitemire Beds with the Amata, since in both Scotland and the Baltic the antiarchs *Asterolepis* and *Bothriolepis* occur together in these latter horizons. However in spite of this, the recognition of psammosteid species common to both provinces (Tarlo, 1961*a*) establishes that the Nairn Sandstones with *Psammolepis undulata*, are equivalent to the Amata horizon, while the overlying Whitemire and Alves Beds with *Psammosteus megalopteryx* seem to be equivalent to the Snetogor and Shelon-Ilmen horizons. From the psammosteids it is now evident that the Scaat Craig Beds which were previously thought to be of the same age as the Alves, are of the higher zone of *Psammosteus falcatus* and consequently equivalent to the e Horizon of the Baltic. Obruchev (in Tarlo, 1961*a*) agrees with this new correlation since it is now known that the same psammosteid species occur in both the Baltic Province and Scotland. According to Gross (1950), Westoll (1951) and Tarlo (1961*a*), the Nairn Sandstones were considered to be Upper Givetian and hence Middle Devonian in age, but since they are known to be equivalent to the Amata horizon, the Nairn Sandstones must be taken to be of Lower Frasnian age, and in view of the revision of the Baltic sequence the Upper Old Red Sandstone of Scotland must now be placed entirely within the Upper Devonian.

Since the same psammosteid species can now be recognized in both the Baltic Province and Scotland, this means not only that the same detailed zonal scheme can be applied to both regions, but it also suggests that there was a free faunal interchange between them in Upper

Devonian times. However, the psammosteid faunas of the Baltic were far more abundant than those of Scotland, and the former Province undoubtedly remained the centre from which waves of migration took place.

Ellesmereland

Kiaer (1915) described a fragmentary vertebrate fauna from the Upper Devonian Series E from the Skrap Valley of Ellesmereland in the Canadian Arctic. As well as containing *Bothriolepis* and crossopterygians, it also included psammosteid remains. These were described by Kiaer as *Psammosteus arcticus* (now referred to *Psammolepis*) and *Psammosteustcomplicatus* (here referred to the genus *Rohonosteus*), while a further fragment named *Psammosteus arcticus* by Kiaer is here referred to the new species *Psammosteus kiaeri*. *Rohonosteus complicatus* is somewhat similar to *R. ornatus* from the Timan, while *Psammolepis arctica* is close to *Psl. venyukovi* from the Baltic Province. With regard to these species the main difference is that the ornamentation of the material from Ellesmereland is of a larger nature, although the pattern is the same. *Psammosteus kiaeri* is rather reminiscent of *P. falcatus*, with which it was erroneously identified by Tarlo (1961*a*).

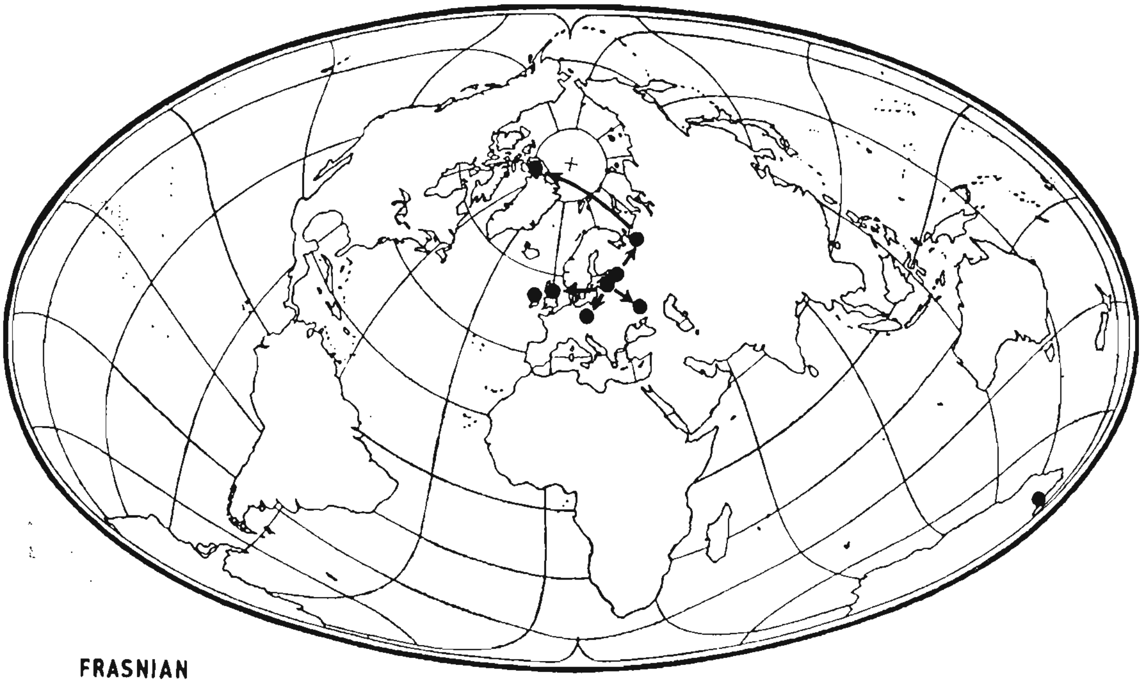

Fig 27.
Distribution of psammosteids during Upper Devonian, Frasnian times

Kiaer (1915) suggested that the fish-bearing Series E belonged to the lower part of the Upper Devonian. Tarlo (1961*a*) on the basis of the identification of *Psammosteus falcatus* made it equivalent to the e Horizon of the Baltic, i. e. in the upper part of the Frasnian. From a comparison of the faunas from the Timan and the Baltic with the Ellesmereland material it now seems clear that this latter fauna is comparable to that of the Amata horizon, and can be correlated with it.

Poland

Gorizdro-Kulczycka (1950) recorded *Psammosteus maeandrinus* together with an Upper Frasnian vertebrate fauna. It seems likely however that the species represented was *P. falcatus*, which was in fact first described and figured by Gross (1933*a*) under the name *Psammosteus maeandrinus*.

?Ireland

McCoy (1848) described two psammosteid species, *Psammosteus granulatus* and *P. vermicularis* from the Yellow Sandstones at the base of the Carboniferous of Kesh, County Fermanagh, Ireland. Woodward (1891*b*) and Rohon (1901) both referred to McCoy's work, but since the material has never been figured little attention has been paid to it. Through the courtesy of Dr. Jackson of the National Museum of Eire the type material has been re-examined, and although *Psammosteus vermicularis* is quite indeterminable, *Psammosteus granulatus* appears to be rather similar to some specimens of *Psammolepis*, in particular *Psl. venyukovi* from the Gauja horizon, and *Psl. undulata* from the Amata horizon of the Baltic Province. There is doubt as to whether this specimen is from the Devonian, but if, as now seems to be the case, it is in fact from Carboniferous rocks then it must belong to some other group. From the specimen by itself it certainly seems to be not unlike a psammosteid.

?Antarctica

During Scott's expedition to the Antarctic, Devonian vertebrates were discovered in the Beacon Sandstone of Granite Harbour, Victoria Land. The fauna which was described by Woodward (1921*b*) included *Bothriolepis*, arthrodires, crossopterygians, acanthodians, and actinopterygians, and also present were a number of isolated dermal tubercles which Woodward considered were referable to either «primitive ostracoderms or to elasmobranchs». Gross (1950) suggested that these might belong to psammosteids, and a re-examination of the specimens shows that they are probably heterostracan and are therefore likely to be psammosteid in nature. From such material it is clearly not possible to effect any correlation with the Baltic Province by means of the psammosteids, although the overall character of the fauna indicates an Upper Frasnian age for these rocks. The significance of this record by Woodward (1921*b*) is that it is the only evidence of the existence of the Heterostraci in the southern hemisphere.

Correlation

At the beginning of the Frasnian the psammosteids were very varied and also had an extremely wide distribution, although as in the Givetian the main centre of evolution and source of waves of migration was in the Baltic. In neighbouring provinces such as Scotland, the Timan and the Donbas, the same species are found, although in the Timan important endemic forms are also present. In such distant provinces as Ellesmereland on the other hand all the psammosteids seem to be endemic, although their relationships to forms in the Baltic and the Timan can still be ascertained. During the remainder of the Frasnian there seemed to be continual faunal interchange between the Baltic and Scotland, and probably also the Timan, although in the case of this latter Province evidence of this is only available so far from the basal Frasnian and the uppermost Frasnian. The picture of psammosteid evolution and distribution in Frasnian times is comparable to that found in the Givetian, in that there seem to have been successive periods of migration outwards from a Baltic centre, and the further away the Provinces are from the Baltic the less detailed a correlation is possible.

Finally, it is of interest to note that *Psammosteus grossi* which occurs at the top of the Frasnian in the Baltic Province is the only psammosteid to survive into the lower part of the Famennian, and is also in fact the last heterostracan so far known in the fossil record.

CONDITIONS OF LIFE

The primitive psammosteids from the Gedinnian of the Welsh Borderland occur in sediments which have recently been demonstrated to be fluviatile in origin, being either river channel or delta top deposits (TARLO, 1962*a*; ALLEN & TARLO, 1963). Since they seem to be confined to such sediments, and are not found in the adjacent brackish intertidal and sub-tidal sediments, it is therefore evident that these psammosteids were freshwater living, as also were those from Spitzbergen (FRIEND, 1961). Nevertheless, in view of the wide distribution of such forms as *Corvaspis*, *Tesseraspis* and *Weigeltaspis*, which are found not only in the Welsh Borderland and Spitzbergen but also in Podolia, it is necessary to postulate that at some time in their lives they must have been tolerant of salt water, since these Provinces could only have been connected by way of the sea.

One explanation might be that the psammosteids were euryhaline, but this does not seem to have been the case as far as the Welsh Borderland forms are concerned. The only other explanation therefore is that their larval stages were spent in the sea, when like the present day eel they were able to travel considerable distances, so that at the onset of metamorphosis they were in a position to invade and colonise freshwater environments. This idea would seem to be the only one capable of explaining the extremely wide distribution of identical freshwater-living psammosteid species during Givetian and Frasnian times.

In Siegenian and Emsian times the psammosteids are best known from marine deposits in South West England and the Rhineland, and although these marine forms were contrasted with the freshwater Emsian psammosteids from central Poland by TARLO (1957), it seems more likely that the Polish fauna represents a secondary colonization of a freshwater environment by formerly marine-living psammosteids. The psammosteids which flourished in the Baltic Province in Middle and Upper Devonian times in every likelihood were derived directly from the Polish Emsian freshwater fauna, and remained freshwater living during their period of radiation. It is also of interest to note that these Baltic forms were also deposited in what seem to be fluviatile and delta-top sediments (see OBRUCHEV, 1933*b*), and although it should be remembered that *Psammosteus maeandrinus* does occur with marine invertebrates, this seems to be exceptional.

This change from freshwater life to marine and then back to freshwater again may seem somewhat unusual, but in fact there are sufficient parallels with modern fish for this to be quite feasible. Indeed the success of the psammosteids in Middle and Upper Devonian times may well have been due in part to their ability to colonize a fluviatile environment as suggested by OBRUCHEV (1944, 1947*a*).

Table 5

CORRELATION OF MIDDLE AND UPPER DEVONIAN PSAMMOSTEID FAUNAS

STAGES		ZONES	BALTIC	SPITZBERGEN	GREENLAND	URALS	DONBAS	ELLESMERELAND	TIMAN	SCOTLAND	POLAND
FRASNIAN	e	*Psammosteus falcatus* zone	*Psammosteus falcatus* *Psammosteus grossi* *Karelosteus weberi* *Obruchevia heckeri*						*Psammosteus falcatus*	*Psammosteus falcatus* *Traquairosteus pustulatus*	*Psammosteus falcatus*
	c	*Psammosteus megalopteryx* zone	*Psammosteus megalopteryx* *Psammosteus pectinatus*							*Psammosteus megalopteryx*	
	b^1	*Psammosteus maeandrinus* zone	*Psammosteus maeandrinus*								
	a^4	*Psammolepis undulata* zone	*Psammolepis undulata* *Psammolepis aerata* *Crenosteus levis* *Psammosteus praecursor/markae* *Psammosteus asper* *Psammosteus livonicus*				*Psammolepis undulata*	*Psammosteus kiaeri* *Rohonosteus complicatus*	*Psammolepis undulata* *Psammosteus praecursor* *Rohonosteus ornatus* *Psammosteus tchernovi*	*Psammolepis undulata*	
	a^3	*Psammolepis paradoxa* zone	*Psammolepis undulata* *Psammolepis paradoxa* *Psammolepis venyukovi* *Psammolepis alata* *Psammolepis abavica* *Ganosteus stellatus*					*Psammolepis arctica*			
						Ganosteus stellatus					
GIVETIAN	a^2	*Pycnosteus tuberculatus* zone	*Pycnosteus tuberculatus* *Ganosteus stellatus* *Tartuosteus maximus* *Yoglinia bergi* *Psammolepis* sp.	*Pycnosteus nathorsti* *Pycnosteus obruchevi*							
		Pycnosteus palaeformis zone	*Pycnosteus palaeformis* *Pycnosteus pauli* *Ganosteus artus* *Ganosteus obtusus* *Ganosteus stellatus* *Tartuosteus giganteus* *Tartuosteus luhai* *Schizosteus asatkini* *Psammolepis proia*		*Psammolepis groenlandica*						
	a^1	*Schizosteus striatus* zone	*Schizosteus striatus* *Pycnolepis splendens*								
		Schizosteus heterolepis zone	*Schizosteus toriensis* *Schizosteus heterolepis*								

ORIGIN AND EVOLUTION OF THE PSAMMOSTEIDS

Any discussion on the origin and evolution of the psammosteids must be based in the main on the evidence provided by the changes seen in time in the morphology of the carapace. Therefore, since views on the relationships of the various heterostracan groups to one another depend largely on the different theories put forward to explain the way in which the carapace has evolved in the Heterostraci, it is necessary to commence with a consideration of this subject. TRAQUAIR (1899, 1900*b*), propounded the view that in the primitive stage, the carapace was composed of isolated denticles, and that such forms as *Drepanaspis* with its complex carapace of numerous plates were somewhat more advanced. He believed that the truly advanced stage was reached by a group such as the pteraspids where the carapace was composed of only a few comparatively large plates. This rather general view of the gradual fusion of dermal elements to form a carapace made up of few large plates was accepted by such authors as GOODRICH (1909), ABEL (1919, 1921, 1924), WOODWARD (1921*a*) and KIAER (1924). However, an alternative view was put forward by JAEKEL (1906, 1911) who suggested virtually the opposite to TRAQUAIR, i. e. that the most primitive stage consisted of one in which the carapace was composed of large plates, and that there was then a gradual breakdown during evolution into smaller elements. Little note seems to have been taken of this idea at the time, possibly because together with it JAEKEL also made the rather far-fetched suggestion that all aquatic vertebrates were derived secondarily from land-living animals. However, STENSIÖ (1927) supported JAEKEL's view on the growth of dermal armour and suggested that the carapace of a typical psammosteid such as *Drepanaspis* was not fairly primitive, but instead seemed to have been derived secondarily from the condition found in a typical pteraspid, by the breakdown of larger plates into smaller ones. This idea was extended to cover other groups, and the view became generally accepted that from the cyathaspids with their simple carapace of four major plates, the pteraspids could be derived by a breakdown, and from these the psammosteids could have evolved in the same way. This view was stated most explicitly by HEINTZ (1938) and due to its being repeated in standard textbooks (ROMER, 1945; YOUNG, 1950, 1962), it became firmly entrenched.

More recently however, OBRUCHEV (1945) demonstrated clearly that in the Heterostraci all the early representatives seem to possess a carapace composed of a mosaic of small plates, and that when the groups are considered in stratigraphical order, the main trend can be seen to be towards a gradual fusion of elements, and not to a breakdown. This view was subsequently accepted and developed by STENSIÖ (1958) and TARLO (1960*b*, 1962*d*). Thus, the type of carapace found in forms such as *Drepanaspis* in which there are fields of tesserae in between the major plates is taken to be a fairly primitive one, just as TRAQUAIR first suggested, while those forms in which the smaller plates have fused together to form only a few larger ones are taken to be more advanced. The psammosteids as a whole, therefore since they are characterized by possessing fields of tesserae between the main plates cannot be considered as highly advanced forms, but in spite of their success in Middle and Upper Devonian times must from the standpoint of their carapace, be taken to be an essentially primitive group.

Although the first convincing evidence of the view put forward earlier by TRAQUAIR was provided by OBRUCHEV, this latter worker still adhered to the idea of STENSIÖ that the psammosteids could be derived from the condition found in the pteraspids, although not for the same reason. OBRUCHEV (1943*b*) noted that the main difference between the psammosteids and the pteraspids was the presence of fields of small tesserae between the main plates, and instead of taking this as a primitive feature which had been retained by the psammosteids, he considered that these tesserae developed secondarily as a neoformation. He believed that they developed in the psammosteids to cover the sensory canals which lie beneath them, for in the young stages of the pteraspids such canals are quite unprotected. This view was reiterated by OBRUCHEV (1945, in TARLO 1961*a*) and was accepted by GROSS (1962). GROSS (1963) refigured the immature *Drepanaspis* first described by KUTSCHER in 1933, which appears pteraspid-like, and indicated that it supported the derivation of the psammosteids from the pteraspids (see Text-fig. 28). However, this specimen can just as easily be used to demonstrate the opposite view. This is especially so with regard to the branchial plates, since in this immature form they are quite unlike those of any pteraspid, being instead highly reminiscent of those of *Weigeltaspis*. There can be little doubt that, as OBRUCHEV stressed, the psammosteids and pteraspids are closely related, but in TARLO (1962*c*) an alternative theory to OBRUCHEV's was put forward to explain their relationship. The suggestion was made that the pteraspids represented a development from the psammosteids, in which the fields of tesserae between the main plates had been lost. An intermediate stage was demonstrated in the traquairaspids, in which the young individuals possessed fields of tesserae, although much reduced from those known in the psammosteids, but lost them as they grew to the adult stage by their becoming incorporated into the median plates.

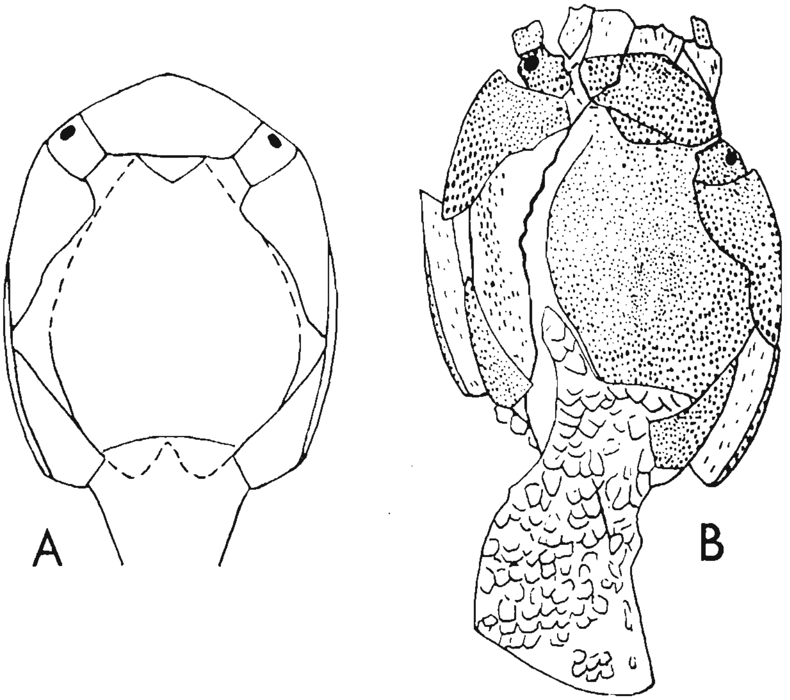

Fig. 28

Drepanaspis gemuendenensis SCHLÜTER — *A* restoration of young stage in dorsal view; *B* immature individual (natural size); (from GROSS, 1963)

OBRUCHEV (in TARLO 1961*a*) suggested that the psammosteids were derived from an advanced pteraspid such as the form described by BROTZEN (1936) under the name *Protaspis*, and renamed *Europrotaspis* by WHITE (1961). This pteraspid, unlike more normal pteraspids has a cornual plate which instead of forming part of the lateral margin of the carapace, just forms part of the median margin of the branchial opening on the dorsal surface. In addition the cornual plate in *Europrotaspis* is smaller than that known in other pteraspids. Thus in this form the cornual plate has a similar position to the cornual plate found in the psammosteids. However, the position of the plate in *Europrotaspis* may well be due in part to the fact that unlike most pteraspids this form was benthonic like the psammosteids, and in consequence had a dorso-ventrally flattened body. Furthermore, the smallness of the cornual plate in *Europrotaspis* may well be merely because it is a remnant of the larger plate found in more primitive pteraspids, since it seems to mark a stage in the gradual reduction and then elimination of this plate altogether, the final stage being found in *Gigantaspis* described by N. HEINTZ (1962). It is probably merely fortuitous that at the stage reached in *Europrotaspis* the cornual plate has come to occupy a position similar to the rather different cornual plate in the psammosteids, which latter acts mainly as a bounding edge to the branchial opening, and not as a means of maintaining stability as is the case in normal pteraspids. What seems likely is that the cornual plate found in these latter forms was produced by the development posteriorly of the cornual plate seen in the psammosteids, with the eventual production of postero-lateral spine-like projections. Then, at a late stage in the evolution of the pteraspids (exemplified by *Europrotaspis*) the posteriorly extended part of the cornual plate came to be reduced (Text-fig. 29).

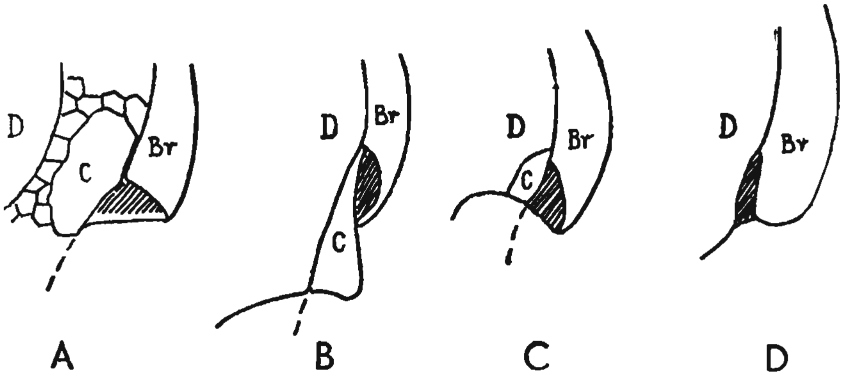

Fig. 29

Diagram indicating gradual reduction and elimination of cornual plates in the pteraspids. *A Drepanaspis* for comparison; *B Pteraspis* (from WHITE, 1935); *C Europrotaspis* (from BROTZEN, 1936); *D Gigantaspis* (from N. HEINTZ, 1962)

It is now generally recognized that the most primitive heterostracans from the Ordovician, possessed a carapace composed of a mosaic of tesserae, and it is from such a tesselated carapace that the patterns of plates known in later heterostracan groups must be ultimately derived. With regard to the psammosteids, there has been discussion as to whether or not such lower Gedinnian genera as *Tesseraspis* which also possess a tesselated carapace (WILLS, 1935; TARLO, 1962*c*) should be regarded as primitive members of this group, or whether the term psammosteid should be restricted to those forms which have the same complement of plates and general organization of the carapace as seen in *Drepanaspis*. OBRUCHEV (in TARLO, 1961*a*) feels that *Tesseraspis* should be considered separately from the psammosteids, this following naturally from his contention that the psammosteids are likely to have been derived from a pteraspid-like ancestor, since *Tesseraspis* is earlier than the pteraspids. However, it is here considered that as the different heterostracan groups must be derived ultimately from forms possessing a tesselated carapace, the simplest method of classification is to include within one group, genera of a particular lineage showing the various stages in the change from tesserae to plates. The psammosteids therefore should not merely include those forms in which the complete complement of plates has been achieved, but also forms showing the stages leading up to this. From this standpoint, forms such as *Tesseraspis* and *Weigeltaspis* in which the tesserae have become either organized into areas foreshadowing later plates, or have already fused into such distinct plates can well be included in an overall grouping with the later more typical psammosteids. Nevertheless, although their carapaces are differentiated towards the condition found in *Drepanaspis*, and despite the fact that they possess the feature characteristic of all psammosteids, i. e. fields of tesserae between what would become the main plates, such forms as *Tesseraspis* and *Weigeltaspis* are here separated from the later more typical psammosteids by being placed in the suborder Tesseraspidida. With regard to the Ordovician forms however, these seem to represent the most primitive structural grade in the Heterostraci as a whole, and from them it is possible to derive any of the later heterostracan orders. It is therefore considered best not to include them in any one of these later heterostracan groups.

Because of the very fragmentary nature of the remains of the tesseraspids *(s. l.)* known so far, it is not possible at present to trace within them evolutionary lineages in detail. It is however possible to recognize the main structural stages which occurred during their evolution. In *Tesseraspis* the carapace is composed entirely of independent tesserae, which although not yet fused together to form plates, are differentiated and organized into groups in areas where plates are known in later psammosteids. The tesserae in the dorsal and ventral median areas of the carapace are thick and are separated by a zone of thin tesserae, from the row of thick wedge-shaped tesserae making up the lateral margins of the carapace, which latter are the precursors of branchial plates. From *Tesseraspis*, *Weigeltaspis* seems to have developed, in which discrete dorsal, branchial, orbital and post-orbital plates are known as well as isolated thin tesserae, but in which the full complement of psammosteid plates does not seem to have yet developed. Since in *Weigeltaspis heintzi* the ornamentation is difficult to distinguish from that of *Traquairaspis symondsi*, it may well be that the traquairaspids which seem to represent a structural stage intermediate between psammosteids and pteraspids, separated off from the main psammosteid line at about this point. Contemporary with *Tesseraspis* there occurs the primitive psammosteid *Kallostrakon macanuffi*, which seems to be a representative of a second side-branch from the main lineage, since it has a rather different type of ornamentation. Discrete plates are known in this form which have been produced by the fusion of cyclomorial tesserae, and numerous isolated tesserae are also known which were presumably part of fields of tesserae. This species seems to grade into *Corvaspis kingi* in which various plates are also known, and as suggested earlier (TARLO, 1960*b*, 1962*c*), this form seems to be on the line leading by the progressive fusion of large plates together, to the cardipeltids known from the Siegenian of North America.

The first incontrovertible evidence of a psammosteid possessing the full complement of plates together with persistent fields of tesserae, which in consequence is placed in the suborder Psammosteida, is found in the genus *Drepanaspis*, and OBRUCHEV (1944, 1947*a*) outlined the major structural changes which occurred during the evolution from this form of *Psammosteus* itself, by way of *Psammolepis*. These changes were mainly concerned with the change in the proportions of the branchial plates. Similar morphological stages were discussed in more detail by TARLO (1961*a*) who showed that in addition to them, there were concomitant changes in other parts of the carapace, particularly with regard to the post-orbital plate. However, a rather fuller account of the evolution of the forms in the suborder Psammosteida is given below.

The first attempt at a detailed study of the evolution of the psammosteids was produced by MARK (1955), although she dealt only with forms from the Tartu and Gauja horizons of Estonia. In this work MARK demonstrated that from the common ancestor represented by *Schizosteus*, there evolved a number of separate lines represented by *Ganosteus*, *Pycnosteus*, *Tartuosteus* (leading to *Psammosteus*), *Yoglinia*, and three main lines of *Psammolepis*: *Psl. abavica*, *Psl. paradoxa* and *Psl. undulata*. More recently, TARLO (1962*c*) suggested from an examination of the growth of ventral median plates in Middle and Upper Devonian psammosteids, that there were two major lineages stemming from *Schizosteus*, one giving rise to *Pycnosteus* and *Tartuosteus*, and the other to *Psammolepis* which then grades into *Psammosteus*. Although this tentative phylogeny unlike that of MARK was not concerned with particular species, it did more to indicate relationships, since it showed how the different genera were likely to be related to each other even though they could be ultimately derived from *Schizosteus*. MARK on the other hand merely had numerous lines coming more or less directly from *Schizosteus*. However, when dealing with the evolution of the Psammosteida as a whole it is necessary to commence with a discussion of the different members of the Drepanaspididae since this is the earliest family belonging to this sub-order. TARLO (1957) suggested that the fauna of freshwater psammosteids recently discovered in central Poland were more likely to have been ancestors of the later Middle Devonian psammosteids than were the drepanaspids, as it was considered that the marine *Drepanaspis* represented a side-branch from the main stock. In the present work however this latter suggestion is discarded and it is now believed that it may well have been from species of *Drepanaspis* that the freshwater living guerichosteids of central Poland were derived, which in turn led to the more advanced forms of the later Middle Devonian.

The only account of evolution within the drepanaspids is due to GROSS (1937) who was able to show changes in the branchial plates from the Upper Siegenian *Drepanaspis schrieli* through *D. gemuendenensis* (Upper Siegenian/Lower Emsian) to the Emsian *D. lipperti*. In the earlier forms, the branchial plate in section is shaped rather like a ridge tile with its dorsal and ventral surfaces meeting at a fairly large angle. Gradually this angle became reduced and the angulated edge became thickened and laterally extended, while the dorsal flange became progressively narrower. By the time *D. lipperti* was reached the dorsal and ventral surfaces of the plate had become more or less parallel, with the ventral part still extending well under the body of the animal, while the dorsal surface extended medially only as far as the median edge of the thick lateral extension to the plate as a whole. GROSS compared the branchial plates of *D. lipperti* with those of *Schizosteus striatus* from the Narowa horizon of the Baltic, but perhaps a closer parallel would be with the earlier guerichosteids.

Unfortunately the other species of *Drepanaspis* recognized in South-West England and the Rhineland, are not known from branchial plates, but only from fragments of median plates, tesserae and scales. *Drepanaspis carteri* is of particular significance since it possesses median plates and tesserae which are ornamented by elongated tubercles very similar to those known in *Tesseraspis*. This would suggest the possibility that *Drepanaspis carteri* could have been derived from this form. Moreover the tubercles of the ornamentation of the plates in *D. carteri* are sharply pointed and fairly well separated from one another, and this suggests a further relationship, this time with *D. gemuendenensis*. In the same fauna as that in which *D. carteri* is found in S. W. England, *Drepanaspis edwardsi* also occurs. In this form the tubercles are larger, more rounded and flatter, and are more closely packed. They seem more like those known in *Guerichosteus kozlowskii*. The problem with the different species of *Drepanaspis* however is that at the moment there is insufficient evidence to demonstrate their relationship to one another or to the later guerichosteids from Poland. The only useful guide is the ornamentation, but since a similar pattern can appear quite independently in different forms, and since in any case it varies in different parts of the carapace, it has its dangers when used alone. For this reason, although parallels in the ornamentation of the different species of *Drepanaspis* and other psammosteid species will be pointed out, only tentative suggestions will be made as to their significance. For example the ornamentation of *D. schrieli*, with its very small closely packed tubercles is rather like that known in *Guerichosteus lefeldi*, while *Drepanaspis jaegeri* seems to be similar to *Guerichosteus kulczyckii. Drepanaspis gemuendenensis* and *Guerichosteus kozłowskii* are the best known species of these two genera as far as the plates are concerned, and it is easy to see how one structural grade could have led to the other. In particular, growth stages are known in the branchial plates of *Guerichosteus kozlowskii*, and it can be seen that in the young stages the plate is similar in shape to that of the adult *Drepanaspis gemuendenensis*. However, as already pointed out, certain drepanaspid species seem to be ornamented in a similar manner to particular species of *Guerichosteus*, and although this may not indicate direct relationships, it may well prove to be the case that the guerichosteids were not necessarily evolved from any one species of *Drepanaspis*. Instead they probably represent a structural stage achieved independently by different drepanaspid lineages.

Provisionally included in the drepanaspids is the genus *Psephaspis*, which is known from a dorsal plate and scales. It is an early form, being of Siegenian age and is found in Utah and Idaho. The ornamentation of the dorsal plate is clearly arranged in concentric rings and in some ways is comparable to that known in *Guerichosteus kozlowskii*. The lateral margins of the plate also show an incorporation of small areas of growth, rather more irregular than the apparently synchronomorial tesserae found at the margins of the median plates in *Drepanaspis gemuendenensis*. These irregular areas are rather reminiscent of those occurring at the margins of the rostral plate in species of *Schizosteus* and *Pycnolepis*. Unfortunately there is as yet no evidence of the nature of the branchial plate of *Psephaspis*, and although it is obviously on the way to the guerichosteids, since its age is closer to that of drepanaspids it is here tentatively included with them.

The guerichosteids from the Emsian of central Poland represent the basic stock from which the main radiation of Middle and Upper Devonian psammosteids seems to have come. As well as the genus *Guerichosteus*, also present in the Polish freshwater fauna is *Hariosteus* which is characterized by the development of small accessory tubercles between the main tubercles of the ornament. It is of interest to note that this development of accessory tubercles is a feature that appears frequently in late members of a particular lineage. The median plates of *Hariosteus* are unusual in the psammosteids, since as well as the normal concentric arrangement of tubercles there are also what appear to be seasonal growth zones. Two species are known — *H. kielanae* and *H. lobanowskii*, the former having rounded tubercles with normal crenulations, while the latter has tubercles which are somewhat elongated. A notable feature of the guerichosteids is that they possess a long wide open posterior notch in the ventral plate. Such a posterior notch is a highly variable feature in the ventral plate of *Drepanaspis*, for sometimes there is a shallow excavation of the posterior margin, while on other occasions there is a long narrow slit, but evidently by the time the guerichosteids are reached this notch has become stable. Also in *Guerichosteus* the branchial plate is far more massively developed than it is in *Drepanaspis*, and the lateral free margin of this plate is more solid and very strong. However, as mentioned above, changes can be traced by means of growth stages in *G. kozlowskii* from the condition in very young individuals where this plate is like that known in *Drepanaspis*, to the adult condition. This adult branchial plate then changes through the various guerichosteids until it approaches the type of plate seen in the advanced guerichosteid *Schizosteus*, where it is drawn out into a comparatively thin solid sheet of bone with a considerable lateral extent.

In the Eifelian of Bohemia there is a single specimen of a young individual in which the ornamentation is reminiscent of that in *Guerichosteus kozlowskii.* Its branchial plate seems much thinner than that of the primitive guerichosteids, with the branchial opening situated some distance medial to the postero-lateral corner. It has thus been placed in *Schizosteus perneri,* although it may well prove to have been derived from *G. kozlowskii.* When the Pernau horizon of the Baltic is reached, two psammosteid species are known. One of these is *Schizosteus heterolepis* which again has an ornamentation rather similar to that of *G. kozlowskii* but has branchial plates which are thinner at the free lateral margins. There is a rather wide variation in the size of the tubercles of the ornament and in this it is reminiscent of the condition in *G. kotanskii.* Furthermore the type of tubercles seen in *S. heterolepis* seems to indicate a possible connection with the later pycnosteids, since they are high and rounded with strong radial ribs, and this species may indicate the point at which the advanced guerichosteids diverge to give the two major lineages of advanced psammosteids *(s. l.).* The other species

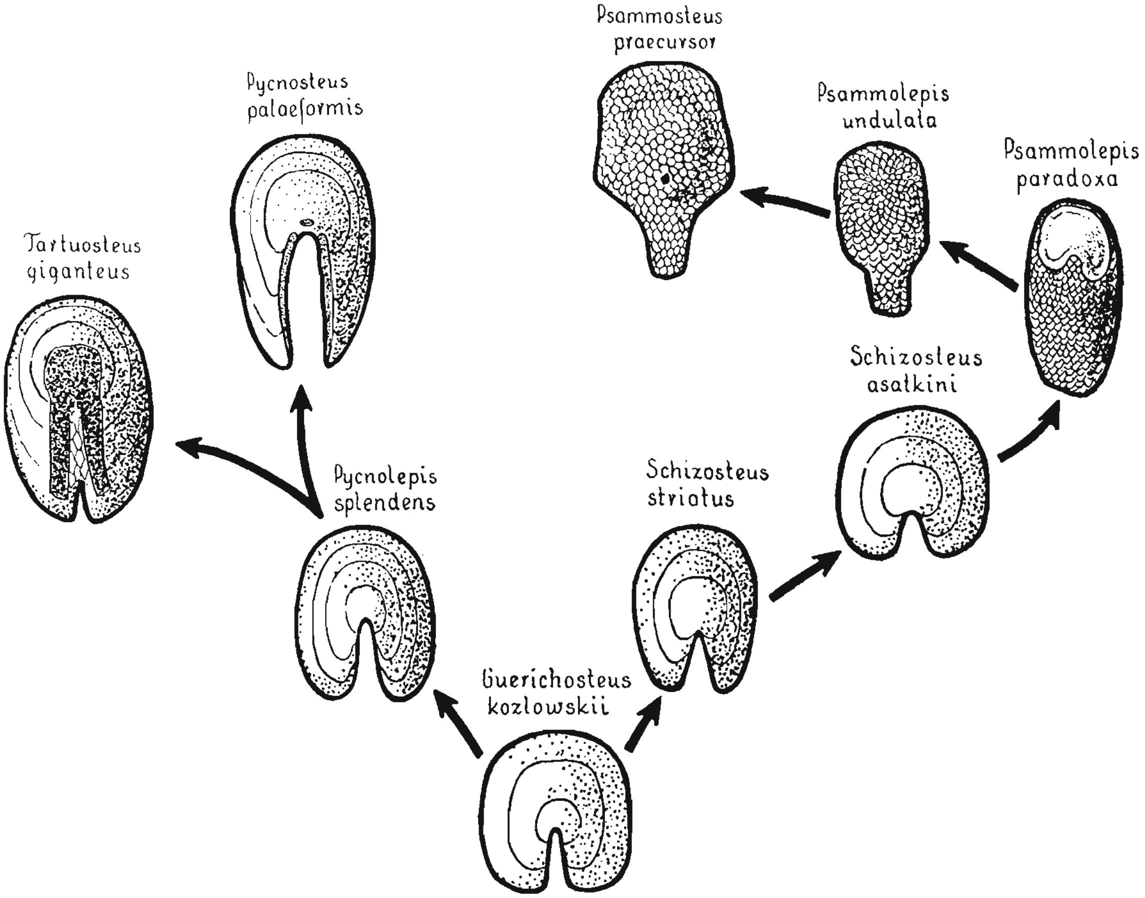

Fig. 30

Diagram of ventral median plates indicating main evolutionary lineages of the Psammosteida in the Pernau horizon is *S. toriensis* in which the ornamentation although similar to that in *S. heterolepis*, is considerably smaller. In the succeeding Narowa horizon, two further psammosteid species are represented, the first of which is *S. striatus*, which is characterized by possessing a basin-shaped ventral median plate with a fairly well developed posterior notch. The contemporary form *Pycnolepis splendens* also has a basin-shaped ventral median plate, but this time the notch is much exaggerated. This form which in many respects is similar to *Schizosteus* is placed in a separate genus since it seems already to have diverged strongly from the typical *Schizosteus* condition. It is well on the way to *Pycnosteus* which is characterized essentially by possessing a very long posterior notch with almost parallel sides. The branchial plates of *Pycnolepis splendens* have very wide lateral extensions, and a nearly contemporaneous species which seems to be closely related to it is *Pycnosteus nathorsti*. This has an ornamentation of fan-shaped tubercles such as are found in *Pycnolepis splendens*, and in addition other tubercles which are more rounded and often possess marked crenulations, which are typical of *Pycnosteus*. Furthermore *Pycnosteus nathorsti* although included in the genus *Pycnosteus*, also seems to show the beginnings of features which characterize the genus *Tartuosteus*. For example, the deep posterior notch in the ventral plate has now become much narrower. Thus *Pyc. nathorsti* seems to represent the stage from which *Tartuosteus* could have branched off from the main pycnosteid line. But although *Pyc. nathorsti* demonstrates this quite clearly, when all its characteristics are taken together it remains itself closer to *Pycnosteus* than to *Tartuosteus*.

The characteristic feature of *Pycnosteus* is that the posterior notch has now become exaggerated, being very deep and wide, and the ventral plate as a whole very elongated. Furthermore, this plate although being flat-bottomed, has steep anterior and lateral portions, so that anteriorly it resembles the stern of a rowing boat. This must have resulted in the mouth of the animal being raised far off the sub-stratum, and as it was obviously a benthonic form since it is strongly abraded on the flat part of the plate, this poses a problem as regards the method of feeding. The most probable explanation is that below the mouth the deep body of the animal housed a pumping organ like the velar organ described by STRACHAN (1958) in the hagfish. This would have enabled *Pycnosteus* to suck in great volumes of water together with small animals from quite a wide area. This same type of deep ventral median plate is also present in *Ganosteus* and *Tartuosteus*, and they may well have fed in a similar manner. Thus within the psammosteids there was a very marked specialization in the carapace, and consequently in feeding habits.

In the Baltic region it is fairly easy to trace the evolution of the genus *Pycnosteus* since several species are represented. *Pycnosteus palaeformis* is found in the lower part of the Arukula horizon, and this form possesses triangular branchial plates which have a lateral margin that is slightly convex in outline, and are ornamented by medium-sized stellate tubercles. This form gives place to *Pycnosteus pauli* from the mid part of the Arukula horizon. Here the tubercles are similar but somewhat larger, while the branchial plates themselves have a fairly straight lateral margin, although there is sometimes the suggestion of a slight concavity in the outline. Finally, *Pycnosteus tuberculatus* appears in the Burtnicki horizon, and in this form the tubercles are larger still and small accessory tubercles are also present between them. The branchial plates are exceptionally wide and they now have a very well marked concave antero-lateral margin along the whole of which there is a zone of even abrasion. Abrasion in this position is difficult to explain, since it could not have been produced by scraping along the sub-stratum, no matter how the plate is orientated. However, a possible solution has been suggested by Dr. J. D. CURREY in a personal communication. He believes that these plates may well have formed almost wing-like projections which would have become abraded as they were dragged through weed. The animals may well have used this method of disturbing the vegetation so that small animals on the weed would have been dislodged and then sucked in for food. A further specialization seen in *Pycnosteus tuberculatus* is the downward extension of the margins of the posterior notch of the ventral median plate. These projected well below the underside of the animal and formed two narrow runners on which the animal could glide over the sub-stratum. *Pycnosteus tuberculatus* which seems not to have survived beyond the Burtnicki horizon, was therefore, one of the most bizarre of the psammosteids.

Closely related to *Pycnosteus* is the genus *Ganosteus* which is contemporaneous with it. This probably represents a side-branch which came off the main line somewhere near to *Pycnosteus palaeformis*. *Ganosteus artus* is the first known species, and although contemporaneous with *Pyc. palaeformis*, since it has a longer range than that species it is also a contemporary of *Pyc. pauli*. Although the branchial plates of *G. artus* are rather badly preserved, they indicate that they were rather similar to those of *Pyc. palaeformis*, as also are the ventral median plates. The ornamentation however is composed of very large, widely separated tubercles. Overlapping *G. artus* in the middle of the Arukula horizon is *Ganosteus obtusus*, known from a single branchial plate which seems to have a very convex outline to the lateral margin while the posterior margin is straight. The anterior part of the lateral margin has been badly bitten, and thus a full outline is not distinguishable. It is possible therefore that it belongs to a rather unusual specimen of *G. artus*. However, the ornamentation although similar to that of *G. artus* is not exactly the same, and for the present it is probably better to consider it as a side-branch from that form and to retain the name *G. obtusus* for it. Found in the upper part of the Arukula horizon, extending right through the Burtnicki and into the Gauja is *Ganosteus stellatus*. This has very large tubercles indeed which are widely separated and have numerous accessory tubercles between them. Again, this seems to be a form at the end of a lineage. Until complete branchial plates belonging to *G. stellatus* were discovered by MARK and OBRUCHEV a few years ago, the branchials were known only from PANDER (1857) and GROSS (1933*a*) and appeared to be narrow plates which were rather solidly built, very similar indeed to those of *Psammosteus* from the Upper Devonian. It therefore appeared that in *Ganosteus* there had been a shortening and widening of the branchial plate that paralleled such changes in the branchial plates of the different species of *Psammosteus*. However, it is now known that the main plate in *Ganosteus stellatus* is comparable to that found for example in *Pycnolepis palaeformis* or *Ganosteus artus*, except that the postero-lateral corner of the plate is drawn out into a very prominent posteriorly-directed spine. Evidently it was merely these posterior spines that had been thought to be the complete branchial plates, and hence led to the misunderstanding. As far as the growth of these plates is concerned, it would seem that in the young stages they had much the same shape as those of the advanced *Psammosteus*. However, instead of merely continuing to grow wider to keep pace with the growth of the animal they then also grew much longer so that eventually they had more the shape of the branchial plates in other species of *Ganosteus*, plus a posteriorly directed extension. A further unusual feature of the ganosteids is that their cornual plate is strikingly similar to that found in *Guerichosteus kozlowskii*, although so far there seems no direct connection between the genera.

A further side-branch from the main pycnosteid line is represented by several species of *Tartuosteus*. Members of this genus, as already noted, show certain close similarities to the Spitzbergen *Pycnosteus nathorsti*, but the main difference between *Tartuosteus* and other pycnosteids is that in its ventral plate the posterior notch has become much narrower, and is partially infilled by lozenge-shaped tesserae which are added on behind each other. However,

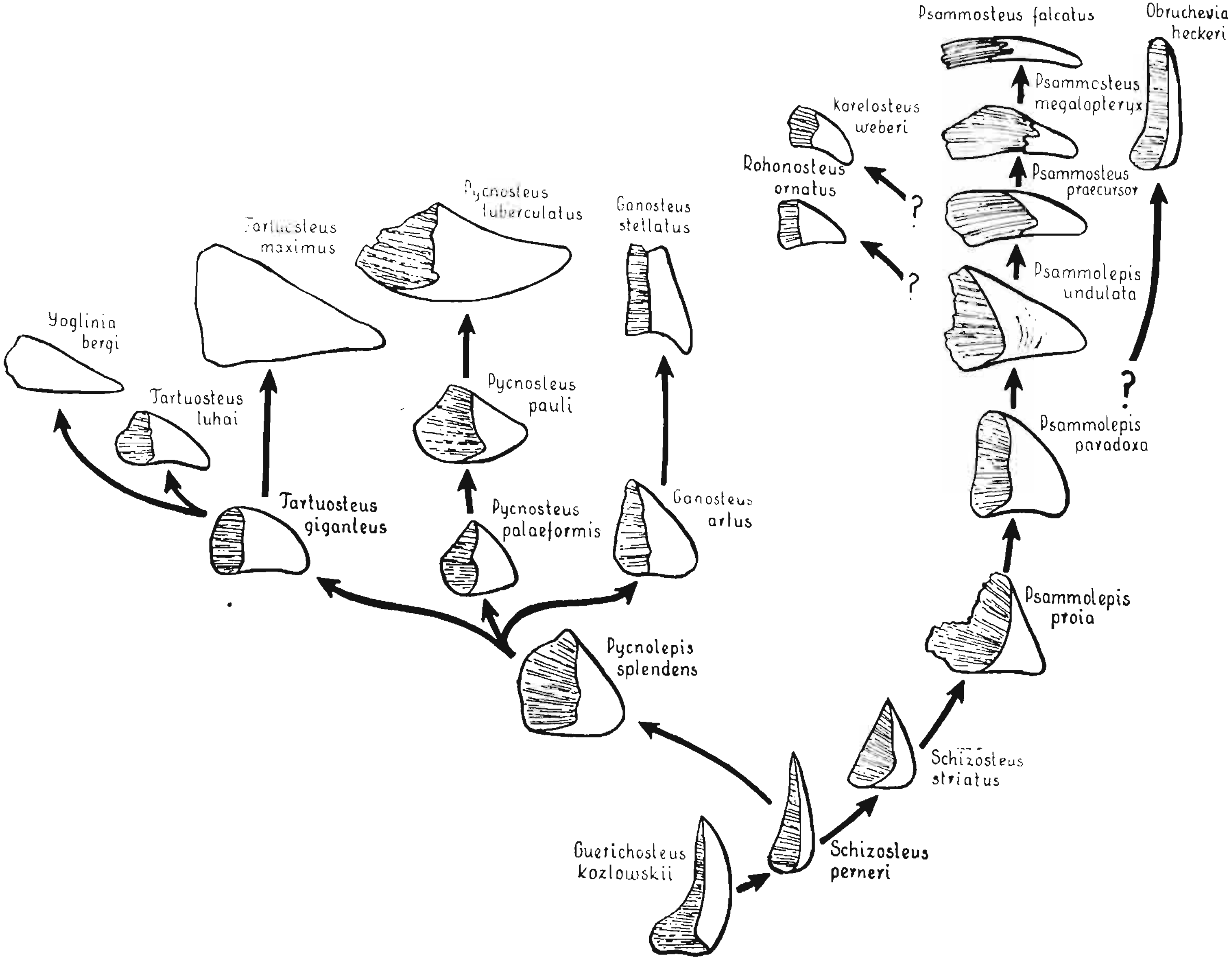

Fig. 31

Diagram of branchial plates arranged according to probable phylogenetic relationships there is always quite a considerable amount of open notch posterior to them. *Tartuosteus* on the other hand is similar to other pycnosteids in that its ventral median plates are very long and boat-shaped, presumably indicating that its feeding habits were the same as theirs. The earliest species — *Tartuosteus giganteus* which occurs throughout the Arukula horizon, is characterized by possessing an ornamentation of minute tubercles which are hardly visible to the naked eye. The branchial plates of this form are fairly long and wide. In the mid part of the Arukula horizon *Tartuosteus luhai* occurs in which the branchial plate is much wider relative to its length, and is also shorter than the branchial plate of *T. giganteus*. In its proportions the branchial plate of *T. luhai* appears to be intermediate between the branchials of *T. giganteus* and *Psammosteus*. The only other form which has a branchial plate with proportions identical to those of *T. luhai* is the psammosteid from the Timan described by ROHON (1899) as *Psammosteus ornatus*. MARK (1955) tentatively suggested that for this reason *Psammosteus* may have been derived from *T. luhai*, while OBRUCHEV (1961) tentatively included the Timan species, here assigned to the new genus *Rohonosteus*, in the genus *Tartuosteus*. The shape of the branchial plate however is not necessarily of any significance with regard to the affinities of the animal concerned, since the proportions of the plate seem to be more an index of the structural stage reached in the evolution of the overall carapace. Animals belonging to quite separate lineages may well have branchial plates which as far as their proportions are concerned are indistinguishable. Since *T. luhai* is early in the succession it seems unlikely that it could have had anything to do with *Rohonosteus*, and as *Tartuosteus* is an offshoot from the pycnosteid line it seems to be quite separate from the psammolepids which grade into the psammosteids *(s. s.)*. From *T. giganteus* there develops *T. maximus* which is found in the Burtnicki horizon, and may also possibly occur in the Gauja. In *T. maximus* the tubercles of the ornamentation are much larger than they are in *T. giganteus*. Furthermore, *T. maximus*, also being the end member of a lineage, is, like *Pycnosteus tuberculatus*, one of the largest psammosteids.

Occurring at the base of the Burtnicki horizon is the unusual form *Yoglinia bergi* which seems to be rather similar to *Tartuosteus maximus* although described first as a pteraspid (OBRUCHEV, 1943*a*). This was because the only fragment known appeared to be a cornual plate ornamented by longitudinal dentine ridges like that of a pteraspid. However it has since been recognized as the posterior part of a branchial plate (MARK, 1955; OBRUCHEV, 1958). *Yoglinia bergi* has extremely wide branchial plates which are comparatively short, and this would seem to make this form similar to *Psammosteus*, but in view of the fact that parts of the ornamentation are almost indistinguishable from *T. maximus* it seems more likely that as MARK (1955) suggested, *Y. bergi* represents a separate side-branch from *Tartuosteus*, in which the main evolutionary trends seen in the psammolepids towards the condition found in *Psammosteus* have been paralleled.

Besides the pycnosteid lineage, there also developed a further separate line from the advanced guerichosteids, in which although the ventral median plates were long and narrow and fairly convex, they were by no means as deep as those of *Pycnosteus*. They were characterized instead by the elimination of the posterior notch early in the development of the individual. In *Schizosteus striatus* from the Narowa horizon, the ventral plates were fairly deep, but instead of being long and narrow were rather round. Furthermore, the margins of the posterior notch were not parallel, but instead they formed a «V», the apex of which reached a point towards the centre of the plate. In *Schizosteus asatkini* from the later Arukula horizon the type specimen is a small carapace with a fairly deep and rounded ventral median plate, but this time the notch is a shallower and broader one, and does not form a «V». The posterior notch in this instance is similar to that found in the young stages of *Psammolepis* which as will be shown also have a similar rounded ventral median plate. The ornamentation of *S. asatkini* is very similar to that found in *S. striatus* and it seems likely that it is a direct descendant from this species. It appears to be evolving towards the typical *Psammolepis* condition in which the rounded plate of the young stage grows posteriorly by the addition of scale-like tesserae, beneath which the main plate continues to grow, to produce in the adult a long narrow and fairly flat plate.

Also found in the Arukula horizon of the Baltic is the first species of *Psammolepis* itself — *Psl. proia* — in which there is a very long narrow ventral plate. The branchial plate has a much greater lateral extent than the branchial in *Schizosteus* and in its proportions is comparable to the contemporary *Pycnosteus palaeformis*. The species *Psl. groenlandica* which is also of Tartu age, appears to be closely related to the Baltic species *Psammolepis proia* since its ornamentation is very similar. The Gauja of the Baltic seems to have been the time when the development of the psammolepids reached its acme, as a whole number of different species are present. *Psl. abavica* and *Psl. alata* seem to be either derived directly from *Psl. proia* or are very close relatives of it. Also found are *Psl. paradoxa* and *Psl. venyukovi*, this latter being characterized by sharply pointed tubercles with accessory tubercles between them. A similar although larger ornament is found in *Psl. arctica* from Ellesmereland, and this may well have arisen from *Psl. venyukovi*. Contemporary with *Psl. paradoxa* is the form described from the Gauja of the Baltic as *Psl. heteraster* by GROSS (1930, 1933*a*). In the ornamentation and character of its branchial plates it seems to be a link between *Psl. paradoxa* and *Psl. undulata*, but as it is somewhat nearer to *Psl. undulata* it is here referred to that species. MARK (1955) placed *Psl. alata* close to *Psl. heteraster* and *Psl. undulata*, while she separated *Psl. abavica* from this particular line. She recognized three lines of development, one leading to *Psl. abavica*, one in which *Psl. proia* is represented at the base, leading to *Psl. paradoxa* and *Psl. venyukovi*, and a third leading to *Psl. alata* and *Psl. undulata*. What seems rather more likely is that most of these species were derived from *Psl. proia* or from a form close to it, and that all of them are very closely related. Many of the differences between them seem to be due merely to the varying shape of the branchial plates, which although showing important differences are hardly sufficient to allow the recognition of separate lines.

As mentioned previously, the ventral median plates in the psammolepids are fairly round in the young stages, having been formed by the cyclomorial growth of tubercles in concentric rings. The young stage of the dorsal median plate is also rather similar. Then, as the animal grows the plates increase in size by the addition of scale-like tesserae beneath which the main plate extends. In the dorsal median plate these tesserae are added on all round the initial cyclomorial plate, but more rapidly posteriorly, while in the ventral plate almost all the new growth is confined to the posterior part of the plate, so that it ends up as a long narrow plate. As the different species of *Psammolepis* are traced in time, the initial cyclomorial area seems to become reduced in size and eventually disappears altogether, and it is of interest to note that the same structural stages seem to have been achieved by the pycnosteid *Tartuosteus*. *Psammolepis undulata* from the Amata horizon which seems to be a direct descendant from *Psl. paradoxa* has reached the stage where there is no longer any sign of the early cyclomorial growth stages, both dorsal and ventral median plates being composed entirely of superficial scale-like tesserae, and with it in this horizon is *Psammolepis aerata* which although known only from a very small branchial plate is remarkable for its large closely packed tubercles. These seem to be the last species of *Psammolepis* and overlapping with them are the first species of *Psammosteus* itself — *P. praecursor* which is known only from branchial plates and ventral median plates, and *P. markae* known only from dorsal plates. Although these two species may eventually be found to belong to one species, since the ornamentation of the dorsal plates of *P. markae* is not exactly the same as that of the ventral and branchial plates of *P. praecursor*, at the moment there is insufficient evidence to unite them. In both cases the median plates are covered with polygonal tesserae typical of *Psammosteus*, and they thus contrast with the ornamentation in *Psammolepis* where the tesserae have a more scale-like appearance. The differences seem to be due to the way in which the tesserae develop, since the tubercles in those of *Psammosteus* seem to grow concentrically, while those in *Psammolepis* grow excentrically, with the centre of growth at one edge. Even so, in some of the tesserae at the margins of the plates of *Psammolepis* concentric growth can be seen, indicating a development towards the *Psammosteus* condition.

From the Amata horizon OBRUCHEV (1964) described a fragment of a median plate under the name *Psammolepis connectens*, but in this work this species is not accepted as valid, since it appears to be equally acceptable as *Psammolepis undulata* or *Psammosteus praecursor/markae*, the superficial tesserae of the fragment showing a graduation from one type of tesserae to the other. However the specimen is important for it emphasizes that at this horizon an advanced *Psammolepis* grades into a primitive *Psammosteus*.

With regard to the ventral median plates of *Psammolepis undulata*, the shape of these is extraordinarily similar to those of *Psammosteus praecursor*, since the posterior part of the plate narrows to form a «neck» so that in outline the plate is shaped like an inverted flask. The posteriorly directed «neck» would seem to suggest that the branchial plates were orientated so that their proximal ends which were covered by branchial tesserae, fitted into the concavities on either side of this «neck». However although their ventral median plates are similar in shape, the branchials of *Psammolepis undulata* and *Psammosteus praecursor* are rather different, since in *P. praecursor* the branchial plates are typical of *Psammosteus*, being very wide and rather short. It seems that in fact the tremendous shortening and widening of the branchial plates to form very strong postero-lateral corners to the carapace first attempted independently by *Yoglinia* and to a lesser extent by *Tartuosteus luhai*, has in the various species of *Psammosteus* been completely accomplished. This must have made the lateral part of the carapace far less vulnerable than in other forms where there were thin projecting sheets of bone. Although there are in the Amata horizon examples of both the most advanced *Psammolepis* and the most primitive *Psammosteus*, also present are a whole variety of other species of *Psammosteus* showing various evolutionary stages, some of them being very advanced indeed. There was probably a burst of rapid evolution early on in the Amata, with primitive forms continuing through, but unfortunately many of the forms are not known from adequate material, so that it is difficult to see how they are related to one another. *Psammosteus asper* for example is rather similar to *P. markae* although it is characterized by tubercles that are rather more widely spaced and have longer crenulations. Another specimen from this Amata horizon described by OBRUCHEV (1964) as *Psammosteus cuneatus* seems rather similar to *Psammosteus megalopteryx* which is known from the Shelon-Ilmen horizon. But in the present work OBRUCHEV's species is not accepted as valid since it appears to be a pathological specimen. It is of interest however since its branchial plates have the same shape as those of typical specimens of *P. megalopteryx*. Also in the Amata is *Crenosteus levis*, which although accepted as a psammosteid *(s. s.)* seems in the proportions of its branchial plates to parallel slightly the condition seen in *Ganosteus stellatus*, since the postero-lateral corners seem to be somewhat drawn out. From the Timan, where both *Psammosteus praecursor* and *Psammolepis undulata* are also found, comes *Psammosteus tchernovi* which appears to be a very advanced species of this genus, as

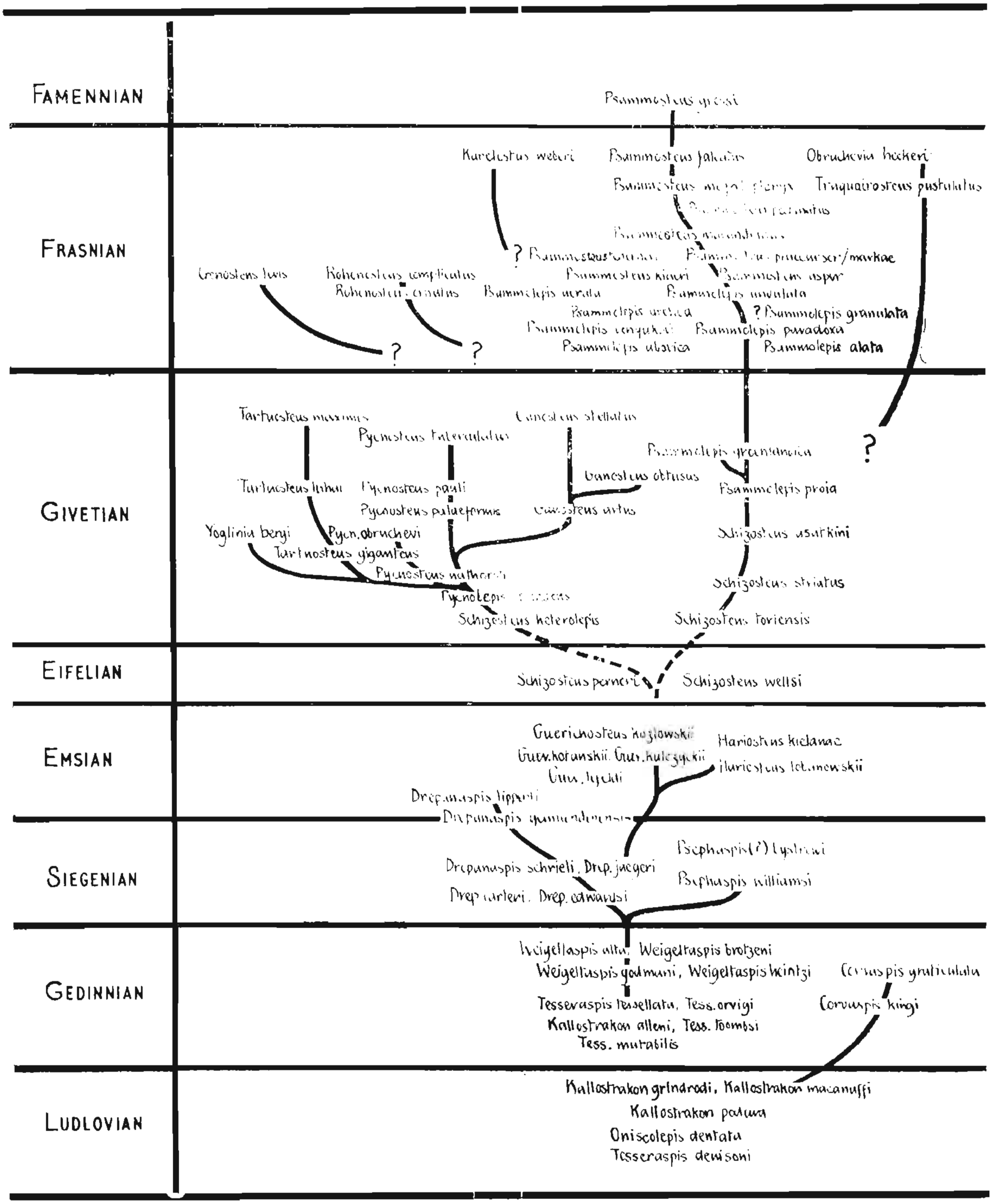

Fig. 32
Tentative phylogeny of the Psammosteiformes

it has branchial plates which appear just like very narrow spines. In the same deposit there occurs *Rohonosteus ornatus*, which as mentioned previously, has branchials which seem to be exactly intermediate in shape between those of typical *Psammolepis* and *Psammosteus* species. *R. ornatus* seems to give rise to *R. complicatus* from Ellesmereland in which although the ornamentation is essentially the same but larger, the branchial plate is rather shorter and wider, i. e. it is getting closer to the *Psammosteus* condition. This seems to suggest that there was more than one line from the *Psammolepis* condition to that of *Psammosteus*. But although *Crenosteus* and *Rohonosteus* could perhaps be considered as advanced psammolepids they are being retained in the Psammosteidae because of the greater emphasis put on their advanced characters.

In the Snetogor horizon, occurs *Psammosteus maeandrinus* in which the branchial plates are shorter and wider than in *P. praecursor*, although the two species are similar in other respects. Indeed there seems to be no reason why *P. maeandrinus* should not have come directly from *P. praecursor*. In the following Shelon-Ilmen horizon is found the very common *P. megalopteryx* in which the branchial plates are again short and wide, but are now much more massively constructed, and show for the first time evidence of their having been moveable to some extent. Very occasionally, branchial plates are found in which the anterior and posterior margins although curved in outline are more or less parallel, like those of the later *P. falcatus*. The ornamentation of *Psammosteus megalopteryx* is fairly variable, but the tubercles which are not very closely packed usually show on the branchial plates well developed basal crenulations which are frequently drawn out proximally. Occurring with *P. megalopteryx* is *P. pectinatus* in which the tubercles are fused into short ridges aligned normal to the main axis of the branchial plates, and possess very delicate comb-like crenulations drawn out proximally. This seems to be a specialized form derived from *P. megalopteryx*, indicating the condition found in the later *P. falcatus*, where in the branchial plates the tubercles are frequently fused into strips aligned normal to the main axis. Fine ribs extend proximally from each strip, and each rib is delicately crenulated. However, although *P. pectinatus* from the Shelon-Ilmen horizon and even *P. kiaeri* from the equivalent of the Amata horizon in Ellesmereland have tubercles fused into flat strips with long proximal extensions, it nevertheless seems most likely that the condition in *Psammosteus falcatus* was a direct development from that found in *P. megalopteryx*, and was not achieved by way of these two somewhat similarly ornamented species.

The branchial plates of *Psammosteus falcatus* from the e Horizon are quite remarkable in their outline, for although both the anterior and posterior margins of the plate are arcuate in outline, they both curve in the same direction, and are thus parallel. However, very occasionally plates are also found with an outline similar to those of *P. megalopteryx*, where the anterior and posterior margins meet at a rounded angle, and as already noted, on rare occasions plates of *P. megalopteryx* are found which resemble in shape those of *P. falcatus*. What appears likely is that the forms with parallel-sided branchial plates had some advantage over those with ordinary branchial plates, so that by the time the e Horizon was reached, the majority of individuals of *Psammosteus* possessed this type of plate. This may perhaps have been connected with bracing and strengthening the posterior part of the carapace. Also found with *P. falcatus* and continuing through into the base of the Famennian is *P. grossi* which has similar branchial plates. The ornamentation in *P. grossi* however is composed of individual tubercles which are divided into proximally directed extensions, so that each tubercle gives the impression of being a short arcuate ridge with proximal projections. *Karelosteus weberi* also appears in the e Horizon, and this is characterized by very large oval tubercles.

It is rather different from the other forms in the e Horizon however, since its branchial plates are reminiscent of those in *Rohonosteus*, and in spite of its very large tubercles which suggest that it is an advanced form, it appears to represent the continued success of a form which has not passed through the highly advanced stages of the late species of *Psammosteus*. It is not possible to indicate with certainty the origin of *Karelosteus*, although it should be noted that *Psammolepis aerata* from the Amata horizon also possesses similar but smaller tubercles. There may well therefore have been a further trend towards the *Psammosteus* condition from yet another species of *Psammolepis*.

A further group of psammosteids are known from the e Horizon of the Baltic and its equivalent in Scotland. These — the obrucheviids — seem to represent a completely separate evolutionary line from the psammolepids. The most primitive of this group is *Traquairosteus pustulatus*, and this is known only from a dorsal median plate and fragments. It seems to indicate the penultimate stage in what is the characteristic of the group as a whole — the reduction and final elimination of dentine tubercles, for its ornamentation is reduced to isolated dentine tubercles each of which is found on the summit of a pustule of aspidin. In the more advanced *Obruchevia [Aspidosteus] heckeri* the dentine tubercles have been completely lost, and the outer layer which is now composed only of aspidin, has been strengthened by an infilling of pleromic dentine. In this form the dorsal median plates are very thick and flat, while the branchial plates are very thin and delicate, and unlike those of all the advanced psammosteids *(s. l.)* seem to have become elongated and narrow — strikingly different from all the contemporary forms. But perhaps the most notable feature of these plates is that they are bent at right angles. This is the reason that it is suggested here that *Obruchevia [Aspidosteus] heckeri* may have evolved from the psammolepids, for in some species of *Psammolepis*, as for example *Psl. paradoxa*, the branchial plates are gently arched from side to side, which does not seem to be the case in any of the pycnosteids. If the curvature in *Psl. paradoxa* were exaggerated, the *Obruchevia [Aspidosteus]* condition could be achieved. It is also evident that this form used the edges of the downturned lateral part of its branchial plates as runners, achieving much the same type of structure as that found in the ventral median plate of *Pycnosteus tuberculatus*. However, since in *Obruchevia [Aspidosteus]* the runner formed by the downturned branchial plates were not as strong as the runners in *Pyc. tuberculatus*, there is every likelihood that the animal possessed a deep ventral plate, like those found in the pycnosteids, which also reached the substratum, so that all the weight of the animal was not concentrated on the rather delicate lateral runners. No fragments of a ventral median plate of *Obruchevia [Aspidosteus]* have however yet been recognized so for the present this theory cannot be verified. Nevertheless, as well as being one of the last of the heterostracans, *Obruchevia [Aspidosteus]* was also one of the most unusual of the Psammosteida.

Thus, as has been demonstrated, as far as the primitive Psammosteiformes are concerned, even though they included a wide variety of forms, it has been possible to recognize only a number of morphological stages which show how a carapace of distinct plates came to be evolved from a tessellated one. Such primitive forms, as can be seen from Text-fig. 32, have been included in the Tesseraspidida. When the Psammosteida are reached however, the situation is rather better. Here again there is a considerable variety of species, and although in the main it is only possible to recognize overall evolutionary trends and morphological stages, in some cases direct phyletic connections can be established between different genera and species. In the chart these are indicated as solid lines. As the chart demonstrates, it is not really possible to show exactly how the different species of *Drepanaspis* are related to one another, or whether the guerichosteids are a separate line, or merely represent a structural stage in the evolution of the carapace. However the pycnosteids and psammolepids seem to represent main evolutionary lineages within which it is possible in certain cases to trace the derivation of one species from another. But within the psammolepid lineage there is the problem of the evolution of the psammosteids *(s. s.)*. It is quite evident that the family Psammosteidae has come from the psammolepids, but what is not certain is whether this has taken place by way of one particular psammolepid, or whether the Psammosteidae merely represents a structural grade which has been achieved independently by several psammolepid lines. This is emphasized particularly by the closeness to various typical Psammolepididae of the rather different psammosteid *(s. s.)* genera *Crenosteus*, *Rohonosteus* and *Karelosteus*. Finally, it is of interest to note that the psammosteids as a whole appear to have died out rather suddenly for no apparent reason, at a time when quite a number of different forms including *Psammosteus grossi*, *Obruchevia [Aspidosteus]* and *Karelosteus* seem to have been flourishing.

APPENDIX

Since reference is made in Part I (General) of the present review to a number of new species which will not be fully described until the subsequent appearance of Part II (Systematic) of this work, it is considered desirable to establish the validity of the new names at the present time, rather than to allow them to continue as *nomina nuda* until the publication of the Systematic Part. The following list therefore, serves to establish the priority of the names of the new taxa in question. Where new species belong to previously established genera, the specific diagnoses are taken as qualifications of the existing generic diagnoses.

Family **TESSERASPIDIDAE** Berg, 1955

Genus **TESSERASPIS** Wills, 1935

Tesseraspis toombsi n. sp.

Holotype: Part of tessellated carapace, P. 29621-P. 29625, P. 29683, housed in the British Museum (Natural History), London.

Type horizon and locality: Lower Devonian (Gedinnian), Lower Dittonian; Mad Bay, Skokholm Island, Pembrokeshire, Wales.

Derivation of name: toombsi — in honour of Mr. H. A. Toombs, of the British Museum (Natural History), London,

Diagnosis. — Tesserae of median areas ornamented by large flat tubercles usually with larger elongated oval tubercle ringed with smaller ones. Some tesserae ornamented by short dentine ridges or elongated tubercles arranged on either side of a median one. Scales ornamented by short longitudinally aligned ridges. Species very close to *T. tessellata*, but distinguished by cyclomorial nature of tesserae being more clearly marked.

Tesseraspis orvigi n. sp.

Holotype: Fragment of tessera, C. 1727, housed in the Swedish Museum of Natural History, Stockholm, figured by Ørvig (1961, Fig. 4).

Type horizon and locality: Lower Devonian (Gedinnian), Upper Czortków beds, *Traquairaspis* zone; Jagielnica Stara, Podolia, Ukraine.

Derivation of name: orvigi — in honour of Dr. T. Ørvig of the Swedish Museum of Natural History, Stockholm.

Diagnosis. — Ornamentation of flat, rectangular tubercles, with well marked crenulations on the margin adjoining a further row of tubercles. Margins between adjacent tubercles in the same row generally smooth.

Tesseraspis denisoni n. sp.

Holotype: Fragment of tessera, P.U. 17096 housed in the Geological Museum, Princeton University, New Jersey, United States, figured by DENISON (1963, Figs. 81*d*, 82*c*).

Type horizon and locality: Upper Silurian (Ludlovian); Beaver River, Yukon, Canada.

Derivation of name: denisoni — in honour of Dr. R. H. DENISON of the Chicago Museum of Natural History.

Diagnosis. — Ornamentation of fairly well separated large round or oval flat-topped tubercles with short prominent crenulations at margins. Also present are similar smaller elongated oval tubercles which may possess a longitudinal median ridge.

Genus **KALLOSTRAKON** LANKESTER, 1870

Kallostrakon macanuffi n. sp.

(Pl. V, figs. 1, 5—7)

Holotype: Median plate, 55505, housed in the Geological Survey Museum, London, figured in the present paper Pl. V, fig. 5.

Type horizon and locality: Silurian (Ludlovian), Downtonian, Lower Red Downton Formation; Bush Pitch near Ledbury, Herefordshire, England.

Derivation of name: macanuffi — in honour of Dr. J. W. MACANUFF of the Nuffield Foundation, London.

Diagnosis. — Plates with superficial tesserae ornamented by short dentine ridges. Large central ridge with shorter ones arranged on either side. Numerous isolated tesserae are found with similar ornament, and also tesserae with large round or oval flat bosses as primordia with short or long, somewhat narrower flat tubercles arranged around them. Further tesserae with elongated oval well-separated flat tubercles with intervening areas filled in by similar irregularly-shaped tubercles.

Kallostrakon grindrodi n. sp.

Holotype: Tessera, P. 8896, housed in the British Museum (Natural History), London.

Type horizon and locality: Silurian (Ludlovian), Downtonian, Lower Red Downton Formation, Bush Pitch near Ledbury, Herefordshire.

Derivation of name: grindrodi — in honour of the late Dr. R. B. GRINDROD, who made the original collection of *Kallostrakon* from Bush Pitch.

Diagnosis. — Tesserae ornamented by large elongated oval widely-separated tubercles. Intervening spaces completely filled by apparently secondarily formed, irregular dentine ridges and tubercles.

Kallostrakon alleni n. sp.

(Pl. V, fig. 4)

Holotype: Median plate, P. 26854-5 housed in the British Museum (Natural History), London, figured in the present paper Pl. V, fig. 4.

Type horizon and locality: Lower Devonian (Gedinnian), Lower Dittonian *Traquairaspis symondsi* zone; Common Bach, Dorstone, Herefordshire, England.

Derivation of name: alleni — in honour of Mr. J. R. L. ALLEN of the University of Reading.

Diagnosis. — Plate ornamented by irregular dentine ridges which although aligned more or less longitudinally are sinuous in outline and also possess lateral projections.

Family **WEIGELTASPIDIDAE** Brotzen 1933

Genus **WEIGELTASPIS** Brotzen, 1933

Weigeltaspis brotzeni n. sp.

Holotype: Fragment of plate, P. 18266, housed in the British Museum, London.

Type horizon and locality: Devonian (Gedinnian), Stage I of Brotzen, *Podolaspis lerichei* zone, Uscieczko, Dnjestr, Podolia, Ukraine.

Derivation of name: brotzeni — in honour of Dr. F. Brotzen, of the Geological Survey Museum, Stockholm.

Diagnosis. — Ornamentation of elongated tubercles with prominent crenulations, similar to those of *W. alta*, but approximately half the size and more closely packed.

Weigeltaspis godmani n. sp.

(Pl. IV, fig. 5; Pl. IX, figs. 5, 6)

Holotype: Ventral median plate with associated branchial plate, P. 23747-23748, housed in the British Museum (Natural History), London.

Type horizon and locality: Lower Devonian (Gedinnian), Middle Dittonian, *Pteraspis crouchi* zone; Castle Mattock Quarry, near Clodock, Herefordshire, England.

Derivation of name: godmani — in honour of the late Dr. F. D. Godman F.R.S., a benefactor of the British Museum, London.

Diagnosis. — Ornamentation of widely separated elongated dentine tubercles of a type similar to those in *W. alta*, but more widely separated, with the individual tubercles relatively wider and more rounded.

Weigeltaspis heintzi n. sp.

(Pl. IV, figs. 6, 7)

Holotype: Dorsal median plate, D. 2440-D. 2441, housed in the Palaeontological Museum, Oslo, figured in the present paper Pl. IV, figs. 6, 7.

Type horizon and locality: Lower Devonian (Gedinnian), Red Bay Series, Ben Nevis Division; Second moraine, Ben Nevis, Spitzbergen.

Derivation of name: heintzi — in honour of Professor A. Heintz, of the Palaeontological Museum, Oslo.

Diagnosis. — Ornamentation of long narrow dentine tubercles with short lateral ribs. Tubercles elongated and narrower than in *Weigeltaspis alta*.

Family **DREPANASPIDIDAE** Traquair, 1899

Genus **DREPANASPIS** Schlüter, 1887

Drepanaspis jaegeri n. sp.

Holotype: Part of median plate, A. Ebert collection, housed in the Geological-Palaeontological Museum, Berlin.

Type horizon and locality: Devonian (Eifelian-Emsian), Herdorfer Schichten, Effelsberger Schichten, Sud Wald, Altenahr, Rhineland, Germany.

Derivation of name: jaegeri — in honour of Dr. H. Jaeger, of the Geological-Palaeontological Museum, Berlin.

Diagnosis. — Ornamentation of regular closely packed round tubercles which are clearly separated from one another, and are larger than those of *D. schrieli* and more closely packed than in *D. gemuendenensis* or *D. lipperti.*

Drepanaspis edwardsi n. sp.

Holotype: Fragment of ?post-orbital plate, P. 13750 housed in the British Museum (Natural History), London.

Type horizon and locality: Lower Devonian (Siegenian), Dartmouth Slates, *Rhinopteraspis cornubica* zone; Lantivit Bay, Polperro, Cornwall, England.

Derivation of name: edwardsi — in honour of Mr. A. P. J. EDWARDS of the Department of Scientific and Industrial Research, London.

Diagnosis. — Ornamentation of closely-packed, rounded tubercles which are large at the lateral margin, but become smaller medially, arranged in regular rows, and clearly separated from one another.

Genus **PSEPHASPIS** ØRVIG, 1961

Psephaspis bystrowi n. sp.

Holotype: Tessera figured by BYSTROW (1959, Text-fig. 7).

Type horizon and locality: Devonian (Emsian); River Nizhni Viluikan, Northern Siberia.

Derivation of name: bystrowi — in honour of the late Professor A. P. BYSTROW, of the University of Leningrad.

Diagnosis. — Ornamentation of large, closely-packed rounded tubercles with few crenulations.

Family **GUERICHOSTEIDAE** nov.

Diagnosis. — Ventral median plate convex with prominent posterior median notch. Branchial plate long with fairly wide free laterally projecting margin; branchial opening situated at postero-lateral corner or medial to it. Post-orbital plate narrows gradually posteriorly.

Genus **GUERICHOSTEUS** nov.

Type species: Guerichosteus kozlowskii n. sp.

Derivation of name: Guerichosteus — in honour of the late Professor G. GÜRICH of Wrocław (Breslau) University.

Diagnosis. — Ventral median plate arched from side to side, with prominent deep posterior median notch. Branchial plate long and fairly wide, branchial opening situated at postero-lateral corner. Post-orbital plate narrows slightly posteriorly. Cornual plate rectangular. Ornamentation of closely-packed rounded crenulated tubercles.

Guerichosteus kozlowskii n. sp.

(Pl. XIII; Pl. XIV, figs. 1—4)

Holotype: Left branchial plate D. 7, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw.

Type horizon and locality: Devonian (Emsian), Placoderm Sandstone, *Rhinopteraspis cornubica* zone; Daleszyce, near Kielce, Holy Cross Mountains, Poland.

Derivation of name: kozlowskii — in honour of Professor R. Kozłowski, of the Polish Academy of Sciences and University of Warsaw.

Diagnosis. — Ornamentation of large rounded tubercles, with prominent short crenulations which form radial ribs, rising almost to the small rounded peaks of the summits of the tubercles.

Guerichosteus kotanskii n. sp.

Holotype: Fragment of plate D. 37, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw.

Type horizon and locality: Devonian (Emsian), Placoderm Sandstone, *Rhinopteraspis cornubica* zone; Daleszyce, near Kielce, Holy Cross Mountains, Poland.

Derivation of name: kotanskii — in honour of Dr. Z. Kotański of the Geological Institute, University of Warsaw.

Diagnosis. — Ornamentation of extremely large closely-packed rounded tubercles, about one millimetre in diameter, with occasional smaller tubercles filling the spaces between the larger ones. Fine crenulations are present at the base of the tubercles. The close packing of the tubercles often produces a somewhat polygonal outline.

Guerichosteus kulczyckii n. sp.

Holotype: Fragment of plate, D. 41, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw.

Type horizon and locality: Devonian (Emsian), Placoderm Sandstone, *Rhinopteraspis cornubica* zone; Daleszyce, near Kielce, Holy Cross Mountains, Poland.

Derivation of name: kulczyckii — in honour of Dr. J. Kulczycki of the Earth Museum, Warsaw.

Diagnosis. — Ornamentation of small rounded dentine tubercles, fairly closely packed, but clearly separated from one another; about 0.5 mm in diameter, with short crenulations at their margins.

Guerichosteus lefeldi n. sp.

Holotype: Fragment of arched plate? ventral median plate, D. 45, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw.

Type horizon and locality: Devonian (Emsian), Placoderm Sandstone, *Rhinopteraspis cornubica* zone; Daleszyce, near Kielce, Holy Cross Mountains, Poland.

Derivation of name: lefeldi — in honour of Dr. J. Lefeld, of the Geological Institute, University of Warsaw.

Diagnosis. — Ornamentation of minute, closely-packed rounded tubercles just visible to the naked eye, approx. 0.3 mm in diameter.

Genus **HARIOSTEUS** nov.

Type species: Hariosteus kielanae n. sp.
Derivation of name: Hariosteus — after the tribe the Harii, inhabiting the region in Roman times.

Diagnosis. — Ornamentation of well separated crenulated tubercles with accessory tubercles between them. Growth lines in alternate bands of larger and smaller ornament, giving characteristic graded growth zones.

Hariosteus kielanae n. sp.

(Pl. XIV, figs. 5, 6)

Holotype: Part of dorsal median plate, D. 48, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw, figured by TARLO (1957, Pl. 1, fig. 2), and in the present paper Pl. XIV, figs. 5, 6.

Type horizon and locality: Lower Devonian (Emsian), Placoderm Sandstone, *Rhinopteraspis cornubica* zone; Daleszyce, near Kielce, Holy Cross Mountains, Poland.

Derivation of name: kielanae — in honour of Professor Z. KIELAN-JAWOROWSKA of the Palaeozoological Institute of the Polish Academy of Sciences, Warsaw.

Diagnosis. — Ornamentation of fairly large, round, widely separated tubercles with prominent crenulations forming radial ribs, which often reach the summits of the tubercles. Surrounding each tubercle and separating it from the others is a ring of much smaller similar tubercles.

Hariosteus lobanowskii n. sp.

Holotype: Part of right branchial plate, D. 60, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw.

Type horizon and locality: Devonian (Emsian), Placoderm Sandstone, *Rhinopteraspis cornubica* zone; Daleszyce, near Kielce, Holy Cross Mountains, Poland.

Derivation of name: lobanowskii — in honour of Mr. H. ŁOBANOWSKI of the Geological Institute, University of Warsaw.

Diagnosis. — Ornamentation of large elongated, widely separated tubercles generally aligned in the same direction, and arranged in single rows with the long axes of the tubercles parallel. Between the rows and also occasionally between the tubercles of a row, are minute accessory tubercles.

Genus SCHIZOSTEUS OBRUCHEV, 1940

Schizosteus wellsi n. sp.

Holotype: Oral plate, 19402, housed in the Geology Museum, University of Ohio, United States, figured by WELLS (1944*a*, Pl. 4 (10), fig. 8).

Type horizon and locality: Devonian (Eifelian), Delaware Formation, Third Bone Bed; locality 8, Franklin County, Ohio, United States.

Derivation of name: wellsi — in honour of Professor J. W. Wells, of Cornell University, New York.

Diagnosis. — Ornamentation of small rounded tubercles with few or no crenulations, generally clearly separated although fairly closely packed.

Family **PYCNOSTEIDAE** Tarlo, 1962

Genus **PYCNOLEPIS** nov.

Type species: Pycnolepis splendens (Eichwald, 1844).

Derivation of name: Pycnolepis — Gr. *pyknos* = dense, and Gr. *lepis* = scale, referring to appearance of ornamentation.

Diagnosis. — Branchial plate broad and long, ornamented by closely-packed dentine tubercles generally fan-shaped, with crenulated margins. Dorsal median plate fairly round in outline with re-entrant angle in anterior margin, ornamented by closely-packed fan-shaped dentine tubercles with fine crenulations along their convex edges. Ventral median plate longer than broad, with deep posterior notch extending halfway into plate. Rostral plate rectangular with wide margin of irregular superficial tesserae.

Genus **PYCNOSTEUS** Preobrajensky, 1911

Pycnosteus obruchevi n. sp.

(Pl. III, figs. 7, 8)

Holotype: Part of median plate (probably dorsal), H. 1570, housed in the Sedgwick Museum, Cambridge, figured in the present paper Pl. III, figs. 7, 8.

Type horizon and locality: Middle Devonian (Givetian), Wijde Bay Series; south of Vatnedalen, Wijdefjorden, North Central Vestspitsbergen.

Derivation of name: obruchevi — in honour of Professor D. Obruchev, of the Palaeontological Institute, Moscow.

Diagnosis. — Ornamentation of well-spaced, rounded or elongated tubercles deeply indented by numerous strong branching crenulations, with areas of larger tubercles similar to those in *Pycnosteus tuberculatus.*

Family **PSAMMOLEPIDIDAE** Tarlo, 1962

Genus **PSAMMOLEPIS** Agassiz, 1845

Psammolepis groenlandica n. sp.

Holotype: Fragment of a plate, 905, housed in the Geological Museum, University of Copenhagen.

Type horizon and locality: Devonian (Givetian), Series with *Asterolepis save-soderberghi;* Sydryggen, Canning Land, E. Greenland.

Derivation of name: groenlandica — after Greenland, where the specimen was discovered.

Diagnosis. — Ornamentation of large, irregularly shaped tubercles with prominent crenulations at their base. These do not appear to extend on to the crowns of the tubercles.

Family **PSAMMOSTEIDAE** TRAQUAIR, 1896

Genus **PSAMMOSTEUS** AGASSIZ, 1845

Psammosteus kiaeri n. sp.

(Pl. II, fig. 2)

Holotype: Branchial plate, A. 13196-A. 13197, housed in the Palaeontological Museum, Oslo, figured by KIAER (1915, Pl. 4, figs. 4, 5), and in the present paper Pl. II, fig. 2.
Type horizon and locality: Upper Devonian (Frasnian), Series E; Skrap Valley, Ellesmereland.
Derivation of name: kiaeri — in honour of the late Professor J. KIAER.

Diagnosis. — Branchial plate ornamented by slightly concave fused rows of dentine tubercles which «V» proximally on the ventral surface; the distal margins of the rows are smooth with comparatively few very short crenulations; the proximal margins of the fused tubercles are drawn out into broad crenulations which tend to subdivide at their extremities.

Genus **CRENOSTEUS** nov.

Type species: Crenosteus levis (OBRUCHEV, 1964).
Derivation of name: Crenosteus — L. *crena* = a notch, referring to the scalloped margin of the dentine tubercles.

Diagnosis. — Branchial plate short and wide, with ornamentation of flat rectangular tubercles with short proximal crenulated fringe.

Genus **ROHONOSTEUS** nov.

Type species: Rohonosteus ornatus (ROHON, 1899).
Derivation of name: Rohonosteus — in honour of the late Professor J. V. ROHON.

Diagnosis. — Branchial plate short and wide; intermediate in outline between *Psammolepis* and *Psammosteus*; ornamentation of closely-packed, lozenge-shaped tubercles aligned parallel to axis of plate.

Family **OBRUCHEVIIDAE** nom. nov.

(to replace **ASPIDOSTEIDAE** BERG, 1955)

Genus **TRAQUAIROSTEUS** nov.

Type species: Traquairosteus pustulatus (TRAQUAIR, 1897).
Derivation of name: Traquairosteus — in honour of the late Dr. R. H. TRAQUAIR.

Diagnosis. — Dorsal median plate with outer surface of aspidin thrown up into conical mounds, each surmounted by a small crenulated dentine tubercle.

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ALPHABETICAL INDICES

I. INDEX OF AUTHORS

II. PALAEONTOLOGICAL INDEX

Systematic names cited only are indicated by *italic*, and names accompanied by diagnosis are indicated by roman letters.

Numerals which indicate the page, on which the species is cited only, are standart; numerals, which indicate pages with diagnosis, are **bold**.

Numerals denoted with asterisks (*) indicate pages with figures.

PLATES

L B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE I

Psammosteus megalopteryx (TRAUTSCHOLD)

(Stolbovo, River Sjass, NW Russia; Upper Devonian Frasnian, Shelon horizon)

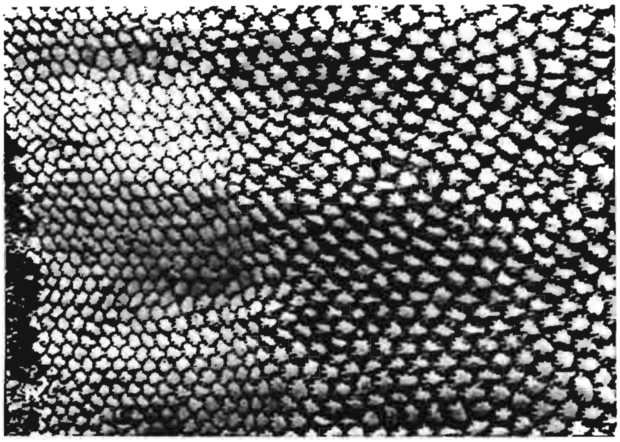
Fig. 1. Branchial plate in dorsal view, showing detail of ornamentation (A. 169. P.M.O.); × 4.
Fig. 2. Polygonal tesserae (220/214. P.M.O.); × 4.
Fig. 3. Proximal margin of ornamentation of ventral surface of branchial plates (A. 169. P.M.O.); × 6.
Fig. 4. Anterior edge of ventral surface of branchial plate (A. 169. P.M.O.); × 7.
Fig. 5. Detail of ornamentation of superficial tesserae (220/214. P.M.O.); × 10.

Photo: P. R. Gurr

Ganosteus stellatus ROHON

Fig. 6. Detail of ornamentation of cornual plate, showing second generation tubercles situated in resorbed cavities in primary tubercles. River Salatsa, Latvia; Middle Devonian, Givetian, Burtnicki horizon (174. G.I.T.); × 4.

Photo from E. Mark



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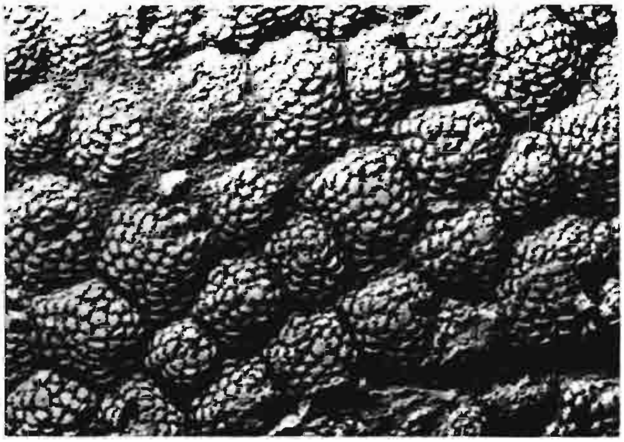

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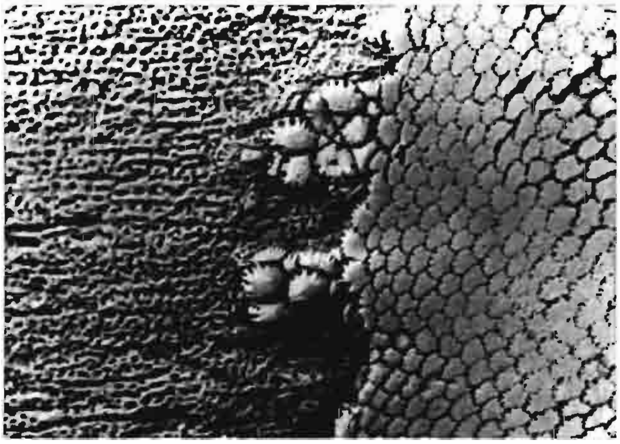

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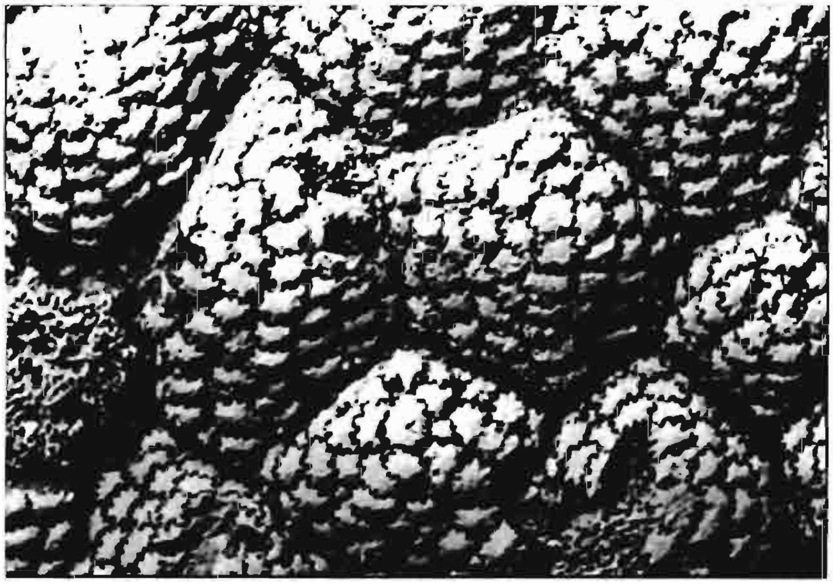

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE II

Psammolepis arctica (KIAER)

Fig. 1. Fragment of plate showing detail of ornamentation, lectotype, specimen figured by KIAER (1915, pl. II, fig. 5, pl. III, fig. 1, 2). Skrap Valley, Ellesmereland; Upper Devonian, Frasnian, Series E (A. 13206. P.M.O.); × 6.

Psammosteus kiaeri n. sp.

Fig. 2. Fragment of branchial plate showing detail of ornamentation, holotype, specimen figured by KIAER (1915, pl. V, fig. 4, 5). Skrap Valley, Ellesmereland; Upper Devonian, Frasnian, Series E (A. 13196-A. 13197. P.M.O.); × 6.

Rohonosteus complicatus (KIAER)

Fig. 3. Fragment of branchial plate showing detail of ornamentation, lectotype, specimen figured by KIAER (1915, pl. V, fig. 1, 2). Skrap Valley, Ellesmereland; Upper Devonian, Frasnian, Series E (A. 13189-A. 13193. P.M.O.); × 6.

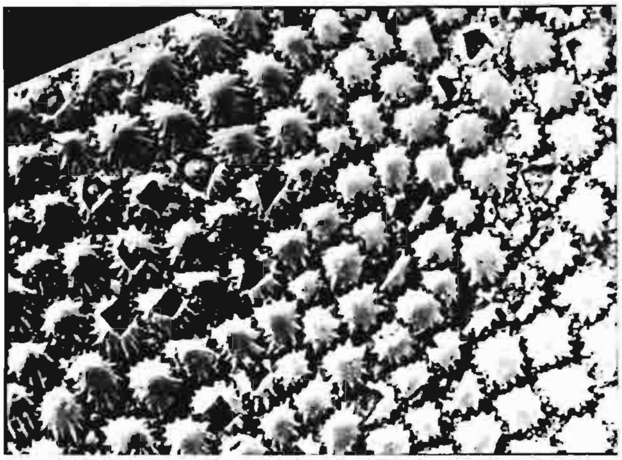
Psammosteus falcatus OBRUCHEV

Fig. 4. Fragment of branchial plate showing detail of ornamentation, specimen figured by TRAQUAIR (1896*b*, pl. VI, fig. 4, 5) as *Psammosteus* sp. and TARLO (1961*a*, pl. VII, fig. 6). Scaat Craig, Elgin, Scotland; Upper Devonian, Frasnian, Scaat Craig Beds (1904.2.12. R.S.M.); × 6.

Psammosteus maeandrinus AGASSIZ

Fig. 5, 6. Distal part of immature branchial plate, showing detail of ornamentation. Kokenhusen, near Riga, Latvia; Upper Devonian, Frasnian, Snetogor horizon; × 6. Fig. 5 (P. 17792. B.M.), Fig. 6 (P. 17793. B.M.).

Photo: P. R. Gurr



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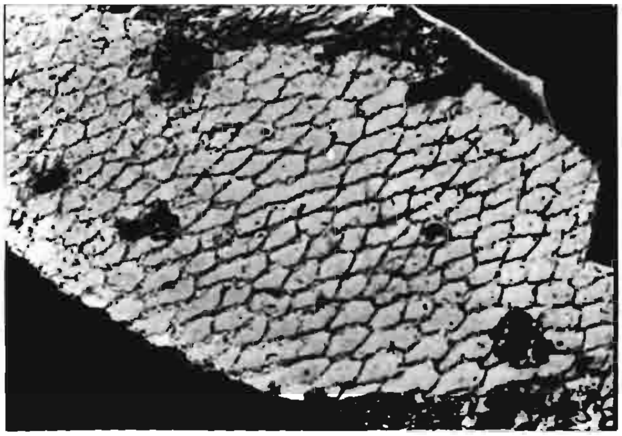

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE III

Pycnosteus palaeformis PREOBRAJENSKY

Fig. 1. Detail of ornamentation. Krasnya Gori, Estonia; Middle Devonian, Givetian, Arukula horizon (A. 28129d. P.M.O.); × 3.

Fig. 3. Fragment of branchial plate showing ornamentation. Haselun, Estonia; Middle Devonian, Givetian, Arukula horizon (A. 28134a. P.M.O.); × 6.

Pycnosteus tuberculatus (ROHON)

(Krasnya Gori, Estonia; Middle Devonian, Givetian, Burtnicki horizon)

Fig. 2. Detail of ornamentation, oblique view. (A. 28135e. P.M.O.); × 6.

Fig. 4. Detail of ornamentation (A. 28135e. P.M.O.); × 6.

Fig. 5. Detail of ornamentation (A. 28135a. P.M.O.); × 6.

Schizosteus heterolepis (PREOBRAJENSKY)

Fig. 6. Detail of ornamentation. Tori, near Pernau; Middle Devonian, Givetian, Pernau horizon (A. 28131d. P.M.O.); × 3.5.

Pycnosteus obruchevi n. sp.

Fig. 7, 8. Fragment of median plate, holotype. Wijdefjorden, Spitzbergen; Middle Devonian, Givetian, Wijde Bay Series (H. 1570. S.M.). Fig. 7×3, Fig. 8×10.

Photo: P. R. Gurr

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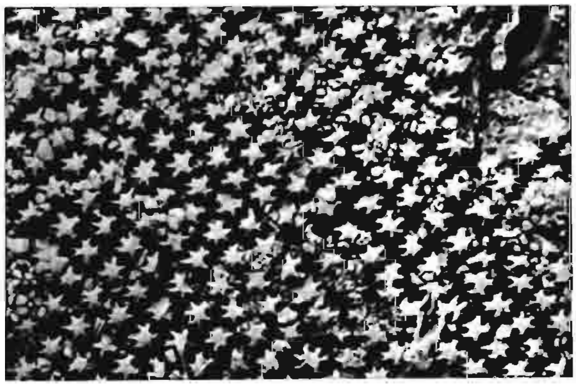

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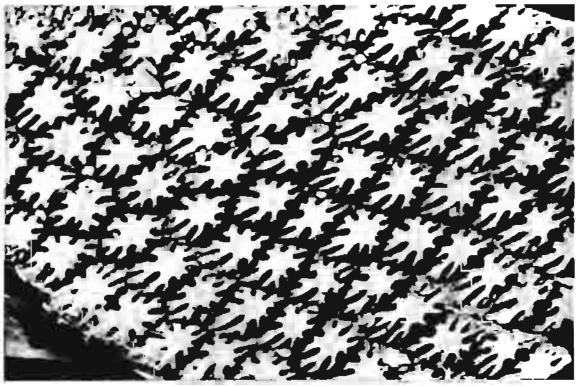

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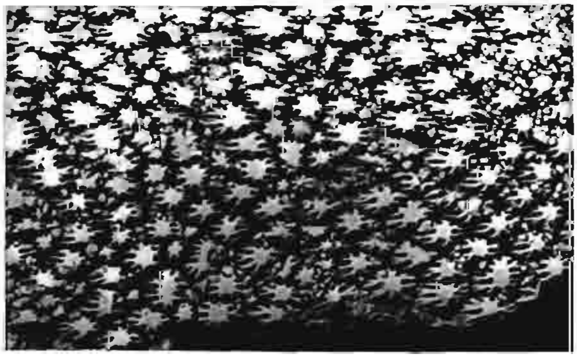

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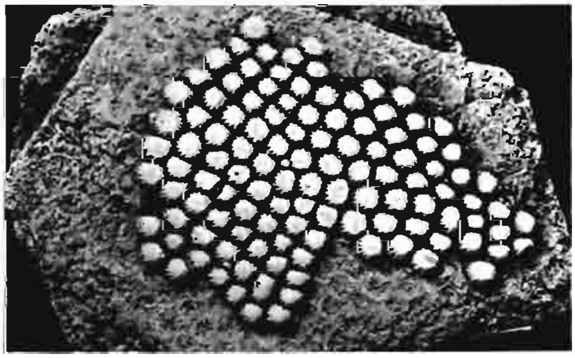

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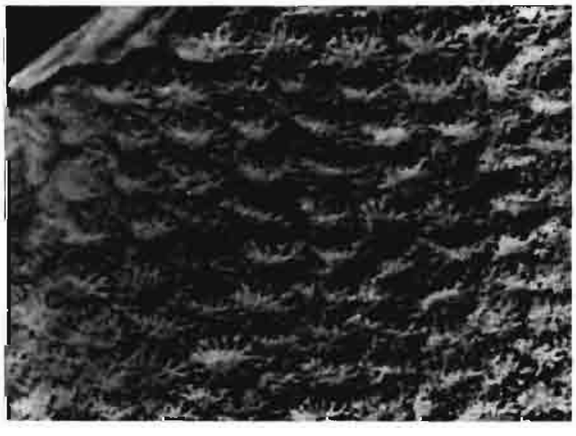

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE IV

Tesseraspis tessellata Wills

Details of ornamentation

(Earnstrey Hall, Shropshire; Lower Devonian, Lower Gedinnian, Dittonian)

Fig. 1, 2. Ornamentation of tesserae of median area (541. B.U.); × 8.

Fig. 3. Ornamentation of body scales (112. B.U.); × 8.

Fig. 4. Ornamentation of thin tesserae situated between median area and lateral margin (539. B.U.); × 8.

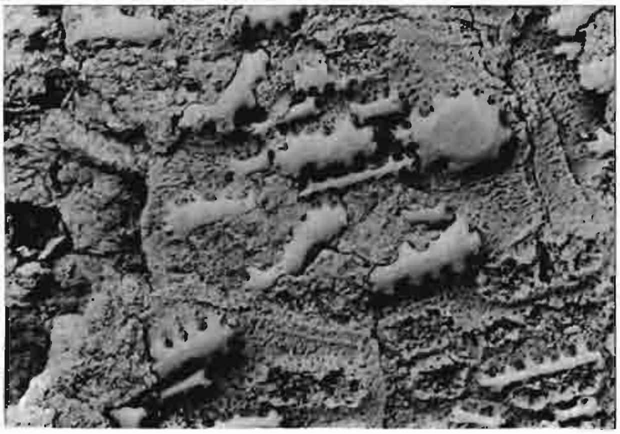
Weigeltaspis godmani n. sp.

Fig. 5. Detail of ornamentation. No locality information; Lower Devonian, Upper Gedinnian, Dittonian (L. 8530. M.M.); × 8.

Weigeltaspis heintzi n. sp.

Fig. 6, 7. Dorsal median plate, detail of ornamentation, holotype. Ben Nevis, Spitzbergen; Lower Devonian, Upper Gedinnian, Red Bay Series, Ben Nevis Division (D. 2440-D. 2441. P.M.O.); × 8.

Photo: P. R. Gurr



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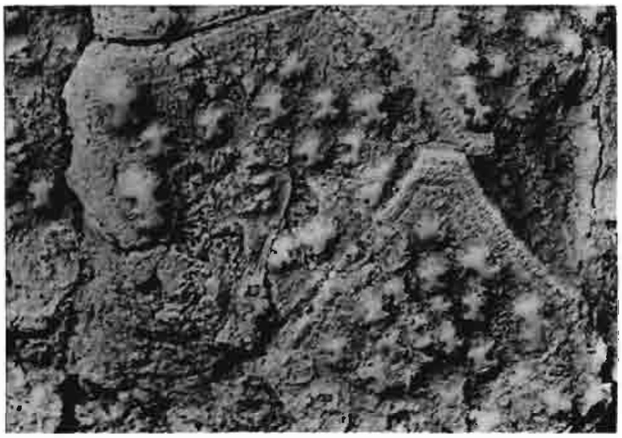

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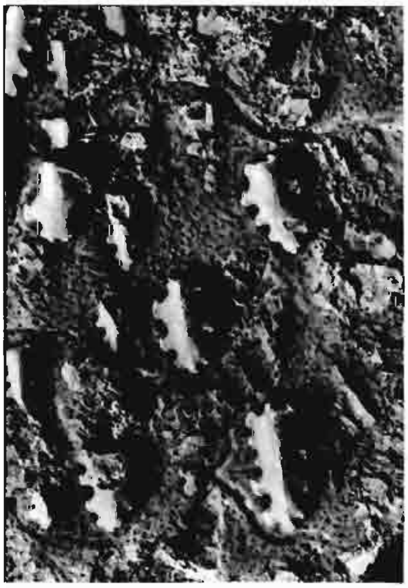

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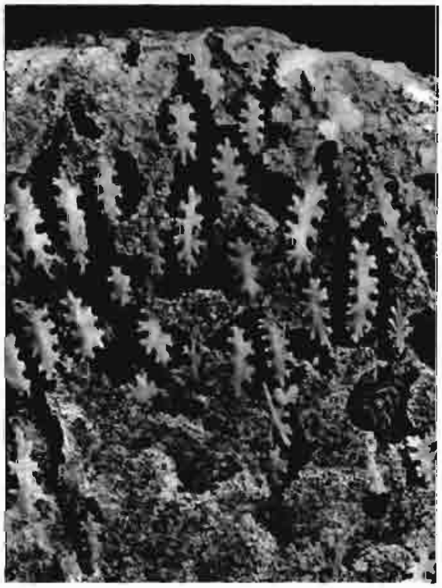

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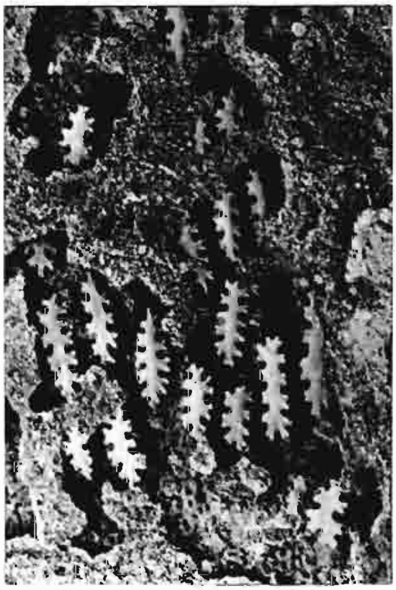

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Palaeontologia Polonica, No. 13, 1964

L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE V

Kallostrakon macanuffi n. sp.

(Bush Pitch, near Ledbury, Herefordshire; Silurian, Upper Ludlovian, Downtonian)

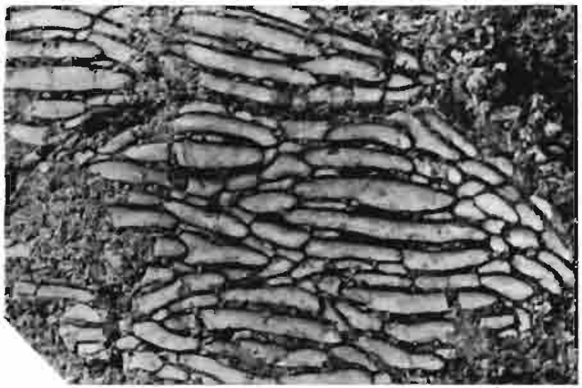
Fig. 1. Superficial tesserae, detail of ornamentation (D. 94. O.U.M.); × 11.
Fig. 5. Median plate ornamented by superficial tesserae, holotype (55505. G.S.M.); × 2.
Fig. 6. Tessera (D. 104. O.U.M.); × 4.5.
Fig. 7. Tessera (D. 85. O.U.M.); × 4.5.

Kallostrakon podura LANKESTER

Fig. 2, 3. Median plate, holotype, specimen figured by LANKESTER (1870, pl. XIII, fig. 20). Bush Pitch, near Ledbury, Herefordshire; Silurian, Upper Ludlovian, Downtonian (D. 96. O.U.M.). Fig. 2×2.5, Fig. 3×5.

Kallostrakon alleni n. sp.

Fig. 4. Fragment of median plate, showing detail of ornamentation, holotype. Common Bach, Dorstone, Herefordshire; Lower Devonian, Lower Gedinnian, Dittonian (P. 26854-5. B.M.); × 8.



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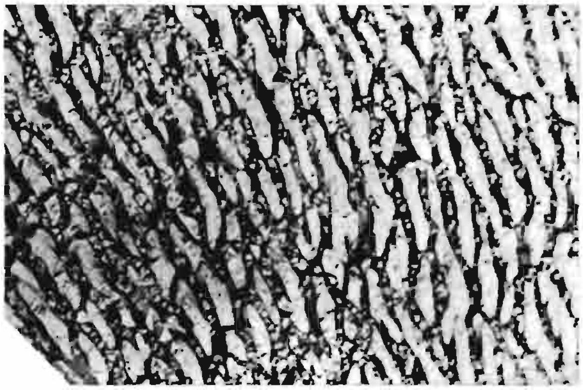

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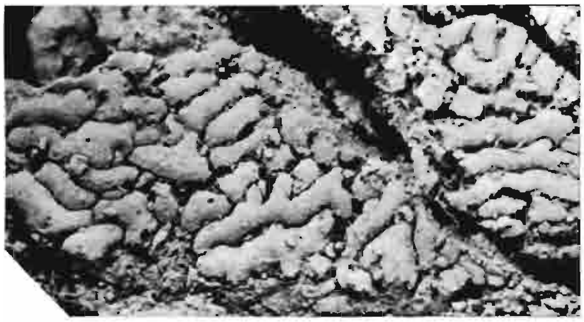

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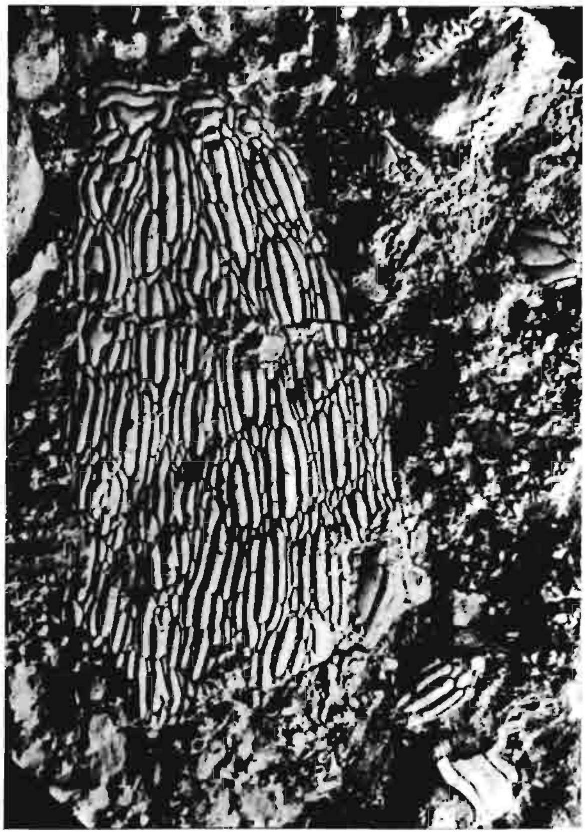

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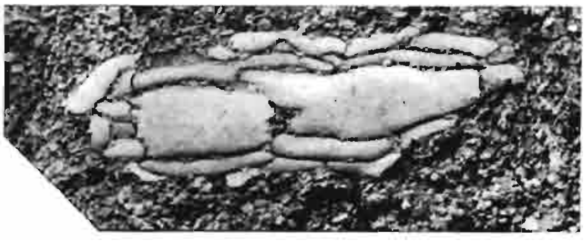

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE VI

Psammosteus megalopteryx (TRAUTSCHOLD)

Sections of aspidin

(Newton Quarry, Elgin, Scotland; Upper Devonian, Frasnian, Alves Beds)

Fig. 1. Aspidin showing random arrangement of aspidinocyte spaces in trabeculae, and parallel alignment in lamellae of aspidones (H. 4813C. S.M.); × 60.

Fig. 2. Enlargement of individual aspidinocyte space (H. 4813C. S.M.); × 400.

Fig. 4, 6. Aspidinocyte spaces showing alignment normal to lamellae of aspidones, probably due to extension of cytoplasmic processes to maintain contact with vascular supply (H. 4813C. S.M.); × 75.

Photo: J. R. Mercer

Fig. 5. Aspidin surmounted by dentine tubercles, specimen figured by TARLO (1961*a*, text-fig. 3a). Stolbovo, River Sjass, north west Russia; Upper Devonian, Frasnian, Shelon horizon (D. 69. U.W.); × 40.

Photo: W. Brackenbury

Recent teleost bone *(Euthynnus alletteratus)* for comparison

Fig. 3. Section of vertebra showing spindle-shaped osteocytes; × 150.

Photo from R. Amprino, A. Barasa and C. Codina


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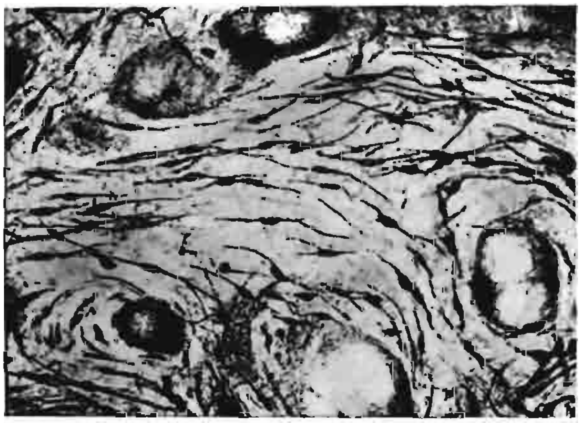
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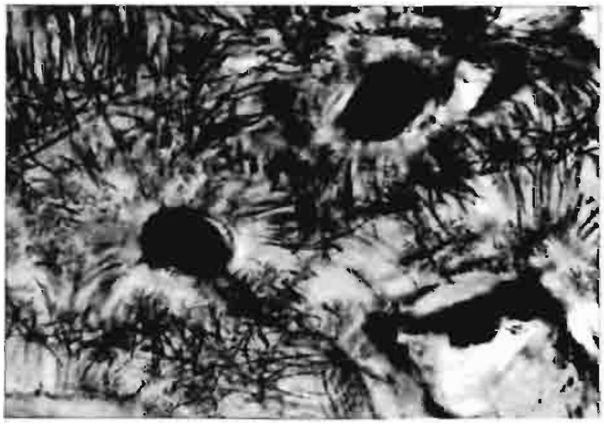
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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE VII

Obruchevia heckeri (OBRUCHEV)

(River Lovat, north west Russia; Upper Devonian, Frasnian, e Horizon)

Fig. 1, 2. Sections of dense aspidin with pleromic dentine (D. 70. U.W.); × 80.
Fig. 4. Section of dense aspidin under polarized light (crossed nicols) (D. 71. U.W.); × 60.

Psammolepis paradoxa (AGASSIZ)

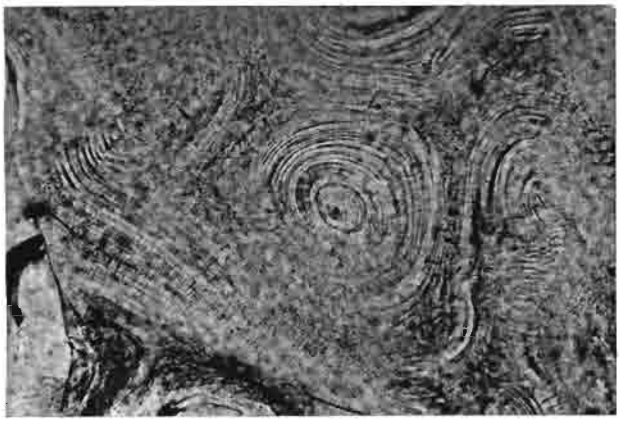
Fig. 3. Section of aspidin under polarized light (crossed nicols). River Aa, Latvia; Upper Devonian, Frasnian, Gauja horizon (D. 72. U.W.); × 60.

Tesseraspis tessellata WILLS

(Earnstrey Hall, Shropshire; Lower Devonian, Lower Gedinnian, Dittonian)

Fig. 5. Section of aspidin under polarized light (crossed nicols) (119. B.U.); × 60.
Fig. 6. Section showing thin aspidin trabeculae and dense aspidin (D. 73. U.W.); × 60.

Photo: J. R. Mercer



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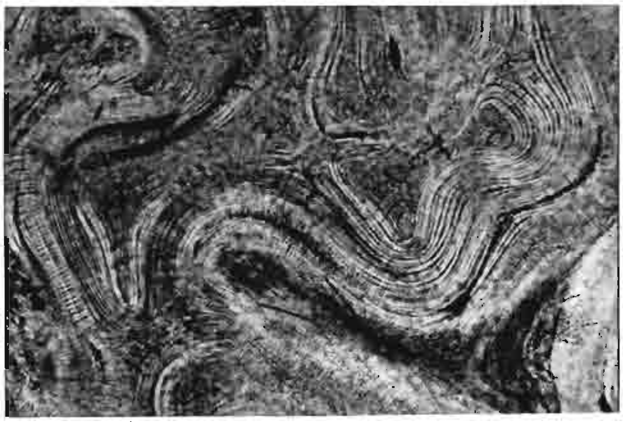

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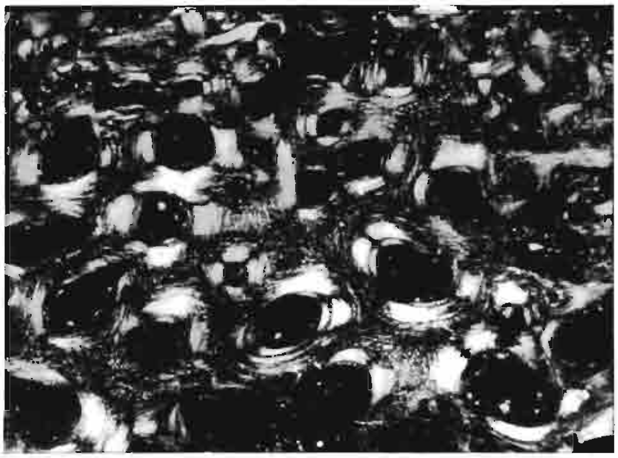

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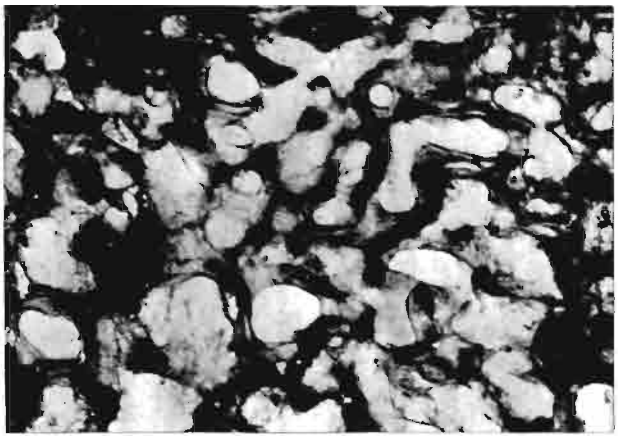

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE VIII

Ganosteus stellatus ROHON

(Lejeji, Latvia; Upper Devonian, Frasnian, Gauja horizon)

Fig. 1, 2. Vertical section of dentine tubercle showing junction of aspidin and dentine (D. 74. U.W.); × 60. Fig. 1 ordinary light. Fig. 2 polarized light (crossed nicols).

Tesseraspis tessellata WILLS

(Earnstrey Hall, Shropshire; Lower Devonian, Lower Gedinnian, Dittonian)

Fig. 3, 4. Vertical section of secondary tubercle surmounting primary tubercle, showing former external surface of plate (538. B.U.); × 60. Fig. 3 ordinary light, Fig. 4 polarized light (crossed nicols).

Fig. 5, 6. Vertical section of dentine tubercle with underlying aspidin, showing random arrangement of aspidinocyte spaces (119. B.U.); × 60. Fig. 5 ordinary light, Fig. 6 polarized light (crossed nicols).

Fig. 7. Vertical section of margin of tessera, showing elongated aspidinocyte spaces aligned normal to edge of plate, parallel to direction of growth (D. 73. U.W.); × 60.

Photo: J. R. Mercer

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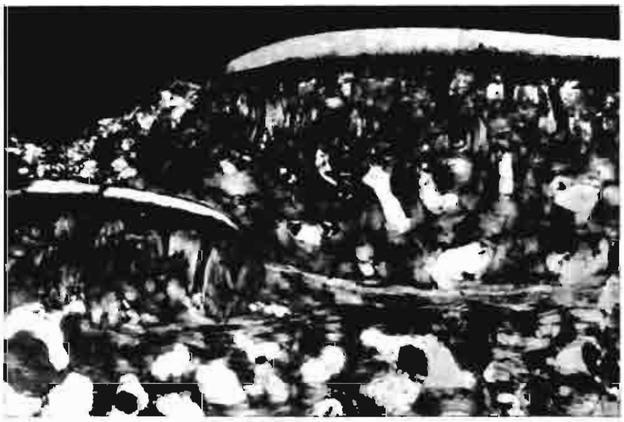

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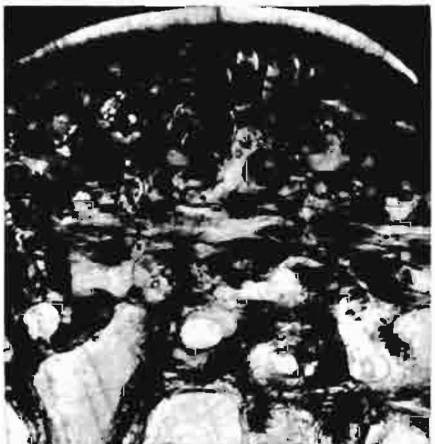

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE IX

Tesseraspis tessellata WILLS

(Earnstrey Hall, Shropshire; Lower Devonian, Lower Gedinnian, Dittonian)

Fig. 1. Vertical section of dentine tubercle showing complex pulp cavity (D. 64. U.W.); × 60.
Fig. 3, 4. Detail of dentine tubules (D. 73. U.W.); × 120.

Corvaspis kingi WOODWARD

Fig. 2. Vertical section showing dentine tubules converging and passing into vertical canal in aspidin. Earnstrey Hall Shropshire; Lower Devonian, Lower Gedinnian, Dittonian (D. 88. U.W.); × 120.

Weigeltaspis godmani n. sp.

Fig. 5, 6. Vertical sections of dentine tubercles showing complex pulp cavities. Dyffryn, Llansoy, Monmouthshire; Lower Devonian, Upper Gedinnian, Dittonian; × 60. Fig. 5 (D. 89. U.W.), Fig. 6 (D. 65. U.W.).

Photo: J. R. Mercer

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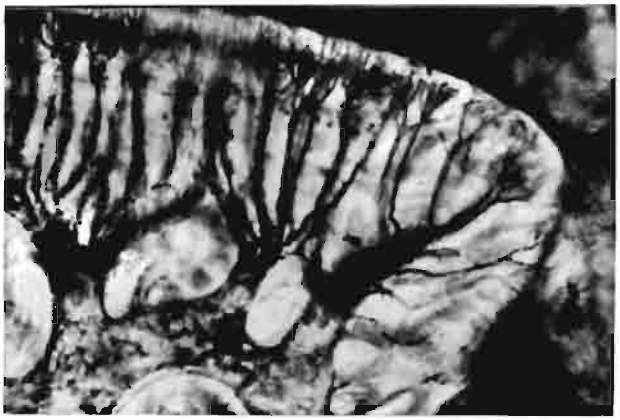

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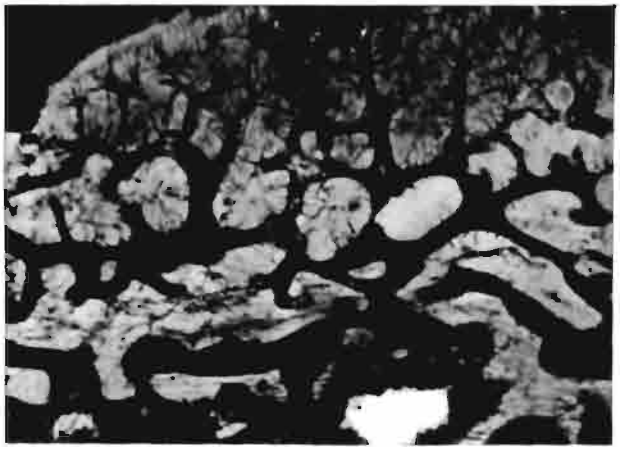

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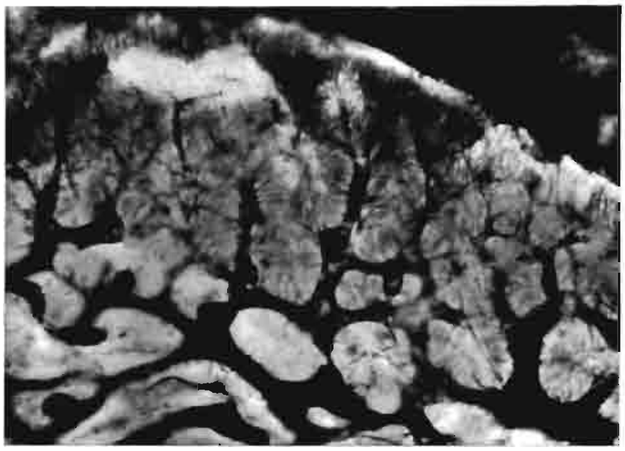

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J. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE X

Ganosteus stellatus ROHON

(Karksi, Latvia; Upper Devonian, Frasnian, Gauja horizon)

Fig. 1. Vertical section of dentine tubercle showing incremental lines (D. 63. U.W.); × 60.
Fig. 3. Detail of tubercle showing junction between dentine and aspidin (D. 67. U.W.); × 120.

Psammolepis paradoxa (AGASSIZ)

(River Aa, Latvia; Upper Devonian, Frasnian, Gauja horizon)

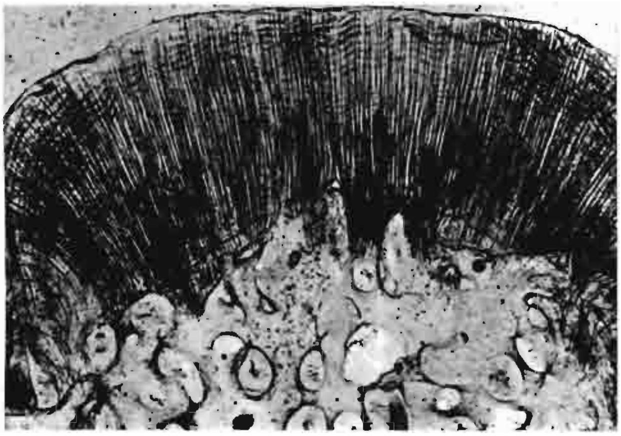
Fig. 2. Vertical section of dentine tubercles overlying aspidin, in polarized light (crossed nicols) (D. 72. U.W.); × 60.
Fig. 5. Detail of dentine tubules in decalcified section (D. 90. U.W.); × 120.

Tartuosteus maximus MARK

(Karksi, Estonia; Middle Devonian, Givetian, Burtnicki horizon)

Fig. 4. Vertical section of tubercle showing dentine tubules (D. 66. U.W.); × 120.
Fig. 6. Detail of fig. 4 showing lateral and terminal branches of dentine tubules (D. 66. U.W.); × 250.

Photo: J. R. Mercer



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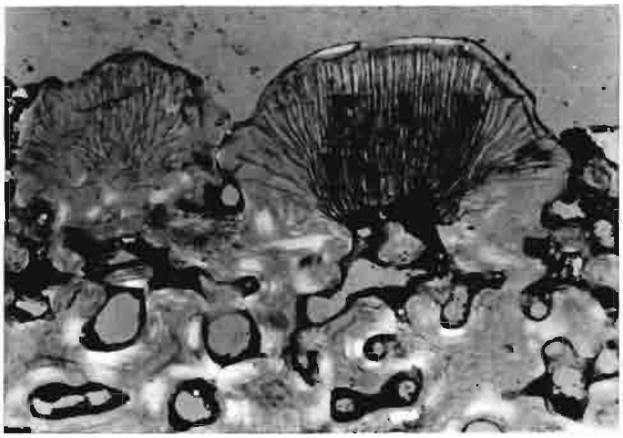

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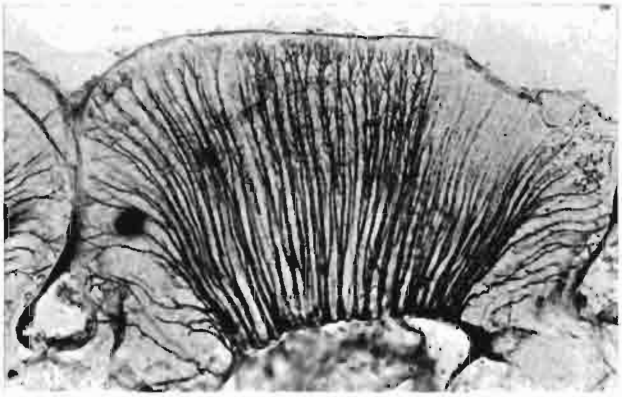

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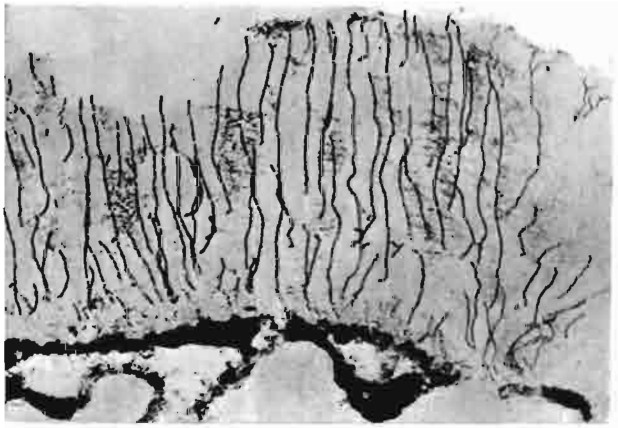

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE XI

Ganosteus stellatus ROHON

Vertical section

(Karksi, Latvia; Upper Devonian, Frasnian, Gauja horizon)

Fig. 1-3. Secondary tubercles overlying dentine tubercles of old surface. Fig. 1 (D. 87. U.W.). Fig. 2 (D. 74. U.W.). Fig. 3 (D. 63. U.W.). All × 25.

Fig. 4. Secondary tubercles overlying primary tubercles showing evidence of resorption (D. 67. U.W.); × 60.

Fig. 5. Secondary tubercle overlying old surface showing gradual infilling of space with new aspidin (D. 63. U.W.); × 60.

Fig. 6. Secondary tubercle overlying old surface showing initial trabeculae of new aspidin forming vertical struts joining old surface (D. 74. U.W.); × 60.

Fig. 7. Aspidin showing areas of resorption cutting into and through lamellae of aspidones (D. 63. U.W.); × 75.

Photo: J. R. Mercer

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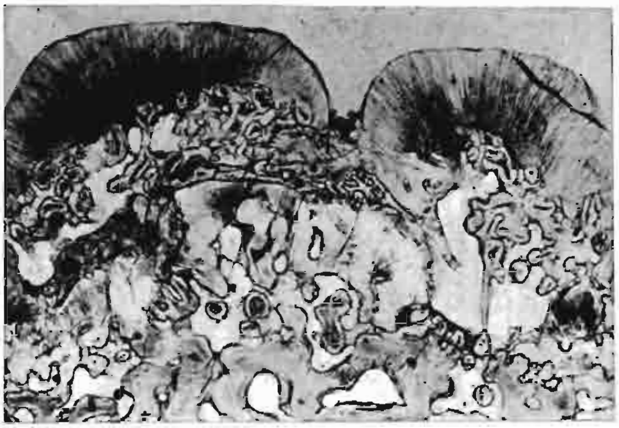

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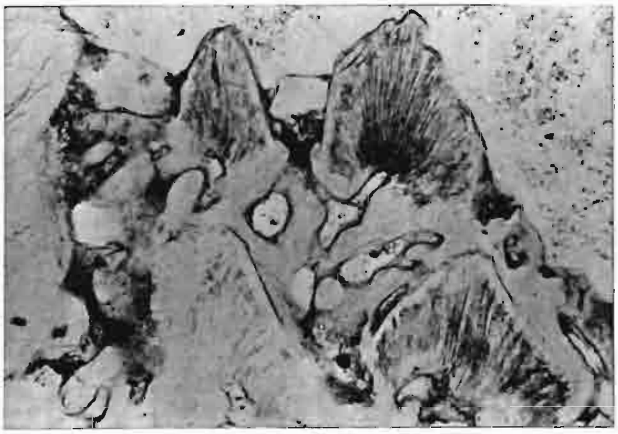

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PLATE XII

Tartuosteus maximus MARK

Pleromic dentine from branchial plate
(Karksi, Estonia; Middle Devonian, Givetian, Burtnicki horizon)

Fig. 1. Pleromic dentine infilling aspidin (D. 68. U.W.); × 60.
Fig. 2. Detail of fig. 1 showing dentine tubules: × 120.
Fig. 4. Edge of infilled aspidin showing development of secondary dentine in pulp cavity of dentine tubercle (D. 68. U.W.); × 120.
Fig. 6. Section of branchial plate showing extent of pleromic dentine (D. 75. U.W.); × 12.

Psammolepis paradoxa (AGASSIZ)

Fig. 3. Decalcified and stained section of aspidin showing differential staining of trabeculae and aspidones (D. 86 U.W.); × 80.

Photo: J. R. Mercer

Obruchevia heckeri (OBRUCHEV)

Fig. 5. Vertical section of aspidin showing dentine tubules of pleromic dentine (D. 70. U.W.); × 120.

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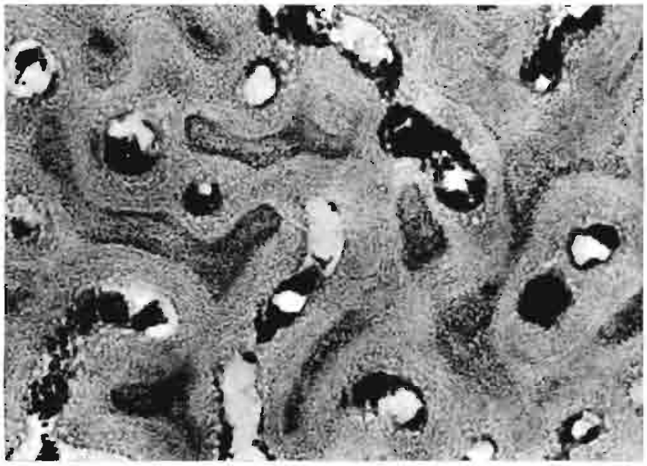

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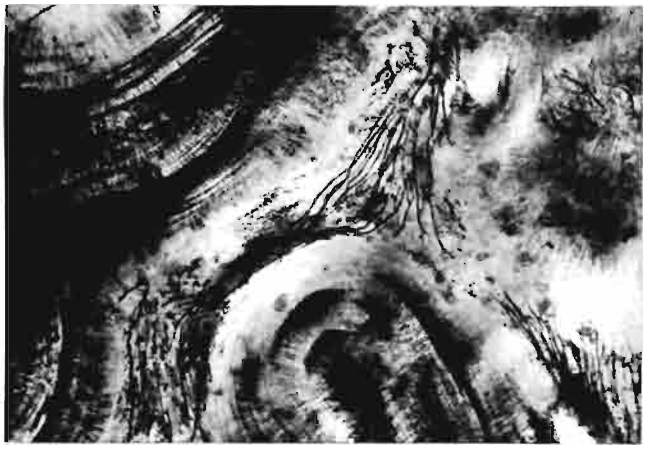

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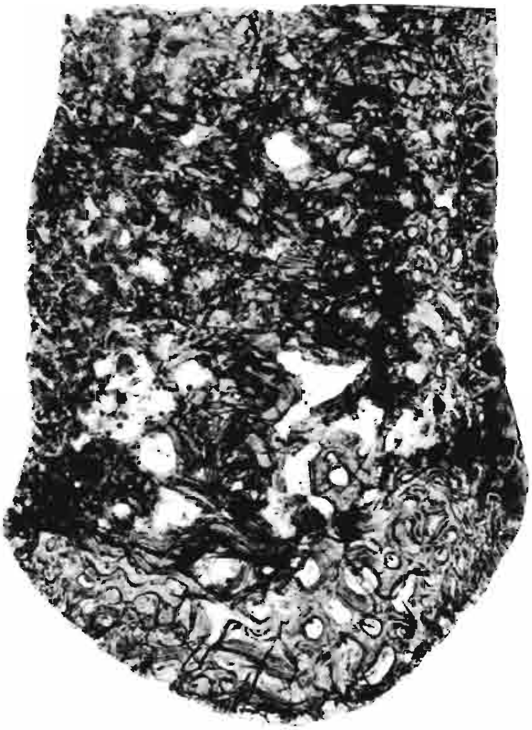

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE XIII

Guerichosteus kozlowskii n. sp.

Fragment of ornamentation

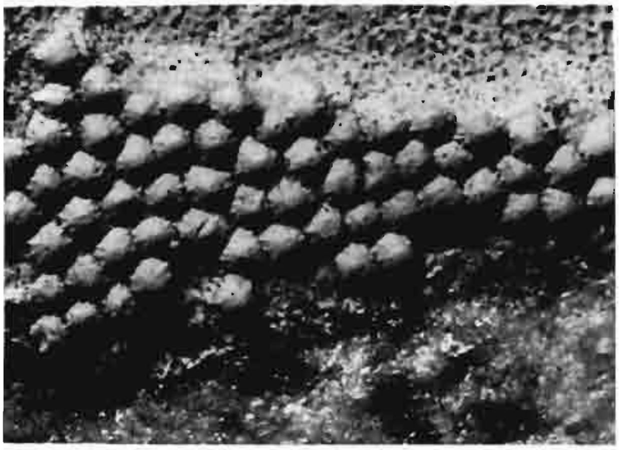
(Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone; D. 35. U.W.)

Fig. 1. Dentine tubercles; × 6.
Fig. 2. Dentine tubercles sprayed with ammonium chloride; × 6.

Photo: P. R. Gurr

Fig. 3. Vertical section of dentine tubercle showing simple pulp cavity; × 60.
Fig. 4. Vertical section of dentine tubercle showing dentine tubules and hyphae of saprophytic fungus; × 120.
Fig. 5, 6. Enlargements of part of fig. 4; × 240.

Photo: J. R. Mercer



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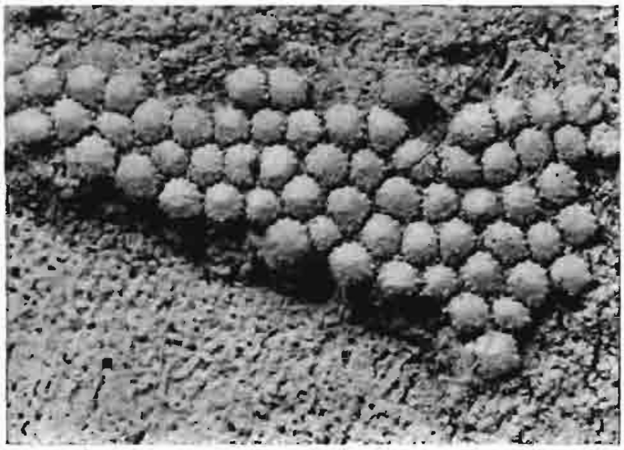

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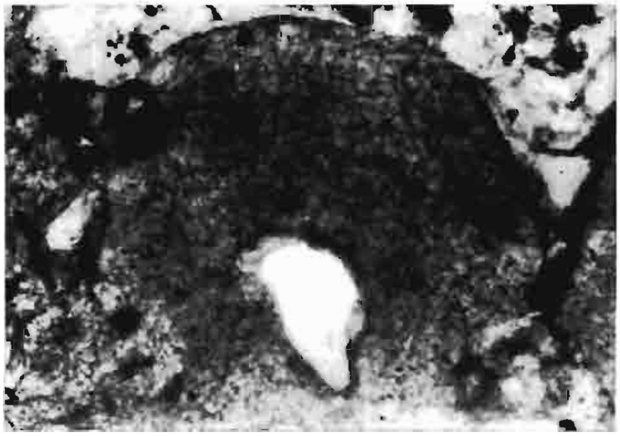

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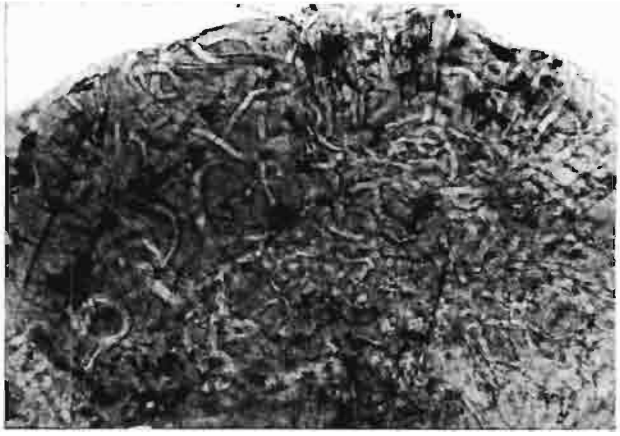

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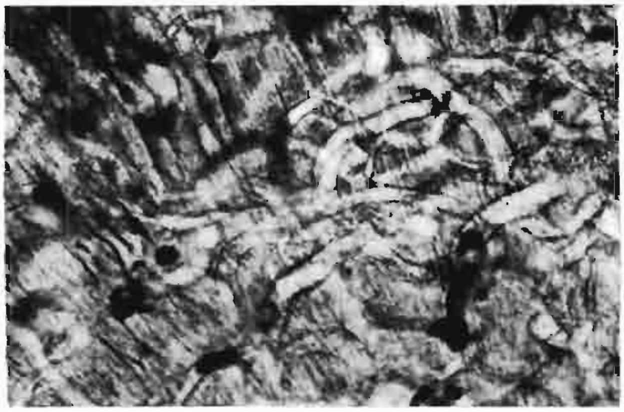

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE XIV

Guerichosteus kozlowskii n. sp.

Detail of ornamentation

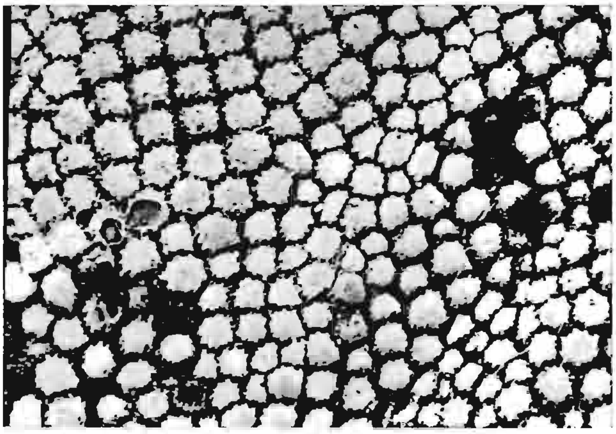
(Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone)

Fig. 1. Dorsal median plate (D. 1. U.W.); × 6.
Fig. 2. Branchial plate (D. 17. U.W.); × 6.
Fig. 3. Natural cast of internal part of ornamentation (D. 36. U.W.); × 6.
Fig. 4. Branchial plate (D. 17. U.W.); × 6.

Photo: P. R. Gurr

Hariosteus kielanae n. sp.

Fig. 5, 6. Detail of ornamentation, holotype. Daleszyce, near Kielce, Holy Cross Mountains, central Poland, Lower Devonian, Emsian, Placoderm Sandstone (D. 48. U.W.); × 7.



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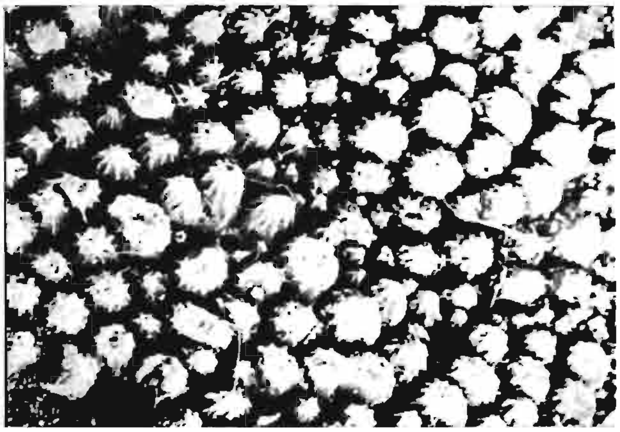

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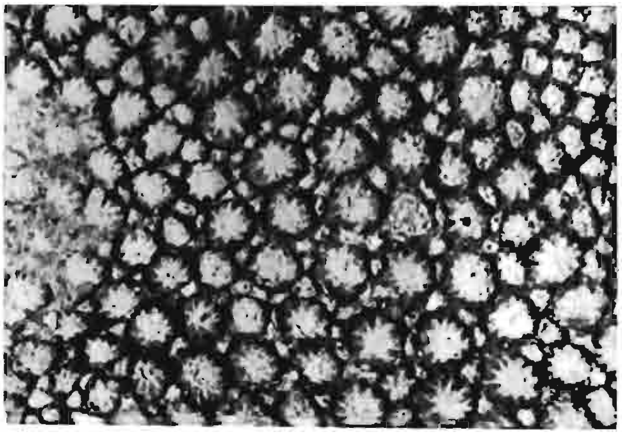

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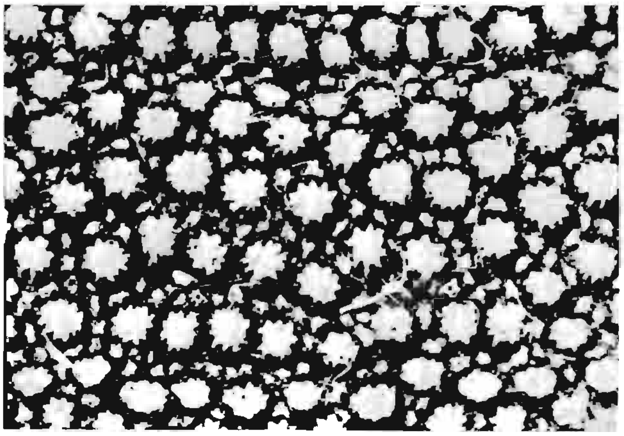

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ACHATS

Pour achat de „Palaeontologia Polonica" à l'étranger prière s'adresser à
Centrala Handlu Zagranicznego „Ars Polona"
Krakowskie Przedmieście 7, Warszawa, Pologne.