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

II. SYSTEMATIC PART

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

II. CZĘŚĆ SYSTEMATYCZNA

BY
L. BEVERLY HALSTEAD TARLO

(WITH 48 TEXT-FIGURES AND 19 PLATES)

WARSZAWA 1965

PAŃSTWOWE WYDAWNICTWO NAUKOWE

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PREFACE

The present work consists of the second part of a comprehensive review of the order Psammosteiformes — a group of the subclass Heterostraci (one of the major divisions of the Agnatha, or jawless vertebrates). Part I (General) of this review, which is published as a separate volume — Palaeontologia Polonica No. 13 — contains an introduction to the Heterostraci as a whole, including a new interpretation of their internal anatomy, as well as sections on the following topics which relate exclusively to the psammosteids: an historical review of previous work; an account of the morphology of the psammosteids together with a discussion of their classification; an account of the growth of the dermal armour based on a detailed examination of its ornamentation; a re-interpretation of the histology of the aspidin and dentine of the dermal armour with particular reference to their fine structure; an account of the stratigraphical range and geographical distribution of the group, and finally a discussion on the origin and evolution of the psammosteids.

This work — Part II (Systematic), contains full descriptions of, and comments on, all available psammosteid material, while in addition problems relating to morphology or evolution are discussed when they pertain to particular specimens. Although much of the material is described here for the first time, previously described material has also been re-examined, enabling a comprehensive critical assessment to be made of the entire order. As can be seen from the List of Contents, the descriptions have been compiled in a systematic way based on the classification discussed in detail in Part I, and outlined briefly in my paper on the Classification and Evolution of the Heterostraci (1962*c*). In consequence of the publication of this review in two distinct parts, an Appendix was included at the end of Part I so that all new taxa could be validated, thus preventing their remaining *nomina nuda* until this Part II appeared.

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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 9 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 Dr. 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-KURIK 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); the late 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-KURIK (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 gemuendenensis*; Dr. F. BROTZEN (Geological Survey Museum, Stockholm) and Dr. S. MATTHES (Halle University) for the loan of the types of *Weigeltaspis alta*; the late 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.

Text-figures 1-10, 20A, 34E, 44 and 45 were drawn by Miss JENNIFER MIDDLETON under my direction, and photographs for plates are by Messrs. W. BRACKENBURY, J. V. BROWN, P. F. GREEN, N. TANTI and K. TAYLOR.

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 the late 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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University of Reading, and
Royal Dental Hospital of London
London, July 1964

SYSTEMATIC PART

Subclass HETEROSTRACI LANKESTER, 1868

Diagnosis. — Jawless (agnathan) vertebrates, anterior part of animal somewhat dorso-ventrally flattened, posterior part laterally compressed. Tail generally inequilobate, lower lobe larger (hypocercal). Carapace covering forepart of body, sometimes composed of mosaic of small tesserae, usually of larger discrete plates comprising unpaired median plates, paired lateral plates, numerous oral plates (exceptions: *Doryaspis* and *Eglonaspis* with no oral plates). Persistent fields of tesserae between main plates in some forms. No lateral fins, cornual plates in Pteraspidida and branchials in Psammosteida laterally extended to aid stability, moveable only in one species of genus *Psammosteus*. Armour composed of basal lamellar layer of aspidin, thick middle layer of spongy aspidin and superficial layer of dentine ridges or tubercles (exception: *Obruchevia [Aspidosteus]* with no dentine layer, but superficial layer of spongy aspidin strengthened with pleromic dentine). Aspidin acellular in early forms, generally permeated by simple spindle-shaped cell spaces; organic matrix shows transition from condition of dentine to that of bone. Trunk and tail with squamation of few deep or numerous rectangular scales overlapping distally; dorsal and ventral median scales form strong fulcra, anterior dorsal fulcral scale can form spine. Histology of scales as in plates. Series of paired branchial pouches (marsupibranch) with longitudinal lateral excurrent canal; common branchial opening at postero-lateral corner of carapace. Well developed endostyle in anterior part of floor of pharynx. Anterior somites distinct, with longitudinal division of muscle blocks; mandibular and hyoidean pre-otic somites unmodified, unconnected with eye (no evidence of pre-mandibular pre-otic somite). Central nervous system simple, primitive fore-, mid- and hind-brain clearly differentiated. Prominent pineal organ, double nasal sacs (diplorhine), nostrils generally opening into buccal cavity (external in Cyathaspidida). Eyes face antero-laterally, auditory apparatus with two semi-circular canals at each side, sensory canal system enclosed within armour with pores to surface, or situated in grooves on external surface.

Order **PSAMMOSTEIFORMES** BERG, 1940

Diagnosis. — Heterostracans characterized by possession of mosaic of small polygonal plates or tesserae between unpaired median plates and plates of lateral margin. Primitive members with tessellated carapace, with tesserae differentiated into groups foreshadowing discrete plates of later forms. More advanced members illustrate progressive fusion of tesserae leading to typical forms with full complement of plates developed, i. e. rostral, pineal, dorsal, ventral and paired orbital, post-orbital, branchial and cornual plates.

Suborder **TESSERASPIDIDA** TARLO, 1962

Diagnosis. — Carapace composed of independent polygonal plates or tesserae which may be fused to form discrete larger plates. In forms where fusion has not taken place the tesserae are differentiated into separate areas foreshadowing such plates. In all forms large areas of the carapace are still composed of discrete tesserae, and the full complement of plates found in the later psammosteids is not achieved.

Family TESSERASPIDIDAE BERG, 1955

Diagnosis. — Carapace composed of tesserae differentiated into separate areas foreshadowing dorsal and ventral median and branchial plates of later forms. Tesserae of certain areas may be fused into discrete plates.

Discussion. — The condition typical of the family is found in *Tesseraspis* in which there are no large discrete plates. In *Kallostrakon macanuffi* large plates have developed probably in both dorsal and ventral median areas, while there is also a variety of tesserae, indicating that these small plates are undergoing a process of differentiation into groups foreshadowing other large plates. In *Kallostrakon podura* and *K. alleni* the evidence of tesserae has almost been lost in the plates known (see section on Ornamentation in General Part of this work (TARLO, 1964*b*) for discussion on elimination of tesserae). However, since these two species are known only from fragments of plates and are placed in *Kallostrakon* merely because of the nature of their ornamentation, the exact position regarding tesserae in these forms is not known.

Genus **TESSERASPIS** WILLS, 1935

Type species: *Tesseraspis tessellata* WILLS, 1935

Diagnosis. — Fully tessellated carapace. Tesserae differentiated into well marked groups: thick tesserae with large tubercles in median areas; thick ridge plates at lateral margins; thin tesserae with smaller tubercles in region between median area and lateral margin; scales small, rhomboid.

Occurrence. — Upper Silurian (Ludlovian); Lower Devonian (Gedinnian), zone of *Traquairaspis-Protopteraspis*; Anglo-Wales, Lithuania, Podolia, and Yukon, Canada.

Discussion. — The organization of the carapace is reminiscent of the Ordovician genus *Astraspis* where there are no large plates, but where the entire carapace consists of tesserae. In *Astraspis* however they are not differentiated or organized into areas, except on the lateral margins where there are ridge plates. In *Tesseraspis* on the other hand, the tesserae are differentiated into groups foreshadowing the plates of later psammosteids and their fields of tesserae. For instance *Tesseraspis* has thick tesserae shaped like ridge tiles at the lateral margins, thick tesserae with large tubercles in the median areas and thin tesserae with smaller tubercles in the region between the median and lateral areas. Until now only one species of *Tesseraspis* has been recognized, and discussion of the genus has been confined to *T. tessellata* which is known from associated tesserae (see pp. 3—6). Associated tesserae are also now known from *T. toombsi*, but the further species referred to this genus, *T. orvigi*, *T. mutabilis*, *T. denisoni* and *T. talimaae* are known only from fragments.

Tesseraspis tessellata WILLS, 1935

(Pl. I, figs. 1-6; Text-fig. 1)

1935. *Tesseraspis tessellata* n. sp.; L. J. WILLS, Rare and new..., pp. 435-439, pl. 3, figs. 1, 2; pl. 4, figs. 1-10; pl. 5, figs. 1-5; pl. 7, figs. 6, 7.
1937. *Tesseraspis tessellata* WILLS; W. GROSS, Die Wirbeltiere..., p. 12.
1946. *Tesseraspis tessellata* WILLS; E. I. WHITE, The genus Phialaspis..., pp. 209-212.
1947. *Tesseraspis tessellata* WILLS; W. GROSS, Die Agnathen und..., pp. 97, 98.
1950. *Tesseraspis tessellata* WILLS; E. I. WHITE, The Vertebrate..., p. 56.
1952. *Tesseraspis tessellata* WILLS; R. H. DENISON, Early Devonian..., p. 270.
1955. *Tesseraspis [tessellata]* WILLS; L. S. BERG, Classification..., p. 28.
1956. *Tesseraspis [tessellata* WILLS*]*; R. H. DENISON, A review of..., p. 393.
1957. *Tesseraspis [tessellata]* WILLS; L. B. TARLO, A preliminary note..., p. 229.
1958. *Tesseraspis [tessellata* WILLS]; E. A. STENSIÖ, Les cyclostomes..., p. 246.
1959. *Tesseraspis [tessellata]* WILLS; W. SCHMIDT, Grundlagen einer..., p. 19.
1960*a*. *Tesseraspis [tessellata* WILLS*]*; L. B. TARLO, The invertebrate..., p. 120.
1961. *Tesseraspis tessellata* WILLS; T. ØRVIG, Notes on some..., pp. 516-518.
1961*a*. *Tesseraspis [tessellata* WILLS*]*; L. B. TARLO, Psammosteids from..., pp. 206-207.
1962*c*. *Tesseraspis tessellata* WILLS; L. B. TARLO, The Classification..., pp. 258-259, text-fig. 5.
1964*b*. *Tesseraspis tessellata* WILLS; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 19, 24, 58, 69, 73; pl. 4, figs. 1-4; pl. 7, figs. 5, 6; pl. 8., figs. 3-7; pl. 9, figs. 1, 3, 4; text-figs. 4, 19*A*.
1964. *Tesseraspis tesselata* WILLS; D. OBRUCHEV, Subclass Heterostraci..., p. 56, text-fig. 16.

Lectotype (here selected): Part of tessellated carapace probably dorsal, 113, housed in the Geological Museum, University of Birmingham, figured by WILLS (1935, Pl. 4, fig. 5) and in the present work (Pl. I, fig. 1, Text-fig. 1*A*).

Type horizon and locality: Lower Devonian (Gedinnian), Lower Dittonian, *Traquairaspis symondsi* zone; Earnstrey Hall, Shropshire, England.

Diagnosis. — Tesserae of median areas ornamented by large flat elongated tubercles with marked crenulations at base; similar smaller tubercles frequently present between the larger. Tesserae situated between median area and lateral margin ornamented by small deeply crenulated rounded tubercles. Lateral margin of carapace formed by thick ridge plates with large oval tubercles at ridge. Scales ornamented by small elongated "fleur-de-lys"-shaped tubercles.

Material. — Groups of tesserae in natural association known from Shropshire, England. Isolated tesserae common in Lower Gedinnian of the Welsh Borderland and also known under London (Streatham borehole).

Description. — The lectotype (113 B. U.) consists of a group of thick polygonal tesserae in natural association. These are characterized by large, oval, flat tubercles with marked crenulations at their margins (Text-fig. 1*A*). A wide longitudinal strip of these tesserae form a median zone in the group which in the specimen is somewhat depressed. This depressed zone is bounded laterally on each side by a row of tesserae set one behind the other. The ornamentation of this second type of tesserae is similar to that of the tesserae of the median zone, but the tesserae are now gently arched from side to side and seem to form two longitudinal raised ridges bounding the median zone, which run at a slight angle to one another, and probably converged posteriorly. One of the ridges is seen to die out at what is presumed to be the anterior region. Lateral to these longitudinal ridges there occur a few small thin tesserae ornamented by small deeply crenulated and often rounded tubercles, reminiscent in shape of gingerbread men. This specimen has been chosen as the lectotype because it shows the way in which the different kinds of tesserae are associated with one another, and also gives an idea of the width of the median area of the carapace. Since it does not seem to show marked

signs of abrasion, the lectotype may well belong to the dorsal side of the animal. A further specimen of associated tesserae (108 B. U.) appears to belong to the left posterior side of the ventral carapace, as the bounding ridge of gently arched tesserae is very severely abraded. The tesserae of the median zone are fairly large, but quickly grade into much smaller lozenge-shaped plates posteriorly, probably the commencement of the squamation. Similarly the tesserae of the severely abraded ridge also become smaller and merge into the squamation. Lateral to this arched ridge are remains of very thin tesserae with a very delicate ornament. An indication of similar thin tesserae is to be found on the right hand side of the specimen, where there seems also to be some evidence of the most posterior part of the right-hand arched ridge.

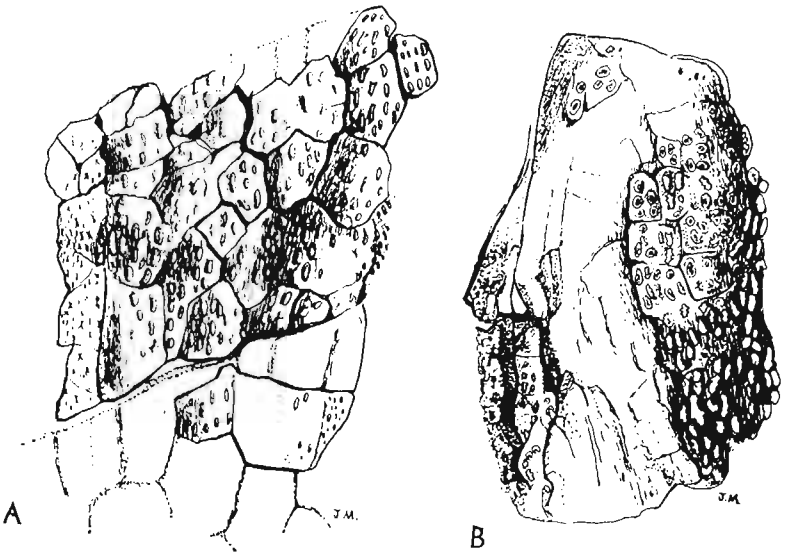

Fig. 1

Tesseraspis tessellata WILLS — *A* lectotype, showing median dorsal area of large tesserae with ornamentation of large tubercles, fragments of thin tesserae at either side with small tubercles (B.U., 113, Earnstrey Hall), × 1; *B* specimen showing ridge plates of lateral margin, large tesserae of anterior part of median ventral area and intervening zone of thin tesserae (B.U., 540 Earnstrey Hall), × 1.

Another important specimen (114 B. U.), possesses thin tesserae with small irregular rounded tubercles. At the margin of these tesserae are four small plates shaped like ridge tiles, aligned horizontally and arranged in a row. One surface of these plates is continuous with the thin tesserae and the other joins it at a marked angle. The tubercles of the ridged plates are small where they adjoin the thin tesserae, but become larger as the summit of the ridge is reached and then become smaller again on the other surface. It is quite clear that these ridge plates formed the lateral margin of the carapace. A further specimen (539 B. U.) also shows such ridge plates with strongly abraded large tubercles at their peak, indicating that this part of the carapace must have rubbed along the substratum. Median to the ridge plates there is a wide zone of thin tesserae with a very small ornamentation, but these are somewhat larger than those in the previous specimen although not as large as the thicker tesserae of the median areas previously described. The smaller tesserae of the previous specimen may have been situated near the posterior margin, where they would grade into the squamation. Unfortunately it is not known what the relationship is between the tesserae of

specimen 539 B. U. and the median area, thus their position in the carapace cannot be judged with any certainty. However, in specimen 540 B. U. the tesserae of the median area and those of the lateral margin are preserved in their natural position (Text-fig. 1 *B*). Those of the median area are badly abraded, indicating a ventral position, while the tubercles appear to swing round to a transverse orientation at one end of the specimen. This seems to contrast with the situation in specimen 108 B. U. where they grade into the squamation. This would indicate therefore that the specimen (540 B. U.) shows the anterior part of the ventral median area on the right-hand side, with the arched longitudinal ridge commencing near the postero-lateral corner.

The ridge plates of the lateral margin in this specimen appear to be aligned at a small angle to the tesserae of the median area, so that the intervening zone of thin tesserae with small tubercles appears to be widening posteriorly. As a result, the ventral carapace can be partially reconstructed, and it can be seen that the median area with its thick tesserae was fairly long and narrow and slightly convex from side to side, and was somewhat upturned near its anterior margin. The lateral ridge plates must have touched the substratum, while between these plates and the median area there was a zone of thin tesserae forming a slight concavity. In specimen 541 B. U. similar ridge plates to those already described are known, but in this instance the thin tesserae are found adjoining both surfaces of them, confirming the fact that in both the dorsal and ventral parts of the carapace, such fields of tesserae were present between the lateral margins and the thicker tesserae of the median areas. Specimen 110 B. U. which seems to represent the anterior part of the ventral carapace shows the abraded median area which then curves upwards to a zone of medium-sized tesserae with rounded tubercles, and as ØRVIG (1961) noted, this specimen also shows evidence of a sensory canal system, short segments of which are visible where tubercles have been lost.

A segment of the squamation (112 B. U.), shows a series of lozenge-shaped scales ornamented by dentine tubercles, which are almost indistinguishable from the very much larger tubercles known in *Weigeltaspis alta*, being shaped rather like multiple „fleur-de-lys". The texture of the aspidin of the plates was well illustrated by WILLS (1935), but when the detailed structure is examined, it can be seen that the aspidin is permeated by randomly arranged spindle-shaped spaces which it is now believed were the site of aspidinocytes (see TARLO, 1963*a*, 1964*a*). WILLS also noted a dentine tubercle below another tubercle in one of his sections and interpreted the underlying one as being a new tubercle prior to eruption. However, as pointed out by DENISON (1952) and ØRVIG (1961), it must be the overlying tubercle which is the new one. WILLS also stated that his underlying tubercle had a cap of enamel, but this is now known not to be so, for although under polarized light the tubercles of *Tesseraspis* show a bright outer rim to the normal dentine, this merely indicates that as in modern teeth, the crystallites in the most superficial layer of the dentine were probably aligned differently from those in the remainder of the tubercle, where they are parallel to the surface of apposition (see W. J. SCHMIDT, 1959). Further details of the histology of *Tesseraspis* are also discussed in the General Part of the present work (TARLO, 1964*b*).

Discussion. — *Tesseraspis tessellata* was first described by WILLS (1935) who demonstrated that there were different types of tesserae in different parts of the carapace. The importance of his work was the recognition of a heterostracan in which the carapace was still composed of discrete tesserae, although it is evident from his material that these were already organized into areas foreshadowing the plates of later forms. Subsequently GROSS (1937, 1947) and BERG (1955) accepted this species as a psammosteid, although DENISON (1952, 1956) for some reason considered it to be a cephalaspid, a point strongly disputed by ØRVIG (1961).

The species was mentioned in passing by TARLO (1957, 1960*a*), STENSIÖ (1958) and SCHMIDT (1959), but little new was added until the nature of the plates of the lateral margin were recognized (TARLO, 1961*a*), parts of the sensory canal system were identified by ØRVIG (1961) and the first tentative restoration was published (TARLO, 1962*c*). This species has been the subject of some controversy, since SCHMIDT (1959) did not feel that there was sufficient evidence to assign it to any particular group, a view echoed by OBRUCHEV (*in* TARLO, 1961*a*) and more recently by STENSIÖ (1964*b*). Nevertheless, as discussed previously (TARLO, 1962*c*), and in the General Part of this work (1964*b*) *Tesseraspis tessellata* can be accepted as a representative of the most primitive structural grade of the Psammosteiformes.

Tesseraspis toombsi TARLO, 1964

(Pl. I, figs. 7-10)

1964*b*. *Tesseraspis toombsi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., p. 110.

Holotype: Part of tessellated carapace, P. 29621-P. 29625, P. 29683, housed in the British Museum (Natural History), London, figured in the present work Pl. I, figs. 7-10.

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

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 similar median one. Scales ornamented by short, longitudinally aligned ridges. Species very close to *Tesseraspis tessellata*, but distinguished by cyclomorial nature of tesserae being more clearly marked.

Material. — Unique holotype.

Description. — The holotype consists of part of an articulated carapace which has been broken up into patches of associated tesserae. The specimen (P. 29683 B. M.) is a group of tesserae from the median area of the carapace, in each tessera of which there is a large central tubercle with others arranged concentrically around it. The central tubercle is an elongated oval shape, while the others may be either round or elongated or form short dentine ridges. In all cases the tubercles are fairly well separated from one another. Associated with this area of large tesserae is a strip of tesserae in which the central tubercle appears as a short dentine ridge, and similar short ridges occur on either side of it. These tesserae are reminiscent of the normal ornament of the plates of *Kallostrakon macanuffi*, but seem in the species described here, to represent a series of median scales which have been displaced through 90 degrees. The tesserae from the median area, with their large central tubercles, on the other hand, are rather similar in their ornament to the isolated tesserae of *Kallostrakon macanuffi*, but their tubercles are more widely spaced and although fairly cyclomorial, seem closer to *Tesseraspis* than to *Kallostrakon*. However, the tesserae could be considered as having an ornamentation somewhere between the two genera. A further area of tesserae similar to the median ones just described is found in specimen P. 29624 B. M., whilst in the fragment P. 29621 B. M. there is a line of somewhat ridged tesserae, in which the ornament consists of elongated tubercles or short ridges aligned longitudinally. Adjacent to these ridged tesserae is a field of tesserae, which unfortunately is not visible in the photograph since it has been preserved beneath the ridged tesserae. These adjoining tesserae unlike the ridged ones, have the normal ornamentation, and indicate that the ridged tesserae are not median scales, but must belong to the lateral margin. Since the tesserae both of the lateral field of tesserae and of the median area of the

carapace have fairly large flattened tubercles, this seems to suggest that the holotype is the major part of the ventral surface of the carapace, where such flattened tubercles are usually found. A small fragment of the squamation of the same individual is also preserved (P. 29622 B. M.) and shows that the scales overlap distally and are ornamented by longitudinally aligned dentine ridges which are fairly well separated. These scales in fact contrast in their ornamentation with those known from *Tesseraspis tessellata*. Thus in the ornamentation of the different parts of the carapace the form here described seems to be quite distinct from *Tesseraspis tessellata*, but the general arrangement of the carapace seems to be basically the same. This form was therefore included in the genus *Tesseraspis* and the name *T. toombsi* was proposed for its reception.

Tesseraspis mutabilis (BROTZEN, 1934)

1934. *Lophosteus mutabilis* n. sp.; F. BROTZEN, Erster Nachweis..., pp. 50-52, text-figs. 5, 6.
1947. *Lophosteus mutabilis* BROTZEN; W. GROSS, Die Agnathen..., pp. 111-112.
1947. *Lophaspis crenulata* BROTZEN; W. GROSS, *Ibid.*, p. 111.
1947. *Strosipherus* sp. PANDER; W. GROSS, *Ibid.*, p. 111.

Lectotype (here selected): Fragment of tessera figured by BROTZEN (1934, Text-fig. 5 *D*).

Type horizon and locality: Lower Devonian (Gedinnian), Beyrichienkalk, *Traquairaspis* zone; Rauhen Bergen, near Steglitz (Berlin), Germany.

Diagnosis. — Ornamentation of small well separated rounded lobate tubercles.

Material. — Fragments from erratic boulders of Beyrichienkalk from Berlin, Germany.

Description. — The lectotype is a small fragment ornamented by several small, well separated tubercles. These are prominent and have short lobe-like extensions which tend to fan out in one main direction. BROTZEN (1934) placed a number of fragments with this type of ornament in the new species *Lophosteus mutabilis*. GROSS (1947), however, believed that the material described by BROTZEN under this name belonged to either *Orthaspis plana* (=*Traquairaspis*) or *Strosipherus indentatus* (=*Oniscolepis*). He also noted that the original material of *Lophosteus*, first described by PANDER (1856) and subsequently by ROHON (1893), consisted of cephalaspid and acanthodian remains. Although the material described by BROTZEN cannot therefore be retained in the genus *Lophosteus*, the nature of the tubercles is so characteristic as to warrant the establishment of a new species, and the similarity of the tubercles to some of those in the scales of *Tesseraspis tessellata* as well as their histology, make it likely that the species described by BROTZEN can be included in the genus *Tesseraspis*. In consequence this form has been listed here as *Tesseraspis mutabilis* (BROTZEN).

Tesseraspis orvigi TARLO, 1964

1961. Drepanaspida gen. et sp. indet.; T. ØRVIG, Notes on some..., pp. 523-524, Text-fig. 4.
1964*b*. *Tesseraspis orvigi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., p. 110.

Holotype: Fragment of tessera, C. 1727, housed in the Swedish Museum of Natural History, Stockholm, figured by ØRVIG (1961, Text-fig. 4).

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

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

Material. — Fragments of tesserae from the Upper Czortkow horizon of Podolia.

Description. — The holotype (C. 1727 R. S.) consists of a fragment of a tessera on which six rectangular tubercles can be made out. These are arranged in two rows of three tubercles, and in both rows the margins between the adjoining tubercles appear to be smooth, while between the rows the margins on both sides are drawn out into fine crenulations. The major surface of the tubercles is flat. The tubercles appear to be very much smaller than any of those known in *Tesseraspis tessellata*, and their character also seems somewhat different, so that obviously a different species is represented. However, the ornamentation is sufficiently close to that of *T. tessellata* to show that the specimen belongs to *Tesseraspis*. The name *Tesseraspis orvigi* was proposed for this form therefore, since although it is based on a fragment only, it is important, as it is the sole record of *Tesseraspis* from the Czortkow of Podolia.

Tesseraspis denisoni TARLO, 1964

1963. *Heterostraci* fam. indet., Type D; R. H. DENISON, New Silurian..., p. 138, figs. 81*D*, 82*C*.
1964*b*. *Tesseraspis denisoni* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., p. 110.

Holotype: Fragment of tessera, 17096, housed in the Geological Museum, Princeton University, New Jersey, United States, figured by DENISON (1963 Text-figs. 81*D*, 82*C*).

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

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.

Material. — Fragments from the Ludlovian of Yukon, Canada.

Description. — This species is known only from a few fragments ornamented by large round flat tubercles with prominently crenulated margins. These grade into rather smaller more elongated, but similar tubercles at one edge of the holotype (17096 P. U.). The main round tubercles which are flat have probably been abraded, since towards the very edge of the specimen the elongated tubercles show less wear, and eventually the outermost tubercles, which appear to be unworn, have a marked longitudinal ridge. DENISON (1963) noted the similarity of this form to fragments of the marginal tubercles of *Cardipeltis*, and also to the Podolian psammosteid described by ØRVIG (1961) (here referred to *Tesseraspis orvigi*). The form described by DENISON is clearly closer to *Tesseraspis* than to *Cardipeltis*, but its ornament distinguishes it from other species of *Tesseraspis*, and in Part I of this work, although it is known only from a fragment, it was considered to warrant specific distinction, and the name *Tesseraspis denisoni* was suggested for it.

Tesseraspis talimaae n. sp.

1962. *Traquairaspis* sp. KIAER; V. KARATAJŪTĖ-TALIMAA, Description of remains..., p. 52, pl. 1, fig. 21, text-figs. 2, 4.
1962. *Tesseraspis* sp. WILLS; V. KARATAJŪTĖ-TALIMAA, Description of remains... p. 53, pl. 1, fig. 15, text-figs. 2, 6.

Holotype: Tesserae No. 5-1199, housed in the Geological Institute, Vilnius, figured by KARATAJŪTĖ-TALIMAA (1962, Pl. 1, fig. 21, text-figs. 2, 4).

Type horizon and locality: Lower Devonian (Gedinnian), Lower Dittonian, *Traquairaspis* zone; borehold at 540 m., Krekenava, Lithuania.

Derivation of name: talimaae — in honour of Dr. V. KARATAJŪTĖ-TALIMAA of the Geological Institute of Vilnius.

Diagnosis. — Ornamentation of small well separated elongated tubercles, generally with three short rounded crenulations at each end. Scales similar to those of *T. toombsi* but with somewhat smaller, short, longitudinally aligned ridges.

Material. — Fragments of tesserae and scales from Lower Dittonian of Lithuania.

Description. — The holotype consists of two naturally articulated tesserae which are roughly hexagonal in outline, with six and eight tubercles on them, respectively. The tubercles are very small when compared with those in other species of *Tesseraspis*, as indeed are the tesserae and scales as a whole. The type of ornament is reminiscent of that found on the thin tesserae situated between the thick tesserae of the median areas and lateral margins. Although known only from a few fragments, the ornamentation is sufficiently distinctive to warrant specific separation from the other species belonging to this genus. The species *Tesseraspis talimaae* is therefore here proposed.

Genus **ONISCOLEPIS** PANDER, 1856

Type species: *Oniscolepis dentata* PANDER, 1856

Diagnosis. — Tesserae ornamented at proximal end by elongated tubercles or short dentine ridges with strong crenulations directed somewhat distally. Ornamentation at distal end of tesserae consists of slightly wider oval tubercles with similar crenulations. In many tesserae the elongated tubercles or short dentine ridges appear to have been added on cyclomorially at either side of a central tubercle.

Occurrence. — K4 horizon, Isle of Oesel, Estonia, and in erratic boulders of Beyrichienkalk on southern shores of the Baltic.

Oniscolepis dentata PANDER, 1856

1856. *Oniscolepis dentatus* n. sp.: C. H. PANDER, Monographie der fossilen..., p. 58, pl. 6, fig. 33.
1856. *Oniscolepis serratus* n. sp.; C. H. PANDER, *Ibid.*, p. 59, pl. 6, fig. 34.
1856. *Oniscolepis crenulatus* n. sp.; C. H. PANDER, *Ibid.*, p. 59, pl. 6, fig. 35.
1856. *Strosipherus indentatus* n. sp.; C. H. PANDER, *Ibid.*, p. 74, pl. 4, figs. 8 a-g.
1856. *Strosipherus serratus* n. sp.; C. H. PANDER, *Ibid.*, p. 75, pl. 4, figs. 9a.
1856. *Strosipherus laevis* n. sp.; C. H. PANDER, *Ibid.*, p. 75, pl. 4, figs. 9 b, c, d.
1893. *Oniscolepis dentata* PANDER; J. V. ROHON, Die obersilurischen..., pp. 90-93, pl. 1, fig. 46; pl. 3, fig. 59.
1893. *Oniscolepis crenulatus* PANDER; J. V. ROHON, *Ibid.*, p. 93.
1893. *Strosipherus indentatus* PANDER; J. V. ROHON, *Ibid.*, p. 93.
1893. *Strosipherus serratus* PANDER; J. V. ROHON, *Ibid.*, p. 93.
1893. *Strosipherus laevis* PANDER; J. V. ROHON, *Ibid.*, p. 93.
1893. *Oniscolepis serrata* PANDER; J. V. ROHON, *Ibid.*, pp. 93-94, text-fig. 19.
1947. *Strosipherus indentatus* PANDER; W. GROSS, Die Agnathen..., pp. 96-98, pl. 9, figs. 1-4, text-fig. 2.
1950. *Strosipherus indentatus* PANDER; W. GROSS, Die paläontologische..., pp. 51, 52.
1950. *Oniscolepis* sp. PANDER; W. GROSS, *Ibid.*, p. 51.
1958. *Strosipherus indentatus* PANDER; D. OBRUCHEV, On the biostratigraphy..., p. 41.
1961. *Oniscolepis dentata* PANDER; W. GROSS, Aufbau des Panzers..., pp. 100-101.
1961. *Oniscolepis* sp. PANDER; W. GROSS, *Ibid.*, pp. 100-108, text-figs. 10, 11, 12 A-L.
1964. *Strosipherus indentatus* PANDER; D. OBRUCHEV, Subclass Heterostraci..., pp. 55-56, text-figs. 14, 15.

Holotype: Tessera figured by PANDER (1856, Pl. 6, fig. 33).
Type horizon and locality: Upper Silurian (Ludlovian), K 4 horizon; Ohhesaare-Pank, Isle of Oesel, Estonia.

Diagnosis. — As for genus, only species.

Material. — Tessera and fragments from the Isle of Oesel, Estonia, and erratic boulders of Beyrichienkalk from the southern shores of the Baltic.

Description. — The holotype is a single tessera in which there is an ornamentation of short dentine ridges with well marked crenulations pointing distally, which have a rather leaf-like appearance. In the distal part of the specimen the tubercles become shorter and wider, being more oval in outline, but again they have prominent distally directed crenulations. In material figured by both PANDER (1856) and ROHON (1893), specimens are found in which the short dentine ridges show a somewhat concentric arrangement, although the main direction of the ridges is a longitudinal one. The species is known only from isolated fragments first described by PANDER (1856) as belonging to seven different species. ROHON (1893) reduced these to two, i.e. *Oniscolepis dentata* and *Oniscolepis serrata*, but in the present work only the former is accepted. Similar material was described by GROSS (1947) from erratic boulders of Beyrichienkalk, but he used the name *Strosipherus indentatus* for it despite the fact that ROHON (1893) had already made this species a synonym of *Oniscolepis serratus*. GROSS suggested that *Strosipherus* (i.e. *Oniscolepis*) might prove to be congeneric with *Tesseraspis*, but he believed that at that stage in our knowledge it was best to keep them separate. The large tubercle he described is somewhat similar to some of the large tubercles of *Tesseraspis*, but the crenulations seem distinct, and furthermore, a smaller fragment shows the concentric alignment of the tubercles which is quite unlike the ornamentation found in *Tesseraspis*. GROSS later (1961) described further similar remains from the Beyrichienkalk which he identified as *Oniscolepis* sp. These too show the cyclomorial tesserae, and it is quite evident that they are distinct from *Tesseraspis*. It is therefore considered reasonable to retain them in a separate genus. However, the tubercles do seem to have a similar arrangement to those known in material described in the present work under the name *Kallostrakon macanuffi*, but the type of ornament and its size enable this latter species to be fairly readily distinguished from the species described here. Although therefore the form from Oesel and the Beyrichienkalk seems to have certain similarities to both *Tesseraspis* and *Kallostrakon*, it appears to be sufficiently distinct from both to justify its retention in a separate genus and species, and despite the fact that it is known so far from poor material only, it is thought reasonable to retain it in the species *Oniscolepis dentata* PANDER (see also pp. 13—14).

Genus **KALLOSTRAKON** LANKESTER, 1870

Type species: *Kallostrakon podura* LANKESTER, 1870

Diagnosis. — Carapace composed of cyclomorial tesserae together with discrete plates formed by fusion of tesserae. Plates may show various stages in progressive elimination of tesserae. Ornamentation of longitudinally aligned dentine ridges; microstructure of dense spongy aspidin.

Occurrence. — Upper Silurian (Ludlovian), Downtonian; Lower Devonian (Lower Gedinnian), Lower Dittonian, zone of *Traquairaspis-Protopteraspis*; Anglo-Wales and Somerset Island, Arctic Canada.

Discussion. — The carapace of *Kallostrakon* is characterized by the possession of large plates formed by the fusion of tesserae. It is not known how many different kinds of plate were present in the carapace, and fusion may have only occurred in the median areas. The abundance of isolated tesserae indicates that a large proportion of the carapace was tessellated,

and hence the inclusion of this genus in the family Tesseraspididae. The ornamentation of the tesserae and plates consists of longitudinally arranged dentine ridges, and suggests an affinity to *Corvaspis*, although fusion into plates seems far less advanced than in that genus. Furthermore, the tesserae in *Kallostrakon* are still cyclomorial in nature in contrast to the synchronomorial type usually found in *Corvaspis*. The main diagnostic features of *Kallostrakon* therefore require its retention in the Tesseraspididae rather than its transfer to the Corvaspididae.

Kallostrakon podura LANKESTER, 1870

1870. *Kallostrakon podura* n. sp.; E. R. LANKESTER, Fishes of the..., pl. 13, fig. 20.
1964*b*. *Kallostrakon podura* LANKESTER; L. B. H. TARLO, Psammosteiformes (Agnatha)..., p. 14, 69, pl. 5, figs. 2, 3.
1965. *Kallostrakon podura* LANKESTER; L. B. H. TARLO, Discussion *in* D. L. DINELEY, Exhibit..., p. 98.

Holotype: Median plate D. 96 housed in the University Museum, Oxford, figured by LANKESTER (1870, Pl. 13, fig. 20) and TARLO (1964*b*, Pl. 5, figs. 2, 3).

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

Diagnosis. — Plate ornamented by short rounded, somewhat irregular dentine ridges which are slightly interdigitated, but are all aligned more or less longitudinally. Evidence of tesserae difficult to make out, although these are suggested by the occasional irregular alignment of the ridges.

Material. — Holotype, and plate from Upper Read Bay Formation, Somerset Island, Arctic Canada.

Description. — The holotype (D. 96 O. U. M.) is part of a discrete plate, and is ornamented by longitudinally aligned, short, rounded dentine ridges. These are not closely packed, and their sides are not exactly parallel, but instead they alter slightly in width and may be somewhat sinuous in outline. They tend to interdigitate with one another, and occasionally they may bifurcate. When the ornament is examined closely, there is no sign of cyclomorial growth or individual tesserae. However, when the specimen is examined as a whole, there is a faint impression of pre-existing tesserae due to the way in which some of the short ridges are arranged, since there is the slight hint that they may have been produced in groups cyclomorially. Occurring with this unique specimen of the species are other remains in which the ornament of dentine ridges shows well marked cyclomorial growth, and distinct tesserae. These latter remains show a great deal of variation, but seem nevertheless to demonstrate that they are obviously related to the species described above, and they should therefore be included in the same genus. However, three different species are represented in the deposit and care must be taken to see that the name *Kallostrakon podura* is used only to refer to the holotype or material directly comparable to it (see TARLO *in* DINELEY, 1965*a*).

Kallostrakon macanuffi TARLO, 1964

(Pl. II, figs. 3-16)

1870. *Kallostrakon podura* n. sp.; E. R. LANKESTER, Fishes of the..., pl. 13, fig. 21; pl. 14, fig. 6.
1870. Fragments of scales; E. R. LANKESTER, *Ibid.*, pl. 13, figs. 6, 6a.
1891*b*. *Kallostrakon podura* LANKESTER: A. S. WOODWARD, Catalogue of..., pp. 175-176.
1893. *Kallostrakon podura* LANKESTER: J. V. ROHON, Die obersilurischen..., pp. 79, 88, 92.

1934. *Corvaspis kingi* n. sp.; A. S. WOODWARD, Note on a new..., p. 567.
1946. *Tolypelepis (Tolypaspis)* sp. PANDER; E. I. WHITE, The genus Phialaspis..., p. 212.
1950. *Tolypaspis* sp. SCHMIDT; E. I. WHITE, The vertebrate faunas..., p. 51.
1950. *Tolypelepis* sp. PANDER; E. I. WHITE, *Ibid.*, p. 56.
1951. *Kallostrakon podura* LANKESTER; D. L. DINELEY, The northern part..., p. 134.
1951. *Oniscolepis* sp. PANDER; D. L. DINELEY, *Ibid.*, p. 134.
1952. *Oniscolepis* sp. PANDER; H. W. BALL & D. L. DINELEY, Notes on the..., p. 213.
1955. *Heterostracan*; B. B. CLARKE, The Old Red Sandstone of..., p. 208, text-fig. 4 on p. 207.
1955. *Kallostrakon podura* LANKESTER; A. P. BYSTROW, On the microstructure..., pp. 495-497, text-figs. 22-24.
1959. *Kallostrakon* sp. LANKESTER; D. L. DINELEY & D. W. GOSSAGE, The Old Red..., p. 223.
1960*b*. *Kallostrakon podura* LANKESTER; L. B. TARLO, The Downtonian..., p. 221.
1961. *Kallostrakon* sp. LANKESTER; E. I. WHITE, The Old Red..., p. 245.
1962*c*. *Kallostrakon* LANKESTER; L. B. TARLO, The Classification..., p. 274.
1962*d*. *Kallostrakon* LANKESTER; L. B. TARLO, Lignées évolutives..., p. 25.
1964*b*. *Kallostrakon macanuffi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 42, 69, 73 96; Pl. 5, figs. 1, 5-7, Text-fig. 15A.
1964. *Kallostrakon podura* LANKESTER; D. OBRUCHEV, Subclass Heterostraci..., p. 49, text-fig. 10.

Holotype: Median plate, 55505, housed in the Geological Survey Museum, London, figured by TARLO (1964*b*, pl. 5, fig. 5, Text-fig. 15A).

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

Diagnosis. — Plates with superficial tesserae ornamented by short dentine ridges. Large central ridge with shorter ones arranged on either side. Isolated tesserae with this type of ornament, and others with large round or oval flat bosses as primordia, with short or longer, somewhat narrow flat tubercles arranged around it. Further tesserae can have elongated oval well separated flat tubercles, with similar but irregularly shaped tubercles filling in the intervening areas.

Material. — Numerous tesserae from the Lower Red Downton of Herefordshire, and Holdgate Sandstones of Shropshire, England, and also from the lower part of the *Psammosteus* Limestones Group, *Traquairaspis pococki* zone, Shropshire.

Description. — The holotype (55505 G. S. M.) appears to be the major portion of a median plate, ornamented by short, longitudinally aligned dentine ridges or elongated tubercles. These are rounded from side to side and their long margins are more or less parallel. Some tubercles bifurcate, but this seems to occur in places where pores of sensory canals open to the surface. The dentine ridges are clearly arranged in a distinct pattern of superficial tesserae, suggesting that the plate was formed by the fusion of separate elements. Each superficial tessera has a central ridge which is somewhat wider than the others, which are arranged at either side of it. This indicates that the initial ridge was a primordium around which the other ridges grew as the animal developed. In the specimen, in what seems to be the anterior extremity of the plate, the dentine ridges are aligned more or less transversely, suggesting a truncated margin. It is not yet possible to tell whether the median plate is from the dorsal or ventral surface of the animal, but as there is little wear on the ridges, it may have been a dorsal median plate. A plate with similar superficial tesserae (D. 94 O.U.M.) appears to have a rather arcuate lateral margin, and seems to narrow considerably at the known end, which is figured (1964*b*) under high power. At the tip of this part of the plate, numerous short oval ridges or large tubercles seem to be marking the natural margin of the plate. Small patches of tesserae, similar to those of the holotype, are also known from Bush Pitch, including specimens P. 41944, P. 41945 and P. 5372 B.M. These specimens each represent either three or four fused tesserae, and each group is delimited by an irregular row of small round tubercles. Similar small round

tubercles are also found at the margins of tesserae in the holotype. In specimen D. 88 O.U.M., the corner of a plate is preserved in which there are typical superficial tesserae, but there is also a wide margin normal to the longitudinal ridges, which is composed of a mass of small, closely packed, irregular rounded tubercles. A further fragment of a plate (P. 41946 B. M.) shows numerous, longitudinally arranged, short dentine ridges, but in this instance it is difficult to make out any sign of superficial tesserae, although some of the ridges tend to wrap round others. Also, there are numerous small narrow ridges intervening between the larger ones. Despite this, the nature of the ridges in the specimen still indicate that it belongs to the species here described, and not to *Kallostrakon podura*, in which latter form the ridges are often distinctly sinuous in outline, and interdigitate with one another. Besides the normal type of tesserae just described, a further type also occurs commonly which is very characteristic. In these tesserae there is a very large, flat oval tubercle with a width about 4-5 times that of a normal dentine ridge. In one specimen (P. 24756 B. M.) such an oval tubercle or flattened boss is the primordium, with somewhat narrower tubercles arranged on either side of it, and these have shorter and still narrower tubercles, arranged concentrically around them. Further examples (P. 41948 and P. 30189 B. M.) have similar but more irregularly shaped primordia, while in P. 41949 and P. 1653 B. M. the primordia are only very slightly wider than the surrounding tubercles.

A further group of remains belonging to this species are represented by specimens P. 1654, P. 1652 and P. 41947 B. M., these being small plates which are arched from side to side and are ornamented by fairly broad, elongated oval tubercles, arranged longitudinally, between which are long, narrow ridges and smaller, rounded tubercles. These specimens are probably dorsal or ventral median scales. Occasionally also, isolated tesserae occur such as D. 104 O. U. M., in which there is a very large rather convoluted primordium with slightly more irregular tubercles than usual around it. However, the ornament still seems to be sufficiently like the normal pattern for it to be retained in the same species as those already described. In fact such convoluted tubercles are also known in parts of *Tesseraspis tessellata* where there has been considerable abrasion, and this variation may therefore not be of great taxonomic significance.

Discussion. — This form is one of the earliest of the psammosteids, and although known only from isolated tesserae and parts of discrete plates, it is important since the tesserae show evidence of cyclomorial growth. Although discrete plates are known, these have quite clearly been formed by the later fusion of such areally growing tesserae. The nature of the ornamentation of the tesserae reveals a considerable degree of variation, and this may indicate merely a difference between tesserae of the dorsal and ventral surfaces, or may suggest a differentiation into specialized groupings such as occurs in *Tesseraspis*. However, the former possibility seems to be the more likely. The tesserae with the large tubercles seem to show more wear than those with narrow ridges, and consequently may well have come from the ventral surface of the animal. It is not yet possible to determine what discrete plates were present in the carapace of this form, but as ROHON (1893) and BYSTROW (1955) recognized, the histology of the plates and tesserae shows the typical spongy texture characteristic of the psammosteids. This is quite distinct from that of the cyathaspids to which this form might have been thought to belong, in view of the fact that *Tolypelepis* has a similar type of ornament although on a much smaller scale. The histology of the species here described was first figured by LANKESTER (1870) who also figured specimens of the species, and subsequently BYSTROW (1955) figured sections of the material. One specimen LANKESTER (1870) referred tentatively to *Kallostrakon podura*, and two further specimens he identified merely as fragments of scales. Sub-

sequently, remains of this species have been referred to by numerous authors although there has been a considerable amount of confusion, for although ROHON (1893) carefully discussed the species and only compared it to *Oniscolepis*, other authors variously identified it as *Corvaspis kingi* (WOODWARD, 1934), *Tolypelepis* (WHITE, 1946), *Tolypaspis* (WHITE, 1950), and *Oniscolepis* (DINELEY, 1951, and BALL & DINELEY, 1952). BYSTROW (1955) gave a further description under the name *Kallostrakon podura*, and also figured the microstructure of an entire plate including the dentine tubercles for the first time. However, his illustration of the ornament appears to be somewhat atypical, and in all probability represents a region towards the margin of a discrete plate. The confusion that has resulted from using four different generic names for the same material can, however, now be eliminated, for since BYSTROW's work it has been generally recognized that the correct generic name is *Kallostrakon.* Since also the material described above has an ornamentation different from that found in *Kallostrakon podura*, it undoubtedly belongs to a distinct species for which the name *Kallostrakon macanuffi* was proposed.

Kallostrakon grindrodi TARLO, 1964

(Pl. II, figs. 1, 2)

1964*b*. *Kallostrakon grindrodi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha).... p. 111.

Holotype: Tessera, P. 8896, housed in the British Museum (Natural History), London, figured in the present work, Pl. II, fig. 1.

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

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

Material. — Several tesserae from the Lower Red Downton of Herefordshire, England.

Description. — The holotype (P. 8896 B. M.) and specimen D. 84 O. U. M. are ornamented by broad, oval tubercles which are fairly well separated from one another. In the intervening spaces are elongated irregular tubercles or ridges which completely fill in any gaps. In these tesserae there is clearly no cyclomorial growth around a primordium, but instead there appear to be two generations of tubercles. Thus since the type of growth seen is quite distinct from that in the tesserae of *Kallostrakon macanuffi*, it is suggested that a new species is represented for which the name *K. grindrodi* was proposed.

Kallostrakon alleni TARLO, 1964

1964*b*. *Kallostrakon alleni* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 73, 111.

Holotype: Median plate P. 26854-5, housed in the British Museum (Natural History), London, part figured by TARLO (1964*b*, Pl. 5, fig. 4).

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

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

Material. — Unique holotype.

Description. — The holotype (P. 26854-5 B. M.) is an oval shaped plate much of which was destroyed during acid development at the British Museum (Nat. Hist.) prior to the development of the acetic acid technique, but fortunately one fragment showing the ornament survived. This form clearly represents a new species of *Kallostrakon*, since it has very characteristic tubercles or dentine ridges with a sinuous outline and short lateral projections. It was provisionally identified as *Tesseraspis*, but the fact that there are short dentine ridges and that the specimen is a discrete plate suggests that this form is closer to *Kallostrakon* to which it has been referred, and the new species *K. alleni* was consequently proposed for its reception.

Family CORVASPIDIDAE DINELEY, 1953

Diagnosis. — Dorsal and ventral median plates with ornamentation of short longitudinal dentine ridges, arranged in superficial synchronomorial tesserae. Branchial plates strongly arched with ornamentation of convoluted dentine ridges at centre. Orbital plates rectangular with dentine ridges arranged concentrically around orbit. All plates with margin of cyclomorial growth with ornamentation of closely packed rounded tubercles.

(New undescribed advanced genus with main plates produced by cyclomorial growth around central primordium [see pp. 19—20 below]).

Genus **CORVASPIS** WOODWARD, 1934

Type species: *Corvaspis kingi* WOODWARD, 1934

Diagnosis. — As for family, only genus (so far described).

Occurrence. — Lower Devonian, Lower and Upper Gedinnian; Spitsbergen, Anglo-Wales, Lithuania, Podolia, southern shores of the Baltic, and Somerset Island, Arctic Canada.

Discussion. — The genus *Corvaspis* was erected by WOODWARD (1934) who considered that it was a new cyathaspid. More recently DINELEY (1953) demonstrated that this genus possessed orbital plates, thus necessitating its exclusion from the cyathaspids. The carapace of this genus comprises median plates, paired branchial and orbital plates, and it is of some significance that there appear to have been tesserae situated between the median plates and those of the lateral margin. For this reason this genus was placed in the psammosteids by TARLO (1960*b*). Since there is insufficient evidence to determine the full complement of plates present in the carapace, however, it seems reasonable to retain the genus and hence the family in the suborder Tesseraspidida, particularly since fragments of the genus are frequently difficult to distinguish from *Tesseraspis* and *Kallostrakon*.

OBRUCHEV (1964) has recently replaced *Corvaspis* in the Cyathaspida (=Cyathaspidiformes), but this procedure is not here accepted.

DINELEY (1965*b*) included a restoration of this genus which was indistinguishable from *Drepanaspis* except for sensory tentacles at the lateral margins of the mouth. There is not sufficient evidence yet for a reconstruction of *Corvaspis* to be feasible, but in any case the branchial plates and median plates known suggest that it would have been rather more „box-like" than indicated by DINELEY. Furthermore, the sensory tentacles were a fiction introduced by STENSIÖ (1958) to explain away the olfactory notches found in the cyathaspids (see TARLO, 1961*c*).

Corvaspis kingi WOODWARD, 1934

(Pl. III)

1927. Palaeaspid; O. JAEKEL, Der Kopf..., pp. 925, text-fig. 53C.
1934. *Corvaspis kingi* n. sp.; A. S. WOODWARD, Note on a new..., pp. 566-567, pl. 19, figs. 1-3.
1953. *Corvaspis kingi* WOODWARD; D. L. DINELEY, Notes on the..., pp. 166-181, pl. 1, figs. 1-5; pl. 2, figs. 1, 2; text-figs. 1-6, 9-14, 16.
1955. *Corvaspis kingi* WOODWARD; A. P. BYSTROW, The microstructure..., pp. 491-497, text-figs. 19-21.
1958. *Corvaspis kingi* WOODWARD; E. A. STENSIÖ, Les Cyclostomes..., pp. 321-326, text-figs. 181A, 182.
1960*b*. *Corvaspis kingi* WOODWARD; L. B. TARLO, The Downtonian..., pp. 217-224, pl. 37, figs. 1-8; pl. 38, figs. 1-6; text-figs. 1-3, 5.
1961. *Corvaspis* sp. indet. WOODWARD; W. GROSS, Aufbau des Panzers..., pp. 96-100, text-figs. 8A-D, 9.
1964*b*. *Corvaspis kingi* WOODWARD; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 19, 42, 73—75, 96; pl. 9, fig. 2, text-figs. 15 B-F.
1964*b*. *Corvaspis kingi* WOODWARD; E. A. STENSIÖ, Les Cyclostomes..., pp. 258-261, text-figs. 83 A-C, 84.
1964*b*. *Corvaspis* sp. WOODWARD; E. A. STENSIÖ, *Ibid.*, p. 259, text-fig. 83D.
1964. *Corvaspis kingi*, WOODWARD; D. OBRUCHEV, Subclass Heterostraci..., pp. 49, 59; pl. 5, fig. 5, text-figs. 9, 20, 21.

Holotype: Part of median plate P. 16446, housed in the British Museum (Natural History), London, figured by WOODWARD (1934, Pl. 19, fig. 1), STENSIÖ (1958, Text-fig. 181A), and in the present work, Pl. III, fig. 1.

Type horizon and locality: Lower Devonian (Gedinnian), Lower Dittonian, *Traquairaspis symondsi* zone; Earnstrey Hall, Shropshire, England.

Diagnosis. — Ornamentation of short, longitudinally aligned dentine ridges arranged in superficial tesserae, generally separated from one another by a narrow groove. Width of ridges greater than in *Corvaspis graticulata*.

Material. — Numerous plates: medial, branchial and orbital, as well as tesserae and scales from the Lower Gedinnian of Anglo-Wales, Spitsbergen and Podolia.

Description. — The holotype (P. 16446 B. M.) is the anterior portion of a median plate which is ornamented by short, longitudinally arranged dentine ridges, separated into superficial tesserae by narrow grooves. The ridges are all the same width, and although similar to those of *Kallostrakon macanuffi*, are distinct, since they appear to have arisen simultaneously. Thus, although superficial tesserae are clearly present, the major growth of the plate was apparently synchronomorial. The margins of the plate are composed of an irregular band of rounded tubercles which are short lengths of the normal ornament, and these indicate that there was a zone of cyclomorial growth around the plate as a whole. This is obviously a characteristic of the form, since most of the plates known possess such a marginal zone. A complete median plate (P. 40575 B. M.) and the median plate 643 B. U. both show that in the posterior part of the plate, the synchronomorial tesserae are separated from one another by narrow zones of round tubercles, and it is at this point that they grade into the squamation. Frequently, as in specimens P. 40573 and P. 42846 B. M., it is clear that isolated tesserae have become incorporated into the margins of the median plate, and this suggests that surrounding the median plate in the carapace was a zone of tesserae — a characteristic feature of the Psammosteiformes. It is true that tesserae are also known incorporated into the median plate of *Traquairaspis*, but this is merely a stage in the normal growth of the plate and is different from the situation in *Corvaspis* where this condition is only rarely found, and isolated tesserae are also known. The median plates as a whole have a very irregular outline, but they are always longer than they are wide and are frequently oval in shape and arched gently from side to side. The fact that they are so irregular again suggests that one large plate of the carapace does not abut directly against another, but that there was a zone of small plates or tesserae

intervening. One of the significant features of the species described here is that it is possible to demonstrate within the ornament every gradation from forms in which the superficial tesserae each have a narrow zone of cyclomorial growth around them to forms where dentine ridges run almost unbroken the whole length of the plate. This final stage is reached through forms where the tesserae are delimited by narrow grooves, then through others where some of the ridges of adjacent tesserae are confluent, and lastly by way of yet others where there are long dentine ridges running the length of the plate, but signs of the earlier growth patterns are still evident in the short transverse grooves present and certain irregularities in the ornament (see TARLO, 1960*b*). This series of changes is also discussed in the General Part of the present work (TARLO, 1964*b*).

Besides the median plates, orbital plates are known, and the major part of one large flat orbital plate (P. 42841 B. M.) indicates that it belonged to a fairly flat carapace, and that the animal was therefore likely to be somewhat dorso-ventrally compressed, with the orbit more on the dorsal surface than lateral. Although one corner is missing, the plate appears to be fairly rectangular, with a wide zone of concentrically arranged arcuate dentine ridges around the orbit. The margin of the plate is ornamented by a zone of small rounded tubercles, but on one side between this marginal zone and the concentric zone of the orbit, there are 4 sensory pores, each of which is surrounded by a series of dentine rings. A branchial plate (P. 42842 B. M.) is roughly oval, but elongated, and is arched from side to side, and when this plate was first described by DINELEY (1953) it was interpreted as a ridge plate which he believed was situated in the median part of either the dorsal or ventral surface of the carapace (see TARLO, 1960*b*). The plate is ornamented by short dentine ridges aligned longitudinally, and is roughly divided up by transverse grooves into a suggestion of superficial tesserae. The ridges run parallel to the dorsal and ventral margins, so that in the mid-line they tend to meet at an angle. A further specimen (653 B. U.) is fairly similar in shape, but is characterized by the fact that in the median zone the ornament is thrown into loops. Fragments of this zone are easy to recognize and are not uncommon. Also in this specimen, a number of sensory pores can be seen running above this area, each of them being surrounded by concentric dentine rings. A small plate (P. 42843 B. M.) which was figured by TARLO (1960*b*) as a lateral plate, now seems to be rather similar in outline to the lozenge-shaped but highly variable pineal plate of *Drepanaspis* (GROSS, 1963). In consequence, it is now tentatively suggested that this plate too is a pineal. The central part of the plate is ornamented by a number of synchronomorial units composed of short, longitudinally aligned dentine ridges, the units themselves being arranged in a random manner. Surrounding them is a wide marginal zone of small tubercles forming the natural limit of the plate.

No post-orbital plates are known in this form, for it now seems that specimen P. 40574 B. M. tentatively identified as such by TARLO (1960*b*) may well be a somewhat asymmetrical median plate, since the general flatness of this plate would seem to militate against it making up part of the lateral margin. Small isolated cyclomorial tesserae are also known occasionally such as specimen P. 42847 B. M., as well as synchronomorial tesserae exemplified by P. 42844 B. M. Scales are also present, these being ornamented by longitudinal dentine ridges in the distal part, with a proximal unornamented portion which in life was covered by the preceding overlapping scale (see DINELEY, 1953).

Discussion. — A fragment of this species from Spitsbergen was figured, although not named, by JAEKEL (1927), but WOODWARD (1934) who was not aware of JAEKEL'S work, gave the first description of the species based on material from England. Subsequently it was recorded from Podolia by STENSIÖ (1944) although material from there was not figured by him

until 1958. When the material from England was first described, it was thought to be cyathaspid in nature, but DINELEY (1953) was able to establish that it could not belong to that group since it possessed discrete orbital plates. He also described plates which he named ridge plates, and thought belonged to the mid-line of the carapace, but these were subsequently recognized as branchial plates (TARLO, 1960*b*) since they were markedly asymmetrical and were similar to the branchials of other heterostracans. DINELEY (1953) whilst recognizing that „it may have been akin to the Drepanaspidae", erected the new family Corvaspidae to receive the genus *Corvaspis*, taking it to be a separate group of the Heterostraci of equal rank to the pteraspids and psammosteids. This was accepted by STENSIÖ (1958) who raised it to the rank of order, calling it the Corvaspida. On the other hand, TARLO (1960*b*) believed that the genus *Corvaspis* could be included within the Psammosteidae, although later (1962*c*) he recognized that although *Corvaspis* should still be retained as a psammosteid within the order Psammosteiformes, it should be placed in the suborder Tesseraspidida as a separate family, the Corvaspididae. Thus, although DINELEY's name is now accepted again, it is in a different context.

After WOODWARD'S original description, DINELEY (1953) described a considerable amount of new material, while BYSTROW (1955) described and discussed the histology of the plates, and STENSIÖ (1958) gave a detailed discussion of the significance of the ornamentation based on the figured material of WOODWARD and DINELEY. TARLO (1960*b*) gave a further description of the genus based on new material and was able to extend STENSIÖ's analysis of the significance of the variation in the ornamentation. STENSIÖ (1958) suggested that *Penygaspis* might be a specialized corvaspid, but TARLO (1960*b*, 1962*d*) was able to demonstrate that it was in fact a pteraspid at the same structural grade as *Corvaspis*, in that it possessed a major central synchronomorial unit in the median plate with a narrow zone of cyclomorial growth surrounding it. DENISON (1953) compared *Corvaspis* with *Cardipeltis*, but he did this immediately before DINELEY'S paper appeared, which is unfortunate, for with its help DENISON could probably have shown rather closer parallels. It was later suggested (TARLO, 1960*b*) that *Cardipeltis* could well be a descendent from *Corvaspis*, and TARLO (1962 *c*, *d*) reiterated the view that the Cardipeltiformes were probably derived from the psammosteids by way of *Corvaspis* or a related form.

Corvaspis graticulata DINELEY, 1953

1953. *Corvaspis graticulata* n. sp.; D. L. DINELEY, Notes on the..., pp. 175-176, pl. 2, figs. 4, 5, text-figs. 7, 8, 15.
1958. *Corvaspis graticulata* DINELEY; E. A. STENSIÖ, Les Cyclostomes..., p. 323, text-fig. 181E.
1964*b*. *Corvaspis graticulata* DINELEY; E. A. STENSIÖ, Les Cyclostomes..., p. 259, text-fig. 84E.

Holotype: Part of a median plate, D. 2664, housed in the Palaeontological Museum, Oslo, figured by DINELEY (1953, Pl. 2, fig. 3), and by STENSIÖ (1958, Text-fig. 181E; 1964*b*, Text-fig. 84E).

Type horizon and locality: Lower Devonian (Gedinnian), Red Bay Series, Ben Nevis horizon; Ben Nevis, Spitsbergen.

Diagnosis. — Ornamentation of short, longitudinally aligned dentine ridges arranged in superficial tesserae, separated from one another by a double row of small round flat-topped tubercles, of similar diameter to width of ridges. Width of dentine ridges less than in *Corvaspis kingi*.

Material. — Fragments of plates from the Ben Nevis horizon, Spitsbergen.

Description. — The holotype (D. 2664 P. M. O.) is part of a median plate ornamented by typical *Corvaspis* synchronomorial superficial tesserae, but in which the dentine ridges are

narrower than in those of the type species. The tesserae are separated from one another by a very characteristic and regular pattern of a double row of small rounded flat-topped tubercles. Although a similar arrangement does occur in some parts of certain specimens of *C. kingi*, the regular nature of the tesserae in *Corvaspis graticulata* enables it to be distinguished easily, as also does the width of the ridges. Furthermore, *C. graticulata* occurs at a higher horizon than does *C. kingi*.

Corvaspis karatajuteae n. sp.

1962. *Corvaspis* cf. *kingi* WOODWARD; V. KARATAJŪTĖ-TALIMAA, Description of remains..., pp. 49-50, 52, pl. 1, figs. 1-14, text-figs. 1, 1-5.

Holotype: Fragment of median plate, No. 5-1184, housed in the Geological Institute, Vilnius, figured by KARATAJŪTĖ-TALIMAA (1962, pl. 1, fig. 1).

Type horizon and locality: Lower Devonian (Gedinnian), Lower Dittonian, *Traquairaspis* zone; borehole at 850.45 m., Stačiūnai, Lithuania.

Derivation of name: karatajuteae — in honour of Dr. V. KARATAJŪTĖ-TALIMAA of the Geological Institute, Vilnius.

Diagnosis. — Ornamentation of short, longitudinally aligned dentine ridges, with very ill defined indication of superficial tesserae.

Material. — Fragments of median, branchial and orbital plates, together with numerous scales from the Lower Dittonian of Lithuania.

Description. — The holotype (5-1184) consists of part of the margin of a median plate. This is shown by the closely-packed, irregularly oval flat-topped tubercles in one corner, since these are characteristic of the periphery of median plates in this genus. Many of the dentine ridges in the main part of the plate are very long with adjacent parallel ridges divided into shorter sections. Some of the ridges appear slightly more prominent than others, and are somewhat reminiscent of the ornamentation of *Kallostrakon macanuffi*. The type of ornamentation falls outside the considerable range described and figured by TARLO (1960*b*), and thus the erection of a new species of *Corvaspis* would seem to be amply justified. The name *C. karatajuteae* is therefore here proposed.

The fragment (5-1185) is clearly part of a branchial plate (formerly erroneously identified as „ridge-plates" by DINELEY, 1953). The central portion of an orbital plate (5-1113) appears to have a much coarser ornament than the rest of the material figured by KARATAJŪTĖ-TALIMAA (1962), but seems to be comparable to that known in *C. kingi*. However, according to measurements in the text, the ornamentation of the figured material is not significantly finer than the type species. The numerous scales figured by KARATAJŪTĖ-TALIMAA (1962) appear to be indistinguishable from those known in *C. kingi* and in fact isolated scales are indeterminable as far as species are concerned.

CORVASPIDIDAE gen. et sp. nov.

DINELEY (1965*a*) recorded the presence of *Corvaspis* n. sp. in the Lower Devonian (Gedinnian), Peel Sound Formation of Somerset Island, Arctic Canada. Later (1965*b*) he figured a dorsal median plate as a corvaspid. The flat-topped dentine ridges of the ornament of this plate are irregular and have coarsely crenulated edges, unlike those found in *Corvaspis* which are smooth. In consequence, this new form cannot be included in this genus. Of much greater significance however, is the concentric arrangement of the ridges themselves, for this indicates that the main plates grew by cyclomorial-areal-growth throughout early development.

This is in contrast to the synchronomorial growth found in *Corvaspis*, at a late developmental stage. This new genus illustrates the same evolutionary trend as that already documented in detail by TARLO (1960*b*, 1962*d*, 1964*b*), but is the first evidence that the corvaspids reached the stage in which cyclomorial growth occurs around a small central primordium, such as is seen, for example, in normal pteraspids. *Corvaspis* itself was at the same stage as the primitive pteraspid *Penygaspis*, but with the discovery of this new form, it is now clear that the corvaspid line evolved considerably further than was previously realized. It is therefore a highly significant form, since it now makes it possible to trace a complete evolutionary sequence in the change from the superficial cyclomorial tesserae of *Kallostrakon macanuffi*, through the synchronomorial superficial tesserae and later synchronomorial plates with narrow surrounding zones of cyclomorial growth, of *Corvaspis kingi*, to the fully cyclomorial plates of the new genus. The new form from Somerset Island further indicates that there was more than one evolutionary line from *Corvaspis* — one leading to the Cardipeltiformes, and the other to this new genus.

Family WEIGELTASPIDIDAE BROTZEN, 1933

Diagnosis. — Dorsal median plate long and narrow, with prominent median ridge in posterior half of plate. Ventral median plate long and narrow with steep sides and fairly flat bottom. Branchial plate forming arcuate lateral margin of carapace, mainly on ventral surface; wide posteriorly, narrow anteriorly; appears to have only a narrow dorsal extent as it curves over at margin just on to dorsal side. Ventral median and branchial plates separated by zone of tesserae. Orbital plate present; irregular post-orbital plate gently arched from dorsal to ventral surface. Ornamentation of widely separated elongated tubercles with marked prominent crenulations.

Genus **WEIGELTASPIS** BROTZEN, 1933

Type species: *Weigeltaspis alta* BROTZEN, 1933

Diagnosis. — As for family, only genus.

Occurrence. — Lower Devonian (Upper Gedinnian), Podolia, Anglo-Wales, Spitsbergen and Latvia.

Discussion. — This genus was erected by BROTZEN (1933*a*) to include the new species *W. alta*, based on a dorsal median plate which was originally incorrectly interpreted as a branchial plate. BROTZEN suggested that this form was related to the psammosteids, although he erected the new family Weigeltaspidae for it. In his description of the histology he considered that there was a thick enamel cap over the tubercles which led WILLS (1935) when discussing the species, to suggest that it was strikingly different from *Tesseraspis* in the histology of its tubercles. In actual fact, there is no enamel cap present in *Weigeltaspis*, and the complex pulp cavities and dentine tubules of the tubercles of both genera are clearly similar in nature. WILLS did however agree with BROTZEN that *Weigeltaspis* was closely related to the psammosteids. WHITE (1935) recorded this genus from the Welsh Borderland, although he considered it to be an arthrodire, but GROSS (1937) like WILLS and BROTZEN regarded the genus as a probable psammosteid, and both BERG (1940) and OBRUCHEV (1941) included the Weigeltaspidae as a grouping of the psammosteids. DENISON (1956) considered this genus

as a heterostracan of uncertain affinities, a view also put forward by ØRVIG (1961). However, TARLO (1961*a*) placed it in the psammosteids and mentioned that the branchial plate was long and narrow and gently arched from side to side. He also mentioned that there was a rectangular post-orbital plate in which the lateral margin was slightly downturned, but this latter plate is now known to be the posterior part of the branchial plate, which is situated on the ventral surface, and the plate identified as a branchial might perhaps be part of a post-orbital plate. Subsequently (TARLO, 1962*c*) the family Weigeltaspididae while still being retained in the Psammosteiformes, was placed in the suborder Tesseraspidida. In this latter work it was suggested that the rostral area of the carapace might also have been composed of tesserae, but it is now known that there is no evidence for this, the error being due to the posterior part of the carapace having been mistaken for the anterior part.

From the new material described in the present work it is evident that the carapace of *Weigeltaspis* is very similar to that of many of the advanced psammosteids. There is, however, insufficient evidence at the moment to determine whether the full complement of plates found in the advanced forms were also present in this genus. It is therefore being retained in the suborder Tesseraspidida.

OBRUCHEV (1964) has included this genus and its family in the Traquairaspidida (= Traquairaspidiformes), but by means of the new material available, this can now be demonstrated to be incorrect.

Weigeltaspis alta BROTZEN, 1933

(Pl. IV, figs. 3, 4; Pl. V, fig. 1; Text-fig. 2*A*)

1933*a*. *Weigeltaspis alta* n. sp.; F. BROTZEN, Weigeltaspis nov. gen..., pp. 648-655, text-figs. 1-4.
1935. *Weigeltaspis* BROTZEN; L. J. WILLS, Rare and new..., p. 439.
1936. *Weigeltaspis alta* BROTZEN; F. BROTZEN, Beiträge zur..., p. 7.
1937. *Weigeltaspis* BROTZEN; W. GROSS, Die Wirbeltiere..., p. 12.
1940. *Weigeltaspis* BROTZEN; L. S. BERG, Classification..., p. 361.
1941. *Weigeltaspis* BROTZEN; D. OBRUCHEV, Remains of..., p. 21.
1950. *Weigeltaspis alta* BROTZEN; J. SAMSONOWICZ, Dewon..., p. 503.
1950. *Weigeltaspis alta* BROTZEN; W. GROSS, Die paläontologische..., p. 49.
1955. *Weigeltaspis* BROTZEN; L. S. BERG, Classification..., p. 28.
1956. *Weigeltaspis* BROTZEN; R. H. DENISON, A review of..., p. 404.
1957. *Weigeltaspis [alta]* BROTZEN; L. B. TARLO, A preliminary note..., p. 229.
1961. *Weigeltaspis alta* BROTZEN; T. ØRVIG, Notes on some..., pp. 518-523, text-fig. 1.
1962*c*. *Weigeltaspis alta* BROTZEN; L. B. TARLO, The Classification..., p. 259.
1964*b*. *Weigeltaspis alta* BROTZEN; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 19, 39, 74, text-fig. 14C.
1964. *Weigeltaspis alta* BROTZEN; D. OBRUCHEV, Subclass Heterostraci..., pp. 62, 63, text-figs. 27, 28.

Lectotype (here selected): Dorsal median plate housed in the Geological-Palaeontological Institute, Halle, Germany, figured by BROTZEN (1933*a*, Text-fig. 1) and in the present work, Pl. IV, fig. 3.

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

Diagnosis. — Ornamentation of large, well separated tubercles with an outline reminiscent of the leaves of an oak tree *(Quercus robur)*, with fine more or less longitudinal striae converging proximally.

Material. — Numerous plates and fragments from the Upper Gedinnian of Podolia.

Description. — The lectotype consists of part of a dorsal median plate in which the characteristic posterior median ridge is strongly developed. A small portion of the original plate is preserved on the specimen which is a natural cast of the inner surface of the plate.

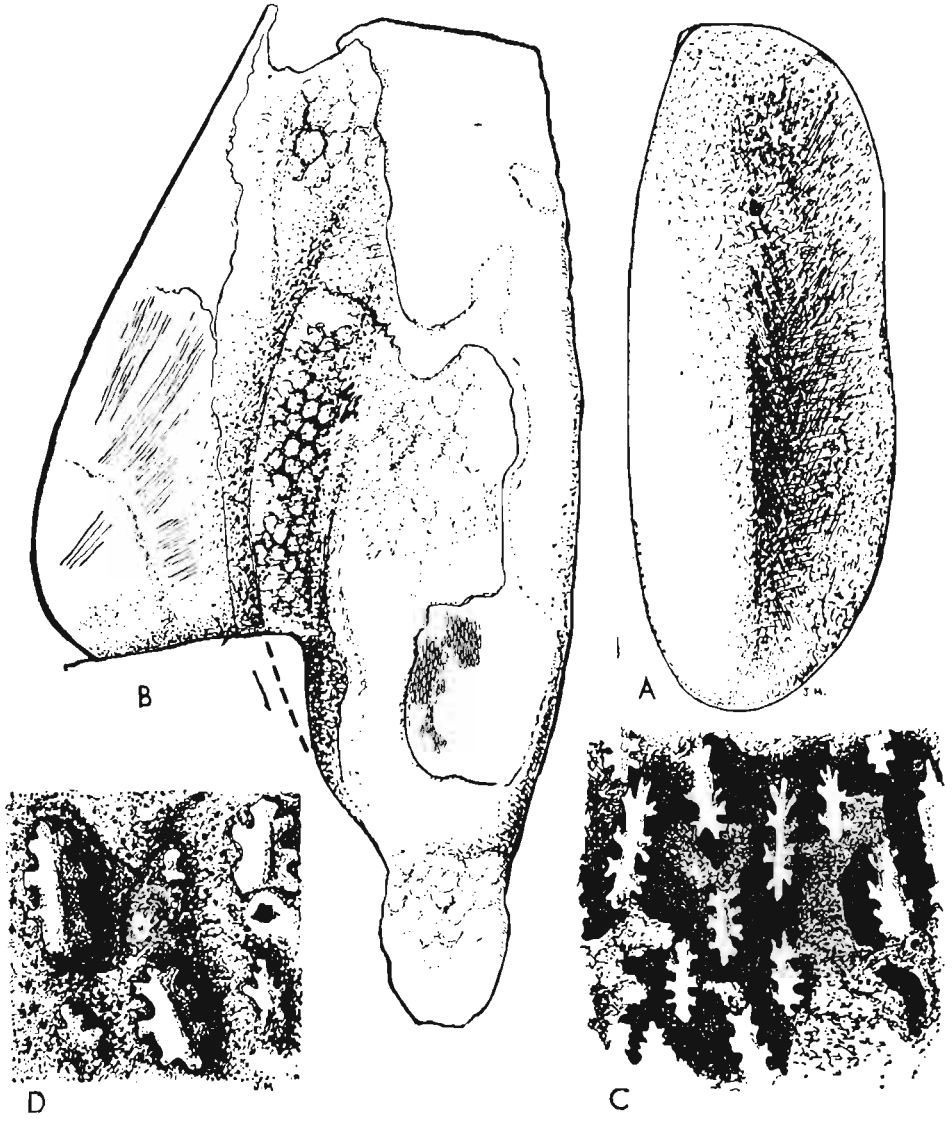

Fig. 2

A Weigeltaspis alta BROTZEN — dorsal median plate (B.M., P. 18221-2, Burakowska), × 1; *B-C Weigeltaspis heintzi* TARLO — *B* carapace in ventral view showing convex ventral median plate, laterally projecting branchial plate, and intervening field of tesserae (P.M.O., E.N.S. Exp. 88, Ben Nevis); × 0·5; *C* holotype, detail of ornamentation (P.M.O., D. 2440-1, Ben Nevis), × 5; *D Weigeltaspis godmani* TARLO, detail of ornamentation (M.M., L. 8530), × 5.

When described by BROTZEN, this plate was interpreted as a branchial plate, but it is now known to be a dorsal median plate. A more complete dorsal median plate (P. 18221, and counterpart P. 18222 B. M.) again shows the characteristic median ridge which is most strongly developed in the posterior part of the plate (Text-fig. 2*A*). It dies out suddenly posteriorly, but flattens gradually anteriorly. In outline, the plate is a long oval, being about three times as long as it is wide, and it is ornamented by the characteristic large, well spaced oak-leaf-like tubercles. These are aligned more or less longitudinally, although in the posterior part of the plate they occasionally swing in towards the mid-line. A fragment of ornament which is a na-

tural mould (un-numbered specimen G. P. I. H.), figured by BROTZEN (1933*a*), is refigured in the present work with reverse lighting and shows the characteristic appearance of the tubercles. Similar although better preserved tubercles were figured by ØRVIG (1961) in specimen C. 1728 R. S.

Discussion. — *Weigeltaspis alta* was described by BROTZEN (1933*a*) as belonging to a new family, the Weigeltaspidae, which he considered to be close to the psammosteids. To some extent this was due to his identification of the plate he figured as a branchial plate, which he compared with the branchials of psammosteids. WILLS (1935) noted that the ornamentation of *Weigeltaspis* seemed to be rather similar to that of *Tesseraspis*, but suggested that in the histology of its tubercles it was "built on exactly the same plan as... in the drepanaspids and psammosteids". He considered, however, that although *Weigeltaspis* was closely allied to the psammosteids, it was different from *Tesseraspis* in the histology of its tubercles, so that it could not be considered to have a close relationship with it. BROTZEN had suggested that the tubercles of *Weigeltaspis* had a very thick development of enamel over them, and this feature according to WILLS served to distinguish the genus from *Tesseraspis*. However, as mentioned previously, when sections of the armour of *Weigeltaspis* are examined, it is evident that no enamel is present, but as in most heterostracans, the dentine tubules break up into fine terminal branches towards the external surface and are only visible under very high power. In fact, in the detail of the histology of the tubercles, *Weigeltaspis* and *Tesseraspis* are very similar.

BROTZEN (1936) listed the species as did SAMSONOWICZ (1950) in his faunal list, and the form seemed to mark BROTZEN's Stage I in the Old Red sequence of Podolia. ØRVIG (1961) who figured part of the ornamentation also followed BROTZEN's interpretation of his material as branchial plates. Later (1962*c*) TARLO pointed out that they were probably dorsal median plates and not branchials.

Weigeltaspis brotzeni TARLO, 1964

(Pl. V, figs. 2, 3)

1964*b*. *Weigeltaspis brotzeni* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., p. 112.

Holotype: Fragment of plate P. 18266, housed in the British Museum (Natural History), London, figured in the present work, Pl. V, fig. 3.

Type horizon and locality: Lower Devonian (Gedinnian), Stage I of BROTZEN, *Podolaspis lerichei* zone; Uscieczko, Dniestr, Podolia, Ukraine.

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

Material. — Several fragments of plates from the Upper Gedinnian of Podolia.

Description. — The holotype (P. 18266 B. M.) consists of a somewhat rectangular convex fragment of a plate on which the ornament of typical tubercles seen in *Weigeltaspis* is aligned more or less parallel to the main axis of the plate. The specimen seems to be quite distinct from the more typical fragments of *Weigeltaspis* found in Podolia which belong to *W. alta*, and hence it warrants specific distinction, since although its ornamentation is of the same character as that of *W. alta*, it is of a quite different order of magnitude. The name *Weigeltaspis brotzeni* was therefore proposed for its reception. A further specimen of this species (P. 20605-4 B. M.) from the same locality, is an orbital plate. This is asymmetrical, with the

orbit situated to one side. Some of the tubercles of the ornament are arranged concentrically around the orbit, while others are arranged radially, and the majority are fairly short with prominent short lateral ribs, giving the characteristic oak-leaf outline.

Weigeltaspis godmani TARLO, 1964

(Pl. V, figs. 4-8; Text-fig. 2 *D*)

1935. *Weigeltaspis* BROTZEN; E. I. WHITE, The Ostracoderm..., p. 385.
1946. *Weigeltaspis* BROTZEN; E. I. WHITE, The genus Phialaspis..., p. 214.
1950. *Weigeltaspis* BROTZEN; E. I. WHITE, The Vertebrate faunas..., p. 56.
1952. *Weigeltaspis* sp. BROTZEN; H. W. BALL & D. L. DINELEY, Notes on the..., p. 213.
1956. *Weigeltaspis* BROTZEN; R. H. DENISON, A review of..., p. 394.
1961*a*. *Weigeltaspis* BROTZEN; L. B. TARLO, Psammosteids from..., p. 207.
1961. *Tesseraspis* sp. WILLS; E. I. WHITE, The Old Red..., p. 245.
1964*b*. *Weigeltaspis godmani* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 58, 74, 112; pl. 4, fig. 5, pl. 9, figs. 5, 6, text-fig. 19B.

Holotype: Ventral median plate with associated branchial plate P. 23747-23748, housed in the British Museum (Natural History), London, figured in the present work, Pl. V, figs. 7, 8.

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

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

Material. — Numerous plates from the Upper Gedinnian of Shropshire, Herefordshire and Monmouthshire, England.

Description. — The holotype (P. 23747-23748 B. M.) consists of a rectangular fragment of a ventral median plate, ornamented by the characteristic but widely spaced and rather stubby tubercles of oak-leaf outline. The lateral margin of the plate is present and it appears to turn up sharply from the fairly flat central area, almost at right angles. This indicates that the plate as a whole was somewhat basin-shaped having steep sides and a flat bottom. Adjacent to the ventral median plate is part of a branchial plate in which the lateral margin, which is slightly arcuate in outline, appears to be abraded. The tubercles are aligned at a slight angle to the margin, and there is a faint indication of growth lines. Unfortunately both the posterior and anterior margins of this plate are missing. A fragment of the posterior part of a branchial plate (P. 20200-20201 (B. M.) however, shows an arcuate lateral margin which swings round into a fairly straight transverse posterior margin, the lateral margin being somewhat upturned. Specimens P. 23751-2 and P. 25053-4 B. M. also appear to represent portions of branchial plates. Such specimens were previously (TARLO, 1961*a*) erroneously interpreted as post-orbital plates, but it is evident that the branchial plates were not merely a fused row of arched elements at the lateral margin, but were prominent plates forming a large proportion of the ventral surface of the carapace. Nevertheless, at the lateral margin they did turn upwards on to the dorsal surface. It is of interest to note that the immature branchial plates of *Drepanaspis* are also flat plates situated on the ventral surface, with merely their lateral edges slightly upturned (GROSS, 1963). Typical dorsal median plates are also known in the species here described, specimens P. 23749-50 and P. 19161 B. M. being elongated narrow plates with a well marked median ridge in the posterior part. A fragment of a plate which is difficult to interpret is P. 19165-6 B. M., for this is elongated and is arched from side to side so that in section it

appears more or less semi-circular. Clearly this plate belongs to the lateral margin since it is not a dorsal or ventral plate. It may perhaps be the anterior part of a branchial plate, but it is more likely to be part of a post-orbital. In some respects it is surprisingly reminiscent of this plate in *Psammosteus* (TARLO, 1961*a*). ØRVIG (1961) mentioned the specimen P. 33149 B.M. which shows the ornamentation, and this is figured in the present work together with a further specimen (L. 8530 M. M., Text-fig. 2*D*).

Discussion. — The first mention of *Weigeltaspis* from the Anglo-Welsh Province was by WHITE (1935) who subsequently (1946, 1950) referred to the presence of this genus. It was mentioned also by BALL & DINELEY (1952), and DENISON (1956). The remarks on this genus by TARLO (1961*a*) were in the main based on material from Anglo-Wales, whilst ØRVIG (1961) referred to a specimen from this region and noted that the ornamentation was highly reminiscent of the Podolian species. In addition, WHITE (1961) mentioned isolated tesserae from this genus, but referred them to *Tesseraspis*. The species from England although reminiscent of *Weigeltaspis alta* from Podolia seems to be quite distinct in its ornamentation, and in consequence placed in the separate species *W. godmani*.

Weigeltaspis heintzi TARLO, 1964

(Pl. IV, figs. 1, 2; Text-figs. 2*B-C*)

1961. *?Weigeltaspis* BROTZEN; T. ØRVIG, Notes on some..., pp. 520-521.
1962*c*. *Weigeltaspis* BROTZEN; L. B. TARLO, The Classification..., p. 259.
1964*b*. *Weigeltaspis heintzi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 25, 96, 112; pl. 4, figs. 6, 7.

Holotype: Dorsal median plate D. 2440—D. 2441, housed in the Palaeontological Museum, Oslo, figured by TARLO (1964*b*, Pl. 4, figs. 6, 7) and in the present work, Pl. IV, fig. 2, Text-fig. 2*C*.

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

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

Material. — Dorsal, ventral and branchial plates from the Upper Gedinnian of Ben Nevis, Spitsbergen.

Description. — The holotype (D. 2440-D. 2441 P.M.O.) consists of a dorsal median plate which is a narrow elongated plate, the posterior margin of which is missing. In the midline there is a characteristic ridge which is very prominent at the posterior part of the plate, but becomes more rounded and dies out anteriorly. Also preserved in the holotype are fragments of the ornamentation of tubercles, these being almost as long as those of *Weigeltaspis alta*, but as much as a third narrower (Text-fig. 2*C*). However, as with other species of *Weigeltaspis*, the fine striae running from the lateral ribs on to the main part of the tubercles can still be made out. In the form here described, the tubercles are all aligned longitudinally. Also from Ben Nevis, is part of a similarly ornamented articulated carapace Field No. 88, discovered by the English-Norwegian-Swedish Spitsbergen Expedition of 1939, and kindly passed on to me by Dr. T. ØRVIG (Text-fig. 2*B*). In the carapace is an oblong ventral median plate which has very steep sides, which then pass into a zone of tesserae. In the posterior part of the carapace behind the ventral median plate, the squamation is visible. Also seen in this specimen is the major part of the lateral margin of the carapace on the right side, in which there is a very large branchial plate with a gently convex lateral margin. The posterior margin of the branchial plate appears to be fairly straight. The shape of the carapace as a whole therefore is similar to that found in more advanced psammosteids, where there is a deep ventral plate and laterally projecting

branchials. In this specimen however it is not possible to ascertain the relationship of the dorsal elements of the carapace.

Discussion. — Although the holotype was discovered in 1928, in VOGT's Expedition, no mention was made of this form until ØRVIG (1961) noted the presence of an undescribed heterostracan from Spitsbergen, probably very closely related to *Weigeltaspis*. The specimen mentioned by ØRVIG (D. 3061 P. M. O.) as consisting of two elongated plates of the carapace behind which are a group of scales, now seems to be the postero-lateral part of a ventral median plate, including part of the flat bottom of this plate and part of one of its steep sides. Because of the angle at which this plate has been preserved it gives the impression of two separate plates. There can be no doubt that all this material belongs to the same species, and that the species belongs to the genus *Weigeltaspis*. However, its ornamentation is sufficiently distinct to warrant it being placed in a separate species for which the name *W. heintzi* was proposed.

Weigeltaspis sp.

LIEPINS (1959) described and figured from Latvia, a tubercle from a heterostracan which he compared with those of *Tesseraspis* and *Weigeltaspis*. From his figure it appears to be referable to *Weigeltaspis*, although it is not possible to make any suggestion as to species. It occurs with a pteraspid which appears to be close to *Pteraspis crouchi*, thus suggesting an Upper Gedinnian age in which only *Weigeltaspis* among the psammosteids is known to occur, thus helping to confirm the genus here suggested for it.

Suborder **PSAMMOSTEIDA** KIAER, 1932

Diagnosis. — Carapace composed of 12 main plates: dorsal and ventral median, rostral, pineal and paired orbital, postorbital, branchial, and cornual. Median plates separated from those of lateral margin by zone of small polygonal plates (fields of tesserae). Anterior margin of ventral surface of carapace formed by "median tesserae", paired "complex-plate", median and lateral marginal plates (GROSS, 1963). Oral plates (seven) with prominent oral tooth lamellae, situated dorsally forming anterior margin of dorsal surface of carapace. Tail almost equilobate, with lower part somewhat longer than upper.

Family DREPANASPIDIDAE TRAQUAIR, 1899

Diagnosis. — Dorsal median plate with anterior and posterior re-entrant angle; ventral median plate convex with variable posterior median notch. Branchial plate long and narrow with branchial opening situated at postero-lateral corner. Post-orbital plate wide anteriorly, narrowing to a point posteriorly.

Discussion. — The family Drepanaspidae was erected by TRAQUAIR (1899) who kept it separate from the Psammosteidae. At first, authors such as BRIDGE (1904) and GOODRICH (1909) also kept the two families separate, but they were later united into one family, some authors employing the name Psammosteidae (e. g. KOKEN, 1911; KIAER, 1915), whilst others used Drepanaspidae (e. g. ABEL, 1919, 1921, 1924; STENSIÖ, 1927; WOODWARD, 1932; WHITE, 1935; ROMER, 1946), although the former name had priority. Subsequently BERG (1940, 1955) and

OBRUCHEV (1941) kept the two families separate as independent groups. Although this procedure was also followed by PARKER & HASWELL (1940) and KUHN (1940), they were merely following the earlier text-books and no further discussion of the relationships of the two families was given. WÄNGSJÖ (1952) listed the name Drepanaspididae for both groups, using the correct spelling of the family name for the first time, and TARLO (1962*c*) following the Russian authors BERG and OBRUCHEV retained the Drepanaspididae as a distinct family separate from the Psammosteidae.

The main distinguishing feature of the Drepanaspididae is their possession of the full complement of plates in the carapace characteristic of the suborder Psammosteida, with little or no development of the lateral extensions to the carapace found in the more advanced families. This family seems to have flourished on the muddy bottoms of shallow seas and may well represent a marine side-branch of the psammosteids (TARLO, 1957), although there seems to be no evidence for PATTEN's (1932) view that they fed on starfish which they scooped up off the substratum. Like most other heterostracans they are likely to have been mud grubbers. The family comprises the genus *Drepanaspis*, of which 6 species are here recognized, and in addition the genus *Psephaspis* containing two species, is tentatively assigned to the family.

Genus **DREPANASPIS** SCHLÜTER, 1887

Type species: *Drepanaspis gemuendenensis* SCHLÜTER, 1887

Diagnosis. — Branchial plates long and narrow with marked postero-median flange on ventral surface and narrow free lateral margin. Post-orbital plates with sinuous medial margin and narrow posterior extension medial to anterior part of branchial plate. Ornamentation of rounded crenulated tubercles.

Occurrence. — Lower Devonian (Siegenian-Emsian); South West England, Ardennes and Rhineland.

Discussion. — The genus *Drepanaspis* was originally described by SCHLÜTER (1887) as a cephalaspid, but TRAQUAIR (1896*a*) claimed that it was a heterostracan representing a new family allied to the pteraspids. However, no figures were given of this genus until TRAQUAIR (1899) produced an attempt at a restoration. TRAQUAIR considered that *Drepanaspis* was closely related to *Psammosteus*, but he was unable to make a direct comparison between the microstructure of the plates in the two genera. However, this was later accomplished by KIAER (1915) who demonstrated that they were similar, thus confirming the close affinity between *Drepanaspis* and *Psammosteus*. TRAQUAIR's main description of the genus *Drepanaspis* (1903) included photographs of fairly complete carapaces, but unfortunately he mistook the dorsal for the ventral surface and in consequence his identification of the plates was reversed. Although at the time DEAN (1904) pointed this out, TRAQUAIR (1905) adhered to his original contention and was supported in this by all other workers at the time. However, KIAER (1915) again demonstrated that DEAN was correct, and was followed by WOODWARD (1921*a*), STENSIÖ (1927) and most subsequent authors.

There has also been some controversy regarding the position of the mouth. TRAQUAIR believed that it was just ventral (i. e. just dorsal), while WOODWARD (1921*a*) and STENSIÖ (1927) thought that it was placed ventrally so that the oral plates were joined to the rostral plates. On the other hand, KIAER (1928) believed that it was terminal. PATTEN (1929) stated that it was in fact dorsal (the position demonstrated by TRAQUAIR, and this was further confirmed by STETSON (1931). However, STENSIÖ (1958) still believed that the mouth was ventral

in *Drepanaspis* and was thus obliged to postulate a soft rostrum projecting anteriorly from the rostral plate. But from the plates present in the carapace it is not possible for this to be achieved, and in fact there is no functional reason why the mouth should be ventral rather than dorsal. In addition until PATTEN's work (1929, 1932) the rostral plate was thought to abut directly on the dorsal plate, but PATTEN stated that there was a pineal plate and a row of small polygonal plates separating the rostral and dorsal plates. The presence of these tesserae has since been confirmed by OBRUCHEV (1943*b*), while GROSS (1963) has recently confirmed that a pineal plate was also present, but was variable in outline. The type of oral plates in *Drepanaspis* was discussed by STETSON (1931) and later by OBRUCHEV (1943*b*). From the specimens previously figured it appeared that there were seven oral plates, three pairs on either side of a median one, but STETSON showed that there were only five elements on the ventral surface of the carapace. This probem was resolved by GROSS (1963) who established that there were in fact two distinct sets of plates present, the oral plates being positioned on top of those of the anterior margin of the ventral surface of the carapace. PATTEN (1932) also figured two external nostrils behind and to the side of the mouth, but these have never been confirmed. However, the impressions of paired nasal capsules have now been figured in the rostral plate by GROSS (1963), although he did not appear to recognize them as such.

Although STENSIÖ (1927) and HEINTZ (1938) considered that the post-orbital plate was the result of a sub-division of the orbital plate of the ancestor to *Drepanaspis*, which they thought was pteraspid-like, OBRUCHEV (1943*b*) first clearly showed that the post-orbital plate curved over from the dorsal on to the ventral surface of the carapace, and in consequence considered that it should really be termed a pre-branchial plate. He based this view on the fact that GROSS (1933*b*) had suggested that *Pteraspis dunensis* (= *Rhinopteraspis cornubica*) had a branchial plate generally consisting of two parts. However, it is clear from FAHLBUSCH (1957) that the post-orbital plate is more closely connected with the orbital than with the branchial, and recently GROSS (1963) has described an orbital with an adjoining post-orbital plate partially fused to it. It could however just as well be that the orbital plate in the pteraspids did not sub-divide to form the two plates in *Drepanaspis*, but that the reverse occurred, although there is no direct evidence either for or against this idea.

OBRUCHEV (1959) suggested that the ventral surface of *Drepanaspis* was as a whole, more convex than the dorsal, but TARLO (1961*a*) disputed this, while still agreeing that the ventral median plate itself was convex. He suggested that the branchial plates were downturned at the sides so that there would be a concavity on either side of the ventral median plate. GROSS (1963) portrayed the transverse section of *Drepanaspis* as very convex ventrally with the laterally projecting branchial plates extending horizontally. This interpretation not only differs markedly from that of TARLO (1961*a*), but also contrasts with the known arrangement in all other psammosteids. With regard to the tail of *Drepanaspis*, this was figured as heterocercal by TRAQUAIR (1899, 1903) [i.e. hypocercal, since TRAQUAIR confused the dorsal and ventral surfaces]. DEAN (1904) and KIAER (1915) recognized that the tail was hypocercal, but STETSON (1931) restored *Drepanaspis* with a symmetrical tail. PATTEN (1932) corrected TRAQUAIR's restoration as far as the anterior part was concerned, but gave the animal a heterocercal tail. OBRUCHEV (1943*b*) restored the hypocercal tail, whilst GROSS (1963) again returned to an almost symmetrical one. Although GROSS added considerable detail to our knowledge of the structure of the tail, in particular of the squamation, it is evident that its overall outline is variable, being nearly equilobate but with the lower portion often slightly larger than the upper. This may suggest that the profile of the carapace is more important with regard to swimming, than the outline of the tail, as previously suggested by OBRUCHEV

(1959). GROSS (1963) also described and discussed a very immature individual, first figured by KUTSCHER (1933) which is remarkably pteraspidlike. This was used by GROSS to support OBRUCHEV's theory on the origin of the psammosteids from the pteraspids, but in fact it would appear to lend somewhat greater support to the alternative theory propounded by TARLO (1962*c*), particularly since the branchial plates are remarkably similar in nature to those of *Weigeltaspis*, and are not like anything one would expect to find in the pteraspids.

Although considerable discussion has ranged over *Drepanaspis*, it was known only from a single species, *D. gemuendenensis*, until GROSS (1933*b*) described the further species *D. schrieli* which differed in the postero-median extent of the ventral part of the median plate, and in the detail of the ornamentation. This same author later (1937) described another species, *D. lipperti*, again distinguished on the proportions of its branchial plates and on its ornament. With regard to the presence of the genus *Drepanaspis* in South West England, TARLO (1961*b*) referred to it, material which MCCOY (1851, 1854, 1855) had described under the name *Steganodictyum carteri*. Furthermore a separate species has now been recognized from South West England, *D. edwardsi*, and another from the Rhineland, *D. jaegeri*, both being distinguished on details of ornament. They are described for the first time in the present work.

Drepanaspis gemuendenensis SCHLÜTER, 1887

(Pl. VI; Text-fig. 3*B*)

1887. *Drepanaspis Gemundenensis* n. sp.; C. SCHLÜTER, Über Panzerfische..., pp. 126-127.
1891*b*. *Drepanaspis gemundenensis* SCHLÜTER; A. S. WOODWARD, Catalogue..., p. 311.
1896*a*. *Drepanaspis Gmundenensis* SCHLÜTER; R. H. TRAQUAIR, On fossil-fishes..., p. 263.
1899. *Drepanaspis Gmundenensis* SCHLÜTER; R. H. TRAQUAIR, Report on fossil..., pp. 844-847, text-fig. 5.
1900. *Drepanaspis gemundenensis* SCHLÜTER; A. S. WOODWARD, Dr. Traquair on..., pp. 68-72, text-fig. 4.
1900*a*. *Drepanaspis Gmundensis* SCHLÜTER; R. H. TRAQUAIR, Notes on..., pp. 153-159, text-figs. 1-3.
1902. *Drepanaspis Gemundenensis* SCHLÜTER; R. H. TRAQUAIR, Additional note on..., pp. 289-291, text-figs. 1, 2.
1902. *Drepanaspis gemuendenensis* SCHLÜTER; C. R. EASTMAN, Text-book of..., p. 51, text-fig. 100.
1903. *Drepanaspis Gemundenensis* SCHLÜTER; R. H. TRAQUAIR, The Lower Devonian..., pp. 725-731, pl. 1, figs. 1-3; pls. 2-5, text-figs. 1-3.
1903. *Drepanaspis* [*gemundenensis* SCHLÜTER]; A. KEMNA, Les récentes découvertes... pp. 366-368, text-fig. 11.
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1904. *Drepanaspis gemündenensis* SCHLÜTER; T. W. BRIDGE, Fishes..., pp. 525-526, text-figs. 314, 315.
1904. *Drepanaspis gemundenensis* SCHLÜTER; B. DEAN, The Lower Devonian..., pp. 64-65.
1904. *Drepanaspis gemundenensis* SCHLÜTER; C. R. EASTMAN, Marginal and ridge..., pp. 703-704.
1905. *Drepanaspis Gemundenensis* SCHLÜTER; R. H. TRAQUAIR, Supplement to..., pp. 469-475, pls. 1-3.
1909. *Drepanaspis gemündenensis* SCHLÜTER; O. ABEL, Bau und Geschichte..., pp. 96-97, text-fig. 93.
1909. *Drepanaspis gemündenensis* SCHLÜTER; E. S. GOODRICH, Vertebrata..., p. 198, text-fig. 169.
1909. *Drepanaspis gemundenensis* SCHLÜTER; L. DOLLO, La Paléontologie..., pp. 398-400, pl. 9, fig. 4.
1911. *Drepanaspis gemündenensis* SCHLÜTER; E. KOKEN, Fische..., p. 30.
1912. *Drepanaspis gemündenensis* SCHLÜTER; O. ABEL, Grundzüge de Paläobiologie..., pp. 437-439, text-fig. 322
1915. *Drepanaspis Gemündenensis* SCHLÜTER; J. KIAER, Upper Devonian..., pp. 29-34, pl. 3, figs. 5, 6; pl. 4, fig. 2; text-figs. 6, 7.
1919. *Drepanaspis Gemündenensis* SCHLÜTER; O. ABEL, Die Stamme der..., pp. 80-82, text-figs. 42, 43.
1920. *Drepanaspis gemündenensis* SCHLÜTER; O. ABEL, Lehrbuch der..., p. 322, text-fig. 510.
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1924. *Drepanaspis gemündenensis* SCHLÜTER; O. ABEL, Lehrbuch der..., p. 333, text-fig. 510.
1927. *Drepanaspis gemündenensis* SCHLÜTER; E. A. STENSIÖ, The Downtonian and..., pp. 327-330, text-fig. 90.
1928. *Drepanaspis gemündenensis* SCHLÜTER; J. KIAER, The structure..., pp. 125—127, text-figs. 4, 5.
1929. *Drepanaspis gemundenensis* SCHLÜTER; W. PATTEN, The structure of..., p. 32.
1931. *Drepanaspis gemündenensis* SCHLÜTER; H. C. STETSON, Studies on the morphology..., pp. 149-152, text-figs. 5-7.
1931. *Drepanaspis gemundenensis* SCHLÜTER; J. R. NORMAN, A history..., p. 345, text-fig. 123B.

1931. *Drepanaspis* [*gemundenensis* SCHLÜTER]; H. G. WELLS, J. HUXLEY & G. P. WELLS, The Science of..., p. 423, text-fig. 219.
1932. *Drepanaspis* [*gemundenensis* SCHLÜTER]; W. PATTEN, Foundations of..., p. 518, text-fig. 6.
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1933. *Drepanaspis [gemundenensis]* SCHLÜTER; F. BROTZEN, Weigeltaspis nov. gen..., pp. 652-653, text-fig. 5, 4.
1933*a*. *Drepanaspis gemündenensis* SCHLÜTER; W. GROSS, Die Fische des..., p. 7, text-fig. 1G.
1933*b*. *Drepanaspis gemündenensis* SCHLÜTER; W. GROSS, Die unterdevonischen..., pp. 55-56, text-fig. 5A.
1933*c*. *Drepanaspis gemündenensis* SCHLÜTER; W. GROSS, Die Wirbeltiere des..., pp. 8-9, pl. 4, fig. 1.
1933*d*. *Drepanaspis gemuendenensis* SCHLÜTER; W. GROSS, Die phylogenetische..., p. 106, text-fig. 1, 1.
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1935. *Drepanaspis [gemundenensis]* SCHLÜTER; E. I. WHITE, The ostracoderm..., p. 442.
1936. *Drepanaspis* [*gemundenensis* SCHLÜTER]; W. K. GREGORY, The transformation..., p. 321, text-fig. 2E.
1937. *Drepanaspis gemuendenensis* SCHLÜTER; W. GROSS, Die Wirbeltiere..., pp. 10-12, text-fig. 6B.
1938. *Drepanaspis* [*gemundenensis* SCHLÜTER]; A. HEINTZ, Ueber die altesten..., p. 52, text-fig. 2h.
1939. *Drepanaspis gemuendenensis* SCHÜTER; J. A. MOY-THOMAS, Palaeozoic..., pp. 9-11, text-fig. 2C.
1940. *Drepanaspis* [*gemundenensis* SCHLÜTER]; O. KUHN, pp. 16, 28, text-figs. 3h, II. 1.
1940. *Drepanaspis gemundenensis* SCHLÜTER; T. J. PARKER & W. A. HASWELL, A text-book..., pp. 131-133, fig. 101.
1940. *Drepanaspis gemündenensis* SCHLÜTER; D. OBRUCHEV, On some psammosteids..., p. 767, text-fig. 1a.
1943. *Drepanaspis gemündenensis* SCHLÜTER; D. OBRUCHEV, A new restoration..., p.p 268-271, text-figs. 1, 2.
1944. *Drepanaspis gemündenensis* SCHLÜTER; D. OBRUCHEV, An attempted..., pp. 143-145.
1945. *Drepanaspis* [*gemundenensis* SCHLÜTER]; D. OBRUCHEV, On the evolution..., pp. 261-262, text-figs. 2, 3.
1947. *Drepanaspis* [*gemundenensis* SCHLÜTER]; D. OBRUCHEV, On the genus..., p. 517.
1947. *Drepanaspis gemündenensis* SCHLÜTER; D. OBRUCHEV, Atlas of the guide..., pp. 193-194, text-fig. 53.
1950. *Drepanaspis gemuendenensis* SCHLÜTER; W. GROSS, Die paläontologische..., p. 58.
1951. *Drepanaspis* [*gemundenensis* SCHLÜTER]; W. K. GREGORY, Evolution..., p. 105, text-figs. 6, 7A.
1955. *Drepanaspis gemüdensis* SCHLÜTER; L. S. BERG, Classification of..., pp. 27-28, text-fig. 8.
1956. *Drepanaspis gemündenensis* SCHLÜTER; E. MARK, On the genus..., pp. 85-88, text-fig. 10a.
1957. *Drepanaspis [gemundenensis]* SCHLÜTER; L. B. TARLO, A preliminary note..., pp. 228-229.
1958. *Drepanaspis gemuendensis* SCHLÜTER; E. A. STENSIÖ, Les Cyclostomes..., pp. 246-252, text-figs. 132, 133.
1959. *Drepanaspis* [*gemundenensis* SCHLÜTER]; D. OBRUCHEV, Body form..., p. 434.
1960. *Drepanaspis* [*gemundenensis* SCHLÜTER]; F. RAW, Outline of a theory..., p. 520, text-fig. 5h.
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1961. *Drepanaspis gemündensis* TRAQUAIR; O. KÜHN, Die Tierwelt..., p. 18, text-figs. 33c, 44.
1961*a*. *Drepanaspis gemundenensis* SCHLÜTER; L. B. TARLO, Psammosteids from..., pp. 207-208, text-figs. 8a, d.
1962*c*. *Drepanaspis gemundenensis* SCHLÜTER; L. B. TARLO, The classification..., pp. 260-262, text-fig. 6.
1963. *Drepanaspis gemuendenensis* SCHLÜTER; W. GROSS, Drepanaspis..., pp. 133-155, pl. 6-9, text-figs. 1-11.
1964*a*. *Drepanaspis gemundenensis* SCHLÜTER; L. B. H. TARLO, The origin..., p. 4, text-fig. 1.
1964*b*. *Drepanaspis gemuendenensis* SCHLÜTER; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 14, 76, 97, 98, 106, text-figs. 1D, 5, 28.
1964*b*. *Drepanaspis gemuendensis* SCHLÜTER; E. A. STENSIÖ, Les Cyclostomes..., pp. 179-182, text-figs. 33, 34.
1964. *Drepanaspis gemuendenensis* SCHLÜTER; D. OBRUCHEV, Subclass Heterostraci..., pp. 69, 70, 74; text-figs. 45, 56*c*.

Holotype: Anterior part of left branchial plate with part of dorsal median plate, housed in the Geological Institute, University of Bonn, cast figured in present paper, Pl. VI, fig. 2.

Type horizon and locality: Lower Devonian (Siegenian-Emsian), Hunsruckschiefer; Gemünden, Eifel, Rhineland, Germany.

Diagnosis. — Ornamentation of small, well separated, sharply pointed high-crowned rounded tubercles, with prominent crenulations forming radial ribs.

Material. — Numerous associated carapaces, from the Siegenian-Emsian of the Rhineland.

Description. — The holotype (G. I. U. B.) consists of part of a dorsal median plate, ornamented by well separated, small, high-crowned, round crenulated tubercles. These are aligned in concentric rings, which however are not well defined. Associated with this median plate is a left branchial plate, the anterior part of which projects beyond the fragment of dorsal

plate, and this is undoubtedly the reason why SCHLÜTER mistook the specimen for a cephalaspid, since the projecting part gives the impression of a lateral cornua. There is a very narrow lateral part to the branchial plate, which is ornamented, and is the free part of the dorsal surface. The bulk of the specimen, however, shows the internal surface of the ventral part of the plate, although the outline only of the posterior part can be made out since this part of the branchial plate lies beneath the dorsal median plate. It can be seen that posteriorly the plate widens out somewhat to form a slight postero-median flange. A complete carapace (1900.52.8. R. S. M.) shows the plates of the dorsal side in natural association. The dorsal median plate is more or less circular, with a broad deep excavation at the anterior margin. Situated directly in front of this, is the rostral plate, the anterior margin of which is slightly angulated. At the left side of the anterior margin of this plate there is a well marked ridge which KIAER (1928) thought represented the front edge of a "maxillary plate", since termed the ascending lamella (STENSIÖ, 1958). STETSON (1931) showed from the specimen 5218 M. C. Z. that this structure was paired, and that it is part of the ascending lamella seems a probable explanation. GROSS (1963) however, described two pairs of such structures as pre-rostral plates, which seem to be the sort of structures STENSIÖ (1958) had in mind when he postulated the existence of upper labial plates. However there does not seem to be sufficient evidence to determine whether these structures described by GROSS as pre-rostral plates are independent plates, or displaced parts of the ascending lamella.

The rostral plate of the carapace (1900.52.8. R. S. M.) has more or less parallel sides which then swing round postero-medially, but since the posterior margin has been lost, TRAQUAIR unfortunately restored the carapace with the rostral plate abutting directly on the dorsal median plate. In the original specimen however, it can clearly be seen that on the left side there is a small plate separating the dorsal and rostral plates. Evidently there was a line of such small plates present between the larger ones, a point confirmed by STETSON (1931) again from his specimen 5218 M. C. Z. GROSS (1963) however described pineal plates from a number of different individuals, where they were situated between the rostral and median dorsal plates, and in some instances the pineal abutted directly against one or other of these plates, while in others it was surrounded by tesserae. With regard to oral plates, those of the carapace 1900.52.8. R. S. M. have a narrow transverse anterior ornamented surface, but the internal surface of the ventral part of these plates which is also visible appears unornamented. It should nevertheless be noted that in specimen 5218 M. C. Z. STETSON demonstrated that this internal surface was in fact ornamented with minute tubercles. In the carapace here described, there appears to be a single median oral plate, on either side of which there seem to be three pairs of further plates, while the lateral margins of the mouth are bounded by a small median marginal plate. Between this plate and the lateral margin of the rostral plate a tessera is situated at each side. This narrow area at each side between the rostral plate and the lateral marginal plate appears in all probability to represent the position of the olfactory opening, and it is of interest to note that GROSS (1963) figured for the first time a rostral plate on which were impressed the underlying paired nasal capsules.

Bordering the lateral margin of the most anterior tessera and the posterior margin of the lateral marginal plate, there occurs a triangular orbital plate with the orbit facing anterolaterally and slightly dorsally. Its posterior margin is straight, and behind it there is a large post-orbital plate, the anterior part of its lateral margin, which is slightly curved, forming part of the margin of the carapace. The posterior lateral margin of this plate abuts on the median margin of the dorsal part of the branchial plate. The post-orbital plate is wide anteriorly, but it tapers to a posteriorly directed point. Its median margin is very irregular, and

separating it from the dorsal median plate is a narrow zone of tesserae. The major part of the lateral margin of the carapace is formed by the branchial plate, which has a long narrow dorsal extent, but expands gradually posteriorly, and then near its posterior end tapers sharply to a point. Below this can be seen the inner surface of the ventral part of the branchial plate, which meets the dorsal part at a sharp angle at the margin of the carapace. The postero-median edge of the dorsal surface of the branchial plate forms the antero-lateral margin of the branchial opening. The median margin of this opening is bounded by a rather oval-shaped cornual plate which tapers somewhat anteriorly, and abuts against the postero-median part of the dorsal surface of the branchial plate. Separating all the plates of the lateral margin from the rostral and dorsal median plates is a zone of polygonal tesserae, which in the posterior part of the carapace grade into the squamation.

A further carapace (1898.103.2. R. S. M.) shows the posterior margin of the dorsal median plate, in which there is a deep excavation in the mid-line. The plate is drawn up into a rounded ridge in this region, this presumably marking the beginning of a line of fulcral scales. The cornual plate in this specimen is slightly angulated at its lateral margin, at the point where it begins to abut against the branchial plate. The posterior part of the lateral margin forms the median margin of the branchial opening. Unlike the cornual plate in the last specimen, the anterior, median and posterior margins are irregular in outline. Specimen 1901.67.6.; 1901.132.1.R. S. M. shows the ventral surface of a carapace in which the branchial plate has a postero-median expansion and then narrows anteriorly. The posterior margin of this plate is fairly straight and transverse to the lateral margins, and it has a gentle postero-median flange beyond which the plate as a whole tapers to a point anteriorly. The ventral median plate is fairly oval in outline, with a more or less straight anterior margin and a shallow posterior notch. In front of the ventral median plate and separating it from the anterior part of the branchial plate is a wide zone of polygonal tesserae. The anterior margin of the carapace as a whole is formed by a composite median plate (called median tesserae by GROSS, 1963), with a large rectangular complex-plate at either side and then a further narrower median marginal plate lateral to it. These 5 plates were previously thought to be the oral plates seen in ventral view, but GROSS (1963) demonstrated that they are quite distinct, and thus the difficulty of attempting to understand how these five plates could be the seven oral plates no longer exists. Between the median marginal plates and the orbital plates are a further pair of fairly narrow plates called lateral marginal plates by GROSS (1963), pre-orbitals by OBRUCHEV (1943*b*) and paraoral plates by STENSIÖ (1958). STETSON (1931) also described the ventral part of the anterior margin of the carapace, this time in specimen 5219 M. C. Z. In this the median tesserae (composite median plate) were rather "Y"-shaped, and had a typical rectangular complex-plate at either side of them. STETSON noted that the "Y" shape of the median tesserae was caused by the composite plate being superficially divided by a longitudinal groove in its anterior part. OBRUCHEV in his restoration (1943*b*) made this superficial division visible on the dorsal surface of the plate, but this is not justified. In fact the median oral plate which is quite distinct from the median tesserae and is on the dorsal surface of them, appears to possess an anteriorly directed angle forming a peak in the mid-line, while the posterior margin of the anterior ornamented part of the plate is also angled somewhat in the mid-line. Thus the ornamented part as a whole (oral tooth lamella) is almost diamond shaped. It should also be noted that on the dorsal surface in other specimens, for example 1900.52.8. R. S. M. and a further specimen housed in the Geological-Palaeontological Museum, Berlin, two oral plates are situated above each of the rectangular complex-plates.

A specimen of a complete carapace, preserved with the dorsal side uppermost (1903.44.

R. S. M.) has the dorsal median plate missing, so that the ventral median plate is seen in internal view. The plate is a wide oval, and its posterior margin has a long narrow slit which is infilled by a number of tesserae. In internal view these appear to be fused, and this specimen is probably the basis on which OBRUCHEV (1943*b*) inserted a dagger-shaped lancet plate in his reconstruction. The notch however seems to be very variable, for in specimen 1898.103.2. R.S.M. it extends much less into the plate. An immature animal formerly in the collection of Mr. BOTTLEY (now in the Geology Department, University of Newcastle) has a ventral plate which is almost circular, with a small shallow posterior median notch and a straight anterior margin. In the adult specimen 1936.38.31. R. S. M. the anterior margin is also straight, and the lateral margins diverge slightly posteriorly then converge somewhat about halfway along their length until the posterior margin is reached.

Discussion. — *Drepanaspis gemuendenensis* was first described by SCHLÜTER (1887), but his original material has not been figured until now. In spite of this, it was obviously seen by TRAQUAIR (1896*a*), and it enabled him to be in no doubt that the material he described (1899, 1900*a*, 1902, 1903, 1905) was conspecific with SCHLÜTER's material. Since TRAQUAIR's work the main discussion in the literature has concerned the different restorations of the carapace, comparatively little new material having been described. However, KIAER (1915) figured both the details of the ornamentation and the histology of the plates for the first time, and also figured the tail, thus establishing the correct orientation of the animal (i. e. which side was dorsal and which ventral). STETSON (1931) added details of the oral region and gave the species a symmetrical tail, while GROSS (1933*c*) figured a small dorsal plate in which he considered sensory canals were preserved radiating from the centre of the plate. This structure however, which is commonly found in psammosteid median plates, and is indicated in BOTTLEY's immature specimen as well as in the dorsal plate of *Schizosteus asatkini*, has nothing to do with the sensory canal system. It is merely connected in some way with the method of growth of the plates. Apart from those mentioned by these few authors together with BOTTLEY (1961), no further remains of *Drepanaspis gemuendenensis* were described until 1963, when GROSS published the first fully comprehensive account of *Drepanaspis* since TRAQUAIR's classic work. GROSS in his paper described a large amount of new material and the importance of this work is discussed above on pp. 27—29.

Drepanaspis schrieli GROSS, 1933

(Text-fig. 3*C*)

1933*b*. *Drepanaspis schrieli* n. sp.; W. GROSS, Die unterdevonischen..., pp. 54-56, pl. 1, fig. 6, text-figs. 5 B-D.
1933*c*. *Drepanaspis schrieli* GROSS; W. GROSS, Die Wirbeltiere..., p. 9.
1933. *Drepanaspis schrieli* GROSS; H. SCHMIDT, Fischreste aus dem..., p. 230.
1937. *Drepanaspis schrieli* GROSS; W. GROSS, Die Wirbeltiere..., pp. 10-12, text-fig. 6C.
1950. *Drepanaspis schrieli* GROSS; W. GROSS, Die paläontologische..., p. 58.

Holotype: Right branchial plate housed in the Geological-Palaeontological Museum, Berlin, figured by GROSS (1933*b*, Pl. 1, fig. 6).

Type horizon and locality: Lower Devonian (Siegenian), *Rhinopteraspis cornubica* zone; Overath, Rhineland, Germany.

Diagnosis. — Ornamentation of closely packed small tubercles. Branchial plate with large postero-median flange, lateral margin strongly convex, with wide laterally projecting free extension.

Material. — Branchial plates and numerous fragments from Overath and Gemünden, Germany, Wihéries, Belgium, and South-West England.

Description. — The holotype is the major part of a right branchial plate which has a strongly convex lateral margin, and a considerable postero-median flange. The branchial plate is sharply angled at the margin of the carapace, the ventral surface being flat and extending a considerable distance medially in its posterior part, forming a well marked postero-median flange (Text-fig. 3*C*). The dorsal part of the plate is set at an angle to the ventral part, and is far less extensive medially. The angulated part of the plate is solid for some distance, and projects freely from the carapace as a whole. A further feature of the ventral part of the plate is that towards its anterior end, its median margin, instead of converging with the lateral margin, swings medially to run parallel to the lateral margin, and only later turns to converge with it. A further specimen in the Berlin Museum is a left branchial plate which again shows a very considerable postero-median flange, which has an even greater medial extent than is apparent in the holotype. However this is due to the fact that in the holotype this part is missing. The lateral margin of the second specimen is very convex, although as in the holotype the anterior limit of the plate is missing. Fragments of median plates are also known housed in the Berlin Museum, and these are ornamented by small closely packed rounded tubercles in contrast to the ornament of *D. gemuendenensis* in which the tubercles are generally rather larger and are well separated.

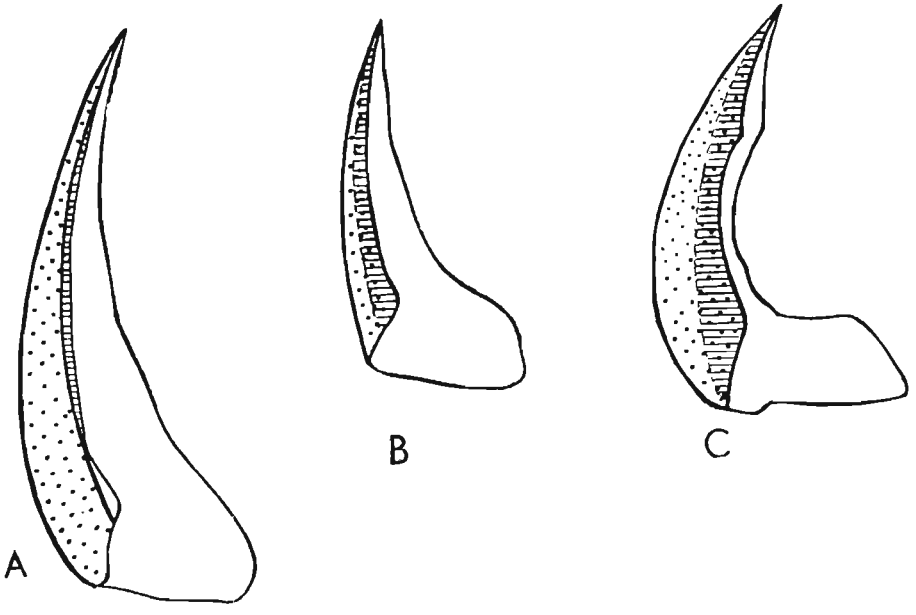

Fig. 3

A-C Drepanaspis, branchial plates in dorsal view. *A Drepanaspis lipperti* GROSS; *B Drepanaspis gemuendenensis* SCHLÜTER; *C Drepanaspis schrieli* GROSS (from GROSS, 1937).

Discussion. — This species was first described by GROSS (1933*b*) and later briefly discussed by him (1937). The lateral margin of the branchial plate is reminiscent of that of *Weigeltaspis heintzi*, and the large postero-median extension of the ventral surface of the branchial plate may well also be a primitive feature.

Drepanaspis lipperti GROSS, 1937

(Text-fig. 3*A*)

1937. *Drepanaspis lipperti* n. sp.; W. GROSS, Die Wirbeltiere..., pp. 10-12, pl. 1, fig. 7; pl. 2, fig. 11; pl. 6, fig. 6, text-figs. 5, 6A.

1950. *Drepanaspis lipperti* GROSS; W. GROSS, Die paläontologische..., p. 58.

Holotype: Left branchial plate P. 2395, housed in the Senckenberg Museum, Frankfurt am Main, figured by GROSS (1937, Pl. 1, fig. 7).

Type horizon and locality: Lower Devonian (Emsian), Klerferschichten; Enz-Tal, near Zweifelscheid, Rhineland, Germany.

Diagnosis. — Ornamentation of closely packed tubercles, elongated longitudinally on lateral part of branchial plate. On dorsal median plate, widely separated tubercles similar to those of *Drepanaspis gemuendenensis*, surrounded by zone of closely packed tubercles similar to, although slightly larger than in *D. schrieli*.

Material. — Branchial, post-orbital and dorsal median plates, from Enzbach near Zweifelscheid, and Willwerath, Rhineland, Germany.

Description. — The holotype (P. 2395, S. M. F.) is a left branchial plate, the lateral margin of which is slightly convex. The median margin of the ventral surface of the plate diverges from the lateral margin posteriorly, and forms a broad postero-medial flange which does not extend as far medially as in *Drepanaspis gemuendenensis* and *D. schrieli*. The dorsal part of the branchial plate, apart from a very narrow medial strip, forms the dorsal surface of the free solid laterally projecting part of the carapace (Text-fig. 3*A*). In the Berlin Museum, there is part of a dorsal median plate, the central region of which is ornamented by high-crowned rounded tubercles, well separated from one another. This region, however, is surrounded by a wide zone of closely packed tubercles which appear to be slightly smaller. The specimen thus appears to combine features of the ornament seen in both *D. gemuendenensis* and *D. schrieli*. A further specimen in the Berlin Museum is a left post-orbital plate, which is ornamented in a similar manner to *D. gemuendenensis*, although the tubercles are more closely packed (see GROSS, 1937).

Discussion. — This species which was described by GROSS (1937) is the youngest member of the genus *Drepanaspis* from the Rhineland, and the medially projecting portion of the dorsal part of the branchial plate which in *D. schrieli* is of considerable width, and is less wide in *D. gemuendenensis*, has to all intents and purposes disappeared in *D. lipperti*. Nevertheless, the width of the free projecting margin of the carapace, although comparatively wider in *D. lipperti* than in the earlier species, is still relatively narrow when compared with the plates of more advanced psammosteids and even the contemporary guerichosteids, and it is evident that the branchial plate of *D. lipperti* which is the holotype, is that of an adult, and is not narrow merely because it has yet to reach its definitive size.

Drepanaspis jaegeri TARLO, 1964

(Pl. VII, figs. 1, 2, 5-9)

1964*b*. *Drepanaspis jaegeri* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 76, 98, 112, 113.

Holotype: Part of median plate, housed in the Geological-Palaeontological Museum, Berlin, figured in the present work, Pl. VII, fig. 1.

Type horizon and locality: Lower Devonian (Siegenian-Emsian), Herdorfer Schichten, Effelsberger Schichten, Süd Wald, Altenahr, Rhineland, Germany.

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 those of *D. gemuendenensis* or *D. lipperti.*

Material. — Fragments and scales from the Effelsberger Schichten and Taunusquartzit, Stephanshausen, Rhineland, Germany.

Description. — The holotype is a rectangular fragment with prominent medium-sized rounded tubercles which are closely packed, but are nevertheless clearly separated from one another. In the specimen it is also possible to make out faint growth lines. A series of specimens which are referred to this species were collected from the Taunusquartzit, and a large rectangular fragment (81 Rose collection G. P. M. B.) appears similar to the holotype, and to further fragments (85, 90, 102, 602, 609 Rose Coll. G. P. M. B.) from the same locality, and they can thus be referred to the same species. The name *Drepanaspis jaegeri* was proposed for this species, since its ornamentation is quite distinct from that of other *Drepanaspis* species, the tubercles being of a different order of magnitude from those in *D. schrieli* besides not being so closely packed, and yet not as widely separated as in *D. gemuendenensis* or *D. lipperti.* A body scale from the Lower Emsian of Steinbrück in which the oval tubercles normally found in such scales are closely packed, but are still distinct from one another, can also be referred tentatively to *D. jaegeri.*

Drepanaspis carteri (McCoy, 1851)

(Pl. VIII, figs. 1-9)

1847. "A small tuberculated specimen"; C. W. Peach, On the Fossil..., pl. 2, figs. 11, 12.
1848. *Asterolepis;* C. W. Peach, On the fossiliferous..., p. 57, pl. 3, figs. 1, 2.
1851. *Steganodictyum Carteri* n. sp.; F. McCoy, On some new..., p. 483.
1854. *Steganodictyum Carteri* McCoy; F. McCoy, Contributions to..., p. 234.
1855. *Steganodictium carteri* McCoy; F. McCoy, British Palaeozoic..., pl. 2A, figs. 4, 4A.
1868*a*. *Steganodictyum carteri* McCoy; E. R. Lankester, On the Discovery..., p. 547.
1870. *Cephalaspis*(?) *carteri* (McCoy); E. R. Lankester, Fishes of the..., p. 42.
1891*b*. *Cephalaspis carteri* (McCoy); A. S. Woodward, Catalogue of..., p. 193.
1893. *Pteraspis carteri* (McCoy); J. H. Collins, A working list..., p. 478.
1932. "*Steganodictyum*" *carteri* McCoy; E. A. Stensiö, Cephalaspids of..., p. 179.
1934. *Cephalaspis carteri* (Woodward); W. W. King, The Downtonian..., p. 545.
1948. *Steganodictyum carteri* McCoy; H. Dewey, South-West..., p. 17.
1961*c*. *Drepanaspis carteri* (McCoy); L. B. Tarlo, Rhinopteraspis cornubica..., p. 370.

Holotype: Fragment of median plate, A. 3466, housed in the Sedgwick Museum, Cambridge, part figured by McCoy (1855, Pl. 2A, figs. 4, 4A), complete specimen figured in the present work, Pl. VIII, fig. 1.

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

Diagnosis. — Ornamentation of large, widely separated tubercles generally round, but may be considerably elongated. Tubercles generally elongated in tesserae.

Material. — Fragments of median plates, an orbital plate and tesserae from the Dartmouth Slates of Cornwall, England.

Description. — The holotype (A. 3466 S. M.) is a small fragment of a median plate ornamented by well separated tubercles which at one end of the specimen are round, but become considerably elongated towards the other. Further fragments (5690 and 82833 G.S.M.) are ornamented by large round tubercles which are also very well separated from one another. Some fragments such as 5691 and 5715 G. S. M. have similar fairly large tubercles, but these

are rather more closely packed than in the previous specimens. A further specimen (8476 G. S. M.) consists of part of the margin of a median plate in which there are large, well separated tubercles, together with a large area of adjoining tesserae or possibly scales, which are difficult to make out since they are not well preserved. However, in this area there is one tessera which is very well preserved,and this is ornamented by several longitudinally aligned elongated tubercles or short dentine ridges, which are well separated from one another. An isolated tessera (1072 G. S. M.) again shows this same ornamentation, several of the well separated tubercles or ridges being greatly elongated. Finally, part of an orbital plate is known (1068 G. S. M.) which besides showing the orbit, has an ornamentation of fairly large well separated tubercles.

Discussion. — As long ago as 1847, PEACH figured a small tuberculated specimen which he identified as being the remains of a fossil fish. Later (1848) he identified such remains incorrectly as *Asterolepis*. However, the material was not validly named until 1851, when MCCOY introduced the name *Steganodictyum carteri* for similar material. He repeated his description (1854), and in 1855 he figured his material for the first time. Although PEACH recognized correctly that his specimen was vertebrate in nature, MCCOY believed the material to be the remains of polyzoa, but nevertheless his name was valid, even though applied to what he thought were invertebrate remains. LANKESTER (1868*a*) was the first person to suggest that *S. carteri* was in fact cephalaspid in nature, and he tentatively assigned it to *Cephalaspis* in 1870, while WOODWARD (1891*b*) listed it as *Cephalaspis carteri*. On the other hand, COLLINS (1893) placed it in the genus *Pteraspis*, but this may well merely have been due to the fact that the type species of the genus *Steganodictyum*, *S. cornubicum*, had since been recognized to be a pteraspid. WOODWARD (1901) described part of a cephalaspid cornua with tuberculated ornament under the name *Cephalaspis carteri*, and subsequently STENSIÖ (1932) listed "*Steganodictyum*" *carteri* as a cephalaspid, while KING (1934) listed *Cephalaspis carteri* (WOODWARD), and DEWEY (1948) also listed the species as a cephalaspid. However, TARLO (1961*c*) assigned the species to the genus *Drepanaspis*. Previously, HENDRICKS (*in* SIMPSON, 1951) had mentioned the presence of *Drepanaspis* in the Dartmouth Slates, and DENISON (1956) also recorded this genus there, but with regard to DENISON's material, this now appears to be referable to arthrodires. In fact, in the Dartmouth Slates remains of arthrodires, cephalaspids and drepanaspids all occur, and all are ornamented by well separated tubercles. Those of the arthrodires are very large, those of the cephalaspids are extremely small, while those of the drepanaspids are between the two others in size. The species *Drepanaspis carteri* is distinguished mainly on the ornamentation, and on the tendency of the tubercles to form short ridges, in some respects reminiscent of the ornament of *Tesseraspis*.

Drepanaspis edwardsi TARLO, 1964

(Pl. VIII, fig. 10)

1964*b*. *Drepanaspis edwardsi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 77, 97, 113.

Holotype: Fragment of ? post-orbital plate P. 13750, housed in the British Museum, Natural History, London, figured in the present work, Pl. VIII, fig. 10.

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

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

Description. — The holotype (P. 13750 B. M.) consists of part of a plate belonging to the lateral margin of the carapace, and appears to be the major part of a post-orbital plate. The tubercles at the margin are large, and become progressively smaller medially. They are rounded and closely packed, and are arranged in regular rows, but there is a slight gap between the adjacent tubercles. In one part of the plate there is a small area of much smaller tubercles. In some respects the ornamentation is comparable to that of *Drepanaspis jaegeri*, but in that species the ornament seems to be very regular in size. Therefore since the tubercles of the ornament of the species here described vary in size, and in any event are quite distinct from those in *Drepanaspis carteri* with which it occurs, it seems justified to place it in a separate species, for which the name *Drepanaspis edwardsi* was proposed.

Genus **PSEPHASPIS** ØRVIG, 1961

Type species: *Psephaspis williamsi* ØRVIG, 1961

Diagnosis. — Dorsal median plate roughly circular in outline with straight anterior margin, convex lateral and rounded posterior margins. Ornamentation of tubercles at centre of plate, dentine ridges at periphery.

Occurrence. — Lower Devonian (Siegenian-Emsian); Utah, Idaho, United States and Northern Siberia, U.S.S.R.

Psephaspis williamsi ØRVIG, 1961

(Pl. XIV, fig. 3)

1958. *Psephaspis williamsi* ØRVIG; E. A. STENSIÖ, Les Cyclostomes..., pp. 252, 423 (nomen nudum).
1961. *Psephaspis williamsi* n. sp.; T. ØRVIG, Notes on some..., pp. 526-533, text-figs. 6-10.
1964. *Psephaspis williamsi* ØRVIG; D. OBRUCHEV, Subclass Heterostraci..., p. 71.

Holotype: Dorsal median plate, C. 1357a, b, housed in the Swedish Museum of Natural History, Stockholm, figured by ØRVIG (1961, Text-figs. 6, 8A, B).

Type horizon and locality: Lower Devonian (Siegenian), Water Canyon Formation; Blacksmith Fork, Cache County, Utah, United States.

Diagnosis. — Ornamentation of rounded and oval tubercles arranged concentrically in median part of plate, and short crenulated dentine ridges aligned parallel to margin of plate at periphery.

Material. — Dorsal median plate and fragments of dorsal median plates and scales from the Water Canyon Formation, Utah, and also from Idaho, United States.

Description. — The holotype (C. 1357 a, b, R. S.) is a dorsal median plate, although it was tentatively identified as a ventral median plate by ØRVIG (1961). It is characterized by the arrangement of its ornament of tubercles in concentric rings. The plate has a fairly straight anterior margin, from which the lateral margins gradually diverge for about half their length. They then converge rather more sharply posteriorly and form a gently rounded posterior margin. The ornamentation consists of rounded crenulated tubercles in the mid part of the plate, and although some of the tubercles which are arranged in concentric rows are rounded, others are about twice as long as they are wide. Towards the periphery of the plate the tubercles are fused into long narrow crenulated strips which are aligned concentrically, parallel to the margins of the plate. In a fragment from Idaho (D. 76 U. W.), there is a zone of concentric

rings of tubercles distal to which the ornament is divided into a number of large fairly rectangular areas. These are very reminiscent of the condition in the rostral plates of *Schizosteus striatus*, where at the periphery large synchronomorial tesserae become incorporated into the margins of the plate. Although ØRVIG remarked that there is no trace of this subdivision in his material, it appears that the beginnings of the development of superficial scale-like tesserae are present, but this is not surprising for even in *Drepanaspis gemuendenensis* tesserae frequently become incorporated into the lateral margins of the median plates (STENSIÖ, 1958). In *Psephaspis williamsi*, however, the condition is well advanced, and seems to be closer to that found in the advanced guerichosteids.

Also present on specimen A. 27946 P. M. O., a fragment of a plate, are patches of second generation tubercles forming tesserae. Some of these have fairly large irregular rounded tubercles arranged concentrically, while others comprise concentrically arranged short narrow dentine ridges, which appear to bear nodes suggestive of the fusion of several tubercles. Also present among the material described by ØRVIG is a fulcral scale (A. 27945 P. M. O.) in which the tubercles are again aligned concentrically in zones parallel to the margins of the scale, forming in particular a series of well marked growth rings parallel to the proximal margin. The alignment of the tubercles in this scale contrast with that of scales in most other psammosteids, where the tubercles usually have a longitudinal arrangement.

Discussion. — *Psephaspis williamsi* which was first described by ØRVIG (1961), is known only from few remains, and these include a large rounded dorsal median plate which is similar in general outline to the plates of some of the advanced psammosteids such as *Schizosteus*, *Pycnolepis* and *Pycnosteus nathorsti*. It is unlikely to be a ventral plate since there is no suggestion of the slightest posterior notch, a feature common to the ventral median plates of all early psammosteids. ØRVIG described *Psephaspis williamsi* as a psammosteid, and this is accepted here, although DENISON (personal communication) considered that it might turn out to be a specialized pteraspid. In some respects the arrangement of the tubercles is reminiscent of the ornament in the advanced pteraspid *Protaspis*, where the typical concentric dentine ridges break up into tubercles, but the shape of the dorsal median plate is quite unlike that of any pteraspid. Furthermore, the development of both second generation tesserae and synchronomorial areas seems to confirm ØRVIG'S interpretation. In addition, the histology of the plate appears to be typically psammosteid rather than pteraspid, this latter being characterized by large open cancellae.

Psephaspis bystrowi TARLO, 1964

1959. *Drepanaspis* sp. SCHLÜTER; A. P. BYSTROW, The microstructure..., pp. 67-69, text-fig. 7.
1964*b*. *Psephaspis bystrowi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 79, 113.

Holotype: Tessera figured by BYSTROW (1959, Text-fig. 7).
Type horizon and locality: Lower Devonian (Emsian), River Nizhni Viluikan, Northern Siberia.

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

Description. — This species is based on an isolated tessera which is ornamented by simple rounded tubercles with virtually no crenulations. These tubercles vary in size, and are rather similar to some of the less regular rounded tubercles of *Psephaspis williamsi*. In section it is clear that the tessera belongs to a psammosteid, and the details of the histology of the tubercles is quite unlike that of the tubercles of *Drepanaspis* as figured by KIAER (1915).

It is also unlike the histology of the tubercles of *Guerichosteus* which is much like that of *Drepanaspis*. From the figures of the histology of the tubercles of *Psephaspis williamsi* (ØRVIG, 1961) the specimen figured by BYSTROW as *Drepanaspis* sp. appears closer to ØRVIG'S species than to any other, and for this reason the tessera is tentatively included in the same genus. It clearly does not belong to any other Emsian psammosteid genus. However, it differs from *P. williamsi* in the details of its ornamentation, as the tubercles are much more closely packed and are more globular. It is also of later age than *P. williamsi*, and it is the only psammosteid so far recorded from Northern Siberia. Since therefore it cannot be referred to any known species, it seems reasonable to create a new species for its reception, and the name *Psephaspis bystrowi* was proposed.

Family GUERICHOSTEIDAE TARLO, 1964

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.

Discussion. — The new family Guerichosteidae has been erected for the reception of psammosteids which show a marked structural advance on the Drepanaspididae, in particular in the development of the branchial and post-orbital plates. This new family includes the Emsian genera *Guerichosteus* and *Hariosteus* and the Eifelian-Givetian genus *Schizosteus*. The guerichosteids appear to be a central group, linking the structural grade exemplified by the drepanaspids with those of the later pycnosteids and psammolepids. In the later guerichosteids belonging to the genus *Schizosteus*, it is possible to recognize from a study of the ventral median plates the way in which the two separate lineages of the later psammosteids developed, i. e. the pycnosteids and psammolepids. As far as the branchial plates are concerned, both experienced a parallel development.

Genus **GUERICHOSTEUS** TARLO, 1964

Type species: *Guerichosteus kozlowskii* TARLO, 1964

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.

Occurrence. — Lower Devonian (Emsian Stage), zone of *Rhinopteraspis cornubica*; Holy Cross Mountains, Poland.

Discussion. — The genus *Guerichosteus*, previously erected, appears quite distinct from the contemporary *Drepanaspis* by virtue of the development of a wide, free, laterally projecting part to the branchial plate, and a much wider posterior part to the post-orbital. At the same time it cannot belong to *Schizosteus* since the branchial opening still appears to be positioned at the postero-lateral corner of the carapace as in *Drepanaspis*, and not some distance medial to it as in *Schizosteus*. In view of these structural features it was felt justified to erect a new genus for this form, of which four species are here recognized.

Guerichosteus kozlowskii TARLO, 1964

(Pls. IX; X; XI, figs. 1-13; XII, figs. 1-4; Text-figs. 4-8)

1896. *Psammosteus* AGASSIZ; G. GÜRICH, Das Paläozoicum,.., p. 392.
1909. *Psammosteus* AGASSIZ; D. SOBOLEV, The Middle Devonian..., p. 246.
1915. *Psammosteus* AGASSIZ; J. KIAER, Upper Devonian..., p. 55.
1937. *Psammosteus* AGASSIZ; J. CZARNOCKI, Überblick der Stratigraphie..., p. 181.
1957. Psammosteid type A; L. B. TARLO, A preliminary note..., p. 230, pl. 1, fig. 1.
1957. *Psammosteus* AGASSIZ; J. CZARNOCKI, Stratigraphy and..., p. 133.
1958. Psammosteids; L. B. TARLO, Specimens of ostracoderms..., p. 8.
1958. Ostracodermi; Z. KOTAŃSKI, Przewodnik geologiczny..., p. 335, pl. 10.
1959. Psammosteids; M. PAJCHLOWA, Atlas Geologiczny..., sheet 5.
1964*b*. *Guerichosteus kozlowskii* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 15, 22, 36, 78, 97-99, 101-2, 114; pls. 13, 14, figs. 1-4.

Holotype: Left branchial plate D. 7, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw, figured in the present paper, Pl. IX, fig. 6, and Text-fig. 4*c*.

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

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

Material. — Numerous fragments of plates: dorsal, ventral, branchial and occasionally post-orbital, cornual, oral and pineal, as well as many fulcral and body scales, from the Placoderm Sandstone, Holy Cross Mountains, Poland.

Description. — *Dorsal median plate.* A large fragment of a median plate (D. 1 U. W.) which is flat and represents the major portion of half of an entire plate, shows well marked growth lines parallel to the lateral margin. At one end of the specimen these curve round to run nearly at right angles to the lateral margin. Unfortunately it is not possible to ascertain the shape of the anterior or posterior margins of the plate, but it appears to be fairly circular in outline. Since it is flat and the details of the tubercles of the plate stand out very clearly, particularly in the median area where they are only slightly abraded, it appears to be a dorsal median plate. A further fragment (D. 2 U. W.,) is part of what may also be a dorsal plate, and this again shows concentric growth lines, although the crenulations on the tubercles are not very distinct in this instance despite the fact that the specimen is not abraded. A notable feature of this fragment is the presence of short radial grooves which in all probability were the site of parts of the sensory canal system.

Ventral median plate. A large severely abraded plate (D. 3 U. W.) is known in which remains of the ornament are preserved only in one or two areas. This plate is very deeply arched, and in view of its severe abrasion on the more convex part, it appears to belong to the ventral surface of the carapace. The curvature is considerably more exaggerated than in any of the drepanaspids, and confirms the more advanced nature of the guerichosteids. A further fragment of a ventral median plate (D. 4 U. W.) appears to represent the right half of the posterior end of the plate (Text-fig. 5*A*). In internal view the natural margin of one side of the posterior notch appears to be preserved as also are the posterior and lateral margins of that part of the plate. The margin of the notch is fairly straight, and the posterior margin of the half plate is almost transverse although it diverges slightly postero-laterally, while the lateral margin which is again fairly straight, tends to converge towards the anterior part of the plate. The margin of the notch swings medially towards its anterior end, so that if the plate is symmetrical, there would be a fairly wide open posterior notch extending about half

the length of the plate. Concentric growth lines are visible more or less parallel to the margins of the plate, which swing round to converge with the notch at an acute angle. Also preserved is part of the external surface of this same fragment, and this shows the ornament of closely packed rounded tubercles arranged in concentric rows. In the anterior part of the fragment these seem to be worn away, and they also appear to be strongly abraded in what was the anterior part of the plate, where the central section of the growth rings form a semi-circle anteriorly, and then turn fairly sharply posteriorly to run parallel to the lateral margin. Since the postero-medial part of the plate is not preserved in this fragment, it is not possible to ascertain the relationship of the growth lines to the posterior notch. A fragment of a ventral median plate (D. 5 U. W.) which appears to be the anterior part of the central area, is severely abraded in its posterior part. Concentric growth lines can be seen running more or less parallel to the abraded zone, but anterior to it. Three short radial grooves are present on the abraded portion, and these seem to indicate the presence of parts of the sensory canal system. A further fragment of a ventral median plate (D. 6 U. W.) again shows concentric growth lines, some parts of which are raised up more than others, so that a series of abraded bands are visible. These fade out to one side of the specimen, suggesting that the fragment belongs to the right side of the central part of the plate, towards the anterior.

Branchial plate. The holotype (D. 7 U. W.) is the mid-section of a right adult branchial plate, the lateral margin of which is arcuate in outline (Text-fig. 4*C*). In dorsal view the dorsal external surface forms just under half the width of the specimen, the remainder being the internal surface of the ventral part of the plate which is at a lower level and divided from the dorsal surface by a very steep vertical edge. The entire lateral part of the branchial plate is thick and solid, forming a very strong lateral margin to the carapace. The ventral surface of this specimen is severely abraded, and shows a certain amount of *post-mortem* crushing. On the dorsal surface there is an ornamentation of closely packed rounded tubercles which gradually increase in size towards the lateral margin, while on the ventral surface the tubercles at the lateral margin are larger still. Running parallel to the margin of this surface are growth lines which tend to swing medially as the posterior part of the plate is approached. Growth lines are very difficult to make out on the dorsal surface. A fragment of a branchial plate (D. 8 U. W.) shows the dorsal surface, and again there is a solid lateral portion in which the median limit of the external surface runs parallel to the almost straight lateral margin, while a large right branchial plate (D. 9 U. W.) shows that in dorsal view the lateral margin is fairly straight, and the dorsal surface is at a marked angle to the ventral surface (Text-fig. 4*B*). The median margin of the dorsal part of this plate forms a medio-dorsal projection somewhat in the manner of specimens of branchial plate in *Drepanaspis*. The posterior part of the plate is not preserved, but the median margin runs more or less parallel to the lateral margin of the ventral surface of the plate when seen in internal view, and then gradually curves medially towards the posterior. It then suddenly swings postero-medially to form a very wide postero-median flange. The ornamentation of the ventral surface is characterized by very large worn tubercles at the lateral margin, medial to which are growth zones which run from the margin posteriorly at a small angle. Close to the medial margin are further growth zones which run more or less parallel to the lateral margin, but in the posterior part of the plate these turn almost at right angles and swing medially. A further specimen, part of the dorsal surface of a branchial plate (D. 10 U. W.), shows growth lines almost identical to those of the ventral surface of the previous specimen. However, it is undoubtedly the dorsal surface because there is a further unornamented portion at a lower level medial to the ornamented part. This specimen is very wide, indicating a considerable free lateral extension to the carapace, comparable to advanced

species of *Schizosteus*. Regarding the growth lines, the fact that two different series of lines are present in the last two specimens mentioned indicates that both the lateral and medial margins of the plates are present. Usually in fragments of branchial plates, as for example in D. 11, D. 12 and D. 13 U. W. one set of growth lines only is present running at an angle to the lateral margin.

The distal tip of a right branchial plate (D. 14 U. W.) shows in ventral view an arcuate lateral margin, at the most posterior limit of which there is a sharp point. The posterior margin of the plate then runs at right angles to the lateral margin for a short distance, and then swings medially in a curve which is convex anteriorly. A further specimen of a distal tip, this time visible in dorsal view, is D. 15 U. W. In this specimen the lateral margin is slightly curved and the median margin of the dorsal part of the plate converges with its posterior corner to form a sharp point. The posterior end of the median margin of the dorsal part of the plate marks the lateral margin of the branchial opening. The median margin of the plate as a whole and of the internal surface of the ventral part runs more or less parallel to the lateral margin, although it swings slightly medially in its posterior part, and at its postero-median corner it meets a rather sinuous posterior margin. A further distal tip of a right branchial plate (D. 16 U. W.) belongs to an immature animal (Text-fig. 4*A*). The plate is sharply angulated, with a narrow dorsal surface set at a considerable angle to the ventral surface. In dorsal view the dorsal surface seems to narrow towards the postero-lateral corner of the plate until it die

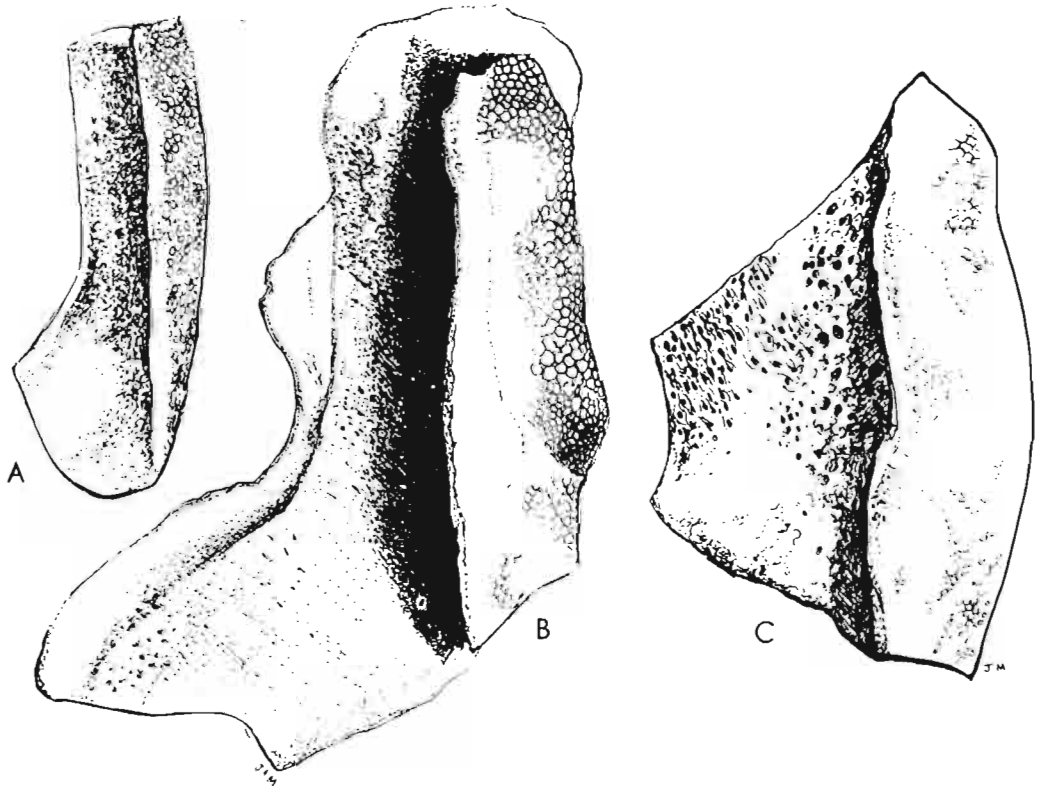

Fig. 4

Guerichosteus kozlowskii TARLO — left branchial plates in dorsal view; *A* (U.W., D. 16); *B* (U.W., D. 9); *C* holotype (U.W., D. 7); Daleszyce, all × 1.

out. The ventral surface which is seen in internal view runs parallel to the lateral margin in the anterior half of the specimen, and then swings postero-medially for a short distance to turn through almost a right angle to run postero-laterally until it grades into the rounded posterior margin of the plate. A gentle postero-median flange is thus produced, which in more mature specimens becomes considerably expanded medially. A specimen of part of a branchial plate (D. 17 U. W.), which appears to be part of the mid section of an adult specimen, has a wide solid free dorsal surface which is somewhat upturned at the margin. On the ventral surface it seems to be severely abraded except at the lateral margin which itself is very strongly arcuate. In *Guerichosteus kozlowskii*, although no complete branchial plates are known, never-

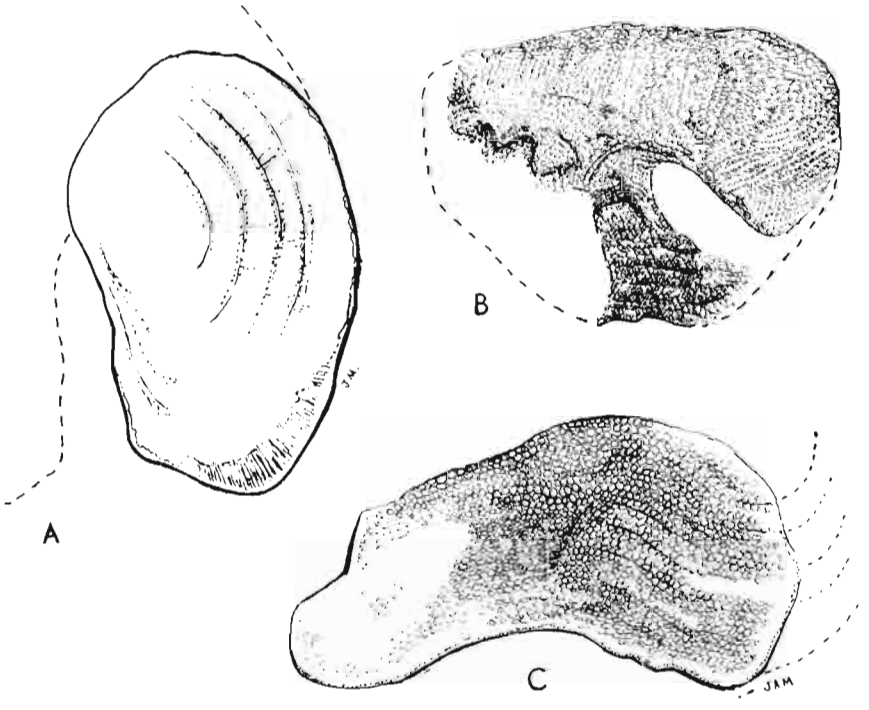

Fig. 5

Guerichosteus kozlowskii TARLO — *A* right posterior part of ventral median plate, internal view (U.W., D. 4), × 0·25; *B* rostral plate (U.W., D. 21), × 0·75; *C* left post-orbital plate (U.W., D. 18), × 0·75; Daleszyce.

theless from the various fragments described above, it is possible to ascertain all the features present. Also, since specimens are known showing different growth stages, it is possible to trace the way in which the various proportions and features of the plates change. In the young stages, the plates appear to be fairly long and narrow with the dorsal and ventral surfaces meeting at a sharp angle, just as if a single plate had been folded to form a "V" in section. As the plate grows the medially projecting extension of the dorsal part of the plate becomes relatively smaller, since the hollow angulated area is gradually infilled with aspidin on the internal surface of the plate to form a solid region. In adult animals the medially projecting part of the dorsal surface may be either very small or absent altogether, so that the dorsal surface is not undercut, and other plates of the dorsal carapace cover all the soft tissue on that side of the animal.

Post-orbital plate. The only recognizable fragment of a post-orbital plate is D. 18 U. W. which is the posterior part of a left plate. The fragment is rather long and narrow, widening anteriorly, and in the posterior part the growth lines run more or less parallel to the lateral margin, which is fairly arcuate (Text-fig. 5*C*). In this region the tubercles of the ornament become somewhat larger. It is not certain whether the exact margin is preserved, but from the tubercles, the margin of the specimen appears to approximate to the true margin of the plate. In the anterior half of the fragment, growth lines are visible which swing medially and then go straight for about one centimetre before they curve medially and swing round anteriorly. Just at the limit of the fragment they seem to turn laterally. The curves are not smooth, but seem to have been arrived at by means of a series of short straight lines of about a centimetre in length following the pattern described. In its natural state the median edge of the specimen is somewhat irregular in this region and in the anterior part the fragment is very reminiscent of the post-orbitals of *Drepanaspis*. However, it differs considerably in the posterior part where it remains fairly wide although still narrower than the anterior part of the plate. In *Drepanaspis* on the other hand the plate quickly tapers to a posteriorly directed point. It is quite evident that with regard to the post-orbital plate, *Guerichosteus kozlowskii* represents a considerable advance on the condition found in *Drepanaspis*, and is close to the condition found in species of *Schizosteus*.

Cornual plate. A very well preserved cornual plate (D. 19 U. W.) seems to belong to the left side of the carapace (Text-fig. 6*A*). The plate has a short lateral margin which forms the median boundary of the branchial opening, and the posterior margin forms a smooth curve for the first two thirds of its length and then gradually swings slightly postero-medially. The centre of growth appears to be in the mid part of the lateral margin, with the posterior growth lines running in a medial direction but slightly posteriorly, and the anterior ones running almost parallel to them. These are joined almost at right angles by the median section of the growth lines which run in an antero-posterior direction, although at a very slight angle to the lateral margins towards which they converge at the posterior end of the plate. Although the fragment has an outline reminiscent of a building keystone, the lateral margin forming the narrow end, it is evident that even though the growth rings are more or less concentric, there was more growth anteriorly and medially than posteriorly. A further cornual plate (D. 20 U.W.) again apparently belonging to the left side, shows a somewhat wider zone of growth posteriorly than in the previous specimen, although the pattern of growth lines is very similar. The cornual plate in this species is thus quite distinct from that known in *Drepanaspis* where it is a fairly oval plate. Unfortunately it is not possible to make comparisons between the cornual plate of the species described here and those of other psammosteids since these plates are only rarely recognized. However, several are known belonging to *Ganosteus stellatus*, and these show a similar quadrangular pattern of growth lines (MARK, personal communication). No firm conclusions can at present be drawn from the similarity of the plates in these two genera, although it does perhaps strengthen the idea of the affinity between the guerichosteids and the pycnosteids.

Rostral plate. An almost complete rostral plate (D. 21 U. W.) shows most of the anterior margin, ornamented by a band of fairly large tubercles which swing postero-laterally on the right hand side (Text-fig. 5*B*). On the left side, the tubercles at the antero-lateral margin are also larger than in the normal part of the plate, indicating that this band of larger tubercles too would have swung round if this part of the plate had not been missing, and in addition that the plate was symmetrical. The major part of both lateral margins is missing although the anterior portion of the right one is present, while the mid part of the posterior margin is

also preserved. This is fairly straight with just one or two small irregularities. The rostral plate appears to be a fairly rectangular plate with the posterior and anterior margins more or less parallel, but it is somewhat wider than it is long. Although the lateral margins diverge initially from the anterior margins, they then straighten out and run more or less at right angles to the anterior margin to swing in again to meet the posterior margin at an angle. In the postero-lateral part of the plate on the left side, three superficial tesserae can be distinguished, and in the central part near the posterior margin further somewhat ill-defined tesserae can also be seen. This type of superficial tessera was also found in a fragment of *Psephaspis williamsi*, and frequently characterizes the rostral plate in species of *Schizosteus* and *Pycnolepis*.

Pineal plate. A single pineal plate (D. 22 U. W.) is known which is somewhat lozenge shaped in outline, although irregular in shape, its major axis being transverse (Text-fig. 6*B*). The central part of the plate is raised somewhat and presumably housed the pineal organ beneath it. The posterior margin is straight in its median portion, and from it the left postero-lateral margin diverges at an obtuse angle, to meet the antero-lateral margin at a fairly sharp rounded angle. On the right side there is a similar straight postero-lateral margin, which however is only about half the length of the left hand one. There is then a lateral flange and this meets a rather more rounded right antero-lateral margin. Anteriorly, the two margins meet at a gentle curve. This pineal plate is rather similar to the single pineal known from the genus *Psammolepis*, belonging to *Psl. abavica*, which is also lozenge-shaped, but in this latter case the surface is completely flat. Furthermore the pineal of *Guerichosteus kozlowskii* is slightly more irregular in outline and is in this respect nearer to the pineal of *Drepanaspis* which although always wider than long, is invariably irregular in outline.

Oral plates. A complete oral plate (D. 23 U. W.) is known, which is somewhat shield-shaped in outline, the anterior margin being straight, with the lateral margins at right angles

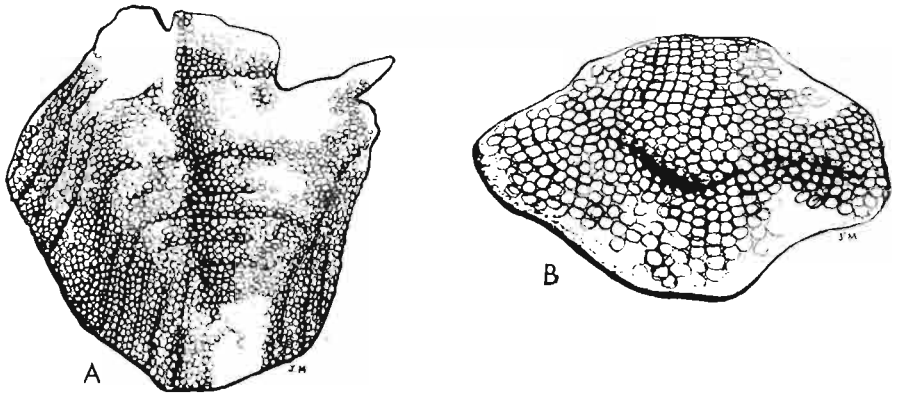

Fig. 6

Guerichosteus kozlowskii TARLO — *A* left cornual plate (U.W., D. 19), × 1; *B* pineal plate (U.W., D. 22), × 2 Daleszyce.

to it and parallel for half their length (Text-figs. 7 *A-C*). These then converge gradually to form a blunt posterior margin. The plate is preserved so that the dorsal surface is visible, and there is a narrow raised strip at the anterior margin which is ornamented by rounded tubercles. This raised area is termed the oral tooth lamella (HEINTZ, 1962), and it partly overhangs the main area of the plate which is the internal surface of the ventral part. This is raised up slightly in the mid-line, but gradually slopes down on either side to produce a faint longi-

tudinal ridge. In lateral view it can be seen that the plate curves over at the anterior margin where it is thinner than in the central part, and also gradually tapers posteriorly. From the symmetry of the plate it does not appear to be a lateral oral plate, but was one of those to one side of the median oral plate, such as are found in *Drepanaspis*. A further oral plate (D. 24 U. W.) is fairly oval in outline, and in dorsal view the anterior part of the plate is raised up from the level of the postero-median two thirds of the plate and is ornamented by rounded tubercles (Text-figs. 7 *D*, *E*). It is clearly an oral plate, but is very asymmetrical, indicating a lateral position. The zone of ornamentation gets narrower to one side, and from the curvature of the anterior margin it would seem to have been situated not only on the right of the median oral plate, but probably at the far end, being the most lateral oral plate of all, forming the antero-lateral margin of the mouth. It seems quite evident that the mouth plates of *Gueri-chosteus kozlowskii* were comparable to those of *Drepanaspis*, and there seems no reason to doubt the fact that all the psammosteids possessed a similar type of oral apparatus. The most striking feature is the prominent development of the oral tooth lamellae which form the anterior margin of the mouth. Until now, such oral plates were known only in *Drepanaspis gemuendenensis*, although their presence has been assumed in other psammosteids (OBRUCHEV, 1947*a*).

Fulcral scales. Numerous scales from both the dorsal and ventral median areas of the carapace are known, and these are symmetrical and greatly elongated. They are also arched from side to side. Specimen D. 25 U. W. is probably from the ventral surface since it appears

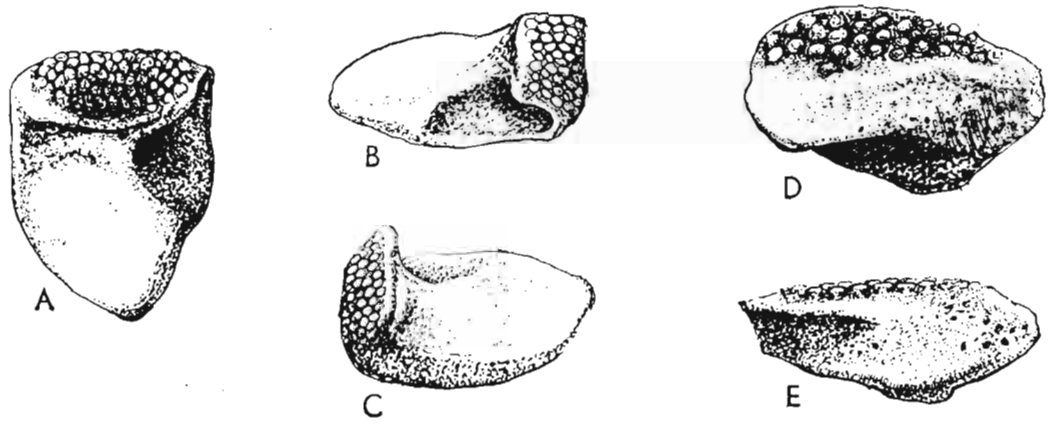

Fig. 7

Guerichosteus kozlowskii TARLO — oral plates; *A-C* oral plate (U.W., D. 23), × 2; *A* dorsal view; *B* left lateral view; *C* right lateral view; *D-E* right lateral oral plate (U.W., D. 24), × 2; *D* dorsal view; *E* left lateral view; Daleszyce.

to be severely abraded along the crest of the proximal two thirds of its length. The notable feature of this particular specimen is the prominence of the tubercles which are fairly closely packed, and are lozenge-shaped, but tend to be more sharply pointed distally. Specimen D. 26 U. W. is the distal tip of a further fulcral scale, possibly from the dorsal surface. The tubercles along its median ridge are aligned more or less longitudinally, while those at either side on the flanks diverge from them in a slightly laterally directed curve which then turns distally. The fulcral scale D. 27 U. W. in which both surfaces are preserved, shows a slight area of abrasion along the crest, and its tubercles are fairly oval with sharply pointed distal ends. On the internal surface there is in the proximal portion, a "V"-shaped broad smooth

groove pointing distally, anterior to which there is a wide "U"-shaped zone also devoid of ornament which shows the characteristic open meshwork of aspidin. The proximal smooth area represents the part of the scale in soft tissue, while the "U"-shaped zone would appear to be the area where most recent dentine tubercles were developing during growth, but had not had time to fuse to the underlying aspidin. Distal to the "U"-shaped zone the entire internal surface of the scale is ornamented by elongated oval tubercles, so that evidently the greater part of the scale was free in the carapace. The scales apparently overlapped one another, their distal part overhanging the proximal part of those succeeding. As the scales grew the free portion must have increased in length by the addition of dentine tubercles at the proximal limit of the ornament. In specimen D. 27 U. W. the tubercles in the distal part are aligned longitudinally and are followed by marked growth zones. First there is an arcuate zone which is convex distally and then a wide zone of elongated pointed tubercles aligned radially around what was the arcuate region inserted in soft tissue. Finally there is a narrow arcuate zone and then smaller tubercles are also aligned radially around the margin of the point of insertion. The internal surfaces of two further fulcral scales (D. 28 and D. 29 U. W.) are also preserved. In these, the elongated tubercles fan out from the apex of the "U"-shaped growing region, but no well marked growth regions can be seen. In contrast to these two specimens, D. 30 U.W. which is also preserved in internal view, is a very wide scale in its proximal part, while in its free distal part the lateral margins converge very sharply. The ornamentation consists of small oval tubercles.

Body scales. Numerous body scales are known which are often asymmetrical, and are much more variable in shape than the fulcral ones. D. 31 U. W. is fairly square in outline, and is gently arched from side to side. The entire internal surface appears to have been inserted in soft tissue, as it is unornamented, while the ornamentation of the external surface is of small oval tubercles aligned longitudinally. The proximal portion of the scale appears to be missing, but in a further fragment of a large body scale (D. 32 U. W.), part of the proximal edge is present and it is devoid of tubercles, suggesting that it was inserted in soft tissue. In this specimen the tubercles are again small, pointed oval ones, and are aligned longitudinally. Faint growth zones can be made out running parallel to the proximal edge. With regard to the distal edge of these scales, as can be seen in specimen D. 33 U. W., here the tubercles are frequently elongated forming what appears to be a fringe, normal to the margin. Specimen D. 34 U. W. shows the unornamented proximal edge, with on the rest of the fragment, closely packed lozenge-shaped tubercles. At the distal margin of the scale a row of elongated "fringe" tubercles are present at right angles to the edge of the scale, whereas the normal lozenge-shaped tubercles are aligned longitudinally, i. e. more or less at right angles to the proximal margin.

Ornamentation. All the plates described above are known from natural moulds, except for one small fragment in which the original tubercles are still preserved (D. 35 U. W.). This shows the details of the individual tubercles remarkably well (Text-fig. 8*A*). They are fairly circular in outline with marked crenulations at their bases which abut or interdigitate with those of adjacent tubercles. These crenulations gradually die out towards the summit of the tubercles, which in well preserved examples, rise to a small rounded peak. The tubercles are fairly closely packed, although they are not markedly deformed for this reason. A photograph of a latex cast of D. 1 U. W. again shows the same type of tubercles, but this time the shapes have been distorted occasionally due to their packing, although the short crenulations are clearly visible. The packing has caused some of the tubercles to become rather rectangular and others more pentagonal, while they are sometimes arranged in rows and at other times

alternately to give the impression of a chess board. As noted earlier, the size of the tubercles varies from one part of the carapace to another, particularly with regard to the plates of the lateral margin, where the tubercles at the margins are considerably larger than those more medially situated. Generally, the tubercles of the lateral edge are much abraded, but in the rather unusual branchial plate (D. 17 U. W.) where the lateral margin is upturned, there are large unworn tubercles on the dorsal surface near the edge (Text-fig. 8*B*). These are very high crowned and the prominent crenulations run almost to their summits, and form a series of radial ribs around the individual tubercles. In many respect therefore they are reminiscent of the tubercles of *Pycnosteus*. With regard to the ornamentation of the scales, the variation of the tubercles has already been noted, but they are always either sharply pointed or naviculate in outline. However, since this type of tubercle occurs in the scales of the majority of psammosteid species it makes recognition on scales alone rather difficult.

Histology. As already mentioned, a single specimen of the actual dermal armour has been found (D. 35 U. W.), and part of it has been sectioned. The texture of the aspidin is normal, being spongy in nature and similar to that known in other psammosteids. The tubercles have a single large pulp cavity, so that in this respect they conform to the tubercles described by KIAER (1915) in *Drepanaspis* and to those in later more advanced psammosteids. They contrast however with the tubercles of the earlier *Weigeltaspis* and *Psephaspis*. The dentine tubules radiate from a single pulp cavity, but in the specimen a considerable part of the dentine has been destroyed by hyphae of a saprophytic fungus. Nevertheless, the dentine tubules stand out in certain parts. The microstructure thus confirms that the material is typically psammosteid in nature and is fairly advanced. A small fragment (D. 36 U. W.) of what appears to be a very unusual type of ornament, with a central tubercle surrounded by a circular rim with radiating ridges, probably belongs to the same species. At first glance it looks like the original material of the armour, but on close examination is seen to be the infilling of the pulp cavities and connected vascular spaces of the normal ornament. The crater rim represents the limit of the tubercle and the supposed tubercle the pulp cavity. The fragment is assigned to the species *Guerichosteus kozlowskii* since the size and arrangement of the separate elements conform to the tubercles previously described (see TARLO, 1964*b*).

Discussion. — As long ago as 1896, GÜRICH recorded *Psammosteus* from the Placoderm Sandstone of the Holy Cross Mountains, and described a specimen which from his description was clearly a branchial plate. Subsequently, SOBOLEV (1909) listed the occurrence of this genus as did CZARNOCKI (1937, 1957) when discussing the stratigraphy of the area. KIAER (1915) in discussing the distribution of *Psammosteus*, mentioned its presence in central Poland (presumably a reference to GÜRICH'S earlier work although it was not directly referred to). However, in all these works, no actual specimens were figured. The first figure to appear was provided by TARLO (1957) who published a photograph of the natural mould of a fragment of a dorsal median plate (D. 2 U. W.) in his preliminary note on the psammosteid remains of the Placoderm Sandstone of Daleszyce. KOTAŃSKI (1958) then figured a block of fossiliferous breccia containing psammosteid fragments from the same locality. The material now identified as *Guerichosteus kozlowskii* was previously (TARLO, 1957) identified as psammosteid type A, and it was suggested that the branchial plate showed some similarities to that of the pycnosteids. It is now evident, however, that the branchial plate in this form is by no means as advanced as in *Pycnosteus* itself, but is obviously much more advanced than the branchial in *Drepanaspis*. *Guerichosteus kozlowskii* therefore clearly belongs to a family from which the more advanced Middle Devonian forms can be derived.

Guerichosteus kozlowskii is by far the commonest species among the psammosteid re-

mains from Daleszyce, and despite the fragmentary nature of the remains as a whole, a greater number of different types of plates are known in this form than in any other psammosteid species with the exception of *Drepanaspis gemuendenensis*, which is known from entire articulated carapaces. Unfortunately, however, because of the incomplete knowledge of the full plates in *G. kozlowskii* it is not possible at the moment to draw any firm conclusions from some of the striking similarities apparent between the parts known and the plates of other groups, such as for example the similarity of the cornual plates to those of *Ganosteus stellatus*, and of the pineal plate to that of *Psammolepis abavica*.

Guerichosteus kotanskii TARLO, 1964

(Pl. XII, figs. 5-7)

1964*b*. *Guerichosteus kotanskii* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 78, 99, 114.

Holotype: Fragment of plate D. 37, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw, figured in the present work, Pl. XII, fig. 7.

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

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

Material. — Fragments of plates from the Placoderm Sandstone, Holy Cross Mountains, Poland.

Description. — The holotype (D. 37 U. W.), is a rectangular fragment ornamented by very large, closely packed, rounded tubercles. Although the fragment is slightly arched, it is not possible to ascertain from which type of plate it comes. A further fragment (D. 38 U.W.), is again ornamented by similar large tubercles, but occasionally much smaller tubercles can be seen filling in spaces between the larger tubercles. This same condition is found in fragment D. 39 U. W. where the tubercles are not quite so tightly packed, and are therefore more circular in outline. In this fragment the fine crenulations at the base of the tubercles can be made out. A fragment of a plate of the lateral margin (D. 40 U. W.), has extremely large tubercles at the lateral edge which are fairly globular, and these give way medially to the more normal large tubercles. In this specimen lines of smaller tubercles are present running at an angle to the lateral margin. Although in *G. kozlowskii* narrow zones of large tubercles are found at the lateral edges of plates of the lateral margin, the normal tubercles of this species are much smaller. Therefore, since the fragments just described show large areas of large tubercles, a separate species is obviously present, for which the name *G. kotanskii* was proposed.

Guerichosteus kulczyckii TARLO, 1964

(Pls. VII, figs. 3, 4; XI, fig. 15)

1964*b*. *Guerichosteus kulczyckii* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 78, 98, 114.

Holotype: Fragment of plate, D. 41, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw, figured in the present work, Pl. VII, fig. 4.

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

Diagnosis. — Ornamentation of small rounded tubercles, packed fairly closely together, but clearly separated from one another. Tubercles, about 0·5 mm. in diameter, with short crenulations at their margins.

Material. — Fragments of plates from the Placoderm Sandstone, Holy Cross Mountains, Poland.

Description. — The holotype (D. 41 U. W.) is a small fragment ornamented by numerous rounded tubercles, all of which are very clearly separated from one another and are more or less circular in outline. A further fragment (D. 42 U. W.), although it is slightly more worn than the previous one, has a similar ornamentation. Specimen D. 43 U. W., which is part of the ventral surface of a right branchial plate, has at the lateral margin tubercles somewhat larger in size than those just described, but these quickly grade medially to tubercles with normal proportions. On this last specimen, there are well marked somewhat arcuate growth lines running posteromedially, but at a sharp angle to the lateral margin. This is characteristic of the growth lines on the ventral surface of branchial plates in this genus. A small fragment (D. 44 U. W.) is part of a body scale, and is ornamented by small oval tubercles which are well separated from one another and show very prominent lateral crenulations. From the size and spacing of the tubercles this specimen is tentatively referred to the same species as the previous fragments. The ornamentation of the material just described, which consists of fairly small clearly separated tubercles is quite distinct from that found in other species of *Guerichosteus*, since not only are the tubercles a different size, but they are also far more uniform in appearance and are hence easy to distinguish. For this reason it is considered justifiable to place material with this ornamentation in a separate species for which the name *Guerichosteus kulczyckii* was proposed.

Guerichosteus lefeldi TARLO, 1964

(Pl. XII, figs. 8, 9)

1957. Psammosteid type D; L. B. TARLO, A preliminary note..., p. 230.
1964*b*. *Guerichosteus lefeldi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 78, 98, 114, 115.

Holotype: Fragment of arched plate, ?ventral median plate, D. 45, housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw, figured in the present work, Pl. XII, fig. 9.

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

Diagnosis. — Ornamentation of minute, closely packed, rounded tubercles just visible to the naked eye, approximately 0·3 mm. in diameter.

Material. — Fragments of plates and scales from the Placoderm Sandstone, Holy Cross Mountains, Poland.

Description. — The holotype (D. 45 U. W.), is a very arched fragment, part of which is devoid of ornament and has clearly been severely abraded. It seems likely therefore that it represents part of a ventral median plate, particularly since the almost unworn area could be the upturned lateral part of such a plate. In the fragment the minute ornamentation of the undamaged part is well preserved, and can be seen to consist of rounded, closely packed tubercles of fairly uniform size. This specimen was previously noted (TARLO, 1957) as psammosteid type D, and it clearly represents a separate species. It appears to be very rare, but this may be partly due to its being overlooked in the field. Although known only from fragments, it seems justifiable to erect a new species for its reception, and the name *Guerichosteus lefeldi*

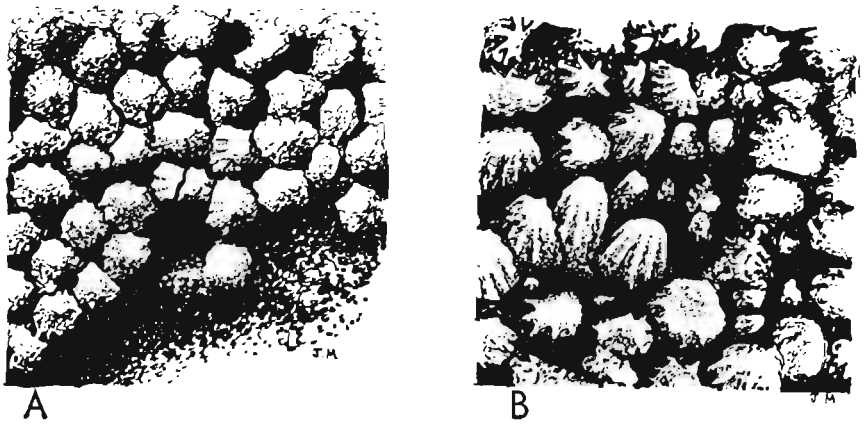

Fig. 8

Guerichosteus kozlowskii TARLO — details of ornamentation; *A* (U.W., D. 35), × 7; *B* (U.W., D. 17), × 7; Daleszyce.

was thus proposed. Two further fragments are also known with the same ornament (D. 46 and D. 47 U. W.). D. 46 is a rectangular fragment, which is angulated and shows well marked growth lines parallel to what is presumed to be a median margin, and then a ridge parallel and slightly lateral to them, which is slightly abraded. Lateral again to this ridge the plate dips, presumably towards the lateral margin of the carapace, suggesting that the fragment might be the median edge of a post-orbital plate. The ornamentation of this specimen is somewhat larger than that of the holotype, but it is still considerably smaller than in *Guerichosteus kulczyckii*, and it is therefore provisionally assigned to *G. lefeldi*. D. 47 is a small fragment, and this has an ornamentation similar both in type and size to D. 46, and appears to be part of a body scale.

Genus **HARIOSTEUS** TARLO, 1964

Type species: *Hariosteus kielanae* TARLO, 1964

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

Occurrence. — Lower Devonian (Emsian Stage), zone of *Rhinopteraspis cornubica*, Holy Cross Mountains, Poland.

Discussion. — The genus *Hariosteus* is closely related to *Guerichosteus*, but is kept separate on account of its remarkable ornament and growth zones. Two species of *Hariosteus* are recognized.

Hariosteus kielanae TARLO, 1964

(Pl. XI, fig. 14; Pl. XIII, figs. 1-4, 6-11; Text-figs. 9, 10)

1957. Psammosteid type B; L. B. TARLO, A preliminary note..., p. 230, pl. 1, fig. 2.
1964. *Hariosteus kielanae* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 15, 22, 78, 98, 115; pl. 14, 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 (1964*b*, Pl. 14, figs. 5, 6) and in the present work Pl. XIII, fig. 1, Text-fig. 9.

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

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.

Material. — Fragments of median, branchial and post-orbital plates, as well as body scales, from the Placoderm Sandstone, Holy Cross Mountains, Poland.

Description. — *Median plate.* The holotype (D. 48 U. W.), is a fragment of a median plate showing a series of very well marked growth zones (Text-fig. 9). The ornament is extremely well preserved and it seems likely that this fragment belonged to a dorsal median plate. The size of the tubercles in the separate zones of growth varies considerably from one

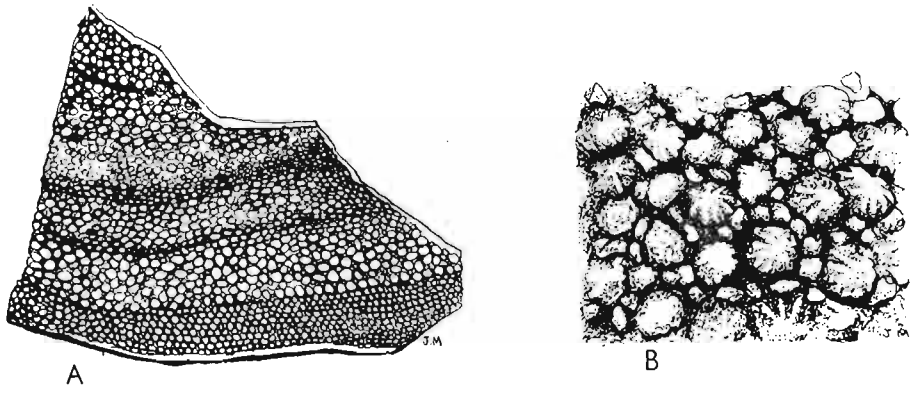

Fig. 9

Hariosteus kielanae TARLO — *A-B* holotype (U.W., D. 48), *A* fragment of median plate showing growth zones, × 1; *B* detail of ornamentation showing accessory tubercles, × 7; Daleszyce.

zone to another, although there is little gradation within each zone. The zones appear to indicate seasonal growth, since there is a broad zone of large tubercles followed by a narrower zone of small tubercles, this pattern being repeated several times. Furthermore, some of the zones are at a slightly higher level than others. This marked banding of the ornament is typical of the species, and probably also the genus, but even more striking than this feature is the nature of the ornament itself. This consists of well separated round tubercles with short crenulations. These continue from the base as radial ribs and converge towards the summits of the tubercles where in some cases they can be seen to meet. Between these main tubercles are situated small rounded ancillary tubercles which appear to form a ring around each main tubercle. Accessory tubercles are known in other psammosteid species, but they are never so numerous or so regularly arranged, with perhaps the exception of the condition in *Ganosteus stellatus*, but there the pattern is very different. A further fragment of a median plate (D. 49 U. W.), again shows the typical ornament and banding, and even in zones where the rounded tubercles are packed closely together, there are nevertheless accessory tubercles in the interstices. The same pattern is even present in the zones with smaller tubercles. A number of fragments (D. 50-54 U. W.), although showing the typical ornamentation of large well

separated tubercles with smaller accessory ones between them, do not show the graded zones to any degree.

Branchial plate. A small fragment (D. 55 U. W.), shows growth zones running parallel to one margin and then swinging round almost at right angles, which would seem to indicate that it is the posterior end of the ventral surface of a branchial plate, where the growth lines swing round to follow the outline of the postero-median flange. Fragment D. 56 U. W. may also perhaps belong to a branchial plate

Post-orbital plate. A large fragment (D. 57 U. W.), is part of a plate which clearly belongs to the lateral margin, since at one edge it is turned over (Text-fig. 10). The striking feature of this fragment however, is again the presence of the alternate zones of growth seen in the fragment of dorsal median plate. Since in fragment D. 57 the zones run at right angles to the lateral margin, this indicates that it cannot be part of a branchial plate, and nor does it seem

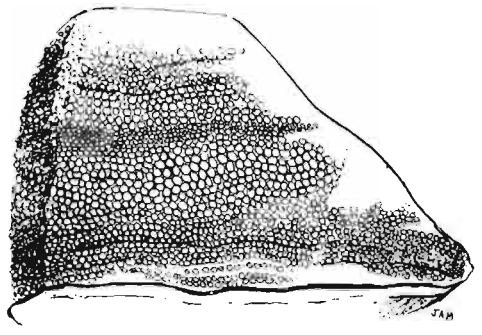

Fig. 10

Hariosteus kielanae TARLO — anterior part of post-orbital plate (U.W., D. 57, Daleszyce), × 1.

likely from what is known of the growth patterns of rostral and cornual plates that it belongs to one of these. However, the post-orbital plate of *Schizosteus heterolepis*, which is wide anteriorly and then narrows posteriorly, has concentric growth rings, and in the wide anterior part these run at right angles to the lateral margin of the plate. Hence, fragment D. 57 would seem to be the anterior part of a post-orbital plate, probably belonging to the right side.

Body scales. A few body scales are known. Specimen D. 58 U. W. shows a proximal unornamented zone distal to which are somewhat elongated tubercles which are sharply pointed distally. These tubercles have prominent crenulations, but the notable feature of the scale is that the tubercles are widely spaced as in the other fragments described above, and there are small accessory tubercles sporadically between them, although in the main the crenulations tend to fill the intervening areas leaving no space for many small tubercles. However, there seems little doubt that it belongs to *Hariosteus kielanae*. A further body scale (D. 59 U. W.), has a fairly straight proximal margin which is unornamented. Of the ornamented part of the plate, the distal half has largely been worn away, while the proximal half is covered by rounded tubercles with small accessory ones between them. The difference in the two scales (D. 58 and D. 59) is probably merely a result of their different position in the body.

Discussion. — Although *Psammosteus* was recorded from the Placoderm Sandstone by GÜRICH (1896), there was no suggestion that more than one genus or even more than one species was represented. Recently (TARLO, 1957) it was recognized that there were several quite distinct types of psammosteid present, and the specimen figured as type B (D. 48 U. W.) which was a natural mould, was distinguished by the zones of minute tubercles separating

larger tubercles. This specimen was referred to the genus and species *Hariosteus kielanae*. The proposal of this new genus and species was considered justified since although the large tubercles in the material here described are themselves comparable to those of *Guerichosteus kozlowskii*, nevertheless by reason of the regularity of the banding seen and the uniform distribution of the accessory tubercles, it would appear essential to place it in a different genus and species.

Hariosteus lobanowskii TARLO, 1964

(Pl. XIII, fig. 5)

1964. *Hariosteus lobanowskii* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 78, 98, 115.

Holotype: Part of right branchial plate D. 60 housed in the Palaeozoological Institute, Polish Academy of Sciences, University of Warsaw, figured in the present work, Pl. XIII, fig. 5.

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

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 individual tubercles of a row, there are minute accessory tubercles.

Material. — Fragments of branchial and median plates from the Placoderm Sandstone, Holy Cross Mountains, Poland.

Description. — The holotype (D. 60 U. W.), appears to be part of the posterior region of a right branchial plate of which the ventral surface is visible. At the lateral margin there are large clearly separated tubercles, medial to which there is a zone of oval or elongated tubercles in which the long axes are parallel to the lateral margin. These tubercles are arranged in a series of sinuous rows running medially, and consisting of single tubercles with their long axes parallel. These rows are well separated by zones of minute tubercles. This pattern begins to die out towards the median part of the fragment which is severely abraded. From the presence of the regular accessory tubercles, it seems quite clear that the species represented by the specimen belongs to the genus *Hariosteus*, but it appears to be quite distinct from *H. kielanae* in the shape and arrangement of the large tubercles. For this reason it was considered justified to propose the new species *Hariosteus lobanowskii* for its reception. Two further fragments (D. 61 and D. 62 U. W.), which appear to be fragments of median plates, again show the same ornamentation, although the rows of large tubercles appear to be in short sections, and there are frequent gaps in the lines of tubercles in which accessory tubercles have formed. However, the tubercles as in the holotype, appear to be elongated and the pattern of the ornament seems to be much the same as in the branchial plate. These further specimens are therefore also referred to the species *H. lobanowskii*.

Genus **SCHIZOSTEUS** OBRUCHEV, 1940

Type species: *Schizosteus asatkini* OBRUCHEV, 1940

Diagnosis. — Dorsal median plate circular in outline with shallow re-entrant angle at anterior margin. Ventral median plate circular in outline, strongly arched from side to side, with wide posterior median notch extending to centre of plate. Branchial plate long and fairly

wide, branchial opening situated some distance medial to the postero-lateral corner. No superficial tesserae known on median plates, but present at margins of rostral plate. Ornamentation of high-crowned, rounded tubercles, with short crenulations or faint radiating ribs.

Occurrence. — Middle Devonian (Eifelian and Givetian Stages), zones of *Schizosteus heterolepis*, *S. striatus* and *Pycnosteus palaeformis*; Baltic province, Bohemia, Ohio and Idaho, United States.

Discussion. — The genus *Schizosteus* was erected by OBRUCHEV (1940) for psammosteids in which there was a well developed posterior notch in the ventral median plate, and in which tesserae were not incorporated into the margins of the median plates. The nature of the posterior notch is highly variable, although it still serves as an aid to the recognition of this genus. A further important diagnostic character is the nature of the posterior margin of the branchial plate and the position of the branchial opening. It is no longer at the lateral margin, as in *Drepanaspis* and *Guerichosteus*, but is some distance medial to the postero-lateral corner, so that the opening is close to the body of the animal, and not near the edge of a wide, laterally projecting extension of the carapace. *Schizosteus* represents a structural grade in advance of that of *Guerichosteus*, from which both pycnosteid and psammolepid lineages can easily be derived.

Schizosteus asatkini OBRUCHEV, 1940

(Text-fig. 11)

1940. *Schizosteus asatkini* n. sp.; D. OBRUCHEV, On some psammosteids..., pp. 766-767, text-figs. 1c, 2.
1964. *Schizosteus asatkini* OBRUCHEV; D. OBRUCHEV, Subclass Heterostraci..., p. 71.

Holotype: Associated dorsal and ventral median plates and posterior part of right branchial plate, 220/489, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1940, Text-figs. 1c, 2), and in the present work, Text-fig. 11.

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Luga River, Leningrad region, Russia.

Diagnosis. — Posterior notch of ventral median plate wide and extending to centre of plate. Ornamentation of small, closely-packed dome-shaped tubercles.

Material. — Unique holotype.

Description. — The holotype (220/489 P. I. M.) consists of part of an associated carapace in which the dorsal and ventral median plates are preserved, together with part of a branchial plate, but there is no evidence of any fields of tesserae (Text-fig. 11). The dorsal median plate is fairly circular in outline, although at its anterior margin there is a shallow, wide re-entrant angle. There are very well marked concentric growth rings present around a central initial growth area, and there is an equal amount of growth on all sides. Also present on the specimen are well marked radial lines which are not part of a sensory canal system, but are likely to be due to the method of growth of the plate. The dorsal median plate although slightly concave in the central part was probably fairly flat in life. In this it contrasts with the ventral median plate which, although again circular in outline, is strongly arched from side to side, the lateral sides being fairly steep and the bottom flat. In this plate too, there are well marked concentric growth rings around a centrally placed initial growth area. There is also a well marked posterior median notch which is fairly broad and extends well into the central area, although it does not reach as far as the centre of the plate. The branchial plate has a convex lateral margin, and its posterior margin has a posteriorly directed rounded lateral projection. Medial to this is a rounded postero-median flange. The ornamentation consists of small dome-shaped rounded

tubercles with marked crenulations, which are packed closely together. Well marked growth zones can also be clearly seen.

Discussion. — This species was first described by OBRUCHEV (1940) who also figured the restored dorsal and ventral median plates. This species which is the type species of the genus *Schizosteus* has a marked posterior median notch in its ventral plate, but this does not

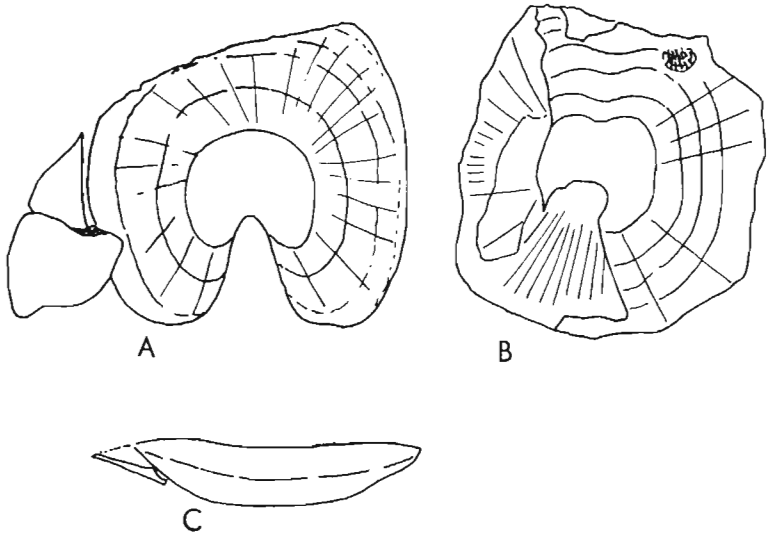

Fig. 11

Schizosteus asatkini OBRUCHEV — holotype, carapace, *A* ventral median plate showing posterior notch, together with adjoining right branchial plate; *B* dorsal median plate; *C* posterior view of specimen, showing profiles of dorsal and ventral median plates (P.I.M. 220/489, Luga); × 0·5.

seem to be as prominent as in other species of the genus. The size of the holotype suggests that it is from a fairly young individual, and in many respects it is reminiscent of the young stages in *Psammolepis*. The posterior notch in the holotype is more strongly developed however than in the young stages of *Psammolepis*, but it is much less developed than in earlier species of *Schizosteus*. Consequently, it seems to be close to the line which led to *Psammolepis*. Thus in *Schizosteus asatkini* it appears that the posterior notch in the ventral median plate has reached a stage where it is being gradually reduced towards the condition in *Psammolepis*, rather than becoming exaggerated to lead to *Pycnosteus*. Furthermore, *S. asatkini* is the only species of *Schizosteus* to be found as late as the Arukula horizon in which *Psammolepis* first appears. The absence of tesserae in the holotype may well be due to their having been lost during burial, but it is more likely that they were not well developed at the stage of growth represented, as also appears to be the case in young stages of *Drepanaspis* (see GROSS, 1963).

Schizosteus heterolepis (PREOBRAJENSKY, 1911)

(Pl. XIV, fig. 4; Text-figs. 12 *B-E*)

1845*a*. *Psammosteus arenatus* n. sp.; L. AGASSIZ, Monographie des poissons..., pp. 105, 130, pl. 31, figs. 7-9.
1911. *Psammosteus heterolepis* n. sp.; I. A. PREOBRAJENSKY, On some representatives..., p. 35, pl. 1, fig. 7; pl. 2, figs. 8, 9.
1933*a*. *Psammolepis heterolepis* (PREOBRAJENSKY); W. GROSS, Die Fische des..., p. 12, pl. 2, fig. 16.

1940. *Schizosteus*(?) *heterolepis* (PREOBRAJENSKY); D. OBRUCHEV, On some psammosteids..., p. 766.
1964*b*. *Schizosteus heterolepis* (PREOBRAJENSKY); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 12, 82, 99, 100; pl. 3, fig. 6.

Lectotype (here chosen): Fragment of branchial plate 372, housed in the Geological Institute, Tallinn, figured by PREOBRAJENSKY (1911, Pl. 1, fig. 7).

Type horizon and locality: Middle Devonian (Givetian), Pernau horizon, *Schizosteus heterolepis* zone; Tori, Estonia.

Diagnosis. — Ornamentation of high-crowned, pointed tubercles with prominent radial ribs which extend to the sharply pointed summits of the tubercles. When abraded, the tubercles are frequently reminiscent of the metal caps surmounting beer bottles. The tubercles vary considerably in size and small tubercles are often found scattered between the larger ones.

Material. — Branchial, post-orbital and orbital plates, together with scales, from the Pernau horizon of Estonia.

Description. — *Branchial plate.* In the lectotype (372 G. I. T.) at the lateral margin there is a row of extremely large tubercles measuring some 2 mm. in diameter, which are severely abraded (Text-fig. 12*B*). Medial to them the tubercles very quickly become much smaller, until they are about a third of the size of the marginal ones. Occasionally small tubercles can be seen filling the interstices between the others. The tubercles as a whole are fairly closely packed, although clearly separated from one another, and they are characterized by possessing very strong, but short radial ribs. The most striking feature of the ornamentation, however, is the variation in the size of the tubercles, — hence the name *Schizosteus heterolepis*. The fragment of a branchial plate is ornamented on both surfaces and consists of part of the completely solid free extension to the carapace. Medially the plate becomes much thicker, and one surface appears to have been horizontal with the other at an angle to it. Presumably this latter is the dorsal surface, the median margin of which approximates to the median limit of the ornamented part of the plate. A further branchial plate (376 G. I. T.) in which the greater part of the lateral margin is preserved, shows that this margin is slightly arcuate in outline, and it curves gently medially in its posterior part, towards the posterior margin (Text-fig. 12*D*). This fragment too, consists of just the free lateral part of the plate and is ornamented on both surfaces. A further lateral part of a branchial plate (A. 28130, P. M. O.) again shows the lateral margin in which the ornamentation consists of very large tubercles, but the rest of the fragment is notable for the high proportion of interstitial tubercles present. The nature of the ornamentation is, however, identical to that of the other fragments.

Orbital plate. An orbital plate (377 G. I. T.) is known belonging to this species, which is strongly arched from side to side (Text-fig. 12*C*). The orbit is situated towards one margin which is thicker in section than the wider part of the plate on the other side of the orbit. In the specimen the orbit is situated about one third of the way down the length of the plate, and it is presumed that the shorter area of plate is anterior, as there is an arched lateral marginal plate anterior to the orbital plate in psammosteids and there is unlikely to be a wide expanse of orbital plate also anterior to the orbit, since this would set the eye back too far in the carapace. However, there is no reason why the orbital plate could not extend posteriorly since there is nothing to limit its backward growth. The orbital plate in question therefore probably belongs to the left side of the carapace.

Post-orbital plate. The major part of a right post-orbital plate (378 G. I. T.) is preserved in which the lateral margin is curved over and is strongly abraded (Text-fig. 12*E*). The growth lines by means of which the plate was identified, run almost at right angles to the lateral margin in the anterior part of the plate, and then make a sharp postero-medial turn to run postero-

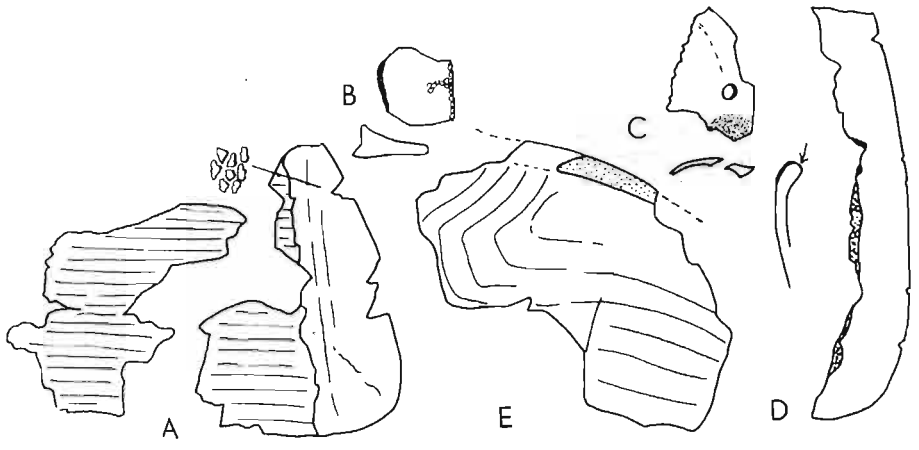

Fig. 12

A Schizosteus toriensis MARK-KURIK — holotype, right branchial plate in dorsal view (G.I.T. 389, Tori), × 0·5; *B-E Schizosteus heterolepis* (PREOBRAJENSKY) — *B* lectotype, fragment of branchial plate (G.I.T. 372, Tori), × 1; *C* orbital plate (G.I.T. 377, Tori), × 0·5; *D* branchial plate (G.I.T. 372, Tori); × 0·5; *E* right post-orbital plate (G.I.T. 378, Tori), × 0·5.

laterally and then gradually converge with the posterior part of the lateral margin. This type of growth pattern is similar to that known in the post-orbital plates of *Guerichosteus kozlowskii* and *Hariosteus kielanae*, and is obviously typical of the guerichosteids.

Discussion. — AGASSIZ (1845*a*) figured under the name *Psammosteus arenatus* (now recognized as a synonym of *Psammolepis paradoxa*) what appears to be a fragment of the same species as the material just described under *Schizosteus heterolepis*. The reason for the present identification of AGASSIZ's specimen is really the colour of his figure, since the material belonging to *Schizosteus heterolepis* is always black, whilst all material of *Psammolepis* from the Baltic is brown in colour. AGASSIZ carefully portrayed the correct colour of the specimens when he figured them, and there is no doubt that he had in his possession a specimen of *S. heterolepis*. However, this form was not properly named until PREOBRAJENSKY (1911) introduced the name *Psammosteus heterolepis* which GROSS (1933*a*) subsequently referred to *Psammolepis*. More recently OBRUCHEV (1940) suggested that this species might be assigned to his new genus *Schizosteus*. From the nature of the branchial plates this species can undoubtedly be placed in the genus *Schizosteus*, although to date ventral median plates which could confirm this identification are not yet known in this form.

Schizosteus toriensis MARK-KURIK, 1965

(Text-fig. 12*A*)

1965. *Schizosteus toriensis* n. sp.; E. MARK-KURIK. Psammosteids from the... (in the press).

Holotype: Branchial plate 389, housed in the Geological Institute, Tallinn, figured by MARK-KURIK (1965, in the press).

Type horizon and locality: Middle Devonian (Givetian), Pernau horizon, *Schizosteus heterolepis* zone; Tori, Estonia.

Diagnosis. — Ornamentation of flat-topped rectangular, or occasionally fan-shaped, tubercles with short crenulations.

Material. — Branchial plate and numerous fragments from the Pernau horizon, Estonia.

Description. — The holotype consists of a right branchial plate (389 G. I. T.). In dorsal view there is a narrow lateral ornamented region taking up about a quarter of the width of the plate (Text-fig. 12*A*). The lateral margin is slightly arcuate and forms a rounded postero-lateral corner which continues into a fairly straight posterior margin. The entire ventral surface is ornamented, but since only a quarter of the dorsal surface is also ornamented, this means that only the lateral quarter of the plate formed the free lateral extension to the carapace. The branchial opening is clearly no longer at the posterior lateral corner of the plate, but is some distance medial to it at the posterior margin, with the solid projecting area of the plate lateral to it. This species is easily distinguishable on the nature of its ornamentation which consists of flat tubercles which are frequently rectangular in outline and have short crenulations, although in some parts they may become rather fan-shaped due to being closely packed. The ornament thus serves to distinguish the species very readily from the contemporary *Schizosteus heterolepis*.

Schizosteus striatus (Gross, 1933)

(Pl. XV, figs. 1, 2; Text-fig. 13)

1933*a*. *Psammolepis striata* n. sp.; W. Gross, Die Fische des..., p. 12, pl. 1, fig. 10, text-fig. 2B.
1935. *Psammolepis striata* Gross; W. Gross, Histologische Studien..., p. 14.
1940. *Schizosteus striatus* (Gross); D. Obruchev, On some psammosteids..., p. 766, text-fig. 1b.
1942. *Schizosteus striatus* (Gross); W. Gross, Die Fischfaunen..., pp. 377, 410.
1947*b*. *Schizosteus striatus* (Gross); D. Obruchev, Atlas of the guide..., p. 195, pl. 50, fig. 7, text-fig. 54.

Holotype: Right branchial plate, 397, housed in the Geological Institute, Tallinn, figured by Gross (1933*a*, Pl. 1, fig. 10) and by Obruchev (1947*b*, Pl. 50, fig. 7).

Type horizon and locality: Middle Devonian (Givetian), Narowa horizon, *Schizosteus striatus* zone; Gorodenko, Estonia.

Diagnosis. — Ornamentation consisting of short dentine ridges aligned in rows at an angle to the lateral margin of branchial plates, and of closely packed rounded tubercles with marked crenulations, somewhat "hat-like with flat brim and crown inclined backwards", on median plates.

Material. — Numerous dorsal, ventral, branchial, post-orbital and rostral plates from the Narowa horizon of Estonia.

Description. — *Dorsal median plate.* An almost complete dorsal median plate (444 G.I.T.) shows well marked concentric growth rings, and a series of radiating lines from the centre of the plate which break up the growth zones into segments (Text-fig. 13*A*). These radial lines which Gross (1933*c*) and Obruchev (1940) considered to be connected with a sensory canal system appear to be simply a result of the manner of growth of the plate. The central growth area has a fairly straight anterior margin divided into three slight lobes, while the lateral sides are arcuate as also is the posterior margin, although it is markedly narrower than the anterior one. The growth zones appear to be wider in the anterior part of the plate than in the posterior part, suggesting that the centre of growth is positioned just to the posterior of the true centre of the plate, with the whole outline of the plate following the shape of that of the central growth area. This seems to contrast somewhat with the dorsal plate of the later *Schizosteus asatkini*, where the central growth area appears to be in the centre of the plate, and it is of interest to note that in such later forms as the various species of *Psammolepis*, the centre of growth appears to move progressively forwards from one species to the next.

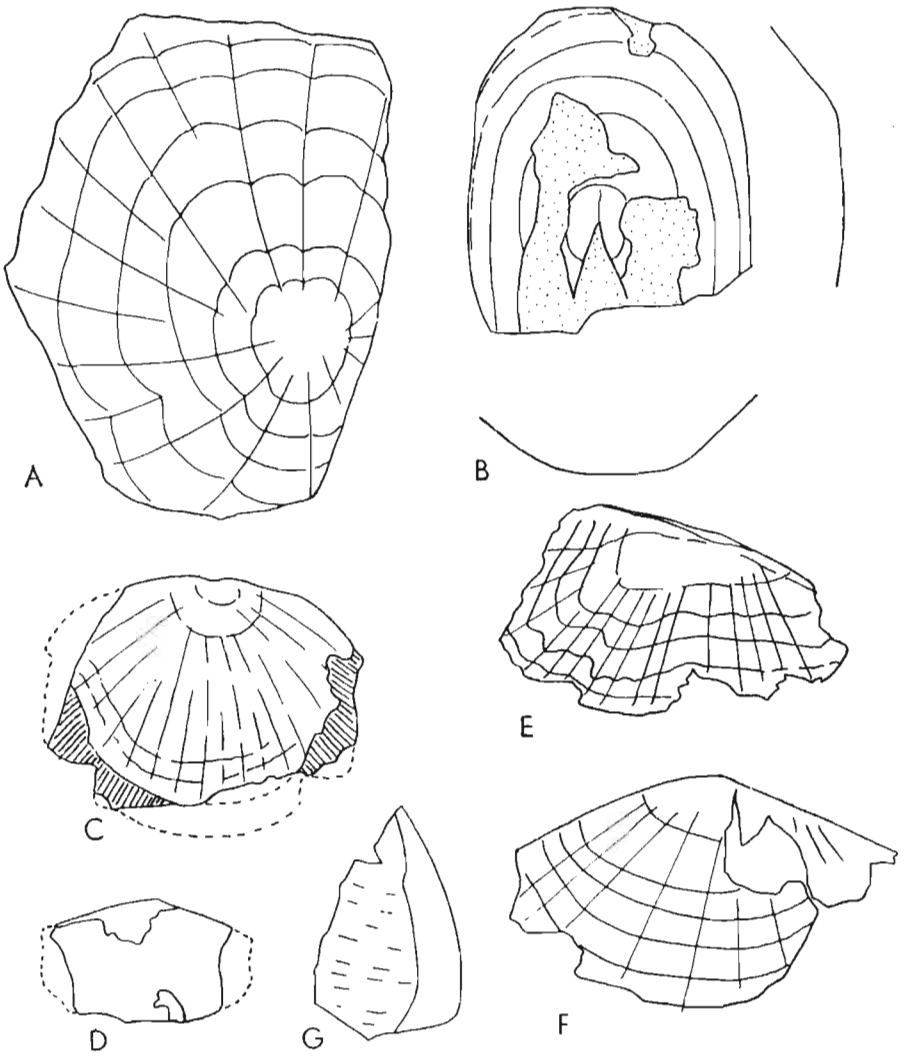

Fig. 13

Schizosteus striatus (GROSS). *A* dorsal median plate showing concentric growth lines (G.I.T. 444, Gorodenko), × 0·5; *B* ventral median plate showing posterior notch, and diagrammatic sections (P.I.M. Colln. Gorodenko), × 0·5; *C* adult rostral plate (G.I.T. 401, Gorodenko), × 0·5; *D* immature rostral plate (G.I.T. 429, Gorodenko), × 0·5; *E* right post-orbital plate (G.I.T. 445, Gorodenko), × 0·5; *F* right post-orbital plate (P.I.M. 220/588, Gorodenko), × 0.5; *G* immature right branchial plate in dorsal view (G.I.T. 424, Gorodenko), × 0·5.

Ventral median plate. The major part of a ventral median plate (220 P. I. M.) belonging to a comparatively immature individual, shows a flat central area with steeply sloping anterior and lateral sides (Text-fig. 13*B*).

Well marked concentric growth rings are visible, and there is also a strong posterior median notch, which reaches the central growth area. The anterior part of the notch forms a sharp angle, thus contrasting with the shallower broader notch in the ventral plate of *Schizosteus asatkini*, even though the specimens appear to represent equivalent growth stages. The development of the notch in *S. striatus*, however, appears to be considerably less than in the contemporary *Pycnolepis splendens* where this feature is greatly exaggerated. This indicates

that *Pycnolepis splendens* is well on the way to the typical pycnosteid condition, whereas *Schizosteus striatus* which is difficult to distinguish from *S. asatkini* except in the development of this posterior notch, may well be on the psammolepid line.

Branchial plate. The holotype (397 G. I. T.) consists of the anterior part of a right branchial plate, the ornamented dorsal side only of which is visible. The lateral margin is slightly convex with large tubercles ornamenting it, and running in parallel rows at a small angle to the lateral margin are rows of short dentine ridges or elongated flat-topped tubercles, giving the impression that the whole surface is striated, hence the name of the species. It is evident even from the anterior part of this plate, that there is an extremely wide lateral free extension or sheet of bony material extending beyond the main part of the carapace for a considerable distance. It is obvious therefore that this is a very advanced member of the guerichosteids, since it is approaching the proportions found in both typical psammolepids and typical pycnosteids. Furthermore a number of immature branchial plates are also known, and a right branchial (424 G. I. T.) which shows a long narrow free lateral margin on the dorsal surface, is in its general proportions comparable to the adult branchials of *Schizosteus toriensis* and *S. heterolepis* (Text-fig. 13*G*).

Post-orbital plate. A well preserved right post-orbital plate (445 G. I. T.) shows the downturned and abraded lateral margin, with in the anterior part of the plate the growth lines running at right angles to the lateral margin (Text-fig. 13*E*). Medially however, these turn and run postero-laterally, converging with the lateral margin posteriorly. The pattern of growth lines is markedly asymmetrical, and is similar to that known in *Schizosteus heterolepis* and the primitive guerichosteids. A further right post-orbital plate (220/588 P. I. M.) again shows part of the lateral margin, and a series of growth lines running at a slight angle to it, but towards the anterior part of the plate they swing round to run towards it at right angles (Text-fig. 13*F*). Even though the plate is not complete, the pattern of growth lines and the asymmetry of the plate show that this is a post-orbital.

Rostral plate. A symmetrical plate from an adult individual (401 G. I. T.) has an arcuate anterior margin in which there is a centre of growth in the mid-line (Text-fig. 13*C*). The lateral margins are fairly straight for part of their length, and they then turn in sharply to run more or less parallel to the anterior margin for a short distance. They then turn again at right angles to run posteriorly where they curve round to form a gently rounded posterior margin. From the outline and symmetry of the plate, with its concentric growth rings and radial lines from the growth centre, it is evident that this is a rostral plate. An immature specimen of the same plate (429 G. I. T.) shows a slightly angled anterior margin and a fairly straight posterior one, but the lateral margins are missing (Text-fig. 13*D*). A further rostral plate (446 G. I. T.), which represents just the left half of the plate, shows concentric growth rings and radial lines, and then at the posterior and postero-lateral margins a wide zone of scale-like superficial tesserae which have become incorporated into the plate. These appear more typically scale-like than those found in the contemporary *Pycnolepis splendens*.

Discussion. — This species was first described by GROSS (1933*a*) under the name *Psammolepis striata*, but was subsequently placed by OBRUCHEV (1940) in the genus *Schizosteus* when he figured the ventral median plate for the first time. GROSS (1942) accepted OBRUCHEV's assignation of this species to *Schizosteus*, and OBRUCHEV (1947*b*) again figured the ventral median plate and the holotype. This species is clearly one of the most advanced guerichosteids as is shown by the development of its branchial plate, and the nature of the posterior notch in its ventral median plate suggests that it may well belong to the psammolepid line.

Schizosteus perneri (RŮŽIČKA, 1929)

(Pl. XIV, fig. 1)

1929. *Psammosteus (Ganosteus) perneri* n. sp.; I. R. RŮŽIČKA, Psammosteus (Ganosteus)..., pp. 1-7, pl. 1 (15), figs. 1-3.
1940. *Schizosteus*(?) *perneri* (RŮŽIČKA); D. OBRUCHEV, On some psammosteids..., pp. 767-768.
1950. *Psammosteus perneri* RŮŽIČKA; W. GROSS, Die paläontologische..., pp. 59, 66.

Holotype: Left branchial plate B.R./123-60, housed in the National Museum, Prague, figured by RŮŽIČKA (1929, Pl. 1 (15), figs. 1-3), and in the present work, Pl. XIV, fig. 1.

Type horizon and locality: Middle Devonian (Eifelian), Chotek Limestones, Horizon $g\gamma$ ($G\text{-}g_3$); Limestone Quarry, Holin, Hlubočepy near Prague, Czechoslovakia.

Diagnosis. — Ornamentation of well separated regular rounded tubercles with prominent radial ribs.

Material. — Unique holotype.

Description. — The holotype (B.R./123-60 N. M. P.), is a left branchial plate, the dorsal surface of which is visible. The specimen although fractured both near the posterior and anterior regions, shows that the lateral margin is slightly convex in outline, and is ornamented by well separated rounded tubercles with prominent crenulations. The lateral margin curves gently in its posterior part to form a rounded postero-lateral corner, and the median margin of the ornamented part of the dorsal surface of the plate curves medially towards the posterior margin, so that the ornamented part is therefore somewhat narrower anteriorly. Medial to the ornamented part there is on the dorsal surface a narrow unornamented area, which is the internal surface of the ventral part of the plate. This part would normally be wider, and it seems likely that the median part of the plate has been lost. Since the median edge of the ornamented part of the dorsal surface swings medially at the posterior margin, the branchial opening must of necessity be situated some distance medial to the lateral margin of the carapace. Beyond the branchial opening there is a free laterally extending projection, and although this is as wide as in such forms as *Drepanaspis lipperti* and *Guerichosteus*, it is not as wide as in say the much later *Schizosteus striatus*. Because of the displacement of the branchial opening medially however, the plate is dissimilar to those known in either *Drepanaspis* or *Guerichosteus*, and it is quite clear that this form belongs to the genus *Schizosteus*, to which OBRUCHEV (1940) tentatively referred it. GROSS (1950) also noted that it seemed to be intermediate between *Drepanaspis* and *Psammolepis*. It is distinguished from the other species of *Schizosteus* by its characteristic ornamentation of regular well separated tubercles.

Schizosteus wellsi TARLO, 1964

(Pl. XIV, fig. 5)

1944*a*. Drepanaspid indet.; J. W. WELLS, Middle Devonian..., p. 285.
1944*b*. Drepanaspid indet.; J. W. WELLS, Fish remains from..., p. 112, pl. 10, figs. 7, 8; pl. 11, figs. 1-4 (non pl. 8, fig. 45; pl. 12, fig. 1).
1955. *Drepanaspis*(?); A. P. BYSTROW, The microstructure..., p. 497.
1964. *Schizosteus wellsi* n. sp.; B. J. TARLO & L. B. H. TARLO, The origin..., p. 7 (nomen nudum).
1964*b*. *Schizosteus wellsi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 21, 61, 80, 115, 116.

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

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

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

Material. — Fragments from Franklin County, Ohio, and Idaho, United States.

Description. — The holotype (19402 G. M. O.) is a small oral plate ornamented by two rows of small rounded smooth tubercles at the anterior part of the dorsal surface, with a smooth unornamented posterior part. As well as this specimen, WELLS (1944*b*) figured a further fragment of a plate with similar clearly separated smooth tubercles (19401 G. M. O.), part of which he showed in section. In addition, a large fragment of a median plate from Idaho (D. 77 U. W.) has very kindly been sent to the author by Dr. R. H. DENISON, and it is evident that it is ornamented with the same type of tubercles. For this reason it can be assigned to the same species as that described by WELLS (1944*b*). The Idaho specimen shows a series of concentric growth rings, and although it is not possible to ascertain the nature of either the ventral or branchial plates, it is evident from the ornament and method of growth of the plate that it is likely to belong to the genus *Schizosteus*. For this reason it is included in this genus, and since the ornamentation is very distinctive, it would appear to be justifiable to erect a new species for its reception, for which the name *Schizosteus wellsi* was proposed.

Family PYCNOSTEIDAE TARLO, 1962

Diagnosis. — Deep ventral median plate, with steep lateral and anterior slopes; persistent open posterior notch (partially infilled secondarily in *Tartuosteus*). Branchial plates as wide as long. Superficial tesserae not present on median plates (except on dorsal median plates of *Tartuosteus* and *Yoglinia*).

Discussion. — The family Pycnosteidae was proposed (TARLO, 1962*c*) for Middle Devonian psammosteids possessing a marked posterior notch in the ventral median plate, which is always open to some extent. This family thus contrasts with the contemporary psammolepids in which only a slight notch is formed in the young stages, which is entirely obliterated as the plate grows. The branchial plates in the family Pycnosteidae are in the main, comparable to those in the Psammolepididae, although in some of the later representatives they become highly specialized. In three of the five genera included in the family Pycnosteidae — *Pycnolepis*, *Pycnosteus* and *Ganosteus*, the posterior notch in the ventral median plate remains fully open throughout life, and in this contrasts with the condition in *Tartuosteus* where although the notch continues to develop as the animal grows, it is gradually infilled at the same time. Thus the length of the open part of the notch is never very great, although the full length of the notch is usually traceable. *Tartuosteus* is included in the Pycnosteidae, however, regardless of the partial secondary infilling of the notch, since the ventral median plate grows in a manner similar to that seen in the three other genera already mentioned. Tentatively included in the family Pycnosteidae is the genus *Yoglinia*, despite the fact that no ventral median plate is yet known in this form, since its ornament is very close to that of *Tartuosteus maximus*. The family Pycnosteidae thus includes the 5 genera mentioned above with the 13 species belonging to them.

Genus **PYCNOLEPIS** TARLO, 1964

Type species: *Pycnolepis splendens* (EICHWALD, 1844)

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.

Occurrence. — Middle Devonian (Givetian), Narowa Horizon; Gorodenko, Estonia and River Slawanka, Leningrad region.

Pycnolepis splendens (EICHWALD, 1844)

(Text-figs. 14, 15)

1844. *Cheirolepis splendens* n. sp.; E. EICHWALD, Über die Fische des... p. 830.
1844. *Cheirolepis unilateralis* n. sp.; E. EICHWALD, *Ibid.*, p. 830.
1844. *Microlepis lepidus* n. sp.; E. EICHWALD, *Ibid.*, p. 830.
1844. *Microlepis exilis* n. sp.; E. EICHWALD, *Ibid.*, p. 830.
1845. *Cheirolepis splendens* EICHWALD; E. EICHWALD, Ueber fossile Fische..., p. 676.
1845. *Cheirolepis unilateralis* EICHWALD; E. EICHWALD, *Ibid.*, p. 676.
1845. *Microlepis lepidus* EICHWALD; E. EICHWALD, *Ibid.*, p. 676.
1845. *Microlepis exilis* EICHWALD; E. EICHWALD, *Ibid.*, p. 676.
1845*a*. *Cheirolepis splendens* EICHWALD; L. AGASSIZ, Monographie des..., p. 155.
1845*a*. *Psammosteus arenatus* n. sp.; L. AGASSIZ, *Ibid.*, p. 155.
1845*a*. *Cheirolepis unilateralis* EICHWALD; L. AGASSIZ, *Ibid.*, p. 155.
1845*a*. *Psammosteus undulatus* n. sp.; L. AGASSIZ, *Ibid.*, p. 155.
1845*a*. *Microlepis lepidus* EICHWALD; L. AGASSIZ, *Ibid.*, p. 155.
1845*a*. *Microlepis exilis* EICHWALD; L. AGASSIZ, *Ibid.*, p. 155.
1845*a*. *Psammosteus maeandrinus* n. sp.; L. AGASSIZ, *Ibid.*, p. 155.
1846. *Cheirolepis splendens* EICHWALD; E. EICHWALD, Nachtrag zu der..., pp. 304-305, pl. 10, figs, 24, 25.
1846. *Cheirolepis unilateralis* EICHWALD; E. EICHWALD, *Ibid.*, p. 305, pl. 10, figs. 26, 27.
1846. *Microlepis lepidus* EICHWALD; E. EICHWALD, *Ibid.*, p. 303, pl. 10, figs. 20, 21.
1846. *Microlepis exilis* EICHWALD; E. EICHWALD, *Ibid.*, pp. 303-304, pl. 10, figs. 22, 23.
1858. *Microlepis lepidus* EICHWALD; G. KADE, Ueber die devonischen..., p. 11.
1858. *Microlepis exilis* EICHWALD; G. KADE, *Ibid.*, p. 11.
1858. *Psammosteus maeandrinus* AGASSIZ; G. KADE, *Ibid.*, p. 11.
1860. *Cheirolepis splendens* EICHWALD; E. EICHWALD, Lethaea Rossica..., pp. 1573-1574, pl. 57, figs. 23 a, b.
1860. *Cheirolepis unilateralis* EICHWALD; E. EICHWALD, *Ibid.*, pp. 1574-1575, pl. 57, figs. 14a, b-d.
1860. *Microlepis lepidus* EICHWALD; E. EICHWALD, *Ibid.*, p. 1576, pl. 57, fig. 13.
1860. *Microlepis exilis* EICHWALD; E. EICHWALD, *Ibid.*, pp. 1576-1577, pl. 57, fig. 12.
1891*b*. *?Cheirolepis canadensis* WHITEAVES; A. S. WOODWARD, Catalogue..., p. 457.
1940. *Cheirolepis splendens* EICHWALD; D. OBRUCHEV, On some psammosteids..., p. 767.
1940. *Cheirolepis unilateralis* EICHWALD; D. OBRUCHEV, *Ibid.*, p. 767.
1940. *Microlepis lepidus* EICHWALD; D. OBRUCHEV, *Ibid.*, p. 767.
1940. *Microlepis exilis* EICHWALD; D. OBRUCHEV, *Ibid.*, p. 767.
1940. *Schizosteus(?) splendens* (EICHWALD); D. OBRUCHEV, *Ibid.*, p. 767.
1958. *Schizosteus splendens* (EICHWALD); D. OBRUCHEV, On the biostratigraphy..., p. 45.
1964*b*. *Pycnolepis splendens* (Eichwald); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 12, 14, 45, 82, 85, 99, 100, 102, 116; text-fig. 16A.
1964. *Schizosteus splendens* (EICHWALD); D. OBRUCHEV, Subclass Heterostraci..., pl. 7, figs. 2, 7.

Lectotype (here selected): Fragment of plate, 1/1296, housed in the Geological Museum, University of Leningrad, figured by EICHWALD (1860, pl. 36, fig. 23).

Type horizon and locality: Middle Devonian (Givetian), Narowa horizon, *Schizosteus striatus* zone; River Slawanka, NW Russia.

Diagnosis. — As for genus, only species.

Material. — Dorsal, ventral, branchial and rostral plates from Estonia, together with numerous fragments from NW Russia.

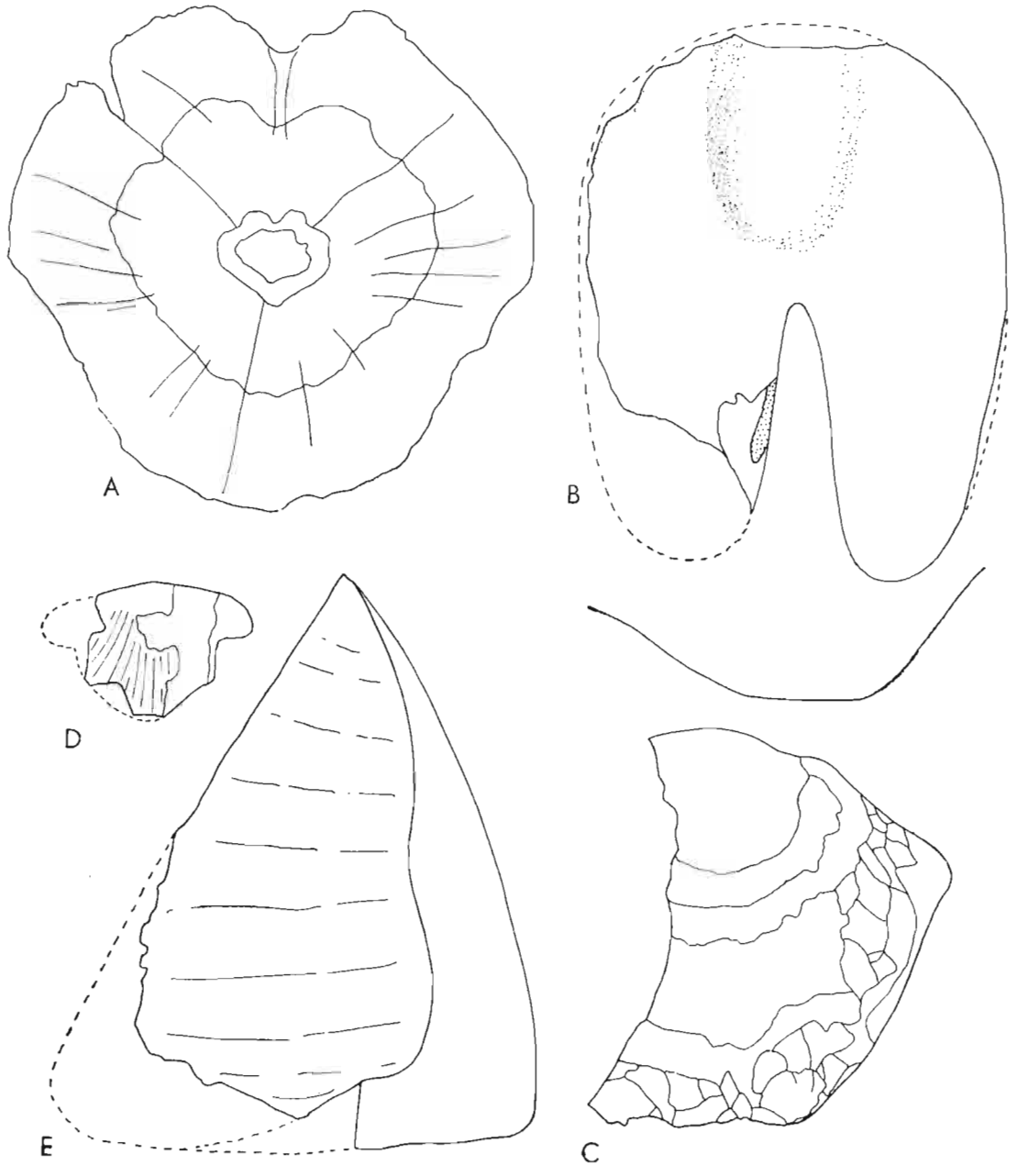

Fig. 14

Pycnolepis splendens (EICHWALD) — *A* dorsal median plate (G.I.T. 426, Gorodenko), × 0·25; *B* ventral median plate (G.I.T. 425, Gorodenko); × 0·25; *C* rostral plate (G.I.T. 420, Gorodenko); × 0·5; *D* immature rostral plate (G.I.T. 428, Gorodenko), × 0·5; *E* immature right branchial plate (G.I.T. 422, Gorodenko), × 0.5.

Description. — *Dorsal median plate.* A flat dorsal median plate (426 G. I. T.) has a fairly wide, shallow re-entrant angle in the centre of the anterior margin (Text-fig. 14*A*). From this the lateral margins diverge strongly, then run parallel for a short distance and finally converge, to reach a gently rounded heart-shaped centre of growth around which concentric zones can be made out, and from which lines radiate. Towards the anterior margin

there is a slight medial groove reaching to the re-entrant angle. The plate is ornamented by closely packed dentine tubercles which are generally fan-shaped, but no superficial tesserae occur.

Ventral median plate. A complete ventral median plate which is strongly arched from side to side (145 G. I. T.) measures 32 cm. in length and 25 cm. in width (Text-fig. 14*B*). The anterior margin is gently rounded, the lateral margins run almost parallel, but gradually converge posteriorly, and in the centre of the rounded posterior margin there is a deep open notch extending 15 cm. into the plate, which is 8 cm. wide at its posterior end, and narrows to under 1 cm. anteriorly. The development of this wide posterior notch clearly establishes the pycnosteid affinities of *Pycnolepis splendens*, and it can be considered as an early member of this family which in the extent of its posterior notch is intermediate between *Schizosteus* and *Pycnosteus*.

Branchial plate. A mature branchial plate (421 G. I. T.) is known in which both the posterior and lateral margins are gently convex and meet at a gently rounded wide angle (Text-fig. 15). The limit of the ornamentation on the dorsal surface is a more or less straight line at right angles to the posterior border, and it continues anteriorly for half the length of the plate and then curves round laterally to form a wide anterior margin. The unornamented part of the plate is much greater in extent in this specimen than in the other pycnosteids. The plate is ornamented by closely packed rounded tubercles, with well developed fine basal crenulations which form fine ribs on the lower sides. A less mature branchial plate (422 G. I. T.) illustrates the marked change in proportions during the growth of the animal (Text-fig. 14*E*).

Rostral plate. The right half of a mature rostral plate (420 G. I. T.) shows the rectangular outline of this plate (Text-fig. 14*C*). The anterior margin is slightly convex in its median part,

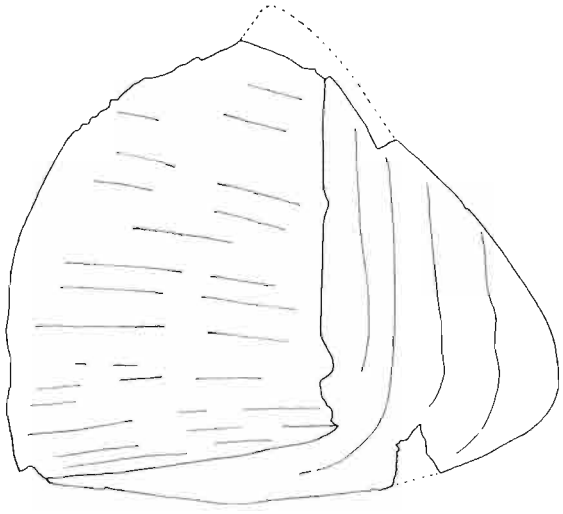

Fig. 15

Pycnolepis splendens (EICHWALD) — right branchial plate in dorsal view (G.I.T. 421, Gorodenko), × 0·33.

and its lateral part slopes slightly posteriorly to meet the straight lateral margin at right angles. The posterior margin forms a very blunt angle in the mid-line, and meets the lateral margin at a slightly obtuse angle. The centre of growth of this plate is in the mid-line at the anterior margin, and around this, elliptical zones of growth can be followed which show that the plate increased in size more rapidly posteriorly than laterally. At the lateral and posterior margins there is a wide zone of irregular superficial tesserae, which are of many different shapes and sizes. This is the only evidence of tesserae in the species. An immature rostral plate (428 G.I.T.)

has a gently convex anterior margin which extends into lateral lappets (Text-fig. 14 *D*). Behind these the lateral margins run directly posteriorly and then converge to form a blunt posterior angle. In this specimen there are no traces of concentric growth, and in all probability it represents the initial growth stage.

Discussion. — EICHWALD (1844, 1845) described several psammosteid fragments under the following names — *Cheirolepis splendens*, *Cheirolepis unilateralis*, *Microlepis lepidus*, and *Microlepis exilis*. In 1845, he was bitterly attacked by AGASSIZ who claimed that this material could be included in AGASSIZ' own *Psammosteus arenatus*, *P. undulatus* and *P. meandrinus*. In 1846 EICHWALD redescribed his species and figured them, and took AGASSIZ to task for trying to make his (EICHWALD'S) names which had priority, synonyms for AGASSIZ' later names. Fortunately the material described by AGASSIZ and EICHWALD was not the same, and as result both sets of names remain valid. PANDER (1857) recognized that EICHWALD'S and AGASSIZ' material was similar, but suggested that it all belonged to *Asterolepis*. KADE (1858) listed *Microlepis lepidus* and *M. exilis* in the synonymy of *Psammosteus meandrinus*, but in 1860 EICHWALD listed both AGASSIZ' and his own species entirely separately. ROHON (1901) also recognized that EICHWALD'S material was in fact psammosteid, and noted as had PANDER, that EICHWALD had confused the dentine tubercles with small scales, and that what he had in fact described was the ornamentation of fragments of body plates, and not as he believed, patches of squamation. GROSS (1933*a*) considered in his description of the new species *Psammolepis striata* (since referred by OBRUCHEV (1940) to *Schizosteus*) that the remains described by EICHWALD might belong to his new species, but he felt that EICHWALD'S material could not be specifically identified. OBRUCHEV (1940) said that the material which EICHWALD assigned to *Cheirolepis splendens*, *Ch. unilateralis*, *Microlepis lepidus* and *M. exilis* in fact represented a single species and he selected the name *Ch. splendens* for it, and this he referred to his new genus *Schizosteus*. This species can be readily recognized by its characteristic fan-shaped tubercles. With regard to the generic designation of this species, *Cheirolepis* could not be used because this was a valid generic name for an actinopterygian which had been erected by AGASSIZ (1835) prior to EICHWALD (1844), and EICHWALD had placed two of his new species in this genus as a result of misinterpreting the remains. At the same time he erected a new genus *Microlepis* which unfortunately was preoccupied having been erected for a reptile by GRAY (1839). It is now recognized that EICHWALD'S 4 new species were the same, and since *Ch. splendens* (the name selected for them) needed to be placed in a new genus, it was included in *Schizosteus* by OBRUCHEV (1940). Further material has, however, come to light which shows that *S. splendens* differs from the material originally called *Schizosteus* by OBRUCHEV. Whilst it is still possible to retain *Schizosteus* for the material described by OBRUCHEV in 1940, a new name must be proposed for EICHWALD'S material. In fact it represents a morphological stage intermediate between *Schizosteus* and *Pycnosteus* since it has a very large well developed posterior notch in its ventral median plate, and as it appears to herald the pycnosteids it is here included as an early representative of the Pycnosteidae, and the name *Pycnolepis* was proposed for it.

Genus **PYCNOSTEUS** PREOBRAJENSKY, 1911

Type species: *Pycnosteus palaeformis* PREOBRAJENSKY, 1911

Diagnosis. — Dorsal median plate more or less circular in outline, with no superficial tesserae. Ventral median plate long and narrow with very long wide persistent posterior notch, the median margins of which are developed as runners; strongly arched from side to side

and towards anterior margin. Branchial plate long and wide, becoming proportionately wider in later species. Ornamentation of high-crowned rounded tubercles with coarse crenulations or radiating ribs.

Occurrence. — Middle Devonian (Givetian Stage), zones of *Pycnosteus palaeformis* and *Pycnosteus tuberculatus*; Baltic province, and Spitsbergen.

Discussion. — This genus was erected by PREOBRAJENSKY (1911) to include his new species *P. palaeformis* which was based on a complete ventral median plate. OBRUCHEV (1940) was able to show that the material described by ROHON (1901) as *Ganosteus tuberculatus*, also belonged to this genus. MARK (1956) re-described *Pycnosteus palaeformis*, *P. tuberculatus* and a new species *P. pauli*, and OBRUCHEV (1965) described the Middle Devonian Spitsbergen psammosteid *P. nathorsti*. The genus *Pycnosteus* is readily recognized by its ornamentation and the extreme length and width of the posterior notch of the ventral median plate. The first attempt at a restoration of this genus is given in the General Part of this work (TARLO, 1964*b*, Text-fig. 6) and also in TARLO & TARLO (1965).

Pycnosteus palaeformis PREOBRAJENSKY, 1911

(Pl. XVIII, fig. 2; Text-fig. 16)

1837. *Trionyx spinosus* KUTORGA; S. KUTORGA, Zweiter beitrag..., p. 12, pl. 4, fig. 11.
1895. *Psammosteus arenatus* AGASSIZ; A. S. WOODWARD, The problem of..., p. 39.
1908. *Psammosteus arenatus* AGASSIZ; E. S. GOODRICH, On the scales..., p. 774, pl. 43, fig. 4.
1911. *Pycnosteus palaeformis* n. sp.; I. A. PREOBRAJENSKY, On some representatives..., p. 34, pl. 1, figs. 1-5.
1911. *Psammosteus imperfectus* n. sp.; I. A. PREOBRAJENSKY, *Ibid.*, p. 35, pl. 1, fig. 6.
1930. *Pycnosteus palaeformis* PREOBRAJENSKY; W. GROSS, Die Fische..., pp. 7-11, pl. 1, fig. 98; pl. 2, fig. 3.
1933*a*. *Pycnosteus palaeformis* PREOBRAJENSKY; W. GROSS, Die Fische des..., p. 13, pl. 2, figs. 22, 23.
1933*a*. *Psammolepis (Pycnosteus?) imperfecta* (PREOBRAJENSKY) W. GROSS, *Ibid.*, pp. 12-13.
1935. *Pycnosteus palaeformis* PREOBRAJENSKY; W. GROSS, Histologische Studien..., pp. 14-15, pl. 2, fig. 1.
1940*b*. *Pycnosteus? imperfectus* (PREOBRAJENSKY) W. GROSS, Acanthodier und..., p. 14.
1940*b*. *Pycnosteus palaeformis* PREOBRAJENSKY; W. GROSS, *Ibid.*, p. 74.
1940. *Schizosteus(?) imperfectus* (PREOBRAJENSKY) D. OBRUCHEV, On some psammosteids..., p. 767.
1940. *Pycnosteus palaeformis* PREOBRAJENSKY; D. OBRUCHEV, *Ibid.*, p. 768, text-figs. 1d, 3.
1947*b*. *Pycnosteus palaeformis* PREOBRAJENSKY; D. OBRUCHEV, Atlas of the guide..., p. 196, pl. 50, fig. 4.
1956. *Pycnosteus imperfectus* (PREOBRAJENSKY); E. MARK, On the genus *Pycnosteus*..., pp. 74-76, text-figs. 1a, 2a.
1956. *Pycnosteus palaeformis* PREOBRAJENSKY; E. MARK, *Ibid.*, pp. 76-77, pl. 1, fig. 1; pl. 2, fig. 1, text-figs. 1b, 2b, 3a.
1962. *Pycnosteus palaeformis* PREOBRAJENSKY; E. MARK, Moningatest..., p. 32, text-fig. 3a.
1964*b*. *Pycnosteus palaeformis* PREOBRAJENSKY; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 12, 15, 17, 19-21, 30, 82, 99-102, 104; pl. 3, figs. 1, 3, text-fig. 7A.
1964. *Pycnosteus palaeformis* PREOBRAJENSKY; D. OBRUCHEV, Subclass Heterostraci..., p. 72, text-figs. 48, 49, 51*a*.

Holotype: Ventral median plate, 102, housed in the Geological Institute, Tallinn, figured by PREOBRAJENSKY (1911, Pl. 1, figs. 1-5), and MARK (1956, Text-fig. 1b), and in the present work, Text-fig. 16*A*.

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Arukula, Estonia.

Diagnosis. — Branchial plate broad and long, ornamented by high-crowned, star-shaped, loosely packed dentine tubercles. Ventral median plate long and narrow, with very wide open posterior notch extending for greater length of plate, strongly arched from side to side and towards anterior margin, with same ornamentation as branchial plate.

Material. — Ventral median and branchial plates from Estonia, Latvia and the Leningrad district.

Description. — *Ventral median plate.* The holotype, (102 G. I. T.), is an almost complete ventral median plate which measures 30 cm. in length and 17 cm. in width (Text-fig. 16*A*). The lateral margins are rather broken and although the anterior margin has been lost since it was described by PREOBRAJENSKY (1911), it was gently rounded. The posterior notch measures 22 cm. in length and 6 cm. in width, and it is fully open. Extending almost all the way down on either side of it are narrow strips some 1-1·5 cm. wide which are much abraded and have been reinforced by pleromic dentine. Anterior to the notch there is a small oval area which is similarly abraded and strengthened. In the anterior part of the plate concentric lines of growth are visible which curve round to end at the notch. The ornamentation consists

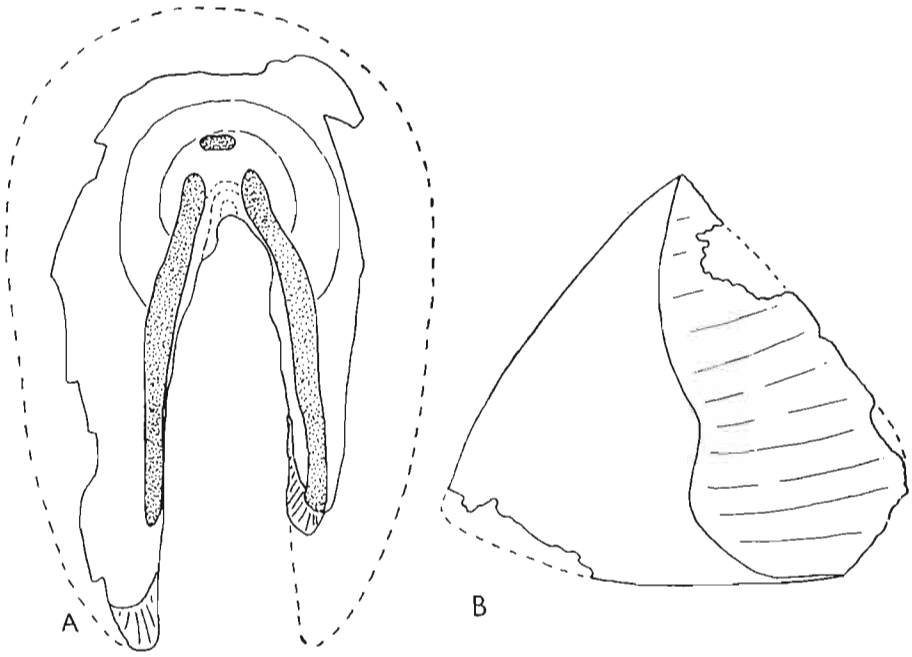

Fig. 16

Pycnosteus palaeformis PREOBRAJENSKY — *A* holotype, ventral median plate showing deep notch with abraded median margins (G.I.T. 102, Arukul; a), × 0·25; *B* left branchial plate in dorsal view (G.I.T. 261, Kallasti), × 0·25.

of loosely packed high-crowned star-like dentine tubercles, the points of the stars being formed by coarse crenulations or short stubby ribs. The plate is strongly arched from side to side, and towards the anterior margin. In lateral view the anterior profile of the plate curves outwards from the flat abraded surface to form a gentle convexity and then forwards and upwards to form a gentle concave slope. From the abraded surface the lateral sides of the plate slope outwards and upwards at a steep angle. A fragment of a ventral median plate (101 G. 1. T.) is the anterior part of the right side and it was originally described as *Psammosteus imperfectus* by PREOBRAJENSKY. It shows the abrasion along the margin of the notch and concentric zones of growth which end at it. The ornamentation in this specimen is indistinguishable from that of the holotype.

Branchial plate. A branchial plate in which the postero-lateral end is complete (1894.61.22 R. S. M.) has a straight lateral border which meets the slightly convex posterior border at a rounded angle of some 70 degrees. The median limit of the ornamentation on the dorsal side

is almost at right angles to the posterior margin, and the ornamentation consists of loosely packed star-shaped tubercles similar to those seen on the ventral plate. A further branchial plate (261 G. I. T.) has a slightly convex lateral margin and a similar posterior margin which it would meet at about 70 degrees (Text-fig. 16*B*). The limit of the ornament on the dorsal side forms a sinuous line running more or less at right angles to the posterior margin, but swings medially as it approaches this margin, to meet it near its median limit. A complete branchial plate is similar in outline to No. 261 G. I. T., but this time the lateral and posterior margins meet at a rather larger angle, this being near to a right angle. The median extent of the ornamentation is less than in the two previous specimens, but the limit of this ornamentation on the dorsal surface takes much the same course as in 261 G. I. T.

Discussion. — KUTORGA (1837) figured a patch of the characteristic tubercles of this species which he believed belonged to the armour of some extinct turtle. In 1895 WOODWARD described the ventral median plate of this same species which he referred to *Psammosteus arenatus*, a species which he had previously noted from Spitsbergen. Since he did not describe the ornamentation and presumably had no knowledge of KUTORGA'S work, it was not realized that WOODWARD'S and KUTORGA'S material belonged to the same species. In 1911, PREOBRAJENSKY redescribed the ventral median plate already described by WOODWARD and this time figured it, together with details of its ornamentation and histology, and erected the new genus and species *Pycnosteus palaeformis* for it. In the same work he described as a further new species under the name *Psammosteus imperfectus*, part of the right side of a similar plate which he thought bordered the notch. GROSS (1930) believed that it belonged to *Pycnosteus*, but in 1933 said that the smallness of its tubercles and their arrangement showed that it was quite different from *Pycnosteus palaeformis*, and stated that he thought that it was more likely to belong to *Psammolepis*, and might well be part of a branchial plate. OBRUCHEV (1940) tentatively referred *P. imperfectus* to *Schizosteus* and recognized that PREOBRAJENSKY had been correct, and that his specimen was part of a ventral median plate. OBRUCHEV also briefly redescribed *Pycnosteus palaeformis*. MARK (1956) again redescribed PREOBRAJENSKY'S material, recognizing that the two ventral median plates described by him were closely related. She therefore referred *P. imperfectus* to *Pycnosteus*, although still keeping it separate from *Pycnosteus palaeformis*. A re-examination of the types of both species in Tallinn shows that in fact their ornamentation is indistinguishable and they therefore both belong to *Pycnosteus palaeformis*, a conclusion tentatively put forward by GROSS (1940*b*).

Pycnosteus pauli MARK, 1956

(Text-fig. 17)

1955. *Pycnosteus pauli* n. sp.; E. MARK, Psammosteidae (Agnatha)..., pp. 4, 7-9, 12, 15, 16.
1956. *Pycnosteus pauli* n. sp.; E. MARK, On the genus *Pycnosteus*..., pp. 82-85, pl. 2, figs. 4, 5; pl. 3, fig. 4, text-figs. 1c, 7, 8 a-d, 9.

Holotype: Ventral median plate, 105, housed in the Geological Institute, Tallinn, figured by MARK (1956, Text-fig. 7), and in the present work, Text-fig. 17*A*.

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Tamme, Estonia.

Diagnosis. — Branchial plate wide and fairly long, ornamented by evenly spaced star-shaped dentine tubercles with longer and more numerous radiating ribs than in *Pycnosteus palaeformis*. Ventral median plate with long open posterior notch.

Material. — Fragments of dorsal and ventral median plates and numerous branchial plates from Estonia.

Description. — *Ventral median plate.* The holotype, (105 G. I. T.) is the posterior part of the left side of a ventral median plate (Text-fig. 17*A*). Bordering the open median posterior notch is a narrow longitudinal strip of severe abrasion which has been strengthened with pleromic dentine. Concentric growth lines can be traced which end at this strip of abrasion. The posterior margin itself is slightly rounded, and the lateral margin gradually diverges from it and then runs more or less parallel to it anteriorly. There is a broad border round the plate devoid of ornamentation, the rest of the plate being ornamented by evenly spaced star-shaped dentine tubercles with moderately long radiating ribs, which tend to bifurcate at their extremities. These are more numerous and are longer than those in the tubercles of *P. palaeformis.*

Branchial plate. Branchial plate 106 G. I. T. has straight lateral and posterior margins which meet at a rounded angle of some 70 degrees (Text-fig. 17*B*). In outline this branchial

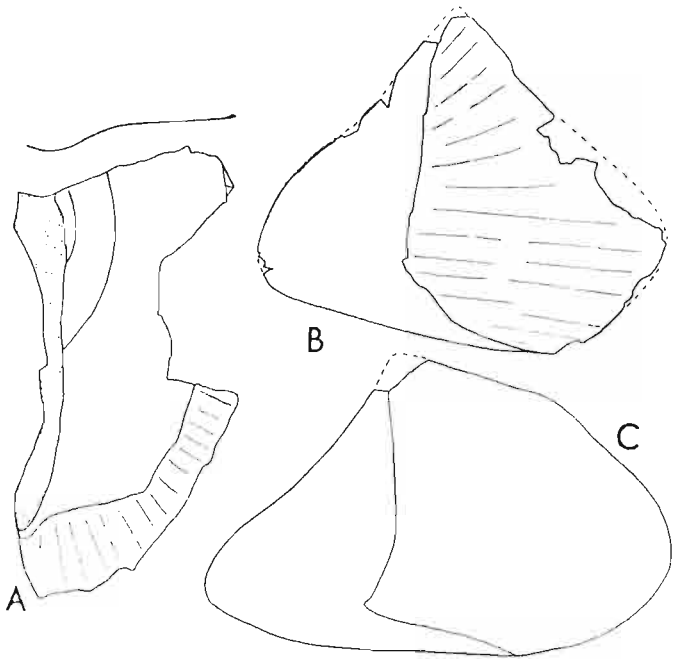

Fig. 17

Pycnosteus pauli MARK — *A* holotype, left posterior part of ventral median plate showing abraded zone at margin of posterior notch (G.I.T. 105, Tamme), × 0·17; *B* left branchial plate in dorsal view (G.I.T. 106, Tamme), × 0·17; *C* left branchial plate in dorsal view (G.I.T. 107, Tamme), × 0·17.

plate is similar to that of *Pycnosteus palaeformis.* On the dorsal surface the limit of the ornamentation runs more or less at right angles to the posterior margin, but turns sharply medially as it approaches this margin, to meet it almost at its medial limit.

A further branchial plate (109 G. I. T.) is drawn out more laterally, the lateral and posterior borders meeting at about 50 degrees. The lateral border is straight, and the posterior slightly convex, and there is a narrow strip of abrasion along the lateral margin. Another branchial plate (107 G. I. T.) has a convex posterior margin and a slightly concave lateral one, and these meet at a fairly wide rounded angle (Text-fig. 17*C*). There is a narrow area of

abrasion along the entire free lateral and posterior borders. On the dorsal surface the medial limit of the ornamentation at first runs at right angles to the posterior margin and then swings laterally, when it turns sharply medially to join the posterior margin some two thirds of the distance from the postero-lateral corner. These branchial plates which have an ornamentation similar to that of the ventral median plate, are intermediate between those known in the earlier *Pycnosteus palaeformis* and the later *Pycnosteus tuberculatus*. Whereas in *P. palaeformis* the lateral margin is generally slightly convex, in *P. tuberculatus* this is always strongly concave, while in *P. pauli* it is usually straight, but may on occasions be slightly concave. Similarly, the ornamentation of *P. pauli* is intermediate between that of the two other species.

Pycnosteus tuberculatus (ROHON, 1901)

(Text-fig. 18)

1836. Fragments des téguments; J. J. F. W. VON PARROT, Essai sur les ossements..., pp. 25. 27, 28, pl. 3, figs. 4, 5, 6, 11, 12.
1837. *Trionyx spinosus* KUTORGA; S. KUTORGA, Zweiter Beitrag..., p. 12, pl. 4, fig. 9.
1901. *Ganosteus tuberculatus* n. sp.; J. V. ROHON, Beiträge zur Anatomie..., pp. 12-13, pl. 1, fig. 2; pl. 2, fig. 23.
1933*a*. *Ganosteus tuberculatus* ROHON; W. GROSS, Die Fische des..., p. 17, pl. 1, fig. 7.
1940. *Pycnosteus tuberculatus* (ROHON) D. OBRUCHEV, On some psammosteids..., p. 768.
1942. *Pycnosteus tuberculatus* (ROHON); W. GROSS, Die Fischfaunen..., pp. 378, 379, 381.
1947*b*. *Pycnosteus tuberculatus* (ROHON); D. OBRUCHEV, Atlas of guide..., p. 196, pl. 50, fig. 6.
1956. *Pycnosteus tuberculatus* (ROHON); E. MARK, On the genus *Pycnosteus*..., pp. 77-81, pl. 1, figs. 2-6; pl. 2, figs. 2, 3; pl. 3, figs. 1-3, text-figs. 3*b*, 4, 5, 6.
1962. *Pycnosteus tuberculatus* (ROHON); E. MARK, Moningatest..., pp. 32, 33, text-figs. 3b, 4.
1964*b*. *Pycnosteus tuberculatus* (ROHON); L. B. H. Tarlo, Psammosteiformes (Agnatha)..., pp. 12, 19, 21, 29, 30, 38, 82, 83, 100-103, 108; pl. 3, figs. 2, 4, 5, text-figs. 6, 7B.
1964. *Pycnosteus tuberculatus* (ROHON); D. OBRUCHEV, Subclass Heterostraci..., p. 72, pl. 7, fig. 4, text-figs. 51, 51b.
1965. *Pycnosteus tuberculatus* (ROHON); B. J. H. TARLO & L. B. H. TARLO, The origin..., p. 20, text-fig. 1.

Neotype (here proposed): Fragment of median plate, 2442/4, housed in the Palaeontological Institute, Moscow, figured by PARROT (1836, Pl. 3, fig. 4).

Type horizon and locality: Middle Devonian (Givetian), Burtnicki horizon, *Pycnosteus tuberculatus* zone; Lake Burtneck, Latvia.

Diagnosis. — Branchial plate short and wide, with concave lateral margin, ornamented by large, round, evenly spaced high-crowned tubercles, with strong radiating ribs which bifurcate towards their extremities, occasionally fused into short strips; occasional similar smaller tubercles among the large ones. Ventral median plate with very long, wide, open posterior notch with prominent runners developed on either side of notch.

Material. — Fragments of dorsal and ventral median plates, numerous branchial plates and single orbital plate from Latvia.

Description. *Ventral median plate*. The posterior part of the right side of a ventral median plate (263 G. I. T.) shows on its external surface a narrow band of severe abrasion strengthened by pleromic dentine at the margin of the posterior notch. Growth lines can be made out running diagonally back to the margin of the notch. This specimen when viewed from the internal surface shows a wide longitudinal zone some 4 cm. in width, bordering the posterior notch, which is ornamented. When the plate is held so that the flat zone of maximum abrasion is in contact with the substratum, the external surface of the plate slopes upwards and outwards, and the ornamentation extends for a short distance on to the internal surfaces which face medially on either side of the notch. In this way, the main body of the carapace is raised up on to a pair of median runners. The ornamentation consists of evenly

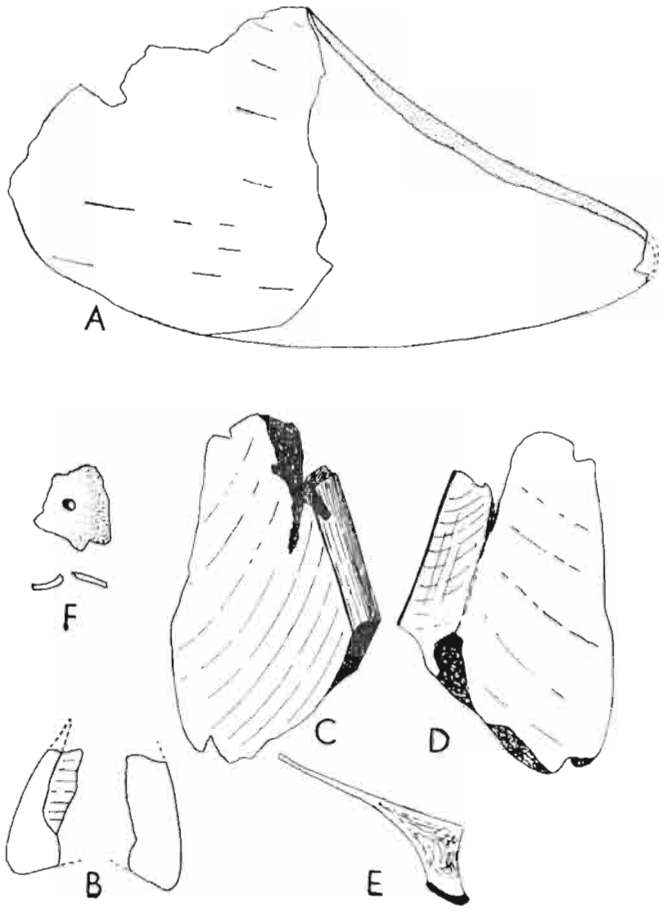

Fig. 18

Pycnosteus tuberculatus (ROHON) — *A* right branchial plate in dorsal view, illustrating concave anterior margin with wide zone of abrasion on dorsal surface (G.I.T. 123, Harma), × 0·25; *B* immature left branchial plate, *a*, dorsal view, *b*, ventral view (G.I.T. 117, Karksi); × 0·5; *C-E* fragment of ventral median plate showing development of runner at margin of posterior notch, *C* external view, *D* internal view, *E* cross-section of median ventral runner (G.I.T. 265, Karksi), × 0·5; *F* orbital plate with cross-section (G.I.T. 116, Karksi); × 0·5.

spaced, large, rounded tubercles with prominent radiating ribs, which branch towards their extremities, with similar smaller tubercles scattered among them. A further fragment of the posterior part of a ventral median plate (265 G. I. T.) shows a median runner extremely well (Text-figs. 18 *C-E*). In external view the plate is curved to form a concavity lateral to the solid runner which thus extends some 3 cm. beyond the main plate. The part of the runner in contact with the substratum is strengthened by pleromic dentine, and the medially facing surface is ornamented. It seems evident that this development of runners is a considerable advance on the condition in the early species where the part of the plate bordering the median notch was abraded extensively, and the soft underpart of the animal's body could also easily be damaged, since it was not covered by an extra plate as believed by GROSS (1933*a*). The runners would not only localise the abrasion, but they would serve to keep the unprotected soft part of the animal well away from the substratum, and in addition would reduce friction as the animal moved over this surface.

Branchial plate. Several complete plates are known, including 123 G. I. T. which has a gently convex posterior margin and a concave lateral margin which meet at a small rounded angle (Text-fig. 18*A*). On the dorsal surface the limit of the ornamentation runs more or less at right angles to the posterior margin for most of its extent, but swings medially as it approaches the margin, to meet it about two thirds of the way along its length.

On this surface the entire lateral margin is abraded to a depth of 1·5 cm., while on the ventral surface this same margin is abraded only to a depth of 0·7 cm., although there is a wider zone of abrasion at the rounded tip. A much larger branchial plate (266 G. I. T.) of which the distal tip and the postero-medial part are missing, measures 50 cm. in width and 15 cm. in length. The posterior margin is gently convex, and the lateral margin concave, and they would probably have met at a rounded angle. The entire lateral margin is abraded to a depth of 1-1·5 cm. on the dorsal surface, and a very narrow strip of abrasion is also present on the posterior margin of this same surface. An immature branchial plate (117 G. I. T.) has an almost straight lateral margin, and a similar posterior margin, which meet at an angle of about 50 degrees (Text-fig. 18*B*). The median limit of the ornamentation on the dorsal side runs more or less parallel to the lateral margin, and then swings medially towards the posterior margin. In outline this plate is similar to the branchial of the earlier *Pycnosteus pauli*. All the branchial plates of *Pycnosteus tuberculatus*, which are ornamented by the characteristic ribbed tubercles, are flat and thin. The narrow even zone of abrasion found along the entire concave lateral margin of these plates is most unusual, and it is difficult to see how such abrasion could have occurred. This advanced species of *Pycnosteus* was obviously very highly specialized, but as yet it is not possible to work out with any certainty exactly how these branchials were used, however a possible explanation has been put forward by Dr. J. D. CURREY (see General Part of this work, 1964*b*, pp. 100-101).

Orbital plate. A single orbital plate (116 G. I. T.) is known belonging to this species (Text-fig. 18*F*). Its median and lateral margins diverge posteriorly and the anterior and posterior margins are irregular. The orbital foramen slopes inwards medially, so that the eye must have faced antero-laterally.

Discussion. — Fragments of this species were first described and figured by VON PARROT (1836) and were in fact the first psammosteid remains ever to be described. One of the fragments he figured is here proposed as the neotype for this species. PARROT'S very careful detailed descriptions have been overlooked by later workers, and his work has fallen into obscurity. This is partly because he did not name any of the material, and as no names appeared in the literature, later workers had little to guide them to his original work. In 1837 KUTORGA figured a fragment of the same species under the name *Trionyx spinosus*, but he did not refer to PARROT'S work. ROHON (1901) described and figured some fragments under the name *Ganosteus tuberculatus*, which had the same ornamentation as those described by PARROT and KUTORGA. Since this was the first time they had been validly named, this became the specific name. GROSS (1933*a*) described some material under the name *Ganosteus tuberculatus*, but OBRUCHEV (1940) showed that in fact part of it belonged to *Ganosteus stellatus*, and that the material described by ROHON as *G. tuberculatus*, should be referred to PREOBRAJENSKY'S genus *Pycnosteus*. Later, (1947*b*) OBRUCHEV figured the details of the ornamentation of *Pycnosteus tuberculatus*, and MARK (1956) described the ventral median plate and branchials of this form for the first time. In the General Part of this work (1964*b*, Text-fig. 6) a restoration of this species was given for the first time.

Pycnosteus nathorsti OBRUCHEV, 1965

(Text-figs. 19, 20*B*)

1884. Bony fragments; E. R. LANKESTER, Fish remains from..., p. 6, pl. 4, fig. 16, 17.
1891*a*. *Psammosteus arenatus* AGASSIZ; A. S. WOODWARD, The Devonian fish-fauna..., pp. 10-11, pl. 2, fig. 11.
1895. *Psammosteus arenatus* AGASSIZ; A. S. WOODWARD, The problem of..., p. 39.
1918. *Psammosteus spinosus* n. sp.; E. A. STENSIÖ, Zur Kenntnis des..., p. 65.
1932. *Psammosteus arenatus* AGASSIZ; E. A. STENSIÖ, The cephalaspids..., p. 195, pl. 66, figs. 5, 6.
1937. *Psammolepis undulata* (AGASSIZ); A. HEINTZ, Lunaspis-arten aus..., p. 19.
1941. *Psammolepis paradoxa* (AGASSIZ); T. NILSSON, Antiarchi..., p. 46.
1943. *Psammosteus* sp.; S. FØYN & A. HEINTZ, The English-Norwegian-Swedish..., p. 48.
1950. *Psammolepis arenata* (AGASSIZ); W. GROSS, Die paläontologische..., p. 42.
1950. *Psammosteus spinosus* STENSIÖ; W. GROSS, *Ibid.*, p. 42.
1951. *Psammosteus* cf. *arenatus* AGASSIZ; T. ØRVIG, Histologic studies..., p. 359, text-fig. 5D.
1955. Psammosteids; D. L. DINELEY, Some Devonian..., p. 255.
1958*b*. Heterostracan; T. ØRVIG, The teeth and..., p. 48, text-fig. 6B.
1960. *Psammolepis* sp.; T. S. WINSNES, A. HEINTZ & N. HEINTZ, Excursion guide..., p. 22.
1965. *Pycnosteus nathorsti* n. sp.; D. OBRUCHEV, Spitsbergen psammosteid... (in the press).

Holotype: Ventral median plate, C. 1004, housed in the Swedish Museum of Natural History, Stockholm, figured by OBRUCHEV (1965, in the press), and in the present work (Text-fig. 19*B*).

Type horizon and locality: Middle Devonian (Givetian), Fiskekløften, Mimersdalen, Spitsbergen.

Diagnosis. — Branchial plate wide and long, ornamented by closely-packed, rounded, crenulated dentine tubercles which may become fan-shaped. Dorsal median plate circular, with ornamentation of high-crowned tubercles with prominent thick crenulations. Ventral median plate moderately arched from side to side, with long narrow open posterior notch.

Material. — Dorsal and ventral median plates and branchial plates from Mimersdalen and Widje Bay Series, Spitsbergen.

Description. — *Dorsal median plate.* A dorsal median plate (P. 598 *a*, *b*, G. I. U.) is almost circular in outline and is quite flat (Text-fig. 19*A*). It measures 29 cm. in length and 27 cm. in width. There is a faint suggestion of a groove near the anterior margin.

Ventral median plate. The holotype is the central part of a ventral median plate (C. 1004 R. S.) which was originally described by WOODWARD (1891*a*). The specimen is divided by the posterior notch which is 2 cm. wide and narrows sharply anteriorly (Text-fig. 19*B*). At either side there is a flat zone which is strongly abraded, and lateral to this the plate slopes outwards and gradually upwards. The sides of the plate are ornamented by loosely packed, rounded tubercles, with strongly developed long crenulations which divide at their extremities. A further fragment of the central part of a ventral median plate (C. 1017 R. S.) has a flat abraded central part from which the plate slopes out and upwards and then again turns to become horizontal. The ventral median plate in this species is reminiscent of that seen in *Tartuosteus*, but from the ornamentation and the fact that the posterior notch is open, it would seem preferable to refer it to *Pycnosteus*. However, it should be noted that the ornamentation of some of the other plates in this species is very close to that of the primitive pycnosteid *Pycnolepis*.

Branchial plate. The postero-lateral corner of a branchial plate (C. 1022 R. S.) shows the fairly straight, slightly convex lateral border and the slightly convex posterior border (Text-fig. 20*B*). This plate is similar in outline to the branchial plate of *Pycnosteus palaeformis*. The median half of another branchial plate (D. 3091 P. M. O.) shows a straight posterior border, and the limit of the ornamented part of the dorsal surface, which runs more or less

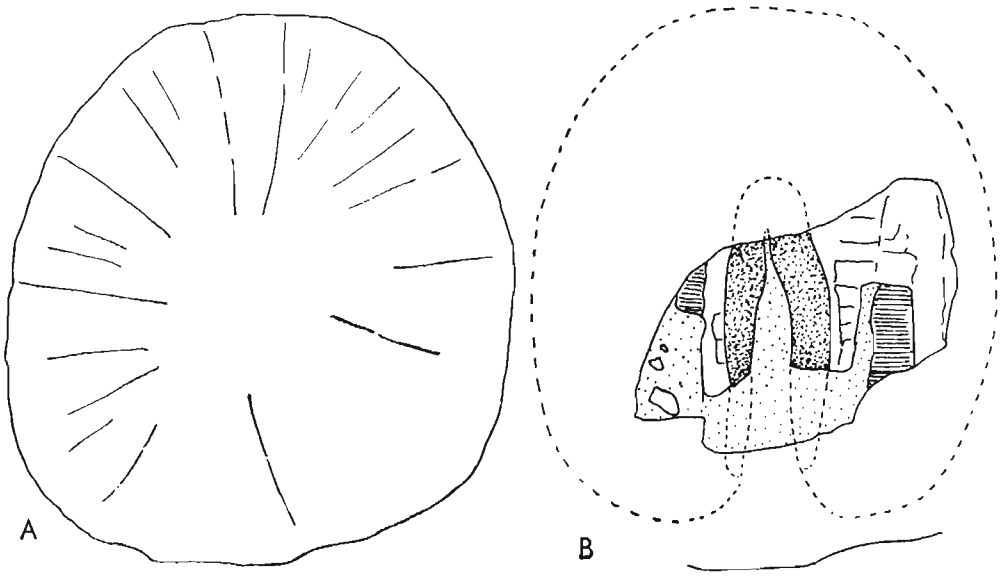

Fig. 19

A-B Pycnosteus nathorsti OBRUCHEV — *A* dorsal median plate with median groove at anterior margin (P. I. U., P. 5986, Mimersdalen), × 0·25; *B* holotype, ventral median plate showing deep narrow posterior notch (R.S., C. 1004, Mimersdalen), × 0·25.

straight and at right angles to the posterior border. The median border of the plate is rather convex. A further branchial plate (D. 3090 P. M. O.) has a convex posterior margin to its lateral half, and a slightly concave one to its medial half. The lateral margin is almost straight, and curves medially at its anterior end. The ornamentation of the branchial plates is somewhat variable. On the ventral surface the tubercles are fairly closely packed and are often fan-shaped with crenulations best developed on the convex margin; on the dorsal side the tubercles are

Fig. 20

A Pycnosteus obruchevi TARLO — holotype, detail of ornamentation (S.M., H. 1570, Wijdefjorden), × 11; *B Pycnosteus nathorsti* OBRUCHEV — branchial plate (R.S., C. 1022, Mimersdalen), × 0·33.

more widely separated, and are generally rounder, and in consequence their basal crenulations are longer and more strongly developed.

Discussion. — LANKESTER (1884) figured some psammosteid remains from the Fiskekløfta horizon, Mimersdalen in Spitsbergen, as "bony fragments". Later, WOODWARD (1891*a*) described and figured further psammosteid remains from the same locality under the name *Psammosteus arenatus*, and included a description of the ventral median plate with its characteristic notch, in his account. In 1895 WOODWARD again mentioned the Spitzbergen material he had identified as *Psammosteus arenatus* while describing a ventral median plate from the Baltic which he placed in the same species. (This ventral median plate however was later made the holotype of *Pycnosteus palaeformis* by PREOBRAJENSKY (1911)). In 1918 STENSIÖ gave an account of the geology of the Mimersdalen area in Spitsbergen and noted the presence of a new species *Psammosteus spinosus*, as well as *Psammosteus arenatus*, although he later (*in* NILSSON, 1941) recognized that only a single species was represented. HEINTZ (1937) placed the Spitsbergen species in *Psammolepis undulata* presumably because GROSS (1933*a*) had suggested that *P. arenatus* described by DOSS (1915) should be included in its synonymy. NILSSON (1941) included the Spitsbergen species in *Psammolepis paradoxa* however, since GROSS (1933*a*) had included the original *P. arenatus* of AGASSIZ in its synonymy.

GROSS (1950) listed both *Psammosteus arenatus* and *P. spinosus* in the Spitsbergen fauna, although he noted that the latter name is a nomen nudum. However, GROSS (1933*a*) showed quite conclusively that AGASSIZ' original *Psammosteus arenatus* was in fact part of a branchial plate of *Psammolepis paradoxa*, and from an examination of it, it is clear that the Spitsbergen material does not belong to this species, or in fact to any species of *Psammolepis*. The Spitsbergen material was first fully described by OBRUCHEV (1965) under the name *Pycnosteus nathorsti*. The generic designation of this species presents some difficulty since sometimes the ornamentation is very similar to *Pycnolepis splendens*. In part of the carapace it is more like *Pycnosteus*, while the characters of the ventral median plate seem to be somewhat similar to those in *Tartuosteus*. However, the consensus of characters suggests that it is somewhat closer to *Pycnosteus* than it is to the other two genera, and hence it is included in this genus.

The confusion with regard to *Psammosteus arenatus* outlined above has resulted in FRIEND (1961) correlating the Spitsbergen beds with the rocks of the Baltic Province which contain *Psammolepis paradoxa* and *Psl. undulata*, and also with the Nairn Sandstones of Scotland which also contain *Psl. undulata*. In fact the Spitsbergen beds should be correlated with the *Pycnosteus* zone (Burtnicki and Arukula horizons) of the Baltic Province.

Pycnosteus obruchevi TARLO, 1964

(Text-fig. 20*A*)

1964*b*. *Pycnosteus obruchevi* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 84, 85, 116; pl. 3, figs. 5, 6.

Holotype: Part of median plate (probably dorsal), H. 1570, housed in the Sedgwick Museum, Cambridge, figured by TARLO (1964*b*, Pl. 3, figs. 5, 6).

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

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*.

Material. — Unique holotype.

Description. — A fragment of a median plate (H. 1570 S. M.) shows clearly the characteristic ornamentation of this species (Text-fig. 20*A*). It consists of well spaced, rounded or slightly elongated dentine tubercles which are deeply indented by numerous, long, rib-like crenulations, which generally bifurcate at their extremities. When the crenulations are taken into account the ornament is fairly closely packed, but the crowns of the tubercles themselves are well separated. On the holotype there is a small patch of large round and fairly high-crowned tubercles with strong radiating ribs which again bifurcate at their extremities, and these large tubercles are very similar to those characteristic of *Pycnosteus tuberculatus*. The type of ornamentation seen in this specimen is well outside the range of variation seen in *Pycnosteus nathorsti*, and in general is more characteristic of the genus *Pycnosteus* than is the ornament of that species. Nevertheless, the ornament of the holotype is quite distinct from that of the other known species of *Pycnosteus*, and hence it is felt that it justifies the erection of a new species for which the name *Pycnosteus obruchevi* was proposed.

Genus **GANOSTEUS** Rohon, 1901

Type species: *Ganosteus stellatus* Rohon, 1901

Diagnosis. — Ventral median plate long and comparatively narrow, with long persistent median posterior notch. Branchial plates broad and long, ornamented by large, high tubercles, with long, thick radial ribs, which branch and re-branch at their extremities; smaller similar tubercles occur among the normal larger ones. Cornual plate quadrangular with centre of growth at lateral margin, around which concentric zones lap.

Occurrence. — Middle and Upper Devonian (Givetian and Frasnian Stages), zones of *Pycnosteus palaeformis*, *Pycnosteus tuberculatus* and *Psammolepis paradoxa*; Baltic province and the Urals.

Discussion. — This genus was originally erected by Rohon (1901) to receive the two species *Ganosteus tuberculatus* and *G. stellatus*. These were considered to be synonymous by Gross (1933*a*) and he took *G. tuberculatus* to be the valid name for them both. However, Obruchev (1940) recognized that they were in fact two distinct species and that *G. tuberculatus* should be referred to Preobrajensky's genus *Pycnosteus*, thus leaving *G. stellatus* as the only species of *Ganosteus*, and hence as the type species (by monotypy). Recent collecting in Latvia and Estonia has established the presence of two further species of *Ganosteus* — *G. obtusus* and *G. artus*, and has also shown that this genus belongs to the family Pycnosteidae on account of the extensive posterior notch found in the ventral median plate.

Ganosteus stellatus Rohon, 1901

(Pl. XIX, fig. 8; Text-figs. 21, 46*B*)

1836. Fragments des téguments; J. J. F. W. von Parrot, Essai sur les..., pp. 26, 28, 29, pl. 3, figs. 1, 3, 9, 10, 13.
1857. Ichthyodorulith; C. H. Pander, Über die Placodermen..., p. 102, pl. 7, fig. 22.
1901. *Ganosteus stellatus* n. sp.; J. V. Rohon, Beiträge zur Anatomie..., pp. 12-13, pl. 1, fig. 7.
1933*a*. *Ganosteus tuberculatus* Rohon; W. Gross, Die Fische des..., p. 17, pl. 1, figs. 4, 5.
1940. *Ganosteus stellatus* Rohon; D. Obruchev, On some psammosteids..., p. 768.
1947*b*. *Ganosteus stellatus* Rohon; D. Obruchev, Atlas of the guide..., p. 196, pl. 50, fig. 5.
1948. *Ganosteus stellatus* Rohon; G. A. Smirnov, On the discovery..., p. 162.
1950. *Ganosteus stellatus* Rohon; W. Gross, Die paläontologische..., p. 27.
1958. *Ganosteus stellatus* Rohon; D. Obruchev, On the biostratigraphy..., pp. 46-47.

1962*b*. *Ganosteus stellatus* ROHON; L. B. TARLO, Dentine 400 million..., pp. 12, 13, text-figs. 2, 3.
1963. *Ganosteus [stellatus* ROHON*]*; L. B. H. TARLO, Aspidin..., pp. 47-8, text-figs. 4, 5.
1964*a*. *Ganosteus stellatus* ROHON; L. B. H. TARLO, The origin..., pp. 8-14, text-figs. 2, 7, 8.
1964*b*. *Ganosteus stellatus* ROHON; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 12, 14, 16, 19, 21, 38, 39, 52, 53, 55, 59, 60, 61, 66, 82, 83, 87, 101, 102, 105; pl. 1, fig. 6; pl. 8, figs. 1, 2; pl. 10, figs. 1, 3; pl. 11, text-figs. 14B, 18, 20.
1964. *Ganosteus stellatus* ROHON; B. J. TARLO & L. B. H. TARLO, The origin..., pp. 35-6, text-figs. 3, 4.
1964. *Ganosteus stellatus* ROHON; D. OBRUCHEV Subclass Heterostraci..., pp. 72, 73, pl. 6, fig. 9; pl. 7, fig. 1.
1965. *Ganosteus stellatus* ROHON; B. J. H. TARLO & L. B. H. TARLO, The origin..., Cover, p. 26, text-fig. 7.

Neotype (here proposed): Fragment of plate, 220/506, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1947*b*, Pl. 50, fig. 5).

Type horizon and locality: Upper Devonian (Frasnian), Gauja horizon, *Psammolepis paradoxa* zone; Eglina, Leningrad district, NW Russia.

Diagnosis. — Branchial plate broad and long, with postero-lateral corner drawn out into narrow posteriorly directed spine; ornamented by very large well spaced high-crowned dentine tubercles, with thick prominent radiating ribs which re-branch towards their extremities, with very small similar tubercles scattered among the larger ones. Ventral median plate long and narrow with well developed posterior notch. Cornual plate generally quadrangular showing concentric zones of growth. Ornamentation as in branchial plate.

Material. — Numerous branchial plates from Latvia and the Leningrad region, ventral median plate and cornual plates from Latvia, and fragments from the Urals.

Description. — *Ventral median plate.* The left posterior half of a ventral median plate (1491-12 G. I. T.) has a fairly straight medial border demonstrating the existence of a very long persistent posterior notch (Text-fig. 21*J*). The posterior margin is narrow and rounded and the lateral margin diverges from it for a short distance and then turns to become only slightly divergent from the margin of the notch.

Branchial plate. A complete branchial plate (1491-8 G. I. T.) has an almost straight lateral margin which turns somewhat medially at its posterior end, and together with the concave posterior margin forms a postero-laterally directed blunt spine (Text-fig. 21*A*). In dorsal view the limit of the ornamentation is a more or less straight line at right angles to the posterior margin, and at approximately 30 degrees to the lateral margin. Specimen 284 G.I.T. shows the postero-lateral part of a plate in which the median part of the posterior margin is straight, and at right angles to the lateral margin (Text-fig. 21*B*). As the posterior margin approaches the lateral one it turns sharply posteriorly to converge gradually with the lateral margin thus producing the characteristic blunt spine. It is more strongly demarcated from the rest of the plate than in the previous specimen. Several broken spines of branchial plates can be seen in the Geological Institute, Tallinn. For example, 1491-11 is part of a mature plate in which the posteriorly directed tip of the spine is truncated, probably having been worn down during life (Text-fig. 21*D*); specimen 279 G. I. T. is a very long and much narrower spine (Text-fig. 21*E*), as also is a further specimen (see Text-fig. 21*C*). A very immature individual (1491-10) is again very narrow, and the tip itself is completely covered by globular tubercles of eruptive dentine which also occur along the lateral margin — clearly a pathological condition (Text-fig. 46*B*). Similar distal tips have been figured by PANDER (1857) and GROSS (1933*a*). These solid fragments, which are ornamented on all surfaces, are very similar to the distal ends of the branchial plates in *Psammosteus*, hence until the complete branchial plates were found during the past few years it seemed that *Ganosteus* might be much closer to *Psammosteus* than is really the case. However, the significance of this apparent similarity of the branchials in the two genera is fully discussed in the General Part of this work (TARLO, 1964*b*, p. 101).

The ornamentation of the branchial plates consists of very large dentine tubercles the summits of which are generally worn flat. From these flat summits thick ribs radiate and these rebranch as they approach the base of the tubercles. Between these large tubercles, very much smaller but similar tubercles are found, with long branching crenulations. Occasionally some of these small tubercles are found overlying the fine distal extremities of the branching ribs of the large tubercles, and this is well seen in specimen 176 G. I. T.

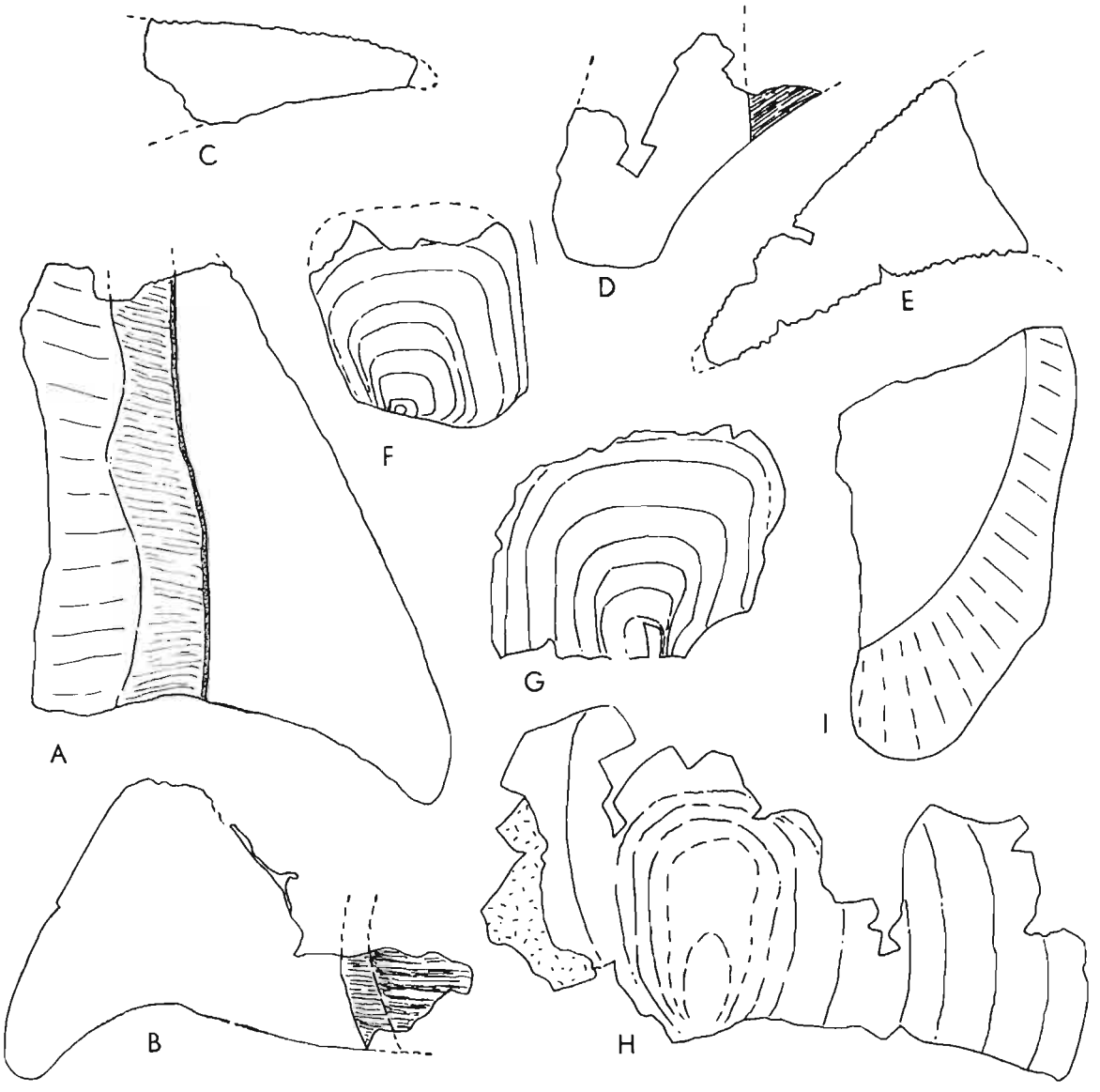

Fig. 21

Ganosteus stellatus ROHON — *A* right branchial plate in dorsal view (G.I.T. 1491-8, Lejeji), × 0·5; *B* posterior part of left branchial plate (G.I.T. 284, river Salatsa), × 0·5; *C* postero-lateral corner of branchial plate (G.I.T. coll., Vezmamnieki), × 0·5; *D* truncated postero-lateral corner of left branchial plate (G.I.T. 1491-11, Lejeji), × 0·5; *E* postero-lateral corner of branchial plate (G.I.T. 279, Karksi), × 0·5; *F* cornual plate (G.I.T. 174, river Salatsa), × 0·5; *G* cornual plate (G.I.T. 282, Lejeji), × 0·5; *H* mature cornual plate (G.I.T. 285, Lejeji), × 0·5; *J* right posterior portion of ventral median plate (G.I.T. 1491-12, Lejeji), × 0·5.

It is thus clear that in the early stages of development, the postero-lateral extremities of the branchial plates are similar in outline to the branchials of *Psammosteus*, and when found alone these spines could be taken as representing entire plates similar to those found in *Psammosteus*. However, now that the complete branchial plate is known in *Ganosteus*, it can be seen that this is quite different from that of *Psammosteus*. In fact the branchial plate as a whole in *Ganosteus* is more like that of *Psammolepis* except for the postero-lateral corner which, as has been demonstrated above, is drawn out into a posteriorly directed spine.

Cornual plate. An almost complete right cornual plate (174 G. I. T.) which lacks only part of the medial border is more or less quadrangular in outline (Text-fig. 21*F*). The centre of growth is towards the posterior half of the postero-lateral margin, and round it are lapped concentric zones of growth which are widest medially and anteriorly, so that the plate increases further in size medially and anteriorly, than it does posteriorly. The zones of growth are marked by lines of large tubercles, the bulk of the zone being filled in by smaller ones. A further cornual plate (282 G. I. T.) is somewhat larger, and the lines of growth are rather more indistinct, but again these can be picked out from the alignment of the large tubercles (Text-fig. 21*G*). This plate is probably a left one. A very large plate (285 G. I. T.) which in all probability is also a cornual plate from the right side of the carapace, has its centre of growth towards the posterior half of the postero-lateral margin, and is comparatively wider than the two other plates on the anterior side of the centre of growth. The medial extent of the plate is unknown, but from the growth lines the plate would probably be rather oblong. The unusual feature of this particular specimen is its very large size.

Discussion. — Fragments of this species were among the first psammosteid remains ever figured. These were described by PARROT (1836) as belonging to the armour of entirely unknown animals which he considered might have been fish, amphibia, or even reptiles. Later, the distal tip of a branchial plate was figured by PANDER (1857) as an ichthyodorulite. Subsequently ROHON (1901) described and figured fragments of this form under the name *Ganosteus stellatus*, and GROSS (1933*a*) included this species in the synonymy of *Ganosteus tuberculatus* ROHON, and figured the spines of two branchial plates. OBRUCHEV (1940) showed that *Ganosteus tuberculatus* should be referred to *Pycnosteus* and that as a result *Ganosteus stellatus* must be taken as the type species of the genus *Ganosteus*. OBRUCHEV referred the material figured by GROSS to *Ganosteus stellatus*, but the fragment of a median plate (pl. I, fig. 7) is in all likelihood referable to *Pycnosteus tuberculatus*. OBRUCHEV later (1947*b*) figured details of the ornamentation of *Ganosteus stellatus*, and the specimen he figured (220/506 P. I. M.) is here proposed as the neotype. SMIRNOV (1948) recorded this species from the Urals, thus extending its geographical range.

Ganosteus artus MARK-KURIK, 1965

(Text-fig. 22)

1955. *Ganosteus artus* n. sp.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 7, 9, 10, 12, 17.
1965. *Ganosteus artus* n. sp.; E. MARK-KURIK, Psammosteids from the... (in the press).

Holotype: Branchial plate, 129, housed in the Geological Institute, Tallinn, figured by MARK-KURIK (1965, (in the press), and in the present work (Text-fig. 22*A*).

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Tamme, Estonia.

Diagnosis. — Branchial plate broad and long, ornamented by rounded, high-crowned tubercles with fine branching radial ribs, arranged more evenly than in *Ganosteus stellatus*;

accessory tubercles rare. Ventral median plate long and comparatively narrow, with long persistent posterior notch.

Material. — Branchial and ventral median plates from Estonia.

Description. — *Ventral median plate.* The anterior portion of a ventral median plate (133 G. I. T.) which unfortunately possesses none of the original margins, shows concentric zones of growth which are gently convex anteriorly. In the posterior part of the fragment the specimen is slightly abraded in the mid-line, and in sagittal section the plate is slightly curved. The anterior part of the plate must have been somewhat basin-shaped. The left posterior part of a further ventral median plate (128 G. I. T.) possesses a complete border (Text-fig. 22*B*). The median margin bordering the posterior notch is straight and a zone about 1 cm. wide along this margin is strongly abraded and is strengthened with pleromic dentine. The posterior margin is gently rounded and the lateral margin curves slightly away from it anteriorly.

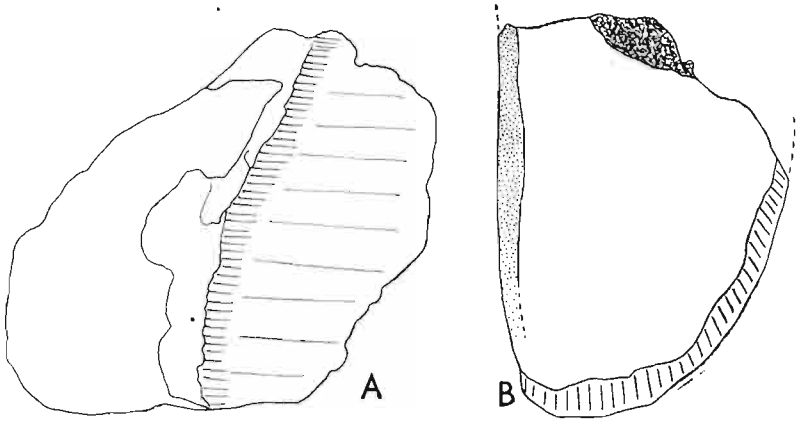

Fig. 22

Ganosteus artus MARK-KURIK — *A* holotype, left branchial plate in dorsal view (G.I.T. 129, Tamme), × 0·5; *B* left posterior part of ventral median plate with narrow zone of abrasion at margin of posterior notch (G.I.T. 128, Tamme), × 0·33.

For a distance of from 1-1·5 cm. from the lateral and posterior margins, the plate is devoid of ornamentation, the rest of it being covered by evenly spaced and fairly closely packed dentine tubercles with well developed branching ribs. These two fragments show quite conclusively that the ventral median plate is in all essentials similar to that seen in *Pycnosteus*, and hence confirms that *Ganosteus* is closely related to this genus.

Branchial plate. The holotype (129 G.I.T.) is a complete branchial plate (Text-fig. 22*A*). The posterior border is straight and the lateral border is convex, although the specimen appears to have suffered some distortion, with the result that the lateral border appears rather irregular. The specimen seems to be somewhat sheared in a postero-lateral direction. The posterior and lateral margins curve to meet in a wide blunt angle. The limit of the ornamentation on the dorsal surface is irregular, and extends about halfway along the posterior margin, gradually approaching the lateral margin anteriorly. In its main proportions this plate is shorter and wider than the branchial of the later *Ganosteus stellatus*, thus suggesting an apparent reversal of the trend seen in other psammosteids.

Ganosteus obtusus MARK-KURIK, 1965

(Text-fig. 23)

1955. *Ganosteus obtusus* n. sp.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 7, 9, 10, 12, 17.
1958. *Ganosteus obtusus* MARK; D. OBRUCHEV, On the biostratigraphy..., p. 46.
1965. *Ganosteus obtusus* n. sp.; E. MARK-KURIK, Psammosteids from the... (in the press).

Holotype: Branchial plate, 132, housed in the Geological Institute, Tallinn, figured by MARK-KURIK, (1965, in the press), and in the present work, Text-fig. 23.

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Haaslava, Estonia.

Diagnosis. — Branchial plate wide and fairly short, ornamented by large high-crowned tubercles with radiating ribs which re-branch at their extremities; occasional secondary tubercles present.

Material. — Unique holotype.

Description. — *Branchial plate.* The holotype (132 G. I. T.) is the lateral free portion of a branchial plate (Text-fig. 23). The posterior margin is straight and the lateral margin

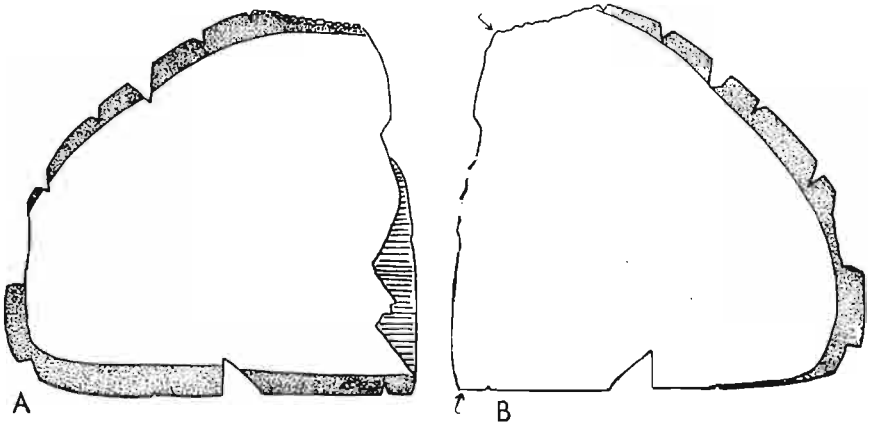

Fig. 23

Ganosteus obtusus MARK-KURIK — holotype, right branchial plate, abraded margins stippled, note healed bite at anterior margin, *A* ventral view, *B* dorsal view (G.I.T. 132, Haaslava), × 0·5.

joins it to form almost a right-angle. Anteriorly the lateral margin curves strongly medially, and at its anterior extremity it is excavated, although this is due to the bite of a predator, which has subsequently healed. In dorsal view the entire surface is ornamented and the lateral margin as far anterior as the damage, is abraded. In ventral view there is a marked band of abrasion along the posterior margin and also along the lateral margin right up to the point where it meets the broken medial edge of the specimen. The ornamentation consists of fairly regularly arranged, large, high-crowned tubercles with strongly marked radiating ribs which bifurcate at their extremities, and generally reach those of adjacent tubercles. Occasionally secondary, smaller similar tubercles are found between the large ones, or lying on the distal parts of the ribs, but these are far less common than in *Ganosteus stellatus*. This species is contemporary with *G. artus*, and may well prove to be a variety of that species when more material becomes available. It is mainly distinguished by the outline of its branchial plate, but it is very difficult to compare directly the branchial of *G. artus* with *G. obtusus*, since the former has suffered

considerable distortion, and the latter has been bitten at its anterior margin. The ornamentation is not strikingly dissimilar, but it seems reasonable for the present to retain the species *G. obtusus*.

Genus **TARTUOSTEUS** OBRUCHEV, 1961

Type species: *Tartuosteus giganteus* (GROSS, 1933)

Diagnosis. — Dorsal median plate with central anterior part devoid of tesserae, and lateral and posterior part of plate ornamented by superficial, scale-like tesserae. Ventral median plate long and narrow, strongly arched from side to side and towards anterior margin; long narrow posterior notch present in mid-line which is partially filled-in in fully mature individuals. Branchial plate wide and fairly long. Cornual plate rather long and somewhat oval in outline. Sensory canal system known in dorsal median plate consisting of two median longitudinal canals with median commissures and one antero-lateral and two lateral canals at each side.

Occurrence. — Middle Devonian (Givetian Stage), Arukula and Burtnicki horizons, zones of *Pycnosteus palaeformis* and *Pycnosteus tuberculatus*; Baltic province.

Discussion. — This genus first appeared in OBRUCHEV (1943*b*), but it was not until MARK (1955, 1956) that it became clear that it referred to the species described by GROSS (1933*a*) under the name *Psammolepis gigantea*, and not until OBRUCHEV (1961) that any reasons were given for the establishment of this new genus. However, although generic distinctions have in the past been recognized on the ornamentation alone, e. g. *Ganosteus*, and it is evident from GROSS's description that in this respect *P. gigantea* differed from all other psammosteids, such a procedure is no longer possible and MARK (1956) cannot be taken as the first valid designation of the genus *Tartuosteus*. OBRUCHEV (1961) therefore properly established the new genus *Tartuosteus* for the form originally described by GROSS (1933*a*).

Tartuosteus giganteus (GROSS, 1933)

(Text-figs. 24, 25)

1933*a*. *Psammolepis gigantea* n. sp.; W. GROSS, Die Fische des..., p. 11, pl. 1, fig. 8, text-figs. 1D, 2C, D, 3.
1940. *Psammolepis gigantea* GROSS; D. OBRUCHEV, On some psammosteids..., p. 766.
1943*b*. *Tartuosteus* [*giganteus* (W. GROSS)]; D. OBRUCHEV, A new restoration..., p. 270.
1950. *Psammolepis gigantea* GROSS; W. GROSS, Die paläontologische..., pp. 27, 28.
1955. *Tartuosteus giganteus* (GROSS); E. MARK, Psammosteids (Agnatha)..., pp. 4, 7-9, 11, 12.
1956. *Tartuosteus giganteus* (GROSS); E. MARK, On the genus..., p. 86.
1958. *Tartuosteus giganteus* (GROSS); D. OBRUCHEV, On the biostratigraphy..., p. 46.
1961. *Tartuosteus giganteus* (GROSS); D. OBRUCHEV, The genus *Tartuosteus*..., pp. 108-110, text-figs. 1-3.
1964*b*. *Tartuosteus giganteus* (GROSS); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 36, 37, 45, 82, 99, 102, 103. text-figs. 12B, 16B.
1964. *Tartuosteus giganteus* (GROSS); D. OBRUCHEV, Subclass Heterostraci..., pp. 71, 72; pl. 7, fig. 6, text-fig. 47.

Holotype: Branchial plate, f. 2, housed in the Geological and Palaeontological Museum, Berlin, figured by GROSS (1933*a*, pl. 1, fig. 8).

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Haaslava, Estonia.

Diagnosis. — Branchial plate long and wide, ornamented by minute, closely packed crenulated tubercles. Dorsal median plate somewhat oval in outline, narrowing anteriorly;

anterior part of plate devoid of superficial tesserae which cover remainder of plate. Ventral median plate oval in outline, narrowing posteriorly; narrow posterior median notch extending almost half-way along plate, partially filled-in in mature specimens; strongly convex from side to side and towards anterior margin. Ornamentation of closely packed crenulated dentine tubercles hardly visible to the naked eye.

Material. — Dorsal, ventral and branchial plates from Estonia.

Description. — *Dorsal median plate.* A large dorsal median plate (151 G. I. T.) which measures 39 cm. in length and 27 cm. at its maximum width, is somewhat oval in outline, but it narrows anteriorly (Text-fig. 24*B*). The anterior margin is truncated and from it the lateral margins gradually diverge until the maximum width of the plate is reached some two thirds of the way from the anterior margin. The margins then run more or less parallel and curve round to form an almost straight posterior margin, which has a short pointed medial extension. In the anterior half of the plate is a large almost circular region, ornamented by minute, closely packed, crenulated tubercles arranged in concentric zones, through which fine ridges radiate from the centre of growth. The centre of growth is in the posterior part of this area and is somewhat oval with a gently rounded anterior margin which is narrower than the posterior margin. In the mid-line of the posterior margin there is a median posteriorly directed lobe. Apart from a border all round the plate measuring 1·5-2 cm. in width which is devoid of ornamentation, the plate is ornamented by minute, closely packed tubercles, similar to those in the anterior part of the plate, except that in this case they are organized into superficial tesserae. The unornamented border of the plate was in all probability covered by similar tesserae which had not yet anchylosed to the underlying plate, and were therefore lost when the carapace disintegrated. A further dorsal median plate (152 G. I. T.) in which the complete sensory canal system is known, has a rather different outline from the one described above (Text-fig. 24*A*). The plate is again somewhat oval, with its narrowest part anterior. The anterior margin in this case is gently rounded with the suggestion of a re-entrant angle. The mid part of the lateral margin is slightly excavated and there is a broad re-entrant angle at the posterior margin. The ornamentation is not preserved and hence the underlying sensory canal system is exposed.

Ventral median plate. A complete ventral median plate (135 G. I. T.) measures 44 cm. in length and 29 cm. at its maximum width (Text-fig. 25*B*). It is rather oval in outline, narrowing somewhat posteriorly. The anterior margin is gently rounded and is continuous with the curve of the lateral margin until the widest point of the plate is reached, some one third of the distance from the anterior margin. From here the lateral margins gradually converge to reach the posterior margin, in the mid-line of which there is a narrow open notch 2 cm. wide which extends some 19 cm. into the plate. The plate is strongly arched from side to side, and is also curved at the anterior margin. Behind the anterior margin there is a zone some 11 cm. wide extending the length of the plate, which is strongly abraded and strengthened with pleromic dentine. Another mature ventral median plate (136 G. I. T.) lacks only the anterior margin, but is otherwise similar in outline to the one previously described, except that the posterior notch is infilled so that it is open for some 8 cm. only (Text-fig. 25*C*). The former extent of the notch can, however, be traced for about 18 cm. until it is obliterated by the abrasion of the ventral surface. This specimen is very much more convex than the one described before, and in the posterior part of the plate is about 10 cm. deep. In the Palaeontological Institute, Moscow, there are two less mature ventral median plates (see Text-fig. 24). The larger of the two specimens measures 27 cm. in length and is 13 cm. wide (Text.-fig. 24*C*). The central part of the plate is strongly abraded and the plate has an infilled posterior notch some 9·5 cm.

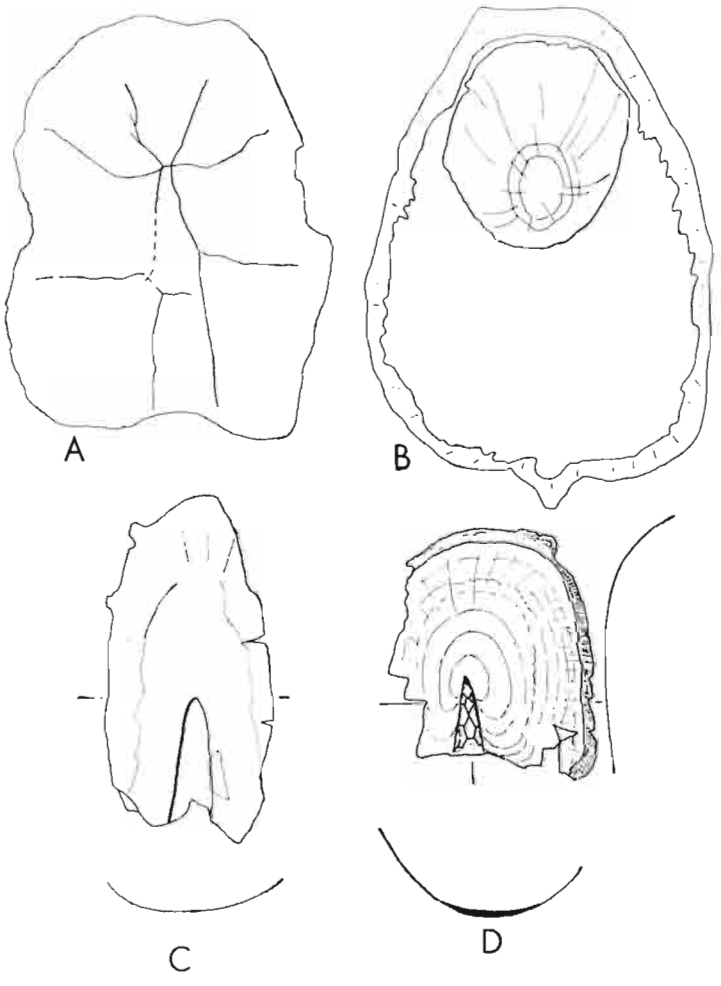

Fig. 24

Tartuosteus giganteus (GROSS) — *A* dorsal median plate showing sensory canal system (G. I.T. 152, Tamme), × 0·17; *B* dorsal median plate showing central area of concentric growth with surrounding region of superficial tesserae (G.I.T. 151, Tamme), × 0·17; *C* ventral median plate showing infilled posterior notch (P.I.M. colln.), × 0·17; *D* ventral median plate with lozenge-shaped tesserae filling posterior notch (P.I.M. colln.), × 0·17.

long and 3 cm. wide, which is inset from the external surface of the bulk of the plate, although in section the aspidin layer of the plate is continuous with that of the infilling of the notch. The other specimen belongs to a much younger individual, and concentric zones of growth can be traced from the centre of the plate (Text-fig. 24 *D*). These are gently rounded anteriorly, and in their posterior part turn anteriorly in the mid-line to produce a strong notch. Although this must originally have been open, in the specimen it is filled-in with lozenge shaped tesserae, but here again, the aspidin layer of the infilling tesserae is continuous with that of the rest of the plate. The central part of the plate is slightly abraded, but the remainder of the plate is ornamented by minute tubercles. The plate is very strongly arched from side to side, and anteriorly.

Branchial plate. The holotype (f. 2 G-P. M. B.) figured by GROSS (1933*a*), is a large branchial plate, measuring 45 cm. in width and 40 cm. in length. The lateral margin is straight and meets the straight posterior margin at an angle of 60 degrees. On the dorsal surface the limit of the ornamentation is a slight curve facing laterally, running at right angles to the

posterior margin for most of its length, and then curving medially to meet this margin. A somewhat smaller branchial plate (153 G. I. T.) has a slightly concave posterior margin and a slightly convex lateral margin which meet at a gently rounded angle of some 60 degrees (Text-fig. 25*A*). The branchial plates are ornamented by the same minute, closely packed dentine tubercles as are found on the median plates.

Sensory canal system. A complete sensory canal system is preserved in a dorsal median plate (152 G. I. T.). It consists of two median longitudinal canals which converge slightly

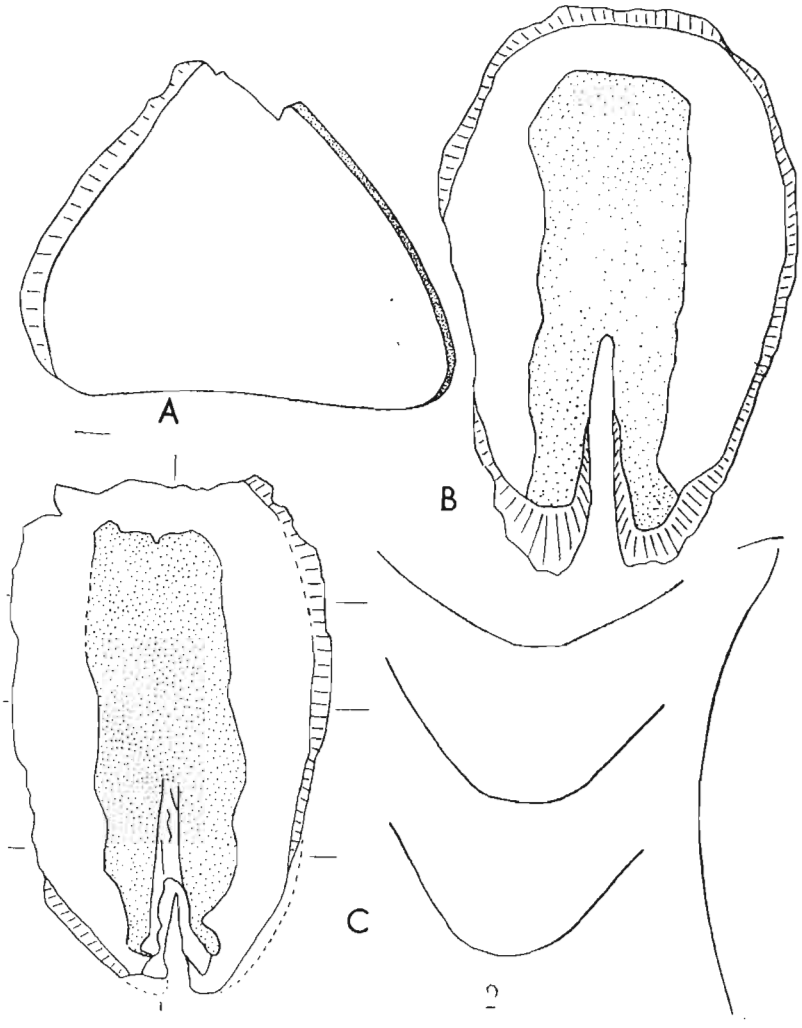

Fig. 25

Tartuosteus giganteus (Gross) — *A* left branchial plate in ventral view (G.I.T. 153, Tamme), × 0·17; *B* ventral median plate showing narrow posterior notch (G.I.T. 135, Tamme), × 0·17; *C* ventral median plate showing partially healed posterior notch, with cross-sections at *a*, *b*, *c*, and longitudinal section at *d* (G.I.T. 136, Tamme), × 0·17.

towards the anterior, and which are joined anteriorly by a short commissure which is produced laterally to form a branch at either side (Text-fig. 24*A*). These branches run laterally and then turn slightly anteriorly. Each longitudinal canal has at its anterior end an antero-lateral branch which diverges from its fellow towards the anterior margin of the plate. The left antero-lateral branch rebranches twice. Halfway down the plate there are two further lateral branches from

the median canals, and just below these there is a further commissure almost joining the two median canals. The middle part of the left longitudinal canal is broken up into short segments. This sensory canal system is somewhat similar to that known in *Psammosteus megalopteryx*, but it is rather more symmetrical.

Discussion. — GROSS (1933*a*) described a large branchial plate characterized by its ornamentation of minute tubercles under the name *Psammolepis gigantea*. OBRUCHEV (1943*b*) first mentioned the genus *Tartuosteus* as having a posterior notch in its ventral median plate, although he gave no indication of the species to which this might refer. MARK (1956) however referred to *Tartuosteus giganteus* (GROSS) thus indicating that OBRUCHEV had GROSS's species *P. gigantea* in mind in his 1943 paper. By the possession of a posterior median notch in the ventral plate GROSS's species clearly did not belong to *Psammolepis*, and hence a different genus was required for its reception. Unfortunately, however, OBRUCHEV's introduction of the new genus *Tartuosteus* was invalid, as was MARK's reference (1956) to the species on which it was based, since no description or diagnosis was given. However, OBRUCHEV (1961) gave a full diagnosis of the genus and a detailed account of its generic characters. This species differs from other pycnosteids because although its posterior notch persists throughout life and can always be clearly recognized, it is rapidly filled in by tesserae, and does not remain fully open. This contrasts with the condition in the psammolepids where a notch is developed in the early stages, but is obliterated and not extended as the animal grows.

Tartuosteus luhai MARK-KURIK, 1965

(Text-fig. 26)

1955. *Tartuosteus luhai* n. sp.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 7, 8, 9, 11, 12, 13.
1958. *Tartuosteus luhai* MARK; D. OBRUCHEV, On the biostratigraphy..., p. 46.
1961. *Tartuosteus luhai* MARK; D. OBRUCHEV, The genus *Tartuosteus*..., pp. 108, 110.
1965. *Tartuosteus luhai* n. sp.; E. MARK-KURIK, Psammosteids from the... (in the press).

Holotype: Branchial plate, 137, housed in the Geological Institute, Tallinn, figured by MARK-KURIK (1965, in the press), and in the present work (Text-figs. 26 *B*, *C*).

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon, *Pycnosteus palaeformis* zone; Haaslava, Estonia.

Diagnosis. — Branchial plate wide and fairly short, ornamented by minute deeply crenulated dentine tubercles generally fused into short irregular strips.

Material. — Branchial plate and fragment of dorsal plate from Estonia.

Description. — *Dorsal median plate.* The posterior half of a dorsal median plate (160 G. I. T.) shows the lateral margins converging posteriorly, and a rounded posterior margin with a median pointed process (Text-fig. 26*A*). In the mid-line there is a faint groove and with the exception of a narrow marginal zone which is devoid of ornament, the plate is covered in superficial tesserae.

Branchial plate. The holotype (137 G. I. T.) is a complete branchial plate measuring 37 cm. in width and 22·5 cm. in length (Text-fig. 26 *B*, *C*). The posterior margin is slightly concave laterally, and slightly convex medially. The lateral margin is slightly convex and joins the posterior margin at a fairly sharp angle. In dorsal view the limit of the ornamentation is at right angles to the posterior border posteriorly, but anteriorly it turns medially to join the anterior margin. In ventral view growth lines can be seen in the ornamentation which are

arcuate, face medially, and at the posterior border swing laterally. The plate is ornamented by very small closely packed dentine tubercles with deep crenulations, which are irregularly fused into short lengths. At the anterior part of the lateral margin the tubercles become much larger, and may reach as much as 0·6 mm. in diameter. This species is distinguished mainly on the outline of its branchial plate which is very short in comparison to the branchials of

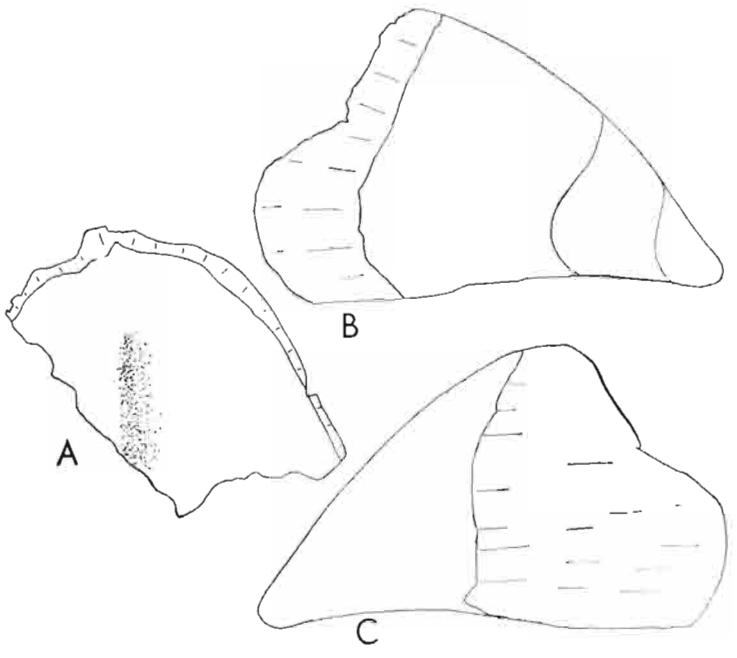

Fig. 26

Tartuosteus luhai MARK-KURIK — *A* anterior part of dorsal median plate showing median longitudinal groove (G.I.T. 160, Haaslava), × 0·17; *B* holotype, left branchial plate in ventral view (G.I.T. 137, Haaslava), × 0·17; *C* in dorsal view.

all other Middle Devonian psammosteids, with the exception of *Yoglinia*. In outline, although not in ornamentation, it is very similar to *Rohonosteus ornatus*, but the difference in stratigraphic position between the two species would seem to suggest that these two forms are not directly related, and that the outline of their branchials has been arrived at independently.

Tartuosteus maximus MARK-KURIK, 1965

(Text-fig. 27)

1955. *Tartuosteus maximus* n. sp.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 5, 7, 8, 9, 11, 12.
1958. *Tartuosteus maximus* MARK; D. OBRUCHEV, On the biostratigraphy..., p. 46.
1961. *Tartuosteus maximus* MARK; D. OBRUCHEV, The genus *Tartuosteus*..., pp. 108, 110.
1962*b*. *Tartuosteus maximus* MARK; L. B. TARLO, Dentine 400 million..., p. 12-13, text-fig. 4.
1964*b*. *Tartuosteus maximus* MARK; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 52, 58, 62, 82, 87, 102, 103; pl. 10, figs. 4, 6; pl. 12, figs. 1, 2, 4, 6, text-figs. 19C, 21.
1965. *Tartuosteus maximus* MARK-KURIK; B. J. H. TARLO, The origin..., p. 13, text-fig. 1.
1965. [*Tartuosteus maximus* MARK-KURIK]; B. J. H. TARLO & L. B. H. TARLO, The origin..., pp. 22, 26, text-figs. 3a, 6.
1965. *Tartuosteus maximus* MARK-KURIK; L. B. H. TARLO & J. R. MERCER, Decalcification... (in the press).
1965. *Tartuosteus maximus* n. sp.; E. MARK-KURIK, Psammosteids from... (in the press).

Holotype: Branchial plate, 138, in the Geological Institute, Tallinn, figured by MARK-KURIK (1965, in the press) and in the present paper, Text-fig. 27*E*.

Type horizon and locality: Middle Devonian (Givetian), Burtnicki horizon, *Pycnosteus tuberculatus* zone; Karksi, Estonia.

Diagnosis. — Branchial plate much wider than long, ornamented by small, closely packed dentine tubercles which are rounded to hexagonal in outline and have very finely crenulated margins. Ventral median plate long and narrow, strongly arched from side to side, with long open posterior notch.

Material. — Ventral median plates, branchial plates and fragmentary cornual plate from Estonia.

Description. — *Ventral median plate.* Specimen 143 G.I.T. is the anterior part and right hand side of a ventral median plate (Text-fig. 27*A*). The complete plate measures 41 cm. in length and must have measured about 20 cm. at its maximum width. The anterior margin was probably rounded and the lateral margins at first diverge from it, and then gradually converge towards the posterior margin. In the central part of the plate there is a very long and broad area of abrasion measuring 34·5 cm. in length, which is reinforced by pleromic dentine. The posterior margin curves anteriorly in the mid-line thus indicating the presence of a posterior notch. The ornamentation consists of small closely packed dentine tubercles which are usually rounded, but may become pentagonal or fan-shaped. They have numerous fine crenulations at their bases. A further fragment (141 G.I.T.) consists of the left-hand posterior part of a ventral median plate (Text-fig. 27*B*). This shows a notch some 23 cm. in length, at the margin of the anterior part of which there is a narrow zone of strong abrasion strengthened by pleromic dentine. The fragment shows concentric zones of growth which run parallel to the lateral and posterior margins, and curve anteriorly towards the mid-line to end at the posterior notch.

Branchial plate. The holotype, (138 G.I.T.) is a complete mature branchial plate measuring 57 cm. in width and 40 cm. in length. The posterior margin is slightly sinuous and is gently excavated just behind the postero-lateral corner, where it meets the straight lateral margin at a small angle (Text-fig. 27*E*). The ornamentation is similar to that seen on the ventral median plate although in this case the tubercles are smaller, and their crenulations are less prominent. A somewhat smaller branchial plate (146 G.I.T.) measures 41 cm. in width and 29 cm. in length (Text-fig. 27*D*). Its fairly straight lateral margin curves posteriorly at its postero-lateral end, to meet the posterior margin in a fairly sharp angle. The posterior margin is gently concave laterally, and then becomes convex medially. On the dorsal surface the limit of the ornamentation reaches from the anterior limit of the lateral margin to the posterior margin, which it meets roughly at right angles. A very immature branchial plate (162 G.I.T.) measures 10·5 cm. in width and 8 cm. in length, although it is not complete anteriorly (Text-fig. 27*F*). The posterior margin is straight, and the lateral margin is gently convex, and they meet at a fairly wide angle, which is just less than a right angle. The limit of the ornamentation on the dorsal surface runs at right angles to the posterior margin and then curves sharply medially to meet it at about 25 degrees. This immature specimen seems in outline to be similar to the mature branchial plates of *Tartuosteus giganteus*, although the mature branchials of *T. maximus* become proportionately wider.

Cornual plate. A single fragmentary cornual plate (187 G.I.T.) is somewhat oval in outline (Text-fig. 27*C*). It shows clearly the concentric growth lines lapping round the centre of growth which lies towards the postero-lateral margin, and also the radial lines running out from the centre of growth. It appears slightly asymmetrical, the centre of growth seeming

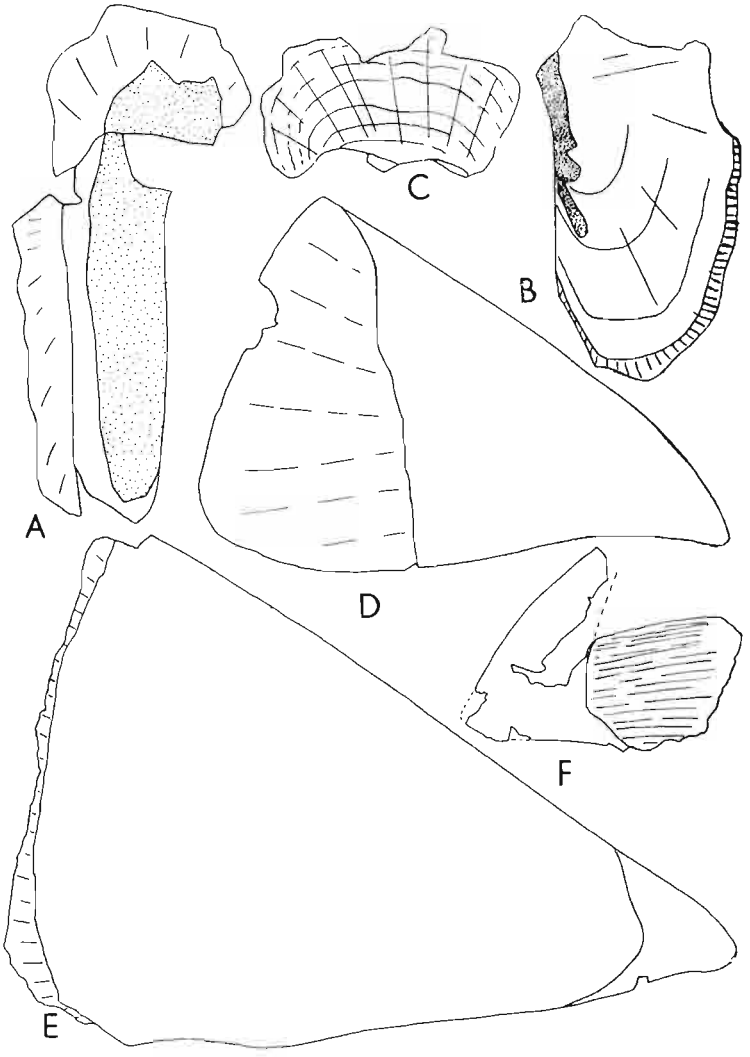

Fig. 27

Tartuosteus maximus MARK-KURIK — *A* right half of ventral median plate showing faint posterior notch (G.I.T. 143, Harma), × 0·17; *B* left posterior part of ventral median plate showing zone of abrasion at margin of deep posterior notch (G.I.T. 141, Karksi), × 0·17; *C* cornual plate showing characteristic growth lines (G.I.T. 187, karksi); × 0·33; *D* right branchial plate in dorsal view (G.I.T. 146, Harma), × 0·17; *E* holotype, left branchial plate in ventral view (G.I.T. 138, Karksi), × 0·17; *F* immature left branchial plate in dorsal view (G.I.T. 162, Karksi), × 0·33.

to lie towards the posterior part of the postero-lateral margin. In the antero-lateral part of the plate the growth lines run at right angles to the postero-lateral margin, whereas in the postero-medial part of the plate they run obliquely.

Fulcral scales. A large ventral fulcral scale (193 G.I.T.) is noted here on account of its large size, as it measures 9·7 cm. in length and 5·5 cm. in width. The distal part of its external surface is strongly abraded, and the distal tip of the internal surface is likewise abraded. In external view it shows concentric lines of growth parallel to the proximal margin, and in internal view the lines of growth run parallel to the proximal limit of the ornamentation, which is a gentle curve facing distally. The proximal half of the internal surface which is embedded

in the skin is unornamented. A further fulcral scale (198 G.I.T.) which is probably from the dorsal side of the body is 10·5 cm. in length and only 3·4 cm. in width. This scale is ornamented in much the same way as the one described above, but is not abraded.

Genus **YOGLINIA** OBRUCHEV, 1943

Type species: *Yoglinia bergi* OBRUCHEV, 1943

Diagnosis. — Branchial plate short and wide, anterior margin fairly straight, posterior margin fairly straight for greater part but markedly concave at distal end producing a very narrow pointed tip; ornamented by short dentine ridges aligned more or less parallel to anterior margin.

Occurrence. — Middle Devonian (Givetian Stage), Burtnicki horizon, zone of *Pycnosteus tuberculatus*; Leningrad district and Estonia.

Yoglinia bergi OBRUCHEV, 1943

(Text-fig. 28)

1942. *Schizosteus* ? n. sp.; W. GROSS, Die Fischefaunen..., pp. 409-410, text-fig. 1.
1943*a*. *Yoglinia bergi* n. sp.; D. OBRUCHEV, *Yoglinia* n. g., Latest pteraspid..., pp. 41-43, text-fig. 1.
1955. *Yoglinia bergi* OBRUCHEV; E. MARK, Psammosteids (Agnatha) from..., pp. 4, 17.
1957. *Yoglinia [bergi]* OBRUCHEV; L. B. TARLO, A preliminary note..., p. 229.
1958. *Yoglinia bergi* OBRUCHEV; D. OBRUCHEV, On the biostratigraphy..., p. 46.
1964. *Yoglinia bergi* OBRUCHEV; D. OBRUCHEV, Subclass Heterostraci..., pp. 74, 75, text-fig. 57.
1965. *Psammosteus bergi* (OBRUCHEV); D. OBRUCHEV & E. MARK-KURIK, Psammosteids of the...(in the press).

Holotype: Branchial plate, 220/504, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1943*a*, Text-fig. 1).

Type horizon and locality: Middle Devonian (Givetian), Upper Tartu horizon (= Burtnicki horizon), *Pycnosteus tuberculatus* zone; River Yoglina, Gdov region, Leningrad district.

Diagnosis. — As for genus, only species.

Material. — Numerous branchial plates from Karksi, Estonia, and the Leningrad region, Russia.

Description. — *Dorsal median plate.* A fragment of a dorsal median plate (161 G.I.T.) shows part of a sensory canal system where the ornamentation has been lost, and superficial tesserae in other areas (Text-fig. 28*A*). The ornamentation of this specimen is somewhat similar to that of *Tartuosteus maximus*, and it is partly for this reason that *Yoglinia* is considered to be closely related to *Tartuosteus* and hence is included in the Pycnosteidae.

Branchial plate. The largest branchial plate (252 G. I. T.) measures 36·5 cm. in width (i.e. along its major axis), and 17 cm. in length (Text-fig. 28*B*). The anterior margin is more or less straight, with a slight convexity in the central part. The posterior margin is fairly straight with a slight concavity towards the distal end, and meets the anterior margin at a fairly sharp angle. The distal part of the posterior margin is slightly bent dorsalwards, and in fact the entire distal tip of the plate is curved in this direction. In ventral view almost the entire plate is ornamented (along the major axis the ornamentation measures 30·5 cm.). The limit of the ornamentation forms a gentle arc facing proximally, and growth lines can be seen which follow the arc but swing distally towards the posterior margin. Near the tip itself they form a gentle sigmoid curve. The ornamentation consists of short dentine ridges aligned more

or less parallel to the anterior margin. A smaller more perfectly preserved specimen (255 G.I.T.) also has a straight anterior margin for the greater part of the width of the plate, but towards the proximal end it swings round to form a fairly straight antero-proximal edge (Text-fig. 28 *D*). The posterior margin is also fairly straight, and also swings round to meet the anterior margin, thus forming a rounded angle at the proximal limit of the plate. The distal part of the pos-

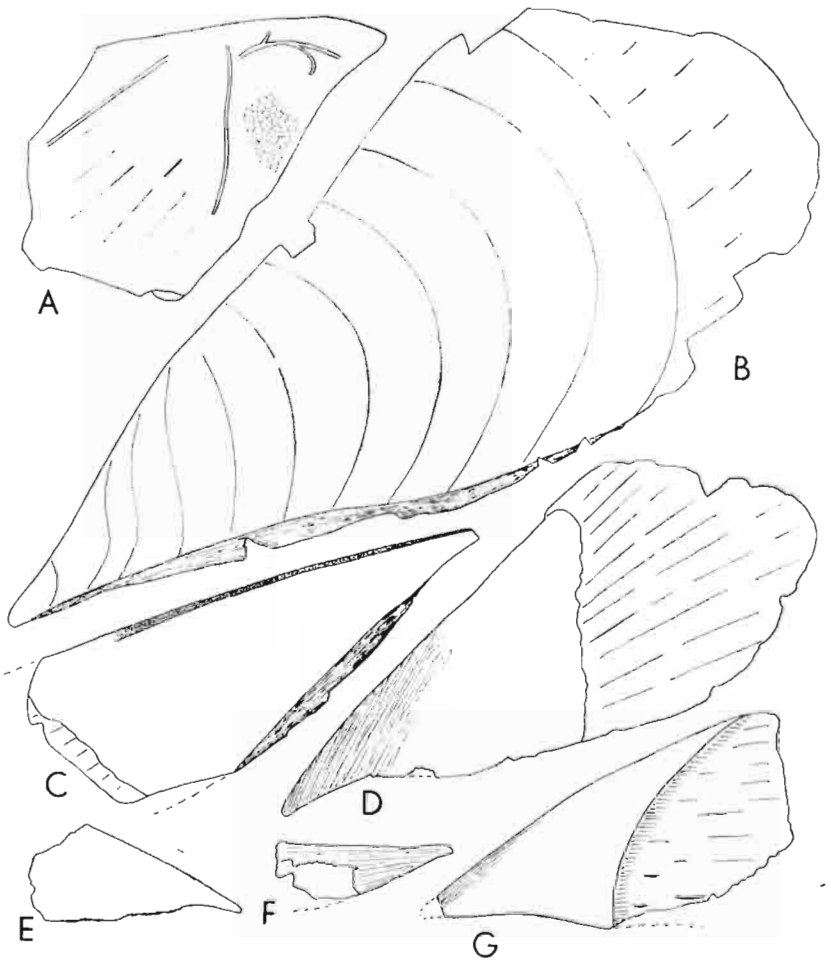

Fig. 28

Yoglinia bergi OBRUCHEV — *A* fragment of dorsal median plate showing part of sensory canal system and superficial tesserae (G.I.T. 161, Karksi), × 0·33; *B* right branchial plate (G.I.T. 252, Karksi), × 0·33; *C* left branchial plate (G.I.T. colln., Karksi), × 0·33; *D* left branchial plate (G.I.T. 255, Karksi), × 0·33; *E* distal tip of branchial plate (G.I.T. colln., Karksi), × 0·33; *F* distal tip of branchial plate (G.I.T. colln., Karksi), × 0·33; *G* left branchial plate (G.I.T. 253, Mazsalaca), × 0·33.

terior margin is markedly excavated to produce a very sharp distal tip. At the distal end the short dentine ridges are aligned more or less parallel to the anterior margin, but proximally they tend to swing round so that they are at a slight angle to this margin, and at a greater one to the posterior margin. The limit of the ornamentation on the dorsal surface is about half way along the width of the plate on the posterior edge, but it extends further proximally at the anterior margin. The lineation of the aspidin on the unornamented region of the plate is

parallel to the major axis. The distal tips of a series of branchial plates showing the different growth stages are illustrated in Text-figs. 28 *C, E, F.* These demonstrate that in the young stage the distal tips are very similar to those of *Psammosteus* species, but the more mature specimens are more reminiscent of those in the psammolepids.

Discussion. — GROSS (1942) described and figured as *Schizosteus* sp. a representative of what OBRUCHEV later recognized as *Yoglinia.* Although the specimen described by GROSS differs slightly from the typical specimens of *Yoglinia bergi*, it can for the present be provisionally included in this species (Text-fig. 28*G*). OBRUCHEV (1943*a*) described and figured the distal end of a branchial plate from the Leningrad district which he considered represented the cornual plate of a pteraspid, although he noted that histologically it consisted of the spongy aspidin typical of the psammosteids rather than the hexagonal cancellae typical of the pteraspids. He suggested that *Yoglinia* represented one of the last members of the pteraspids which had independently evolved specialized cornual plates for the purpose of anchoring, a function carried out by the specially developed branchials of psammosteids. Since that time it has been recognized (MARK, 1955; TARLO, 1957; OBRUCHEV, 1958) that in fact *Yoglinia* is a psammosteid, and not a pteraspid and hence that the plates interpreted as cornuals are branchials.

The familial placing of this genus is rather difficult as apart from a few fragments of median plates, only branchial plates are known, there being no knowledge as to whether or not the ventral plate has a posterior notch. The young branchial plates are very short and wide and if found isolated would probably be taken as belonging to *Psammosteus.* More mature plates are quite distinctive however, having become proportionately longer. Nevertheless, they always remain shorter and wider than the branchials of any contemporary species although the proportions of *Tartuosteus luhai* and *T. maximus* are not too dissimilar. Since the ornamentation of the median plates of *Yoglinia* approaches that of *T. maximus* it seems likely that *Y. bergi* is closely related to *Tartuosteus*, and for this reason it is included in the family Pycnosteidae.

OBRUCHEV (1964) placed *Yoglinia bergi* in the family Psammosteidae, and more recently OBRUCHEV and MARK-KURIK (1965) have even referred this species to the genus *Psammosteus.* It is more likely however that *Yoglinia* represents a sidebranch of the pycnosteids close to *Tartuosteus*, in which the branchial plates have become short and wide, paralleling the trend seen later in the psammolepid line which gave rise to the true psammosteids *(sensu stricto).* In view of this, OBRUCHEV and MARK-KURIK'S (1965) procedure is not here accepted.

Family PSAMMOLEPIDIDAE TARLO, 1962

Diagnosis. — Dorsal median plate ornamented by superficial scale-like tesserae, produced mainly by cyclomorial growth. Ventral median plate long and narrow, with anterior region of concentric cyclomorial growth and posterior of superficial scale-like tesserae. Branchial plate broad and long, entire ventral surface and lateral half of dorsal surface ornamented by rounded dentine tubercles. Post-orbital plate oval in outline, forming same proportion of lateral margin as branchial plate. Cornual plate oval; rostral plate somewhat pentagonal in outline. Pineal plate lozenge-shaped, with major axis aligned transversely. Sensory canal system (known only in ventral median plate of *Psammolepis undulata*) consisting of transverse arcuate canal near anterior margin, and two median longitudinal canals each with two lateral branches.

Discussion. — This family represents a separate development from the Guerichosteidae, which somewhat paralleled the Pycnosteidae, and later gave rise to the Psammosteidae. The psammolepids are characterized by narrow, solid ventral median plates which differ from the notched plates of the pycnosteids, and by broad and long branchial plates which contrast with the short branchials of the psammosteids *(sensu stricto)*. The Psammolepididae includes only the type genus *Psammolepis* of which nine species are recognized. The closely related genera *Karelosteus*, *Crenosteus* and *Rohonosteus*, which are known only from their branchial plates, are considered under the Psammosteidae.

Genus **PSAMMOLEPIS** AGASSIZ, 1845

Type species: *Psammolepis paradoxa* (AGASSIZ, 1845)

Diagnosis. — As for family, only genus.

Occurrence. — Middle and Upper Old Red Sandstone, Middle and Upper Devonian (Givetian and Frasnian Stages), zones of *Pycnosteus palaeformis*, *Psammolepis paradoxa* and *Psl. undulata*; Baltic province, Timan, Donbas, Scotland, and Ellesmereland (Canadian Arctic).

Discussion. — This genus was first introduced by AGASSIZ (1844), but it was a *nomen nudum*. The following year (1845*a*) he described four species under the generic name *Psammosteus* and the same year (1845*b*) he used the generic name *Psammolepis* for one of them — *P. paradoxa*. This was therefore the first valid use of this generic name, although it was abandoned by all subsequent workers until 1933. GROSS then showed that the material described under the name *Psammosteus* belonged to two separate genera, and these were represented typically by *Psammosteus maeandrinus* on the one hand, and *Psammolepis paradoxa* on the other. Since the time of AGASSIZ, there have been important contributions on the genus *Psammolepis* by GROSS (1930, 1933*a*), OBRUCHEV (1944, 1945, 1947*b*), HEINTZ (1957), MARK (*in* HEINTZ, 1957, 1958), and TARLO (1961*a*). Until recently only branchial, dorsal and ventral median plates were known, and this led STENSIÖ (1958) to the conclusion that the cornuals had become incorporated into the dorsal plate by fusion, and that the rostral, orbital and post-orbital plates had either disappeared or had disintegrated into smaller elements which were impossible to identify. However, as a result of the extensive collections made by Dr ELGA MARK and her colleagues, cornuals, rostrals, orbitals and post-orbitals are known belonging to this genus, and in one instance a post-orbital and branchial plate have been found in natural association. From this new material MARK (*in* HEINTZ 1957, 1958) was able to give a detailed reconstruction of the dorsal side of *Psammolepis*. A previous attempt was due to OBRUCHEV (1944) which was based on dorsal and ventral median plates and branchials alone. It should be noted that the genus *Psammolepis* is readily recognized by its ornamentation of superficial scale-like tesserae.

Psammolepis paradoxa (AGASSIZ, 1845)

(Pl. XVIII, fig. 1; Text-fig. 29)

1844. *Psammolepis paradoxus* n. sp.; L. AGASSIZ, Recherches sur les... p. XXXIV (nomen nudum).

1844. *Placosteus arenatus* n. sp.; L. AGASSIZ, *Ibid.*, p. XXXIII (nomen nudum).

1845*a*. *Psammosteus paradoxus* n. sp.; L. AGASSIZ, Monographie des poissons..., pp. 104-105, 130, pl. B, figs. 5, 6; pl. 27, figs. 2-4.

1845*a*. *Psammosteus arenatus* n. sp.; L. AGASSIZ, *Ibid.*, pp. 105, 130, pl. 28a, figs. A, b; pl. 31, fig. 10 (*non* 7-9).

1845*b*. *Psammolepis paradoxus* (AGASSIZ); L. AGASSIZ, Lettres sur les..., p. 406.
1845*b*. *Placosteus arenatus* (AGASSIZ); L. AGASSIZ, *Ibid.*, p. 404.
1846. *Psammosteus arenatus* AGASSIZ; E. EICHWALD, Nachtrag zu der..., pp. 306-307, pl. 10, figs. 40, 41.
1857. *Psammosteus* sp.; C. PANDER, Über die Placodermen..., pp. 20-21, pl. 7, fig. 16.
1858. *Psammosteus arenatus* AGASSIZ; G. KADE, Ueber die devonischen..., pp. 10-11, pl. 1, figs. 14 a, b.
1860. *Psammosteus paradoxus* AGASSIZ; E. EICHWALD, Lethaea Rossica..., p. 1517.
1891*b*. *Psammosteus Paradoxus* AGASSIZ; A. S. WOODWARD, Catalogue of fossil..., p. 128.
1893. *Psammosteus paradoxus* AGASSIZ; J. V. ROHON, Die obersilurischen..., pl. 1, fig. 41.
1894. *Psammosteus paradoxus* AGASSIZ; R. H. TRAQUAIR, On Psammosteus taylori..., p. 226.
1901. *Psammosteus* sp.; J. V. ROHON, Beiträge zur Anatomie..., pp. 5-12, 13-21, pl. 1, figs. 1, 3-6, 9-13.
1908. *Psammosteus paradoxus* AGASSIZ; E. S. GOODRICH, On the scales..., p. 774, pl. 43, fig. 3.
1911. *Psammosteus undulatus* AGASSIZ, I. A. PREOBRAJENSKY, On some representatives..., pp. 28-29.
1915. *Psammosteus maeandrinus* AGASSIZ; J. KIAER, Upper Devonian Fish..., p. 36, pl. 4, fig. 1.
1930. *Psammosteus paradoxus* AGASSIZ; W. GROSS, Die Fische des..., pp. 5-14, pl. 1, figs. 3-9 A, 9 C-11; pl. 2, figs. 1, 2, 8
1933*a*. *Psammolepis paradoxa* (AGASSIZ); W. GROSS, Die Fische des baltischen..., pp. 5-8, pl. 2, figs. 8-10, 17, 18, 27, 28, text-figs. 1 A, B, 2 A.
1935. *Psammolepis paradoxa* (AGASSIZ); W. GROSS, Histologische studien am..., pp. 12-16, pl. 2, figs. 2, 3, 6; pl. 3, figs. 1-3; pl. 4, fig. 2, text-fig. 6.
1944. *Psammolepis paradoxa* (AGASSIZ); D. OBRUCHEV, An attempted restoration..., pp. 143-145, text-figs. 1, 2.
1945. *Psammolepis [paradoxa]* (AGASSIZ); D. OBRUCHEV, On the evolution..., pp. 262-263, text-figs. 4, 5.
1947*b*. *Psammolepis paradoxa* (AGASSIZ); D. OBRUCHEV, Atlas of the guide forms..., p. 196, pl. 50, figs. 1-3, text-fig. 55.
1955. *Psammolepis paradoxa* (AGASSIZ); A. P. BYSTROW, On the microstructure..., pp. 499-508, text-figs. 26-35.
1956. *Psammolepis paradoxa* (AGASSIZ); A. P. BYSTROW, On the damage caused..., pp. 40-41, 43-45, text-figs. 9, 13.
1957. *Psammolepis paradoxa* (AGASSIZ); A. HEINTZ, The dorsal shield..., pp. 153-162, pl. 17, figs. 1, 2; pl. 18, figs. 1-3; pl. 19, figs. 1-6, text-figs. 1 A, B, 2, 3.
1961*a*. *Psammolepis paradoxa* (AGASSIZ); L. B. TARLO, Psammosteids from..., p. 208, text-fig. 8e.
1962. *Psammolepis [paradoxa* AGASSIZ]; E. MARK, Moningatest..., p. 31, text-fig. 2.
1964*b*. *Psammolepis paradoxa* (AGASSIZ); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 14, 19, 21, 31, 61, 63, 64, 84, 86, 87, 97, 99, 102, 104, 108; pl. 7, fig. 3; pl. 10, figs. 2, 5; pl. 12, fig. 3, text-figs. 8 B, C, 22 B, C.
1964. *Psammolepis paradoxa* (AGASSIZ); B. J. TARLO & L. B. H. TARLO, The origin..., p. 5, text-fig. 1.
1964. *Psammolepis paradoxa* (AGASSIZ); E. A. STENSIÖ, Les Cyclostomes..., pp. 182, 183, text-fig. 35.
1964. *Psammolepis paradoxa* (AGASSIZ); D. OBRUCHEV, Subclass Heterostraci..., pp. 73, 74, pl. 6, figs. 1, 2, text-fig. 56b.
1964. *Psammolepis* sp. AGASSIZ; D. OBRUCHEV, *Ibid.*, pp. 50, 54, 74, text-figs. 11, 12, 53.
1965. [*Psammolepis paradoxa* (AGASSIZ)]; B. J. H. TARLO & L. B. H. TARLO, The origin..., p. 23, text-fig. 4.
1965. *Psammolepis paradoxa* (AGASSIZ); L. B. H. TARLO & J. R. MERCER, Decalcification..., pl. 1, figs. 1, 3-6.

Neotype: Ventral median plate, f. 12, housed in the Geological and Palaeontological Museum, Berlin, figured by GROSS (1930, Pl. 1, fig. 3), and in the present work, Text-fig. 29*B*.

Type horizon and locality: Upper Devonian (Frasnian), Gauja horizon, *Psammolepis paradoxa* zone; River Aa, Latvia.

Diagnosis. — Branchial plate broad and long, ornamented by closely packed, rounded tubercles with short, well marked crenulations. Dorsal median plate fairly round in outline drawn out to a median point posteriorly, and with a shallow re-entrant angle anteriorly, ornamented by superficial scale-like tesserae arranged concentrically around central area devoid of tesserae. Ventral median plate long and narrow, with anterior region of concentric zones of growth and posterior of superficial scale-like tesserae.

Material. — Dorsal median and ventral median plates, branchial plates, and orbital plate together with numerous body scales and fulcral scales from Latvia, and N. W. Russia, and also from erratic boulders from the southern shores of the Baltic.

Description. — *Dorsal median plate.* GROSS (1933*a*) published a reconstruction of a dorsal median plate based partly on a specimen in the Palaeontological Museum, Oslo. This specimen (A 172 P. M. O.) was subsequently described in detail by HEINTZ (1957). The plate measures 27 cm. in length and 25 cm. at its maximum width; the anterior margin is fairly straight with

a slight suggestion of a re-entrant angle in the midline (Text-fig. 29*A*). The lateral margins diverge slightly and just over halfway down the plate they are gently rounded and converge to a small median point in the middle of the posterior margin. The centre of growth of the plate is well marked by an area devoid of tesserae, and lies in the anterior half of the plate. Superficial tesserae are arranged concentrically around it, and in the lateral and posterior

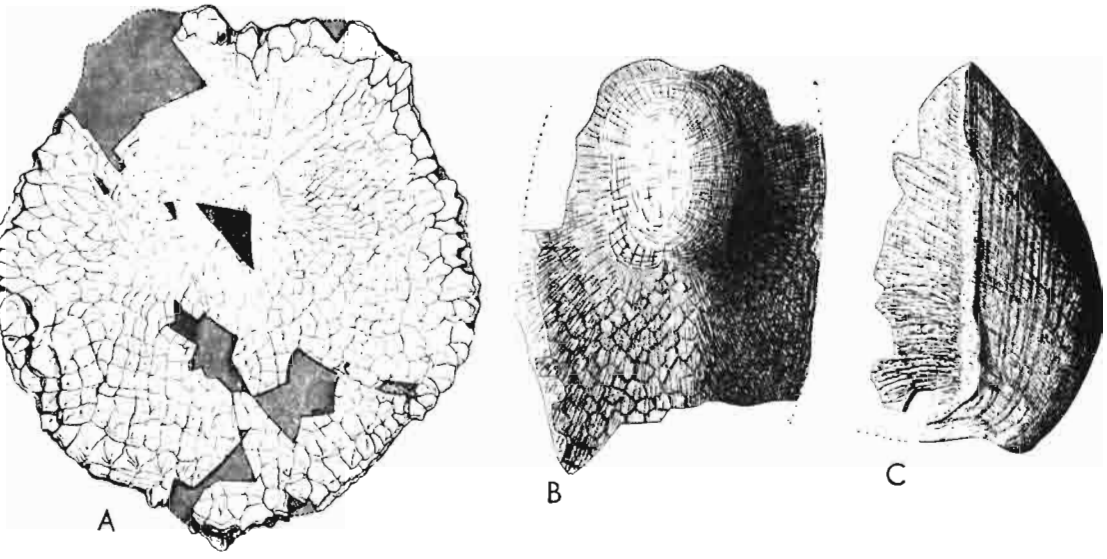

Fig. 29

Psammolepis paradoxa (AGASSIZ) — *A* dorsal median plate (P.M.O. A. 172, river Aa), × 0·25 (from HEINTZ, 1957); *B* neotype, ventral median plate showing shallow posterior notch and superficial tesserae (G-P. M.B. f. 12, river Aa), × 0·25; *C* right branchial plate in dorsal view (G-P. M.B. f. 13, river Aa), × 0·25 (from GROSS, 1930).

sectors of the plate these tesserae are scale-like, while at the margins they take on an imbricate appearance. HEINTZ (1957) also described a further fragment of a dorsal median plate probably referable to this species (A 173 P. M. O.), which differs from the complete specimen by having a very wide central area devoid of tesserae in which concentric zones of growth are very clearly seen.

Ventral median plate. GROSS (1930) figured a ventral median plate (f. 12 G-P.M.B.) and subsequently (1933*a*) proposed it as the neotype. This specimen is the greater part of a plate which lacks only the anterior and posterior margins (Text-fig. 29*B*). The specimen as preserved measures 20·5 cm. in length and 15 cm. in width. The anterior part of the plate is somewhat convex, but it gradually flattens out posteriorly. The domed part, which is almost circular in outline, is abraded, and has a very shallow, rounded re-entrant angle in the mid-part of its posterior boundary. This slight notch is infilled by superficial tesserae which make up the posterior half of the plate, and are also found along the lateral margins of the anterior part of the plate. It seems clear that the central domed area with its posterior notch represents an early growth stage, and that the plate increased in size by the addition of superficial tesserae which were added on mainly posteriorly. OBRUCHEV (1944) reconstructed this plate and portrayed a broad shallow re-entrant angle along the anterior margin and a marked notch on the posterior margin, but this specimen offers no justification for such a reconstruction. The anterior border in all likelihood followed the outline of the central domed area and was thus

in all probability convex anteriorly, and although the young individuals possessed a small posterior notch, this was very quickly eliminated by the addition of superficial tesserae.

Branchial plate. An almost complete branchial plate (f. 13 G-P M.B.) was figured by GROSS (1930). The lateral margin is very curved and the curvature reaches its maximum about four fifths of the way down the plate (Text-fig. 29*C*). The posterior margin is excavated to give a characteristic sinuous appearance. On the dorsal surface the edge of the ornamentation forms a straight line from the anterior almost to the posterior margin, but then swings sharply in a medial direction to gradually converge with the posterior margin. The entire ventral surface of the plate is ornamented, and the plate as a whole is convex from side to side to form a concavity on the ventral side of the carapace. A somewhat less mature specimen (P. 7465 B.M.) has a nearly straight lateral margin, and a rather less developed excavation on the posterior margin. Towards the anterior part of the plate the lateral margin tends to curve medially. The lateral part of the branchial in this instance formed a thin, laterally projecting sheet of bone extending beyond the body of the animal. According to OBRUCHEV (1944), this development of the branchial plates was a response to the taking up of a fluviatile life, as not only did the branchials function as gliding planes, but the sucking action of the vacuity beneath them helped them to act as anchors permitting the animals to hold against the current.

Orbital plate. A single orbital plate (246 G.I.T.) which probably belongs to the right side of the carapace is complete apart from the antero-medial corner. It has a slight projection postero-medially, and is arched from side to side. The opening for the eye slopes inwards and is more or less circular in outline, so that the eye must have faced dorso-laterally. So far this is the only orbital plate known in the family Psammolepididae.

Scales. Dorsal and ventral fulcral scales, together with body scales have been described and figured by numerous authors including PANDER (1857), ROHON (1901), GROSS (1930, 1933*a*), and OBRUCHEV (1947*b*). In general, these are similar to the scales known in most, psammosteids, the ornamentation being elongated along the scales to give a characteristic naviculate or lozenge shape to the tubercles.

Discussion. — In 1844 AGASSIZ listed the species *Psammolepis paradoxa*, but this was a *nomen nudum* and when the species was first described and figured by AGASSIZ (1845*a*), he established the name *Psammosteus paradoxus* for a fragment of median plate showing the characteristic scale-like tesserae. In the same paper he described and figured a fragment of a branchial plate of the same species under the name *Psammosteus arenatus*. Later (1845*b*) AGASSIZ' letters to MURCHISON (written in 1842) were published, in which he had used his earlier name *Psammolepis paradoxa* which by 1845 he had discarded. This species he characterized as having «scales irregular, unequal, of rhombohedral form», and thus inadvertently validated the generic name *Psammolepis* distinct from *Psammosteus*. It was not, however, until 1933 that such a separation of these two genera was accepted by GROSS (1933*a*), and then by all subsequent workers on the group. It should be noted that GROSS resurrected AGASSIZ' name from his 1844 paper which, since it was a *nomen nudum* was not available. GROSS was apparently unaware of AGASSIZ' second work of 1845 which was the first valid use of the name *Psammolepis paradoxa*. Our main knowledge of this species is due to the work of GROSS (1930, 1933*a*), but since that time OBRUCHEV (1944) gave an attempted reconstruction of the species, and HEINTZ (1957) gave a detailed description of the dorsal median plate. A revised restoration of the ventral surface is given in the General Part of the present work (TARLO, 1964*b*, Text-fig. 8*B*).

Psammolepis venyukovi OBRUCHEV, 1965

(Text-figs. 30, 31)

1955. *Psammolepis venyukovi* (OBRUCHEV) M. S.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 6, 8, 9, 12.
1957. *Psammolepis venyukovi* (OBRUCHEV) M. S., E. MARK, *in* A. HEINTZ, The dorsal shield..., pp. 153-154, text-fig. 1c.
1958. *Psammolepis* [*venyukovi* OBRUCHEV]; E. MARK, Devoni ajastu..., p. 52, text-fig. 29.
1958. *Psammolepis venyukovi* OBRUCHEV; D. OBRUCHEV, On the biostratigraphy..., pp. 47, 48.
1959. *Psammolepis* [*venyukovi* OBRUCHEV]; A. S. ROMER, The Vertebrate..., text-figure on p. 41.
1961*a*. *Psammolepis venyukovi* OBRUCHEV; L. B. TARLO, Psammosteids from the..., p. 208, text-fig. 8b.
1962*b*. *Psammolepis venyukovi* OBRUCHEV; L. B. TARLO, Dentine 400 million..., p. 12, text-fig. 1.
1962. *Psammolepis* [*venyukovi* OBRUCHEV]; E. MARK, Moningatest..., p. 30, text-fig. 1.
1964*b*. *Psammolepis venyukovi* OBRUCHEV; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 31, 38, 44, 45, 52, 60, 87, 90, 91, 104; text-figs. 8A, 16C.
1964. *Psammolepis venyukovi* OBRUCHEV; B. J. TARLO & L. B. H. TARLO, The origin..., p. 5, text-fig. 2.
1964. *Psammolepis wenjukovi* OBRUCHEV; E. A. STENSIÖ, Les Cyclostomes..., p. 184, text-fig. 36A.
1964. *Psammolepis venyukovi* OBRUCHEV; D. OBRUCHEV, Subclass Heterostraci..., pp. 73, 74, text-figs. 52, 54.
1965. *Psammolepis venyukovi* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).
1965. *Psammolepis venyukovi* OBRUCHEV; B. J. H. TARLO & L. B. H. TARLO, The origin..., p. 23, text-fig. 5.

Holotype: Branchial plate, 240, housed in the Geological Institute, Tallinn, figured by OBRUCHEV (1965, in the press), and in the present work, Text-fig. 31*A*.

Type horizon and locality: Upper Devonian (Frasnain), Gauja horizon, *Psammolepis paradoxa* zone; Joksi, Estonia.

Diagnosis. — Branchial plate broad and long, length exceeding width; ornamented by sharply pointed crenulated tubercles, with the crenulations continuing up the slope of the tubercles as ribs; minute secondary tubercles occurring among the normal high-crowned ones. Dorsal median plate covered by superficial scale-like tesserae except in small rectangular area in anterior third of plate where concentric zones of growth are visible; peripheral tesserae showing cyclomorial growth.

Material. — Dorsal median plates, branchial plates together with a post-orbital and rostral plate from Estonia.

Description. — *Dorsal median plate*. An almost entire dorsal median plate (236 G.I.T.) is known (Text-fig. 31 *D*). In outline it is very similar to the complete dorsal median plate of *Psammolepis paradoxa* described by HEINTZ (1957). There is a shallow re-entrant angle in the anterior margin, while the lateral margins gradually diverge and then about halfway along the length of the plate converge, to form a fairly rounded posterior margin. As with *Psl. paradoxa*, although most of the plate is ornamented by superficial scale-like tesserae, there is a small area which represents the centre of growth of the plate, in which there are no tesserae, but instead narrow concentric zones of rounded tubercles are visible. In *Psl. venyukovi* however, this region is very much smaller than it is in *Psl. paradoxa*, and it is situated much further anteriorly, being in this case within the anterior third of the plate. The centre of growth is seen even more clearly in a further specimen (237 G.I.T.) where it is set in a shallow depression in the plate. Anterior to it there is a shallow groove running towards the anterior margin, and although the plate as a whole is covered by superficial scale-like tesserae, these are not developed in the sector of the plate immediately anterior to the centre of growth. The main distinguishing feature of *Psl. venyukovi* is its ornamentation of very high-crowned pointed tubercles with well marked radial ribs, which extend into short crenulations at the base of each tubercle. Between the normal tubercles minute secondary dentine tubercles frequently occur.

Branchial plate. The holotype (240 G.I.T.) is an adult branchial plate with a curved lateral margin which meets an excavated posterior margin at almost a right angle (Text-

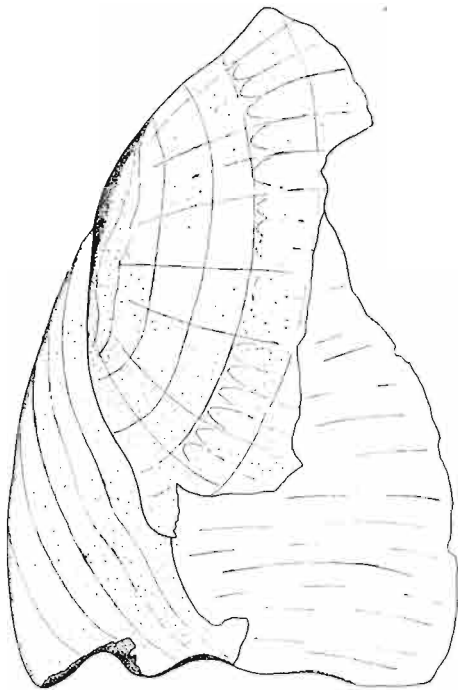

Fig. 30

Psammolepis venyukovi OBRUCHEV — Left branchial and post-orbital plates in natural association (G.I.T. 239, Joksi), × 0·33.

fig. 31 *A*). Just within the posterior half of the lateral margin there is an arcuate notch measuring 3·5 cm. which was clearly caused by the bite of a predator and has been completely healed by the growth of a new generation of dentine tubercles. The unornamented portion of the dorsal surface is somewhat greater in extent than the ornamented part. The limit of the ornamentation is somewhat sinuous and runs at right angles to the posterior margin, but as it approaches this margin it swings medially to end about three quarters of the way along it. A further adult branchial (241 G.I.T.) is remarkable for the extensive damage to its posterior margin which has been very severely bitten (Text-fig. 31 *B*). Although completely healed, the jagged edge of this margin still bears withness to the attentions of a predator. A further mature branchial plate (239 G.I.T.) is particularly important since it occurs in natural association with the post-orbital plate (Text-fig. 30). The lateral margin is smooth and convex but its posterior margin is damaged by three adjacent bites.

Post-orbital plate. A complete post-orbital is known (239 G.I.T.) which is in natural association with a branchial plate (Text-fig. 30). It adjoins the plate along the medial limit of the ornamentation of the latter's dorsal side, overlying the anterior two thirds of its unornamented part, and its antero-lateral margin forms a smooth curve continuous with the lateral margin of the branchial plate. The lateral margin of the post-orbital is slightly curved over and shows evidence of abrasion in its central part. This area at the margin is the centre of growth, as is evidenced by the growth lines which lap round it. Towards the median margin of this plate superficial tesserae begin to develop which first appear like scales pointing towards the centre of growth, but then are continued to give a characteristic column-like appearance, the pointed summits of the columns being directed towards the centre of growth of the plate.

The bulk of the plate is set at an angle of about 50 degrees to the branchial plate, with only its lateral margin actually in contact with it. Although there must have been some *post-mortem* distortion, it seems evident that the two plates must have had much the same relationship during life.

Rostral plate. The left half of a rostral plate (186 G.I.T.) is known (Text-fig. 31 *C*). This has a fairly straight anterior margin which is slightly bevelled, and it must have formed the

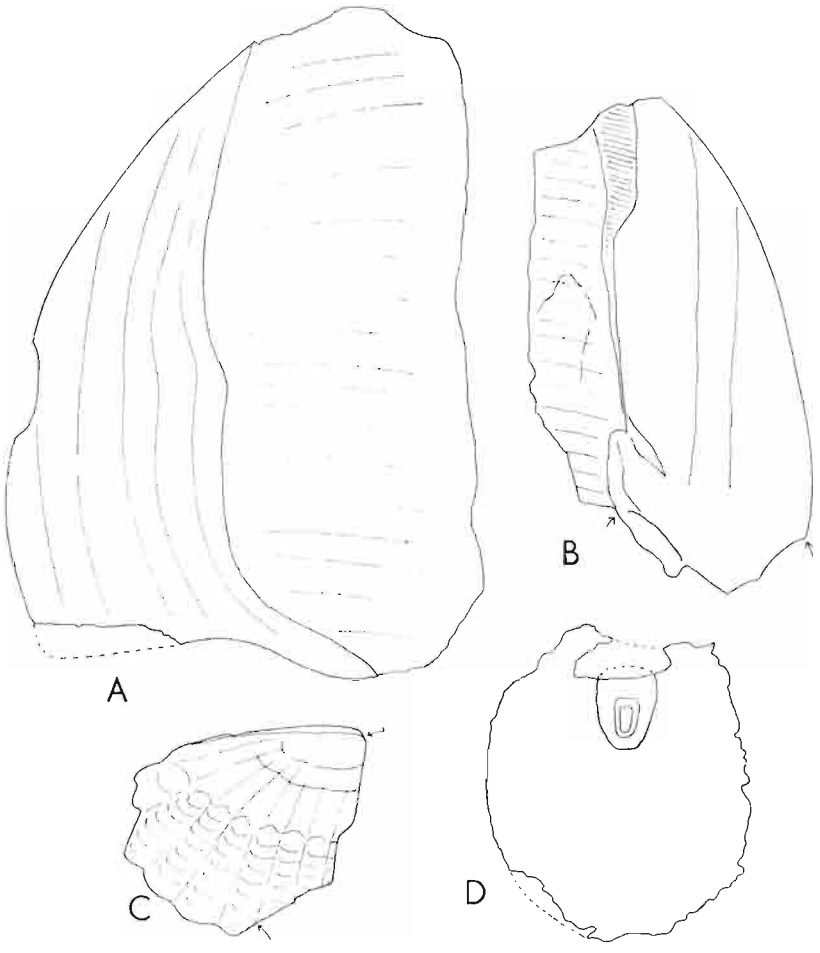

Fig. 31

Psammolepis venyukovi Obruchev — *A* holotype, left branchial plate in dorsal view showing rounded notch in lateral margin caused by bite of predator (G.I.T. 240, Joksi), × 0·33; *B* right branchial plate in dorsal view showing badly bitten posterior margin, damaged area located between arrows (G.I.T. 241, Joksi), × 0·33; *C* rostral plate (G.I.T. 186, Joksi), × 0·33; *D* dorsal median plate showing central area of concentric growth situated near anterior margin (G.I.T. 236, Joksi), × 0·17.

posterior edge of the mouth. Concentric growth lines can be seen curving round from a centre of growth at the mid-point of the anterior margin showing that in its younger stages the plate must have been rather oblong, although the lateral margins diverged slightly anteriorly. As in the post-orbital plate, towards the periphery tesserae began to develop. Then chevron shaped zones of growth were built on posteriorly, which pointed opposite to the initial tesserae, and produced the characteristic radial columns of the ornamentation.

Discussion. — This species was first mentioned by MARK (1955) and subsequently by OBRUCHEV (1958). HEINTZ (1957), however, published MARK's reconstruction of this species which showed the relationships of the plates of the dorsal side of the carapace. MARK (1958) published a restoration of the animal in life drawn by Professor BYSTROW, and this was repeated by ROMER (1959) and TARLO (1962*b*), and also in a slightly modified form by MARK (1962) and OBRUCHEV (1964), while TARLO (1961*a*) refigured MARK's 1957 reconstruction. This species, which is important from an anatomical point of view, unfortunately poses a taxonomic problem, since the species was only fully described by OBRUCHEV (1965), yet the publication by MARK (*in* HEINTZ, 1957) of a full reconstruction which was named as *Psammolepis venyukovi* could perhaps be taken as a validation of the species. In view of the fact that no indication was given of the details of the ornamentation in the 1957 reconstruction and as this is the main diagnostic feature of the species, OBRUCHEV's 1965 description is here taken as the first valid use of the name. A modified reconstruction of this species is given in the General Part of this work (TARLO, 1964*b*).

Psammolepis undulata (AGASSIZ, 1845)

(Pl. XVII, fig. 2; Text-fig. 32)

1844. *Placosteus undulatus* n. sp.; L. AGASSIZ, Recherches sur les..., p. XXXIII (nomen nudum).
1845*a*. *Psammosteus undulatus* n. sp.; L. AGASSIZ, Monographie des..., p. 106, 130, pl. 31, figs. 11, 12.
1845*b*. *Placosteus undulatus* (AGASSIZ); L. AGASSIZ, Lettres sur les..., p. 404.
1860. *Psammosteus undulatus* AGASSIZ; E. EICHWALD, Lethaea Rossica..., pp. 1517-1518.
1897. *Psammosteus tessellatus* n. sp.; R. H. TRAQUAIR, Additional notes on..., p. 377, pl. 11, figs. 1, 2.
1899. *Psammosteus undulatus* AGASSIZ; J. V. ROHON, Die devonischen..., p. 14.
1911. *Psammosteus undulatus* AGASSIZ; I. A. PREOBRAJENSKY, On some representatives..., pp. 28-30.
1915. *Psammosteus arenatus* AGASSIZ; B. DOSS, Ein Fund von..., pp. 77-78, pl. 1.
1933*a*. *Psammolepis tessellata* (TRAQUAIR); W. GROSS, Die Fische des..., p. 15.
1933*a*. *Psammolepis undulata* (AGASSIZ); W. GROSS, Die Fische des..., p. 8-9, pl. 1, figs. 3, 6.
1937. *Psammolepis tessellata* (TRAQUAIR); A. HEINTZ, Lunaspis-arten aus..., folding table.
1942. *Psammolepis undulata* (AGASSIZ); W. GROSS, Die Fischfaunen des..., p. 410, text-fig. 2A.
1950. *Psammolepis undulata* (AGASSIZ); W. GROSS, Die paläontologische..., p. 29.
1958. *Psammolepis undulata* (AGASSIZ); D. OBRUCHEV, On the biostratigraphy..., p. 48.
1958. *Psammolepis timanica* n. sp.; D. OBRUCHEV, *Ibid.*, p. 48.
1961*a*. *Psammosteus tessellatus* TRAQUAIR; L. B. TARLO, Psammosteids from..., pp. 193, 203.
1961*a*. *Psammolepis undulata* (AGASSIZ); L. B. TARLO, *Ibid.*, pp. 202-4, pl. 7, figs. 4, 5, text-fig. 7.
1964*b*. *Psammolepis undulata* (AGASSIZ); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 15, 17, 19, 22, 31, 32, 36-38, 44, 84-89, 91, 97, 99, 102, 104, 105; text-fig. 12A.

Neotype: Branchial plate, f. 16, housed in the Geological and Palaeontological Museum, Berlin, figured by GROSS (1933*a*, R. 1, fig. 6).

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon, *Psammolepis undulata* zone; Kuke, Latvia.

Diagnosis. — Branchial plate long and wide; ornamented by rounded crenulated tubercles which tend to coalesce into irregular short strips. Dorsal median plate entirely covered by superficial scale-like tesserae. Ventral median plate somewhat flask-shaped in outline with narrow part posterior.

Material. — Dorsal and ventral median plates from Scotland, fragments of plates from the Timan, branchial plates from the Donbas, and dorsal, ventral and branchial plates from the Baltic province.

Description. — *Dorsal median plate.* An almost entire dorsal median plate from Scotland (132 E.M.) lacks only the anterior margin. The lateral margins are rounded and they con-

verge gradually towards the posterior margin. The plate is gently arched from side to side and is very thin, measuring about 1 mm. in thickness. It is covered by superficial scale-like tesserae, which are arranged somewhat concentrically around a centre which lies in the anterior part of the plate. A further fragment of a dorsal median plate also from Scotland (P. 10187 B.M.) is perhaps the anterior half of the plate, although as it is broken at the margin, it is not possible to ascertain whether or not a re-entrant angle is present. As with the former specimen the plate is entirely covered by superficial scale-like tesserae, and is gently curved from side to side. A fragment of a further dorsal median plate from Scotland (1906. 139, 31 R.S.M.)

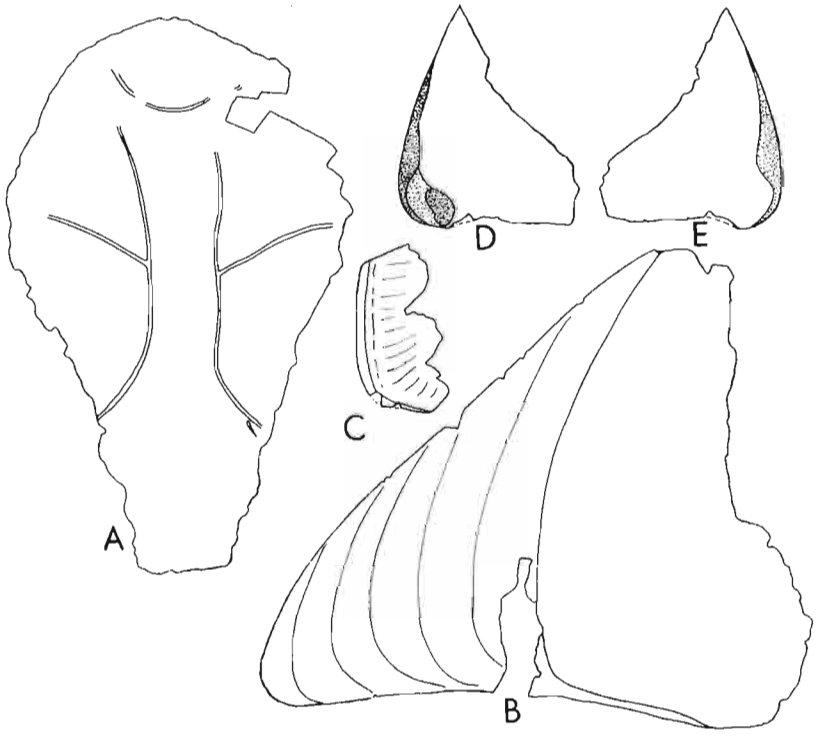

Fig. 32

Psammolepis undulata (AGASSIZ) — *A* ventral median plate showing sensory canal system (G.I.T. 247, Kuke), × 0·33; *B* left branchial plate in dorsal view (G.I.T. 249, Kuke), × 0·33; *C* immature left branchial plate in dorsal view (G.I.T. 251, Riga-Pskow Highway 1 km on left bank river Amata), × 0·33; *D* senile right branchial plate showing abrasion on both surfaces *a*, ventral view, *b*, dorsal view (G.I.T. colln., Kuke), × 0·33.

shows the typical ornamentation of closely packed rounded tubercles in the superficial tesserae. The anterior part of a dorsal median plate from the type locality Kuke (184 G.I.T.) as preserved has a fairly irregular outline, is gently arched from side to side, and is entirely covered by superficial scale-like tesserae, and shows no evidence of a re-entrant angle at the anterior margin.

Ventral median plate. A complete ventral median plate (133 E.M.) is known from Scotland, and this is somewhat flask-shaped in outline, with the narrow end facing posteriorly. The anterior margin forms a broad angle and from it the lateral margins run almost parallel until about halfway down the plate, when they converge to reach a narrow truncated posterior

margin. The plate is gently arched anteriorly, flattening out posteriorly, and it is very thin. No trace of ornament can be seen. A further ventral median plate from Scotland (1906.139.1 R.S.M.) has a rounded anterior margin from which the lateral margins diverge slightly until halfway down the plate, when they converge rather more sharply to reach the posterior margin which is unfortunately somewhat damaged. The plate is gently arched from side to side in the anterior part, flattening out posteriorly. The general proportions and shape of this particular specimen are reminiscent of the large adult ventral median plate of *Psammosteus praecursor* (see below). A single complete ventral median plate from Kuke (247 G.I.T.) has recently been collected, and again this is flask-shaped (Text-fig. 32*A*). The anterior border is rounded and the lateral margins diverge for a third of the way down the plate, and then run almost parallel for a short distance before they converge sharply to reach the narrow truncated posterior margin. This plate is again very thin, and is gently arched from side to side in the anterior part, flattening out in the posterior part. The ornamentation is faintly preserved in the central part of the plate, where superficial tesserae can be made out. The plate is particularly important since the sensory canal system is clearly visible. It consists of a semi-circular transverse canal near the anterior margin, facing posteriorly, together with two longitudinal canals running parallel in the centre of the plate which, two thirds of the way down the plate curve laterally and almost reach the lateral margins. Halfway down each median longitudinal canal a lateral branch runs somewhat anteriorly to again almost reach the lateral margin. The anterior semi-circular canal is similar to that seen in both the pteraspids and traquairaspids, as also are the median longitudinal canals, but the canal system in *Psammolepis undulata* differs from them by possessing paired lateral branches which are not known in the ventral canal system in any other heterostracan.

Branchial plate. A complete branchial plate (249 G.I.T.) is known from Kuke (Text-fig. 32*B*). The plate is somewhat wider than it is long, and the antero-lateral margin is fairly straight, and meets the slightly concave posterior margin in a gently rounded angle. The plate is ornamented by closely packed rounded tubercles which have a tendency to coalesce into short irregular strips. On the dorsal surface the ornamentation covers the lateral half of the plate, and in addition a narrow strip almost reaching the proximal end of the posterior margin. The median border of the ornamented part forms a gentle arc facing laterally. A very immature branchial plate (251 G.I.T.) is known from a locality on the left bank of the River Amata (Text-fig. 32*C*). The lateral margin of the plate is almost straight, but it curves to join a much shorter posterior margin which is also more or less straight. In dorsal view only a narrow lateral border 4 mm. in width is ornamented, and this continues along the posterior margin for the greater part of its length. In this young individual the branchial plates extended only a short distance laterally from the body of the animal, and in this respect the plate is very similar to the adult branchial plates of some of the species of *Schizosteus*. The postero-lateral part of the branchial plate of a very mature individual is also housed in Tallinn, and is notable for the extreme abrasion of the ventral surface of the postero-lateral corner, which is somewhat irregular due to the uneven nature of the plate in this region (Text-fig. 32*D*). Part of the dorsal surface of the lateral margin is also abraded.

Discussion. — AGASSIZ (1845*a*) described two fragments of a branchial plate under the name *Psammosteus undulatus*, and this species was mentioned only in passing by EICHWALD (1860), ROHON (1899), and PREOBRAJENSKY (1911). In 1897 TRAQUAIR described part of a ventral plate under the name *Psammosteus tesselatus* and in 1915 DOSS described a dorsal median plate which was entirely covered by superficial scale-like tesserae under the name *Psammosteus arenatus* AGASSIZ. GROSS (1933*a*) redescribed AGASSIZ' species *P. undulatus*,

and referred it to *Psammolepis*, and at the same time correctly included Doss's material in this species. In addition he suggested that TRAQUAIR's species should also be referred to *Psammolepis*. TARLO (1961*a*) was able to show that *Psammosteus tesselatus* in fact belonged to *Psammolepis undulata*, and proposed as a neotype for this species the branchial plate figured by GROSS (1933*a*). The material that ROHON (1899) mentioned under *P. undulatus* was given the name *Psammolepis timanica* by OBRUCHEV (1958), but this name was a *nomen nudum* and an examination of the original material housed in Moscow now shows that it belongs to *Psammolepis undulata*.

Psammolepis proia MARK-KURIK, 1965

(Text-fig. 33)

1955. *Psammolepis proia* n. sp.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 8, 14.
1958. *Psammolepis proia* MARK; D. OBRUCHEV, On the biostratigraphy..., p. 46.
1964*a*. *Psammolepis proia* MARK; L. B. H. TARLO, The origin..., p. 12, text-fig. 5.
1965. *Psammolepis proia* n. sp.; E. MARK-KURIK, Psammosteids from the... (in the press).

Holotype: Left branchial plate, 167, housed in the Geological Institute, Tallinn, figured by MARK-KURIK (1965, in the press), and in the present work (Text-fig. 33*C*).

Type horizon and locality: Middle Devonian (Givetian), Arukula horizon (Lower Tartu horizon), *Pycnosteus palaeformis* zone; Tamme, Estonia.

Diagnosis. — Branchial plate with straight lateral margin forming fairly sharp angle with straight posterior margin. Ventral median plate oblong with considerable posterior notch in young stage, filled by superficial tesserae. Ornamentation of rounded crenulated tubercles

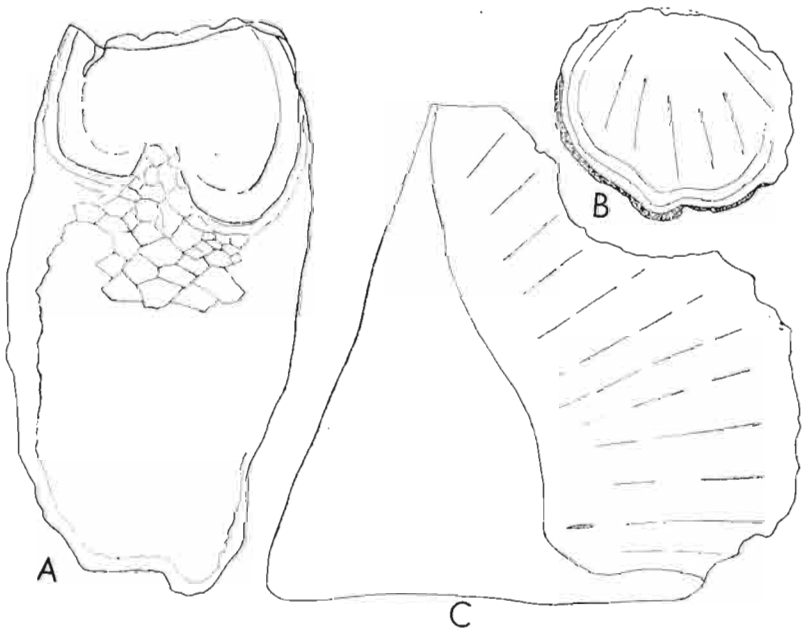

Fig. 33

Psammolepis proia MARK-KURIK — *A* ventral median plate, showing anterior part with zones of concentric growth and posterior notch, together with superficial tesserae covering remainder of plate (G.I.T. 148, Tamme); × 0·33; *B* cornual plate (G.I.T. 165, Tamme), × 0·33; *C* holotype, left branchial plate (G.I.T. 167, Tamme), × 0·33.

with fine ribs on to summits of tubercles. Tubercles fused into short strips at lateral margin of branchial plate.

Material. — Branchial plates, ventral median plate and cornual plate from Estonia.

Description. — *Ventral median plate.* A ventral median plate (148 G.I.T.) which lacks only the anterior border is more or less rectangular in outline, although the posterior margin is somewhat narrower than the anterior (Text-fig.33*A*). The plate measures 23 cm. in length and 11·5 cm. in width, and the anterior part is somewhat abraded, but it is still possible to make out the zones of concentric growth which indicate the round plate of the immature animal, with its characteristic posterior notch. This particular young growth stage is asymmetrical, the left-hand side being longer than the right. The notch is filled in with superficial tesserae and the rest of the plate is covered by similar, but larger scale-like tesserae. This specimen demonstrates the characteristics of the ventral plate of *Psammolepis* extremely well.

Branchial plate. The holotype, an almost complete branchial plate (167 G.I.T) has a fairly straight lateral margin which forms a sharp angle with the nearly straight posterior margin (Text-fig. 33*C*). The entire posterior margin on the dorsal surface is ornamented, although the postero-medial corner is defective. The border of the ornamented part of the dorsal surface is slightly sinuous, but more or less normal to the posterior margin except that where it approaches the margin it swings round and runs parallel to it. The unornamented portion has a greater medial extent than in the branchials normally found in this genus. The ornamentation consists of rounded dentine tubercles which are fairly closely packed, and these have crenulations which are produced into fine ribs towards the summits of the tubercles themselves. At the lateral margin the tubercles are frequently fused into short rows parallel to the margin. A further branchial plate (166 G.I.T.) is similar to the above specimen except that the lateral border is somewhat convex anteriorly.

Cornual plate. The only cornual plate known in the family is 165 G.I.T. This is oval in outline, and shows concentric growth from an area on the postero-lateral margin which in all probability covered the common branchial opening (Text-fig. 33*B*).

Discussion. — The name *Psammolepis proia* first appeared in the summary of MARK's thesis which was published in 1955, and was later mentioned by OBRUCHEV (1958); the species was only validated however, by MARK-KURIK (1965). The importance of this species lies in its stratigraphical position, as it occurs in the Arukula horizon whereas the other known species of the genus are found in the Gauja and Amata horizons which are considerably higher. It shows that *Psammolepis* was contemporary with the early species of *Tartuosteus*, *Pycnosteus* and *Ganosteus*, and did not arise later than these other genera as might previously have been supposed.

Psammolepis abavica MARK-KURIK, 1965

(Text-fig. 34)

1955. *Psammolepis abavica* n. sp.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 12, 14.
1965. *Psammolepis abavica* n. sp.; E. MARK-KURIK, Psammosteids from... (in the press).

Holotype: Branchial plate, 168, housed in the Geological Institute, Tallinn, figured by MARK-KURIK (1965, in the press), and in the present work (Text-fig. 34*A*).

Type horizon and locality: Upper Devonian (Frasnian), Gauja horizon, *Psammolepis paradoxa* zone; Lejeji, Latvia.

Diagnosis. — Branchial plate incompletely known, but lateral margin somewhat convex; ornamented by closely packed tubercles varying from rounded to pentagonal, and in some cases fan-shaped, with fine comb-like basal crenulations best developed along their proximal

edges. Ventral median plate with anterior area devoid of tesserae, but showing concentric zones of growth with posterior notch, and zoned scale-like tesserae in posterior part.

Material. — Ventral median plates and branchial plates together with single pineal plate from Latvia.

Description. — *Ventral median plate.* Part of a ventral median plate (1491-4 G.I.T.) shows the right posterior portion of the area of concentric growth in the anterior part of the

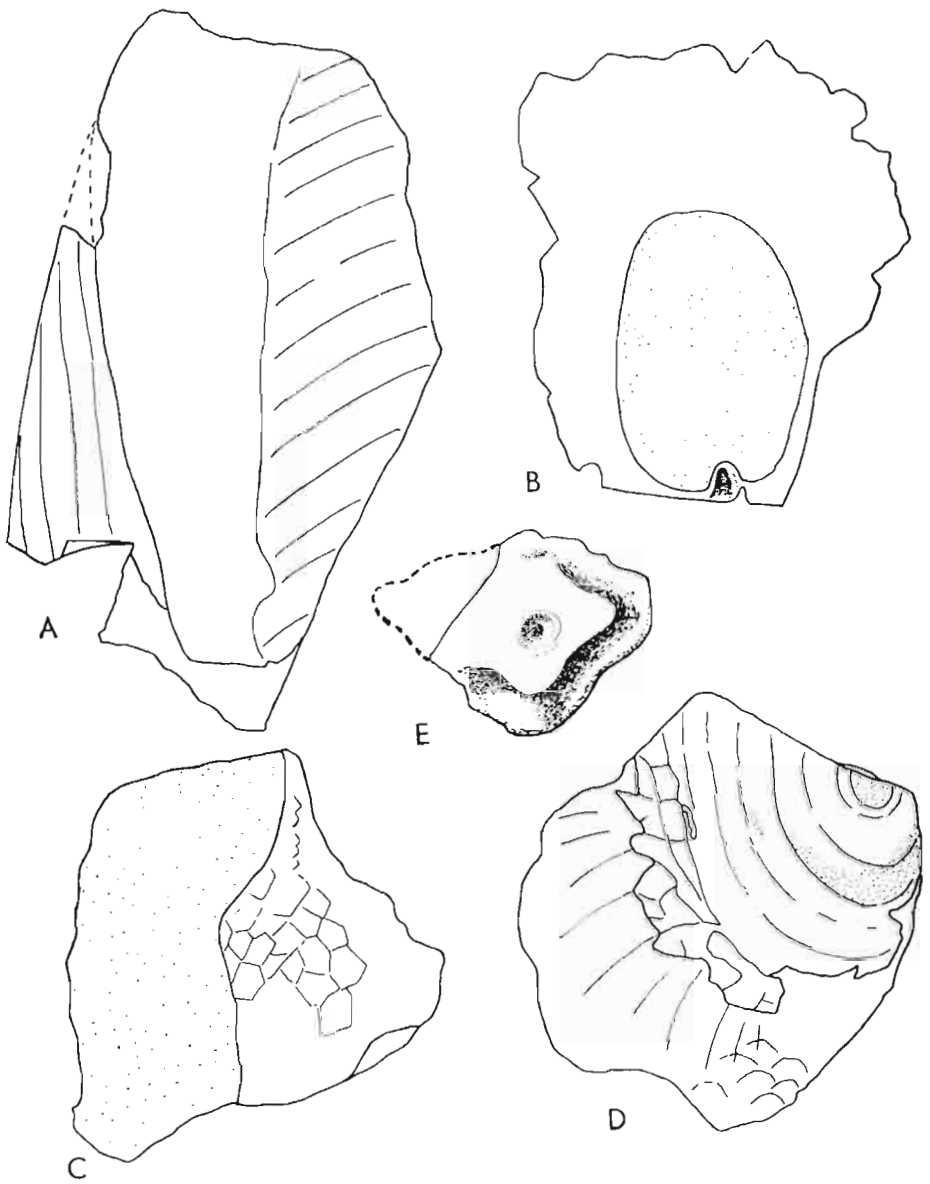

Fig. 34

Psammolepis abavica MARK-KURIK — *A* holotype, left branchial plate in dorsal view (G.I.T. 168, Lejeji), × 0·5; *B* ventral median plate with faint evidence of posterior notch (G.I.T. 1491-6, Lejeji), × 0·5; *C* ventral median plate showing abrasion which has obliterated evidence of posterior notch (G.I.T. 1491-7, Lejeji), × 0·5; *D* ventral median plate showing shallow posterior notch and irregular tesserae at margin of concentric growth (G.I.T. 1491-4, Lejeji), × 0·5; *E* pineal plate with depression for pineal organ (G.I.T. 1491, Lejeji), × 1.

plate, which is devoid of tesserae, and behind it the very irregular superficial tesserae which are the first to develop (Text-fig. 34*D*). The concentric zones marking the early growth stages turn anteriorly as they reach the mid-line posteriorly, and in this way produce the characteristic posterior notch of the young *Psammolepis*. These concentric zones, which are fairly wide, are ornamented by closely packed dentine tubercles which are fairly high crowned and have basal crenulations continuing upwards as ridges on to the crowns themselves. Behind the concentric zones there is a transitional zone of much the same width, ornamented by very irregular superficial tesserae, and these in turn give way to more normal scale-like tesserae which are not arranged in zones, but give the appearance of squamation. A further specimen although only a fragment of the posterior part of a ventral median plate, shows the scale-like tesserae very well, with their characteristic narrow zonation arranged concentrically from the anterior corner of each individual tessera. The anterior half of a mature individual (1491-7 G.I.T) is strongly abraded, especially in the central oval area which is entirely flat, and is strengthened by pleromic dentine (Text-fig. 34*B*). In the middle of the posterior border of this area, a very small posterior notch is visible. An even more mature specimen (1491-6 G.I.T.) shows the postero-lateral corner of the early growth area which is strongly abraded and strengthened by pleromic dentine (Text-fig. 34*C*). There is no evidence of a posterior notch since in the mid-line the area is continuous with a longitudinal tract which is similarly abraded and strengthened. The lateral part of the fragment still retains evidence of superficial tesserae, but these have been obliterated in the medial part.

Branchial plate. The holotype (168 G.I.T.) consists of the anterior part of a left branchial plate (Text-fig. 34*A*). The lateral margin is very slightly convex, but the remaining borders are missing with the exception of the anterior part of the medial border, which diverges slightly posteriorly from the lateral border. The ornamentation on the dorsal surface of the plate extends most of the way along the lateral margin, from which its border runs at an angle posteriorly, but is more or less parallel to the anterior part of the medial margin. The ornamentation itself consists of closely packed dentine tubercles which vary somewhat in size, there being zones of larger and smaller tubercles running through the normal pentagonal or fan-shaped tubercles. These have fairly long crenulations, particularly on their proximal edge, where they generally appear somewhat comb-like. A further specimen (147 G.I.T.) is the anterior half of a branchial plate. Its lateral border is more convex than in the holotype and the medial border diverges fairly strongly from it. In this instance on the dorsal side, the limit of the ornamentation is more nearly parallel to the lateral margin.

Pineal plate. A single pineal plate (1491 P.I.M.) is known belonging to this species, and it is also the only pineal plate known in the family Psammolepididae (Text-fig. 34*E*). In all probability it was fairly symmetrical with its major axis transverse. In external view the plate is entirely flat, but internally there is in the centre a deep round pit some three-quarters of the thickness of the plate which must have housed the pineal organ. At the margins on the inner side of the plate there is a very marked step. This plate is strikingly similar to the single pineal plate of *Guerichosteus kozlowskii* described above (Text-fig. 6*B*).

Psammolepis alata OBRUCHEV, 1965

(Text-fig. 35)

1955. *Psammolepis alata* (OBRUCHEV) M. S.; E. MARK, Psammosteids (Agnatha)..., pp. 4, 6, 8, 9, 12, 14.
1958. *Psammolepis alata* OBRUCHEV; D. OBRUCHEV, On the biostratigraphy..., p. 47.
1965. *Psammolepis alata* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).

Holotype: Branchial plate, 258, housed in the Geological Institute, Tallinn, figured by OBRUCHEV (1965, in the press), and in the present work (Text-fig. 35*B*).

Type horizon and locality: Upper Devonian (Frasnian), Gauja horizon, *Psammolepis paradoxa* zone; Kuradihoopast, Estonia.

Diagnosis. — Branchial plate long and wide, ornamented by large, globular, rounded dentine tubercles with short basal crenulations, generally with small rounded tubercles between them. Ventral median plate long and narrow, tapering somewhat posteriorly,where it is ornamented by scale-like tesserae.

Material. — Branchial plates, ventral median plate and fragments of dorsal plate from Estonia.

Description. — *Ventral median plate.* A complete ventral median plate (172 G.I.T.) is well preserved except for part of the anterior margin, although it is still possible to make

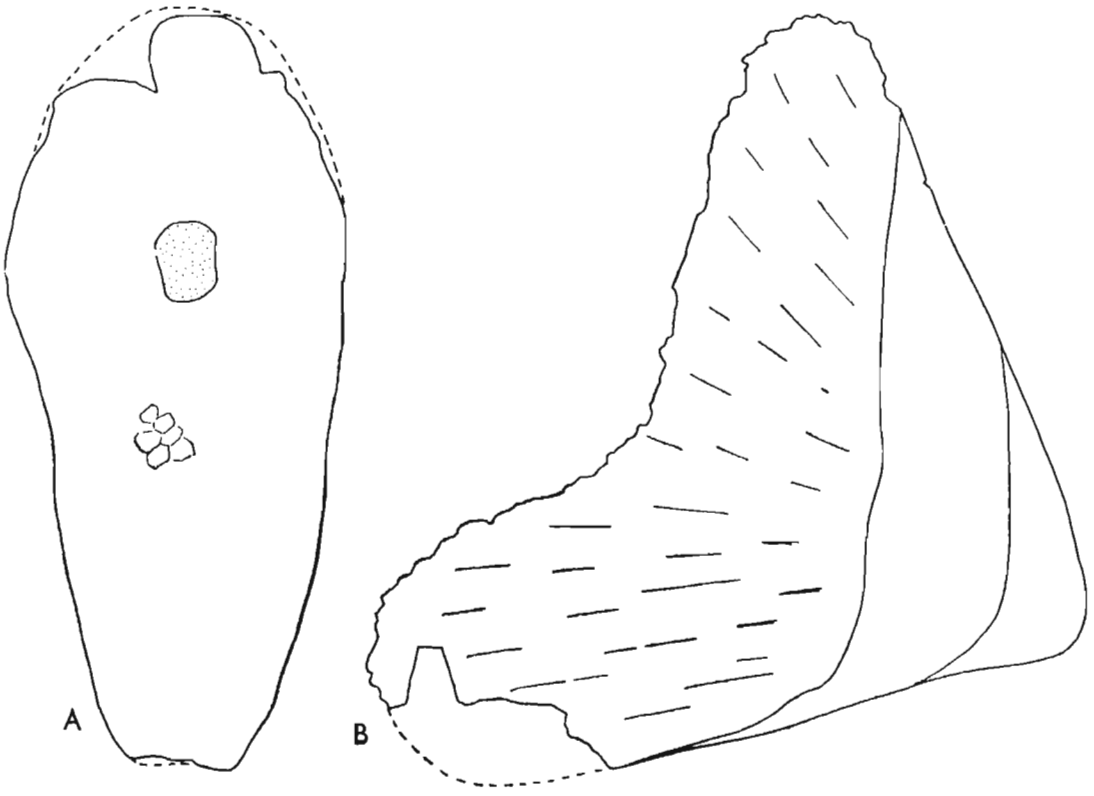

Fig. 35

Psammolepis alata OBRUCHEV — *A* ventral median plate showing initial point of abrasion and superficial tesserae (G.I.T. 172, Joksi), × 0·5; *B* holotype, right branchial plate in dorsal view (G.I.T. 258. Kuradihoopast), × 0·5.

out the full outline (Text-fig. 35*A*). The anterior margin is gently rounded and the lateral margins diverge for about a third of the length of the plate, and then very gradually converge to the truncated posterior margin. In the mid-line, at the point of maximum width of the plate, there is a small round patch which is strongly abraded and has been strengthened by the laying down of pleromic dentine. This probably represents the centre of growth of the plate. In this anterior part of the plate there is no indication of superficial tesserae, although in the posterior

half, faint outlines of such tesserae can be made out. The plate is very thick and is slightly curved from side to side in the anterior part, and flattens out posteriorly.

Branchial plate. The holotype (258 G.I.T.) is a complete branchial plate lacking only the postero-medial corner (Text-fig. 35*B*). The lateral border is straight and is almost at right-angles to the straight posterior border which it joins in a gently rounded angle. On the dorsal surface the limit of the ornamentation is a straight line running from the anterior part of the lateral margin towards the posterior margin where it would form an angle of about 70 degrees. However, as it approaches this margin it swings medially, and runs almost parallel to the margin. The median edge of the plate runs almost parallel to the limit of the ornamentation for about half the length of the plate, and then it swings medially to run nearly parallel to the posterior margin, thus forming a postero-medial flange. The plate is ornamented by well-rounded tubercles with short crenulations. These often appear globular, and between them there occur very small round accessory tubercles. A further branchial plate (173 G.I.T.) shows the median and lateral margin but the greater part of the posterior margin is missing. The lateral margin is fairly straight and the median limit of the ornamented part is again a straight line running towards the posterior margin. In this case the median edge of the plate diverges slightly posteriorly from the limit of the ornamentation but again swings sharply medially to produce the characteristic postero-medial flange, which in this instance is complete at the postero-medial corner, and is gently rounded. The entire posterior margin is preserved in branchial plate 260 G.I.T., although only the postero-median and postero-lateral corners are preserved in addition. This plate shows the extent of the ornamentation on the dorsal side along the posterior margin, which gradually converges with this margin and meets it about four-fifths of the way along it from the postero-lateral corner.

Psammolepis aerata OBRUCHEV, 1965

(Pl. XIX, fig. 9)

1965. *Psammolepis aerata* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).

Holotype: Branchial plate, 220/527, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1965, in the press), and in the present work, Pl. XIX, fig. 9.

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon, *Psammolepis undulata* zone; Milodej, NW Russia.

Diagnosis. — Branchial plate ornamented by very large roof-shaped tubercles with very short basal crenulations produced into faint striae on to the main part of the tubercle.

Material. — Unique holotype.

Description. — *Branchial plate.* The holotype (220/527 P. I. M.) is a fragment of a branchial plate, the lateral margin of which is straight. The tubercles are closely packed and very high crowned, and vary in size. The larger tubercles have roof-like summits, whereas some of the smaller ones are pointed. Their basal crenulations are very short and stubby, but are produced on to the main part of the tubercles as faint striae. The larger tubercles are reminiscent of those seen in *Karelosteus weberi* but differ by having more angular summits and by being considerably smaller, measuring 1-2 mm. along their major axis. This species may well be a precursor of *Karelosteus*, but from the form of the branchial plate, as far as it can be determined, this species can still be assigned to *Psammolepis*.

Psammolepis arctica (KIAER, 1915)

1915. *Psammosteus arcticus* n. sp.; J. KIAER, Upper Devonian fish..., pp. 23-24, pl. 2, fig. 5; pl. 3, figs. 1-3.
1950. *Psammosteus arcticus* KIAER; W. GROSS, Die paläontologische..., p. 46.
1964*b*. *Psammolepis arctica* (KIAER); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 17, 90, 104. pl. 2, fig. 1.

Lectotype (here selected): Fragment, A. 13206, housed in the Palaeontological Museum, Oslo, figured by KIAER (1915, Pl. 2, fig. 5, Pl. 3, fig. 1, 2, 3), and TARLO (1964*b*, Pl. 2, fig. 1).

Type horizon and locality: Upper Devonian (Frasnian), Series E; Skrap Valley, Ellesmereland, Arctic Canada.

Diagnosis. — Ornamentation of fairly large high-crowned pointed dentine tubercles with very prominent crenulations forming radial ribs.

Material. — Fragments from Ellesmereland, Arctic Canada.

Description. — This species is known only from small fragments, the best preserved of which (A. 13206 P. M. O.) is here chosen as the lectotype for the species. Its ornamentation is very similar to that in *Psammolepis venyukovi*, but it differs from it by the greater size of its tubercles. It is clearly a different species from *Psl. venyukovi*, but nevertheless is obviously very closely related to it. KIAER (1915) described this form and its histology and included in the same species a branchial plate which is referred below to the species *Psammosteus kiaeri*.

Psammolepis groenlandica TARLO, 1964

(Pl. XV, fig. 3)

1961. *Psammolepis* sp.; T. ØRVIG, Notes on some..., p. 515.
1961. *Psammolepis* sp.; E. JARVIK, Devonian..., p. 199.
1964*b*. *Psammolepis groenlandica* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 22, 85, 104, 116.

Holotype: Fragment of a plate, 905, housed in the Geological Museum, University of Copenhagen, figured in the present work, Pl. XV, fig. 3.

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

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.

Material. — Unique holotype.

Description. — The holotype (905 G.M.U.K.) is a fragment of a plate which does not show any division into superficial tesserae, and since the ornament is similar to that of *Psammolepis*, there seems every likelihood that it belongs to part of a branchial plate from a member of this genus. The tubercles are fairly large, closely packed and rather irregular in outline, with what appear to be fairly smooth crowns. They possess well marked basal crenulations. The species represented by this specimen appears to be rather similar to *Psammolepis proia*, which first appears in the Arukula horizon of the Baltic Province, and this can be equated with the horizon from which the holotype comes. However, although the specimen is similar to *Psl. proia*, its ornamentation is sufficiently different to warrant the erection of a new species, for which the name *Psammolepis groenlandica* was proposed. It should be noted that the specimen was first recorded by ØRVIG (1961) and later by JARVIK (1961).

?Psammolepis granulata (MCCOY, 1848)

(Pl. XIV, fig. 2)

1848. *Psammosteus granulatus* n. sp.; F. MCCOY, On some new..., p. 7.
1891*b*. *Psammosteus granulatus* MCCOY; A. S. WOODWARD, Catalogue..., p. 128.
1901. *Psammosteus granulatus* MCCOY; J. V. ROHON, Beiträge zur..., p. 4.
1964*b*. *Psammosteus granulatus* MCCOY; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 13, 91.

Holotype: Fragment of a plate housed in the National Museum of Ireland, Dublin, figured in the present work, Pl. XIV, fig. 2.

Description. — The specimen is preserved in a black silty shale. Part of it is preserved as a natural mould, and part is the actual material. The ornamentation consists of well separated tubercles with what appear to be accessory tubercles between them, and although they do not appear to have been as high crowned as those of *Psammolepis venyukovi*, the ornament is somewhat reminiscent of that species. From the ornament alone, the specimen appears to belong to a psammosteid, and if this is the case, it would seem reasonable to assign it to the genus *Psammolepis*. Furthermore, sections of the material have been made and these are not inconsistent with the specimen being a psammosteid. However, when first described by McCoy (1848) as *Psammosteus granulatus*, it was said to be from the Yellow Sandstone of Lower Carboniferous age, and although subsequent authors (including Charlesworth, 1963) have suggested that the Yellow Sandstone Group might be of Upper Devonian age, it is not certain whether this particular specimen is from rocks of Devonian age. Further stratigraphical work is required in the area from which the specimen has come before it can be placed in the Psammosteida without any doubt. According to Dr. A. E. Griffith and Dr. J. S. Jackson (personal communications, 1961, 1964) the area in question is covered by rocks of Carboniferous Limestone age (Visean Stage).

However, more recently Dr. Griffith, having carried out further field work in the area, has stated (personal communication, 1965) that the "succession may in fact not be all Visean, but could extend down through the Tournasian into the Upper Old Red Sandstone — the great thickness of sediment below [the zone of] S_2 could be argued to support this view". McCoy gave a very careful description of the specimen, and later Woodward (1891*b*) and Rohon (1901) listed this species as a psammosteid, but since the title of McCoy's original paper was "On some new Fossil Fish of the Carboniferous Period" the majority of authors have ignored the description. This is probably partly because the material has until now not been figured, for although at the time McCoy described it he deposited drawings of his material at Cambridge, unfortunately these are no longer extant. (Dr. C. L. Forbes' personal communication). The further specimen described as *Psammosteus vermicularis* by McCoy (1848), is quite indeterminable.

Family PSAMMOSTEIDAE Traquair, 1896

Diagnosis. — Dorsal median plate with shallow re-entrant angle at anterior margin, ornamented by superficial polygonal cyclomorial tesserae. Ventral median plate long and narrow; ornamentation as in dorsal median plate. Branchial plate flat, very short and wide, generally falcate in outline. Post-orbital plate long and narrow, forming major portion of lateral margin of carapace.

Discussion. — The family Psammosteidae was erected by Traquair (1896*b*) to receive the genus *Psammosteus*, and Rohon (1899) proposed the same family independently of Traquair. Since Traquair's time, this family has come to include all the Middle and Upper Devonian psammosteids, but the recent increase in our knowledge of these, has meant that it becomes no longer feasible to retain them all within a single family. For this reason, the Psammosteidae is here restricted to include only forms in which the branchials are short and wide, solid and falcate in shape, and in which the dentine tubercles of the dorsal median plates (where known) are arranged concentrically in polygonal superficial tesserae. These features

enable the family Psammosteidae to be readily distinguished from the Psammolepididae, Pycnosteidae and Obrucheviidae. The family Psammosteidae thus includes 10 species of *Psammosteus*, and the following are provisionally referred to the family: *Crenosteus levis*, *Karelosteus weberi*, *Rohonosteus ornatus* and *R. complicatus*.

Genus **PSAMMOSTEUS** AGASSIZ, 1845

Type species: *Psammosteus maeandrinus* AGASSIZ, 1845

Diagnosis. — Dorsal median plate ornamented by superficial polygonal tesserae produced by cyclomorial growth. Ventral median plate long and narrow with superficial tesserae ill-defined. Branchial plate flat and solid with distal portion ornamented on all surfaces; always very short and wide, falcate in outline. Lateral margin of carapace formed mainly by post-orbital plate. Cornual and rostral plates imperfectly known. Pineal known only from a single example which is very small and mushroom-shaped. Sensory canal system poorly known, but comparable to that seen in *Tartuosteus*.

Occurrence. — Upper Devonian (Frasnian Stage), zones of *Psammolepis undulata*, *Psammosteus maeandrinus*, *P. megalopteryx*, and *P. falcatus*; Baltic province, central Poland, Timan, Scotland and Ellesmereland (Canadian Arctic).

Discussion. — This genus was originally erected by AGASSIZ (1845*a*) to include four species — *P. maeandrinus*, *P. paradoxus*, *P. undulatus* and *P. arenatus*. *P. arenatus* is included in the synonymy of *P. paradoxus*, which together with *P. undulatus* was referred to the genus *Psammolepis* by GROSS (1933*a*). Thus *P. maeandrinus* by virtue of the elimination of the other species, became the type species of *Psammosteus*. Since the time of AGASSIZ important contributions on the genus *Psammosteus (sensu stricto)* have been made by TRAUTSCHOLD (1880), TRAQUAIR (1894, 1896*b*, 1897), WOODWARD (1911), KIAER (1915), GROSS (1933*a*, 1942), OBRUCHEV (1945, 1947 *a*, *b*) and TARLO (1961*a*). The different species of *Psammosteus* are of considerable value in the stratigraphy of the Upper Devonian, as they provide the basis for a zonal scheme in the Baltic province, which can be applied to some degree in other regions such as the Timan and Scotland.

The genus *Psammosteus* is readily recognized by the characteristic cyclomorial ornamentation of the superficial tesserae of the dorsal median plates, and by the small solid branchial plates. Normally these are not found together (only in one instance have both branchial and dorsal median plates been found in natural association), and the systematics of the genus are in fact based entirely upon differences of ornamentation in the branchial plates. As a result, it is often difficult to assign isolated fragments of other plates to the correct species.

The fact that branchial and dorsal plates are generally the only parts of *Psammosteus* that are found, led STENSIÖ (1958, p. 249) to the conclusion that the cornuals had become incorporated into the dorsal plates by fusion, and that the rostral, orbital and post-orbital plates had either disappeared or had disintegrated into smaller elements which were impossible to identify. However, it can be seen from the associated carapace of *Psammosteus megalopteryx* from Scotland, which was briefly described by WOODWARD (1911), that all the elements known in the Lower Devonian *Drepanaspis* are still present in the Upper Devonian *Psammosteus* (see TARLO, 1961*a*).

The first attempted reconstruction of the genus was by OBRUCHEV (1947*a*) and was based on a ventral median plate of *Psammosteus praecursor*, and on WOODWARD'S description of *P. megalopteryx*, but as WOODWARD'S figure and description were incomplete, it was not

possible for the outline of the carapace to be ascertained correctly. A recent re-examination of the associated carapace (TARLO, 1961*a*) has enabled the dorsal side of *Psammosteus* to be reconstructed for the first time, and has established the presence of the rostral, post-orbital and cornual plates. Since this second reconstruction of *P. megalopteryx*, specimens of this species have been examined in Moscow, and in consequence it was necessary in Part I of this work to modify the reconstruction (TARLO, 1964*b*, Text-fig. 10 *A-B*).

Since *P. megalopteryx* is of considerable importance to any understanding of the organisation of the plates of the carapace in *Psammosteus*, although it is not the type species, it will be dealt with first.

Psammosteus megalopteryx (TRAUTSCHOLD, 1880)

(Pls. XV, figs. 4, 5; XVI: XVII, figs. 3-7; XVIII, figs. 5, 7; XIX, figs. 6, 7; Text-figs. 36, 37)

1880. *Coccosteus megalopteryx* n. sp.; H. TRAUTSCHOLD, Ueber *Dendrodus*..., p. 152, pl. 6, fig. 1; pl. 7, fig. 2.
1880. *Coccosteus megalopteryx* n. sp.; H. TRAUTSCHOLD, Ueber Dendrodus..., p. 156.
1889. *Coccosteus megalopteryx* TRAUTSCHOLD; H. TRAUTSCHOLD, Ueber vermeintliche..., p. 136.
1890. Selachian appendages; R. H. TRAQUAIR, On the structure..., p. 134.
1890. *Megalopteryx* TRAUTSCHOLD; H. TRAUTSCHOLD, Ueber *Megalopteryx*..., pp. 575-6.
1891. *Psammosteus* [*megalopteryx* TRAUTSCHOLD]; G. GÜRICH, Ueber Placodermen..., pp. 911-2.
1891*b*. *Psammosteus megalopteryx* (TRAUTSCHOLD); A. S. WOODWARD, Catalogue of fossil..., p. 126.
1891*b*. *Psammosteus maeandrinus* AGASSIZ; A. S. WOODWARD, *Ibid.*, p. 126.
1894. *Psammosteus taylori* n. sp.; R. H. TRAQUAIR, On *Psammosteus taylori*..., p. 225, 1 text-fig.
1896*b*. *Psammosteus taylori* TRAQUAIR; R. H. TRAQUAIR, The extinct vertebrata..., pp. 260-3, pl. 6, fig. 1-3.
1897. *Psammosteus taylori* TRAQUAIR; R. H. TRAQUAIR, Additional notes on..., pp. 378-9, pl. 11, fig. 5.
1901. *Psammosteus* AGASSIZ; I. V. ROHON, Beiträge zur..., p. 30, pl. 2, figs. 18-20.
1911. *Psammosteus taylori* TRAQUAIR; A. S. WOODWARD, On the Upper Devonian ostracoderm..., pp. 649-52, pl. 9 fig. 1-6.
1932. *Psammosteus taylori* TRAQUAIR; A. HEINTZ, Beitrag zur..., p. 7-8, text-fig. 3.
1933*a*. *Psammosteus megalopteryx* (TRAUTSCHOLD); W. GROSS, Die Fische des..., pp. 14-5, pl. 1, fig. 1; pl. 2, fig. 21.
1935. *Psammosteus megalopteryx* (TRAUTSCHOLD); W. GROSS, Histologische Studien..., p. 12, pl. 2, fig. 5.
1945. *Psammosteus* [*megalopteryx* (TRAUTSCHOLD)]; D. OBRUCHEV, On the evolution of..., p. 262, text-figs. 6 a-d.
1947*a*. *Psammosteus megalopteryx* (TRAUTSCHOLD); D. OBRUCHEV, On the genus *Psammosteus*..., pp. 519-20, text-fig. 2c.
1947*b*. *Psammosteus megalopteryx* (TRAUTSCHOLD); D. OBRUCHEV, Atlas of the..., p. 197, pl. 51, figs. 1, 2, 5.
1956. *Psammosteus megalopteryx* (TRAUTSCHOLD); A. P. BYSTROW, On the destruction..., pp. 41-43, text-figs. 10-12.
1961*a*. *Psammosteus taylori* TRAQUAIR; L. B. TARLO, Psammosteids from the..., pp. 193, 195.
1961*a*. *Psammosteus megalopteryx* (TRAUTSCHOLD); L. B. TARLO, *Ibid.*, pp. 194-200, 208-9, pl. 7, figs. 1-3, text-figs. 1, 2, 3 a, b, 4, 5, 8 c, f.
1963. *Psammosteus* [*megalopteryx* (TRAUTSCHOLD)]; L. B. H. TARLO, Aspidin..., pp. 46-47, text-figs. 1, 2.
1964*a*. *Psammosteus megalopteryx* (TRAUTSCHOLD); L. B. H. TARLO, The origin..., pp. 9-11, text-figs. 3, 4.
1964*b*. *Psammosteus megalopteryx* (TRAUTSCHOLD); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 15, 17, 19, 21, 22, 32, 33, 37, 39, 46, 47, 51, 52, 60, 86, 87, 89, 102, 105, 107; pl. 1, figs. 1-5; pl. 6, figs. 1, 2, 4-6; text-figs. 9, 10 A-C, 13, 14 A, 17.
1964. *Psammosteus megalopteryx* (TRAUTSCHOLD); E. A. STENSIÖ, Les Cyclostomes..., p. 184, text-figs. 36 B, C.
1964. *Psammosteus megalopteryx* (TRAUTSCHOLD); D. OBRUCHEV, Subclass Heterostraci..., pp. 74, 75, text-figs. 55, 58a

Neotype: Branchial plate, 220/325, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1945, Text-fig. 6a; 1947*a*, Text-fig. 2c; 1964, Text-fig. 58a), BYSTROW (1956, Text-fig. 10), and in the present work Text-fig. 37*A*.

Type horizon and locality: Upper Devonian (Frasnian), *Psammosteus megalopteryx* zone; Stolbovo, River Sjass, Russia.

Diagnosis. — Branchial plate short and wide; ornamented by closely packed crenulated tubercles which narrow distally. Dorsal median plate with generally oval but variable outline;

superficially divided into polygonal tesserae with crenulated tubercles arranged concentrically round larger tubercle. Ventral median plate narrow, naviculate in outline, with superficial tesserae indistinct. Ornamentation of closely packed rounded dentine tubercles with crenulated margins.

Material. — Numerous dorsal median plates from Scotland and Russia; one ventral median plate from Scotland and two fragments from Russia; innumerable branchials showing all stages of growth; scales, body and fulcral; fragments of dorsal median plates showing parts of sensory canal system; patches of tesserae from branchial plates, dorsal median plates and fields of tesserae; single associated carapace from Scotland.

Description. — *Dorsal median plate.* The first complete dorsal median plate known of *P. megalopteryx* (1895.143.1 R.S.M.) was described by TRAQUAIR (1896*b*). This plate is somewhat oval in outline with its posterior half somewhat wider than the anterior. The posterior margin is slightly pointed, while the anterior margin has a broad shallow re-entrant angle. The plate is gently convex from side to side, flattening out towards the anterior margin. The holotype of *P. taylori* (1894.169.1 R.S.M.) (since transferred to *P. megalopteryx*), although lacking the anterior margin is in all other respects identical to the previous specimen. A similar plate is also known from Russia (220/545 P.I.M.) although in this case the convexity in the posterior part is very slight, the plate being almost flat. Furthermore, this plate is only about one third of the thickness of the ones known from Scotland.

Comparative sizes of dorsal median plates (in mm.):

Catalogue number		Length	Width
P. 10956	B.M.	31	27
102	E.M.	*25·5	24
1894.169.1	R.S.M.	27	16
1895.143.1	R.S.M.	26	16
P. 10957	B.M.	22	16
220/545	P.I.M.	20	11·3
104	E.M.	*13·5	12

* estimated

In marked contrast to these plates is the specimen (P. 10956 B.M.) described by WOODWARD (1911). The anterior margin is again marked by a re-entrant angle but this time the lateral margins flare out forming almost a semi-circle on either side, until they are excavated towards the posterior end. They then run more or less parallel for a short distance until they reach the broad blunt angle of the posterior margin. The posterior part of the plate is markedly convex, but again it flattens out anteriorly. Similar plates are housed in the Elgin Museum (e. g. 102 E.M.). A further specimen (P. 10957 B.M.) which is also strongly convex posteriorly, has however an outline closer to the specimen described by TRAQUAIR (1896*b*). The dorsal median plate has an ornamentation of superficial tesserae in which small dentine tubercles are arranged concentrically around a large central one. The tesserae are normally pentagonal or hexagonal, and cover the entire surface. One fragment from the Leningrad district (housed in the P.I.M.) shows the change that occurs in the shape of the tesserae as the margin of the

plate is reached; the normal polygonal tesserae become rather scale-like in appearance and are reminiscent of the superficial tesserae seen in *Psammolepis*.

It is thus clear that the dorsal median plates are variable in outline and in consequence caution must be exercised when attempting to use such differences to distinguish species. Marked differences are also apparent in the degree of convexity of the plates, as well as in their thickness. The differences in outline might well be due to the age of the individual, as in general the narrower plates are usually also smaller. In any case however, such differences

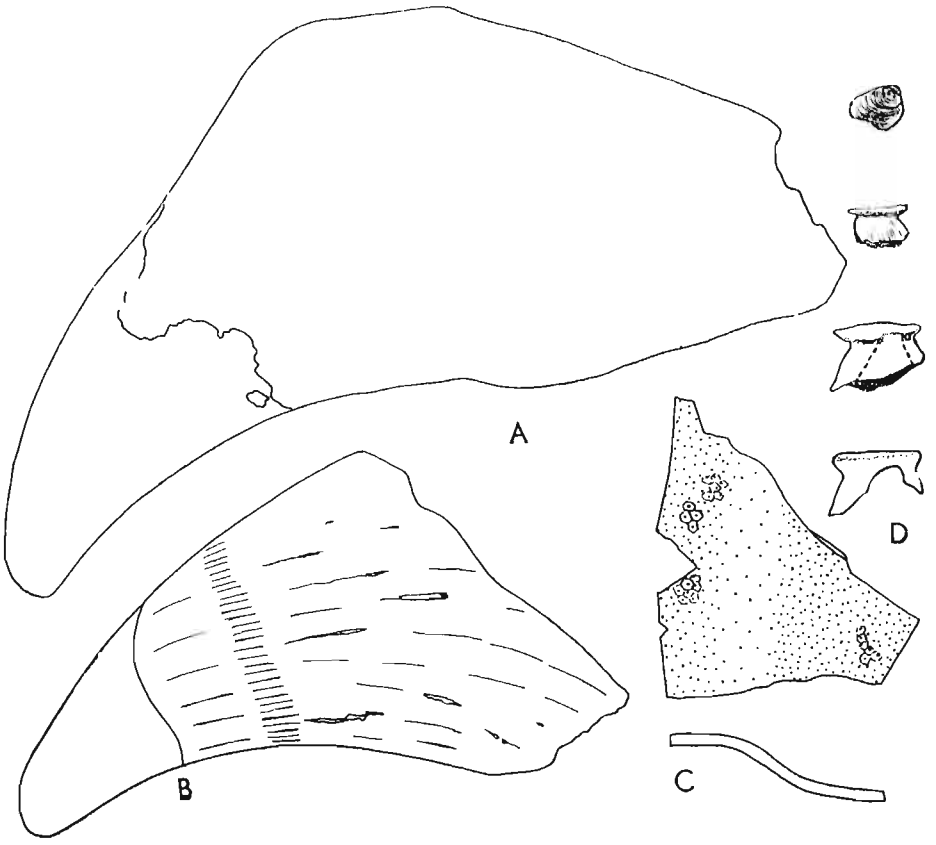

Fig. 36

Psammosteus megalopteryx (TRAUTSCHOLD) — *A* neotype, left branchial plate (P.I.M. 220/325, Stolbovo), × 0·5; *B* left branchial plate (P.I.M. 220/153, Stolbovo), × 0·5; *C* fragment of ventral median plate (P.I.M. 220/265, Stolbovo), × 0·5; *D Psammosteus* sp. — pineal plate (P.I.M.), upper figs. natural size.

can be expected since as the median plate is surrounded by a mosaic of small elements, i. e. fields of tesserae, it can increase in size at the expense of the tesserae. Such an increase is likely to have taken place by the areal growth of the plate beneath the tesserae which later became fused to it. This would explain the fact that frequently in the dorsal plates the superficial tesserae are missing and there is a pattern of shallow polygonal depressions giving the surface of the plate a rather honeycomb appearance. The superficial tesserae in these cases could not have been completely anchylosed to the plate. It would also serve to explain the fact that in the specimen (220/545 P.I.M.) figured by OBRUCHEV (1947*b*) on which two patches of tesserae are preserved, those in the posterior part are fused to the plate, while

the tesserae of the anterior patch have become detached and have been preserved in a disordered condition.

With regard to the differences in thickness and convexity seen in the plates from Russia and Scotland, it has been suggested (TARLO, 1962*d*) that these are directly related to differences in the environment, different profiles of the carapace being a response to particular conditions. Whatever the explanation of these differences, however, it is clear that the carapace of *Psammosteus* was much more variable than was previously believed.

Ventral median plate. The only complete specimen of a ventral median plate known comes from the articulated carapace from Scotland (P. 10956 B.M.). This plate was partly figured by WOODWARD (1911) and was included in the reconstruction of *P. megalopteryx* by TARLO (1961*a*). It is flat and naviculate in outline, being pointed anteriorly and truncated posteriorly, as is clearly seen in Text-fig. 10*B* (TARLO, 1964*b*). The plate is seen in internal view, and is preserved in two pieces. At the break it is possible to observe small patches of the ornamentation of the external surface. This consists of large rounded dentine tubercles which do not appear to be organised into tesserae. The only other remains of ventral median plates of this species are two fragments (220/203, 220/265 P.I.M.) which were recently identified by the author in the large collection of psammosteid material in Moscow (Text-fig. 36*C*). In section both fragments show a curvature resembling somewhat a gentle monoclinal fold. In both cases, one limb of the fold is more abraded than the other, indicating that this portion of the fragment formed part of the central median area of the complete plate. In the smaller of the two fragments (220/203), tesserae are clearly visible; on the other hand, in the larger specimen tesserae are hardly discernable, but scattered prominent tubercles are visible with rows of smaller tubercles arranged concentrically around them. With strong oblique lighting however, it can be seen that in fact superficial tesserae are present.

It is obvious therefore that there are striking differences between the Russian and Scottish forms. In transverse section the Russian specimens are curved while the one from Scotland is flat, and whereas in the Russian fragments faint superficial tesserae are visible, it is not possible to recognize such tesserae in the Scottish specimen.

It is evident that the Russian fragments come from ventral plates which would have been considerably larger than the one known from Scotland, and the differences noted above may therefore well be due to the Scottish form being a younger individual. If it were, one could envisage the fields of tesserae surrounding the ventral plate becoming incorporated into its margins as the animal approached maturity. This would make the edges of the ventral plate curve upwards away from the central flat area, as the fields of tesserae do along the margins of the plate in the Scottish specimen. The significant point is, that whether the concavities between the branchial plates and the central flat region of the ventral surface of the carapace were formed by the fields of tesserae alone, or by lateral extensions of the ventral median plate, the cross-section of both the Russian and Scottish animals must have been essentially the same. The shape of the mature ventral median plate must have been reminiscent of that of *Psammolepis*, and therefore the contrast between this plate in *Psammolepis* and in *Psammosteus* noted by TARLO (1961*a*) is now seen to be not so marked.

The differences between the Russian and Scottish specimens of ventral median plates belonging to *P. megalopteryx* would therefore appear to be due to the relative age of the individuals concerned, rather than to environmental factors.

Branchial plate. The neotype of *Psammosteus megalopteryx* is a branchial plate (220/325 P.I.M.), the distal end of which is ornamented on all surfaces by closely packed dentine tubercles. The sides of the tubercles converge to a point distally, but are rounded and crenulated

proximally (Text-fig. 36*A*). This part of the plate is strongly abraded on its antero-ventral margin, and to a lesser degree on its antero-dorsal margin, indicating that it projected from the carapace, and that its anterior margin was in contact with the substratum. This distal portion of the plate is flat and solid, and is roughly triangular in outline; its anterior margin is somewhat convex while its posterior margin is rather concave, and the posteriorly directed apex of the triangle is bluntly rounded. Although this is the only part of the plate normally found preserved, in the neotype almost the entire plate is known. The bulk of the plate is formed of a comparatively thin sheet of bone which flares out from the triangular ornamented apex, especially in an anterior direction. It is devoid of ornamentation, and must have been covered by other elements of the carapace. On its ventral surface there is a clearly marked zone in which the spongy bone shows a fine lineation aligned parallel to the major axis of the plate. This zone is adjacent to the distal portion of the plate described above, and in other specimens it is seen to be covered by characteristic branchial tesserae (see below under *Tesserae*). Proximal to this zone the spongy bone shows a coarser lineation with occasional deep grooves, and it is likely that this region was covered by soft tissue. This specimen which is large and well developed is clearly from a mature individual. A similar but smaller and less complete branchial (220/153 P.I.M.) also has a large proximal unornamented region, although this does not appear to flare out quite so much anteriorly (Text-fig. 36*B*).

The distal end of a somewhat younger branchial (220/545 P.I.M.) has a rather different outline, the triangular portion being more acutely angled (Text-fig. 37*A*). This specimen is of particular interest since on the dorsal side, the ornamentation of dentine tubercles is covered by a thin sheet of smooth eruptive dentine. At first glance it looks as if the plate is strongly abraded, but where the ornamentation ends it can be seen that the layer of dentine is lying on top of the normal tubercles. The distal tip of branchial 220/327 P.I.M. although more rounded than the previous one, also shows this secondary dentine layer (Text-fig. 37*B*).

A number of immature branchials are also in the Moscow collection, and of special interest is the fact that the dentine tubercles of their ornament are larger than those in the ornament of the more mature specimens, and are also more widely separated from one another. Occasionally as in specimen 220/112 P.I.M., the dentine tubercles on the ventral surface are arranged in arcuate rows, pointing proximally, and not distally as is more normal. As with mature branchials, these immature ones are generally flat, although specimen 220/46 P.I.M. is downturned ventrally (Text-fig. 37*E*). In plan the tip of this specimen is rounded, contrasting with 220/45 in which the tip is sharply pointed (Text-fig. 37*H*), and a further specimen (Text-fig. 37*K*) in which the tip is bent posteriorly. In contrast to all the specimens previously mentioned is a further immature branchial (No. 220/157 P.I.M.) in which both the anterior and posterior margins are almost parallel, instead of forming two sides of a triangle (Text-fig. 37*J*). This is in fact similar to the condition seen in the adult specimen 220/69 P.I.M. (Text-fig. 37*D*), and is reminiscent of the normal adult condition seen in the succeeding species *P. falcatus*.

In the associated carapace from Scotland both branchial plates are preserved in their natural position, although the specimen as a whole has been somewhat sheared. Unfortunately only the distal dorsal parts are clearly visible but these are important as they indicate the orientation of the branchials in the carapace during life, showing that the distal portions of the plates are directed posteriorly. From the other branchials described above it can be seen that the anterior edge of the distal portion is usually abraded as also is the rounded apex, particularly on its ventral surface. Commonly the entire anterior edge of the distal portion of the branchial is worn flat although in some adult specimens the antero-ventral edge is

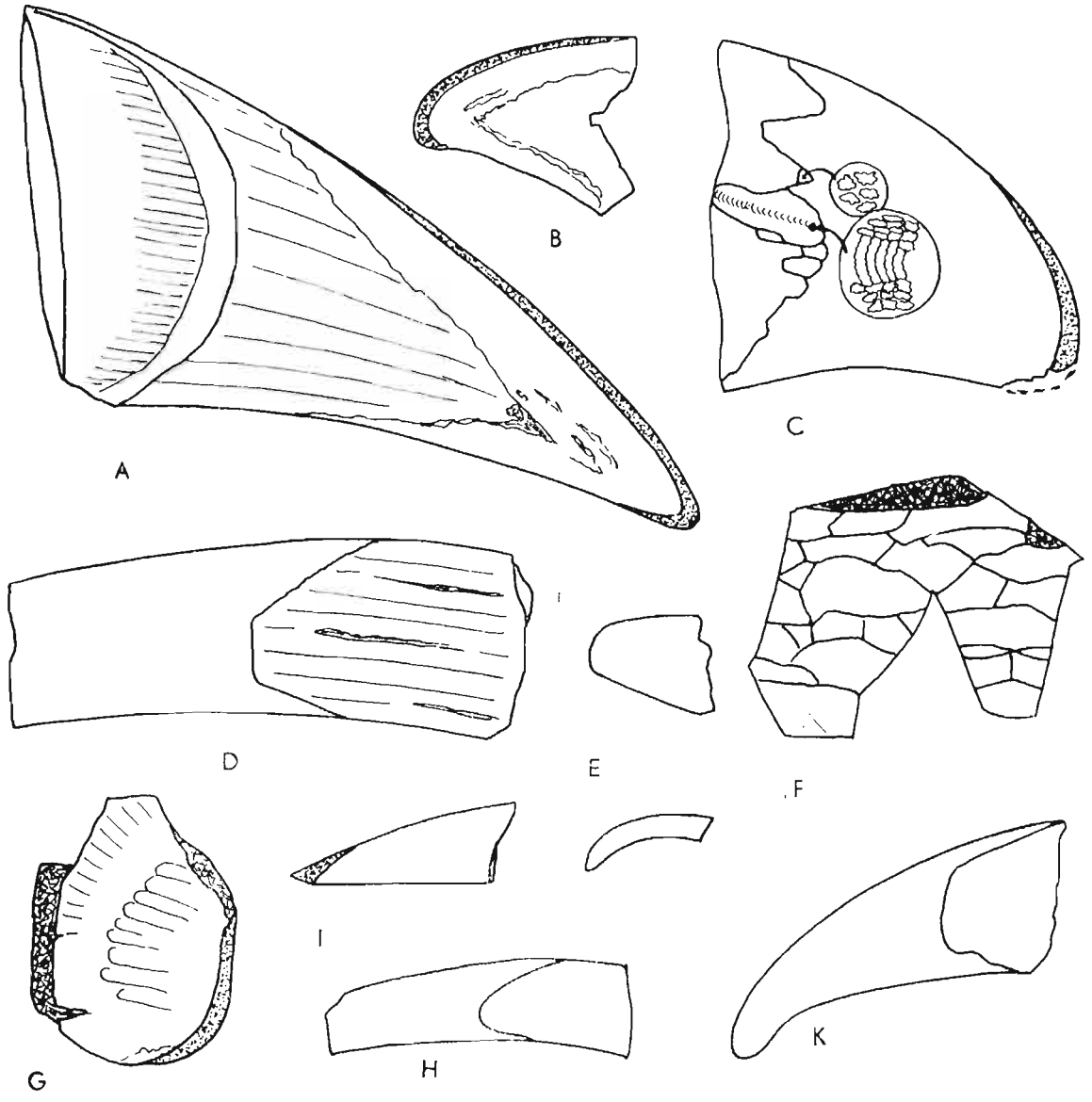

Fig. 37

Psammosteus megalopteryx (TRAUTSCHOLD) — *A* left branchial plate in ventral view, showing thin sheet of eruptive dentine (P.I.M. 220/545, Stolbovo); *B* distal tip of right branchial plate showing thin sheet of eruptive dentine (P.I.M. 220/327, Stolbovo); *C* left branchial plate showing characteristic ventral tesserae adhering to proximal part of plate (P.I.M. 220/44, Stolbovo); *D* branchial plate (P.I.M. 220/69, Stolbovo); *E* distal tip of branchial plate (P.I.M. 220/46, Stolbovo); *F* fragment of proximal part of branchial plate with adhering branchial tesserae (P.I.M. 220/191, Stolbovo); *G* senile branchial plate (P.I.M. 220/298, Strelna); *H* distal tip of branchial plate (P.I.M. 220/45, Stolbovo); *J* branchial plate (P.I.M. 220/157, Stolbovo); *K* branchial plate with posteriorly directed distal tip (P.I.M., Colln., Stolbovo); all figures natural size.

strongly abraded to form a rounded angle with a further facet of wear on the antero-dorsal edge. In either case the greatest wear is always at the distal tip of the branchial, and although all surfaces show signs of abrasion, this is least on the dorsal surface. The distal portion of one

senile specimen (220/298 P.I.M.) has been so extensively abraded that virtually the entire free portion of the branchial has been worn away (Text-fig. 37*G*).

From their position in the Scottish carapace, it would appear that the distal extremities of the branchial plates would not have been subject to a great deal of abrasion, and this would also seem to be the case in the immature specimens from Russia, where the ornamentation is almost perfectly preserved. Hence it would seem that the branchials were only brought into a position in which they could be abraded as the animal grew. The branchial plates must have been pushed further out from the carapace by the addition of zones of tubercles along the proximal margin of the free distal end, and occasionally, as in specimens P. 4493, B.M. and A. 169, P.M.O., such zones of growth stand out very sharply. The differential wear on some of the branchials (see TARLO, 1964*b*, Text-figs. 9 *B-C*) would seem to indicate that they could be held in at least two different positions, since if the branchials were in a fixed position in the carapace, it is hard to conceive of any manner in which two opposed facets of wear could have been produced. In view of the considerable medial extent of the branchials within the carapace, it can only be concluded that the branchial plates were to a certain extent moveable appendages as WOODWARD (1911) suggested. Thus it appears that in *Psammosteus* the heterostracans had evolved rudimentary paired fins.

Post-orbital plate. This plate is known only in the associated carapace P. 10956 B.M., originally described by WOODWARD (1911). He noted that the lateral border of the carapace anterior to the branchial plate, was formed by a thin layer ornamented with large rounded tubercles. However, as only a small portion of the ornamentation was figured, it was not possible from his paper, to ascertain the correct outline of the carapace. A recent re-examination of the specimen has shown that in fact this thin layer represents the post-orbital plate (TARLO, 1961*a*). The plate, which is on the left side, is incomplete, and its full extent cannot be ascertained even though the whole of the lateral margin is visible. The maximum length of the plate is 34 cm. and in its posterior part where it is widest, it measures 5 cm. In this region it is separated from the dorsal median plate by a narrow zone of tesserae. At the lateral margin the plate is curved right over and is gently rounded in section, so that part of it is present on the ventral margin of the carapace. Unfortunately as the specimen is incomplete it is not possible to establish the median extent of the plate on the ventral surface. The margin of the carapace produced by the post-orbital plate forms a smooth curve which is continuous with the anterior edge of the branchial plate. A striking feature of the plate is its remarkable thinness, as also is the fact that it does not seem to have suffered much abrasion. In the reconstruction based on the associated carapace (TARLO, 1961*a*) the post-orbital covers the ventral surface of the branchial, but this is now known to be incorrect since this area is covered by branchial tesserae. At the same time the post-orbital does not abut the cornual plate as was suggested, but is separated from it by several tesserae of the dorsal field.

Cornual plate. Again the only evidence of this plate is in the associated carapace described by WOODWARD, although in this instance WOODWARD failed to notice that there was an area on the dorsal surface composed of isolated rounded tubercles, in the angle formed by the posterior margin of the branchial and the posterior lateral margin of the dorsal plate. This area obviously represents the remains of the cornual plate (TARLO, 1961*a*) which would have been situated between the dorsal and branchial plates, partly covering the latter on its dorsal surface, and probably marking the position of the branchial opening. As already noted above, the tesserae on the posterior margin of the post-orbital plate indicate that the cornual plate did not abut it directly. Unfortunately the outline of the cornual plate cannot be ascertained.

Rostral plate. According to WOODWARD (1911) «in the region of the head, just in front of the median dorsal plate, there are also traces of dermal armour, but these are too imperfect for their nature to be determined». It seems likely that the quadrangular area in the mid-line represents part of the rostral plate, but here again it is not possible to trace the full outline of the plate. All that can be said is that it exists, and that it is extremely thin.

Pineal plate. WOODWARD figured «a mass of calcified tissue lying in the anterior angle of the median dorsal plate», which he considered to be a «displaced fragment». Unlike the remains of the post-orbital and rostral plates, this rounded element is as thick as the dorsal plate, and it seems likely that it represents a pineal plate. In this connection it should be noted that a single pineal plate of *Psammosteus* sp. is known from Russia. This is oval in outline in dorsal view, measuring 9 × 6 mm. The outer part is ornamented, beneath which the plate is somewhat constricted before it widens out again, so that in lateral view it is somewhat spool-shaped (see Text-fig. 36 *D*). In internal view the plate is hollow, where it housed the pineal organ.

Tesserae. Between the median plates and the plates of the lateral margin, there are zones of small thin polygonal plates or tesserae. These are ornamented by rounded dentine tubercles with crenulated margins, which are generally arranged concentrically around a larger central tubercle. The margins of the tubercles are not deeply indented, the crenulations rarely measuring more than a fifth of the total width. There are usually about ten crenulations to each tubercle, although occasionally some of these bifurcate at their extremities. Similar tesserae are found fused to the median plates to form the characteristic ornamentation of *Psammosteus* dorsal plates. A fairly immature dorsal median plate from Russia (220/545 P.I.M.) shows the «honeycomb» appearance noted by TRAQUAIR (1899). This occurs when the tesserae are lost, the individual "cells" representing the former position of tesserae, and the "walls" the point at which the tesserae were first fused to the plate beneath. It is thus clear that the tesserae were not firmly fused to the plates until the animal was mature. In the Russian specimen all the tesserae have been lost with the exception of two small patches, one of which is in the posterior part of the plate. Here the tesserae are firmly affixed to the plate, and the "walls" of the "honeycomb" where visible appear to be thicker than in the central part of the plate. Towards the anterior part of the plate there is a further patch in which the individual tesserae are heaped up at different angles. This suggests that they had become detached from the plate, but had not been completely lost before fossilization. As already noted above under *Dorsal median plate*, towards the periphery of the dorsal median plate the tesserae tend to become more scale-like in outline.

Superficial tesserae also occur on the part of the ventral surface of the branchial plates adjacent to the distal portion. These are again ornamented by crenulated dentine tubercles arranged concentrically, but this time most of the tesserae are elongated along the main axis of the branchial plate, and frequently there is a medial line of arcuate tubercles pointing proximally, along the main axis of the tesserae. These are clearly visible in specimens 220/44 P.I.M. (Text-fig. 37 *C*) and 1902.72.1 R.S.M. Between these elongated tesserae are smaller interstitial tesserae, and specimen 220/258 P. I. M. shows that in addition at the point where the free distal part of the branchial begins, some free tubercles seem to be filling the spaces between the tesserae (see also OBRUCHEV, 1947*b*).

Scales. These are essentially of two distinct kinds — body scales and fulcral scales. The body scales are found on the trunk behind the carapace, and the anterior ones are difficult to distinguish from the posterior tesserae with which they are confluent. In fact, the posterior tesserae gradually become imbricate and come to possess anteriorly, narrow unornamented areas which are overlapped by the scales in front. These body scales have an ornamentation

similar to that seen in the normal tesserae, although the concentric arrangement of the tubercles is not so pronounced. This is well seen in specimen 139 E.M. from Scotland.

The fulcral scales occur in the mid-line on both the dorsal and ventral surfaces of the body. These scales are symmetrical and are narrow, elongated and strongly arched from side to side. The specimen from Scotland (1904.2.11 R.S.M. + P. 10959 B.M. (counterpart)) tapers posteriorly, and is ornamented along its crest by tubercles which converge to a point distally, and are rounded and crenulated proximally. The flanks of the scale are ornamented by naviculate crenulated tubercles aligned longitudinally.

Sensory canal system. The sensory canal system is situated below the dentine tubercles in the upper part of the spongy aspidin layer of the dorsal median plate. It is not known in the other plates. In the fragments of dorsal plates from which the superficial tesserae have been lost, the canals may appear as faint straight ridges running across the «honeycomb». Two specimens from Stolbovo (220/201 and 220/211 P.I.M.) show small segments of the sensory canal system in which the cross commissures join the two median canals. In specimen 220/201 short lengths of the lateral canals can also be seen (TARLO, 1964*b*, Text-fig. 13*C*). Two further specimens showing parts of the sensory canal system are known from Scotland. The less complete fragment (1894.169.3 R.S.M.) shows part of a median canal and a lateral one (*l. c.*, Text-fig. 13*A*), while in the more complete specimen (1960.9. R.S.M.) — the posterior part of a dorsal median plate — two median longitudinal canals with their lateral branches are visible (*l. c.*, Text-fig. 13*B*). No lateral longitudinal canals can be seen, but it is possible that the lateral branches could turn as they approached the sides of the carapace, to run longitudinally. In this latter Scottish specimen the lateral branches are somewhat asymmetrical, but this is not very unusual (see above under *Tartuosteus*) and it is not necessary to postulate missing branches in order to restore the symmetry as was done by TARLO (1961*a*).

Discussion. — TRAUTSCHOLD (1880) described and figured a psammosteid branchial plate from Russia under the name *Coccosteus megalopteryx*. This he interpreted as the lateral spine of an arthrodire, but in 1891 both GÜRICH and WOODWARD recognized that it belonged to *Psammosteus*, although WOODWARD incorrectly considered that it was conspecific with *Psammosteus maeandrinus* AGASSIZ. TRAQUAIR (1894, 1896*b*, 1897) described dorsal median plates from Scotland which were ornamented by superficial polygonal tesserae, under the name *Psammosteus taylori*, and in 1911, WOODWARD described the associated carapace of *P. taylori*. This included the branchial plates, which were smaller and not so well preserved as the one described by TRAUTSCHOLD. GROSS (1933*a*) figured from Russia the major part of a mature branchial plate of *P. megalopteryx*, together with a fragment of a dorsal median plate showing superficial tesserae, and noted that *P. megalopteryx* and *P. taylori* were very closely related. Subsequently, OBRUCHEV figured further Russian branchial plates (1945, 1947*a*), and later (1947*b*) a dorsal median plate and a fragment of a branchial showing the characteristic branchial tesserae. TARLO (1961*a*) suggested that the Scottish species *P. taylori* (TRAQUAIR) was conspecific with the Russian *P. megalopteryx* (TRAUTSCHOLD).

The various plates of *P. megalopteryx* described above, demonstrate the great variation that can occur in the outlines of the different plates. It is therefore not possible to use the outline of branchial plates to distinguish species as GROSS (1942) attempted to do. The safest character to use for the recognition of species is the ornamentation of the branchial plates, but even here care must be taken, as in some young forms of *P. megalopteryx*, where the tubercles are well separated from one another, the ornamentation resembles that seen in *P. falcatus*. However, in this latter species the crenulations of the tubercles have numerous fine secondary spurs, and in young individuals the tubercles are fused into rows transverse to the main axis of the plate.

Psammosteus maeandrinus AGASSIZ, 1845

(Pl. XVIII, figs. 3, 4; Pl. XIX, fig. 5)

1844. *Placosteus maeandrinus* n. sp.; L. AGASSIZ, Recherches sur les..., p. XXXIII (nomen nudum).
1845*a*. *Psammosteus maeandrinus* n. sp.; L. AGASSIZ, Monographie des..., p. 104, 130, pl. 27, fig. 5, 6.
1845*a*. *Ctenacanthus serrulatus* n. sp.; L. AGASSIZ, *Ibid.*, p. 119, 131, pl. 33, fig. 24.
1845*b*. *Placosteus maeandrinus* (AGASSIZ) L. AGASSIZ, Letters sur les poissons..., p. 404.
1845*b*. *Ctenacanthus serrulatus* AGASSIZ; L. AGASSIZ, *Ibid.*, p. 404.
1845. *Placosteus maeandrinus* AGASSIZ; R. I. MURCHISON, The Geology of Russia..., p. 47.
1857. *Asterolepis*?; C. PANDER, Über die Placodermen..., p. 20, pl. 7, fig. 17, 18.
1858. *Psammosteus maeandrinus* AGASSIZ; G. KADE, Ueber die devonischen..., pp. 11-15, pl. 1, fig. 4.
1860. *Ctenacanthus serrulatus* AGASSIZ; E. EICHWALD, Lethaea Rossica..., p. 1516.
1860. *Psammosteus maeandrinus* AGASSIZ; E. EICHWALD, *Ibid.*, pp. 1516-1517.
1891*b*. *Ctenacanthus serrulatus* AGASSIZ; A. S. WOODWARD, Catalogue of fossil..., p. 126.
1891*b*. *Coccosteus megalopteryx* TRAUTSCHOLD; A. S. WOODWARD, *Ibid.*, p. 126.
1891*b*. *Psammosteus maeandrinus* AGASSIZ; A. S. WOODWARD, *Ibid.*, p. 126.
1901. *Psammosteus maeandrinus* AGASSIZ; J. V. ROHON, Beiträge zur Anatomie..., pp. 1, 2, pl. 2, fig. 21, 22.
1901. *Ctenacanthus serrulatus* AGASSIZ; J. V. ROHON, Beiträge zur Anatomie..., p. 4.
1915. *Psammosteus meandrinus* AGASSIZ; J. KIAER, Upper Devonian Fish..., pp. 34-36, pl. 6, fig. 4-6, text-fig. 8. (non pl. 4, fig. 1).
1930. *Psammosteus (Dyptychosteus?) maeandrinus* AGASSIZ; D. OBRUCHEV, The significance of..., p. 94.
1932. *Psammosteus maeandrinus* AGASSIZ; E. A. STENSIÖ, The Cephalaspids..., p. 195, text-fig. 70.
1933*a*. *Psammosteus? serrulatus* (AGASSIZ) W. GROSS, Die Fische des..., pp. 15-17, pl. 2, fig. 13-15, text-fig. 5.
1942. *Psammosteus maeandrinus* AGASSIZ; W. GROSS, Die Fischfaunen..., p. 411, text-fig. 2B.
1947*a*. *Psammosteus maeandrinus* AGASSIZ; D. OBRUCHEV, On the genus *Psammosteus*..., p. 518, text-fig. 2a.
1947*b*. *Psammosteus maeandrinus* AGASSIZ; D. OBRUCHEV, Atlas of the..., p. 197, pl. 51, fig. 3, 4.
1950. *Psammosteus meandrinus* AGASSIZ; W. GROSS, Die paläontologische..., pp. 30, 33.
1958. *Psammosteus maeandrinus* AGASSIZ; D. OBRUCHEV, On the biostratigraphy..., p. 48.
1964*b*. *Psammosteus maeandrinus* AGASSIZ; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 12, 14, 19-21, 39, 86, 87, 91, 92, 107; pl. 2, figs. 5, 6
1964. *Psammosteus maeandrinus* AGASSIZ; D. OBRUCHEV, Subclass Heterostraci..., p. 74, pl. 5, fig. 3; pl. 6, figs. 3, 7.

Neotype (here proposed): Branchial plate, 220/684, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1947*b*, Pl. 51, fig. 3, 4), and in the present work, Pl. XIX, fig. 5.

Type horizon and locality: Upper Devonian (Frasnian), Snetogor horizon, *Psammosteus maeandrinus* zone; Andoma, NW Russia.

Diagnosis. — Branchial plate short and wide, ornamented by small crenulated tubercles which are generally fused to form narrow dentine ridges running parallel to the main axis of the plate.

Material. — Numerous branchial plates from the Leningrad region, Estonia and Latvia.

Description. — *Branchial plate.* The neotype of *Psammosteus maeandrinus* is a branchial plate (220/684 P.I.M.), only one surface of which is visible. The distal part of the plate is ornamented by crenulated tubercles fused into short dentine ridges, and in general these are aligned along the major axis of the plate. The anterior margin of the plate is straight, although at the distal extremity it is slightly curved posteriorly, while the posterior margin is gently concave, and together with the anterior margin, forms a sharp pointed distal tip which is curved slightly posteriorly. The proximal limit of the ornamentation cannot be ascertained as the proximal portion of the plate is broken. OBRUCHEV (1947*a*) gave a generalized sketch of part of another branchial plate (220/802 P.I.M.). This specimen is the distal portion of a branchial plate, and on it the short lengths of fused tubercles are well separated from one another, and have very fine basal crenulations, some of which bifurcate at their extremities. Towards the proximal part of the specimen the short dentine ridges are more closely packed.

A further specimen (220/653 P.M.O.) is part of a mature branchial showing the proximal portion of the ornamented surface. The anterior margin is almost straight, and the posterior very slightly concave. The margin of the ornamentation on the dorsal surface forms a gentle sigmoid curve, extending from the anterior margin in a postero-proximal direction, and then in a posterior direction, and then again in a postero-proximal direction to reach the posterior margin. Thus the ornamentation reaches further proximally on the posterior margin than it does on the anterior. The ornamentation consists of exceedingly fine short dentine ridges aligned parallel to the sigmoid curve. Towards the distal end the dentine ridges are somewhat broader and they tend to be aligned diagonally across the plate, antero-distally. On the ventral surface the short dentine ridges of the proximal part of the ornamentation are aligned roughly transverse to the main axis of the plate, although they run slightly diagonally in an antero-distal direction. Further distally the ridges swing round to become almost parallel to the main axis.

A fourth specimen (A. 171 P.M.O.) is part of the distal portion of a branchial plate, together with the impression of the greater portion of the distal end, proximal to the preserved fragment. This specimen is the original from which KIAER (1915) made the block diagram showing the histology of *Psammosteus maeandrinus*. The plate is ornamented by closely packed short dentine ridges aligned along the major axis of the plate. These have very fine short crenulations. At the margins of the plate the dentine ridges are fairly well separated and their basal crenulations are longer, and are drawn out in a proximal direction.

The sharply pointed distal tips of two small, delicate immature branchials (P. 17792 and P. 17793 B.M.) are ornamented by short dentine ridges or elongated tubercles which are aligned parallel to the major axis of the plate, are well separated from one another, and have long basal crenulations. These are drawn out posteriorly in the same way as the marginal dentine ridges of A. 171 P.M.O. The basal crenulations continue as ridges up to the crest of the tubercles themselves. Some of the elongated tubercles may also be drawn out into two or three prongs at their proximal margin. Three further specimens (f. 144, f. 145, and f. 146 G-P.M.B.) are similar to the last two, as they also have very sharp distal tips, and well separated unworn elongated tubercles with very long crenulations, which form characteristic ridges on the main tubercles.

Although at first glance the adult branchial plates appear to be quite different from the immature specimens, in fact this is not so. It is true that the immature specimens have larger tubercles which are well separated, and being well separated there is room for their basal crenulations to be longer. However, as the animal grows, the branchials increase in size by the addition of tubercles proximally, and these become progressively smaller and more closely packed. This is similar to the situation noted above in *Psammosteus megalopteryx*. The alignment of the dentine ridges also tends to change, as they swing round until eventually when the animal is quite mature, the alignment of the last ridges is more or less normal to those in the greater part of the ornamented section of the plate.

Tesserae. A small fragment of a dorsal median plate (220/257 P.I.M.) would seem to belong to this species. The tesserae are generally hexagonal with very sharp straight margins, and the tubercles which ornament them are very small and are arranged in some 10—12 concentric rings around a central larger one. This is an unusual condition, as fewer rings are usually found in other species. The tubercles tend to be arcuate in outline with fine crenulations. There is no direct evidence that these tesserae belong to *Psammosteus maeandrinus*, but as they come from Montseva, a locality which has yielded only this species, it is most probable that they belong to it.

Discussion. — AGASSIZ (1845*a*) described and figured under the name *Psammosteus maeandrinus*, part of an adult branchial plate. At the same time he described and figured under the name *Ctenacanthus serrulatus* the distal tips of two immature branchials, and in an appendix to his paper he discussed the work of EICHWALD (1844, 1845) who had described two fragments under the names *Microlepis lepidus* and *M. exilis*. AGASSIZ claimed that EICHWALD should have used the name *Psammosteus maeandrinus* for them, but EICHWALD's names have priority over those of AGASSIZ. Fortunately they do not represent the same species as those of AGASSIZ, hence the two sets of specific names do not conflict with one another. Also in 1845 MURCHISON'S Geology of Russia was published, which included several of AGASSIZ's letters on the psammosteid remains, and these dealt with *Psammosteus maeandrinus* under the name *Placosteus maeandrinus* which AGASSIZ published in 1844, but which was at that time a *nomen nudum*. His *Psammosteus maeandrinus*, however, was the first valid name for the Russian material, and *Placosteus* (*in* MURCHISON, 1845) is an objective junior synonym. Subsequently PANDER (1857) discussed the branchial plates of *Psammosteus maeandrinus* which he considered represented lateral plates of *Asterolepis*, in spite of the fact that he demonstrated that their histology was entirely different from that of *Asterolepis*. The specimen which he figured clearly belongs to *P. maeandrinus*.

In the following year, KADE (1858) described psammosteid remains from erratic blocks, including several fragments which he identified as *Pst. maeandrinus* but from his figures only one of these would seem to belong to this species. In his synonymy of the species he includes *Microlepis lepidus* and *M. exilis* which were first described by EICHWALD in 1844, but were not figured until 1846. Clearly KADE was of the opinion that EICHWALD's names were not validated until he had published figures of them. In 1860, EICHWALD redescribed his species and also listed AGASSIZ', but was of the opinion that they were in no way related — a view which has since been confirmed. At the same time he included *Ctenacanthus serrulatus* in the synonymy of *Psammosteus maeandrinus*. He considered (as is now known to be correct), that the material concerned represented a single species. In this he was followed by WOODWARD (1891*b*) who at the same time erroneously included TRAUTSCHOLD'S *Coccosteus megalopteryx* in the same species. ROHON (1901) also recognized that *Ctenacanthus serrulatus* was a psammosteid, but he did not consider that it belonged to *P. maeandrinus*. KIAER (1915) gave a careful description of the histology of *P. maeandrinus* and figured a specimen of a dorsal median plate showing tesserae under this name. An examination of this particular specimen shows that in fact it belongs to *Psammolepis paradoxa*. GROSS (1933*a*) described and figured three immature branchial plates under the name *Psammosteus*? *serrulatus*, since he was of the opinion that they represented a species distinct from *Psammosteus maeandrinus*. He used the name *P. maeandrinus* for two further branchials which were quite unlike the other three. In 1942, however, GROSS, on information provided by OBRUCHEV, accepted that *P. serrulatus* was in fact identical to the true *P. maeandrinus*, and that what he had considered to be *P. maeandrinus* represented a distinct new species. OBRUCHEV (1947*a*) described *Psammosteus maeandrinus* and gave a new name *(P. falcatus)* to the material called *P. maeandrinus* by GROSS (1933*a*). In 1947*b*, OBRUCHEV figured a further branchial plate of *P. maeandrinus* together with its ornamentation. This specimen is here chosen as the neotype, since the whereabouts of AGASSIZ' material is no longer known, and as *Psammosteus maeandrinus* is the type species of the genus, it is necessary for a neotype to be proposed. The branchial plate (220/684 P.I.M.) has been mutually agreed by the specialists on the group, as the most suitable specimen for this purpose.

Psammosteus praecursor OBRUCHEV, 1947

(Pl. XIX, fig. 3; Text-figs. 38-40, 46*C*)

1899. *Psammosteus arenatus* AGASSIZ; J. V. ROHON, Die devonischen..., pp. 12-14, text-figs. 4,5.
1947*a*. *Psammosteus praecursor* n. sp.; D. OBRUCHEV, On the genus..., pp. 517-19, text-figs. 1, 2b.
1958. *Psammosteus praecursor* OBRUCHEV; D. OBRUCHEV, On the biostratigraphy..., p. 48.
1961*b*. *Psammosteus praecursor* OBRUCHEV; L. B. TARLO, Middle and Upper..., p. 46.
1964*b*. *Psammosteus praecursor* OBRUCHEV; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 16, 17, 21, 32, 33, 87, 88, 99, 104-107; text-fig. 10D.

Holotype: Branchial plate, 220/384, housed in the Palaeontological Institute Moscow, figured in the present paper Text-fig. 40*A*.

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon (*Psammolepis undulata* zone); Yam-Tesov, River Oredesh, Russia.

Diagnosis. — Branchial plate short, wide and very thin, with wide free distal end; ornamented by small tubercles with comparatively long delicate basal crenulations. Ventral median plate with narrow median extension posteriorly.

Material. — Two ventral median plates and numerous branchial plates from the Leningrad region and several branchial plates from the Timan.

Description. — *Ventral median plate.* Two complete ventral median plates (4680 G.P. M.L.) are known, the smaller specimen of which was figured by OBRUCHEV (1947*a*). In outline

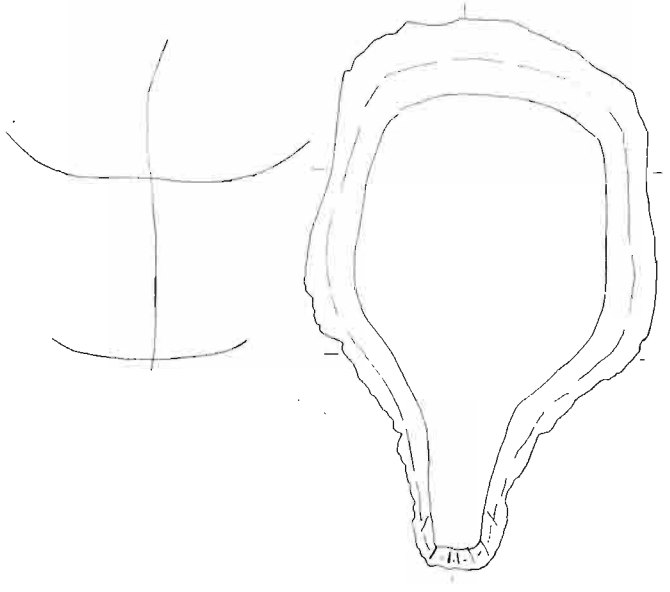

Fig. 38

Psammosteus praecursor OBRUCHEV — immature ventral median plate (G.P.M.L. 4680), × 0·25.

this plate resembles an inverted flask measuring 28 cm. in length and 18 cm. at its maximum width, which is approximately halfway along its length (Text-fig. 38). From the point of maximum width towards the anterior the sides of the plate converge very slightly, and the anterior border is almost straight with the exception of the lateral corners which are rounded. In the posterior half of the plate, the lateral margins converge very sharply for about 7 cm. and then tend to become parallel, ending in a truncated posterior margin measuring approximately

3 cm. The anterior part of the plate is convex from side to side, the central part being flat, with the sides curving up. The plate tends to flatten out posteriorly. In longitudinal section the plate is flat but convex at the anterior margin.

The larger plate measures 31 cm. in length and is 21 cm. at its maximum width which is just in the posterior half of the plate (Text-fig. 39). The sides gradually converge from the point of maximum width to reach the anterior margin which is somewhat rounded. In the posterior part of the plate, the lateral margins also converge, but slightly more strongly than the anterior ones, to end in a truncated posterior margin which measures 7 cm. in width. In cross-section, the plate is strongly arched anteriorly, gradually flattening out towards the pos-

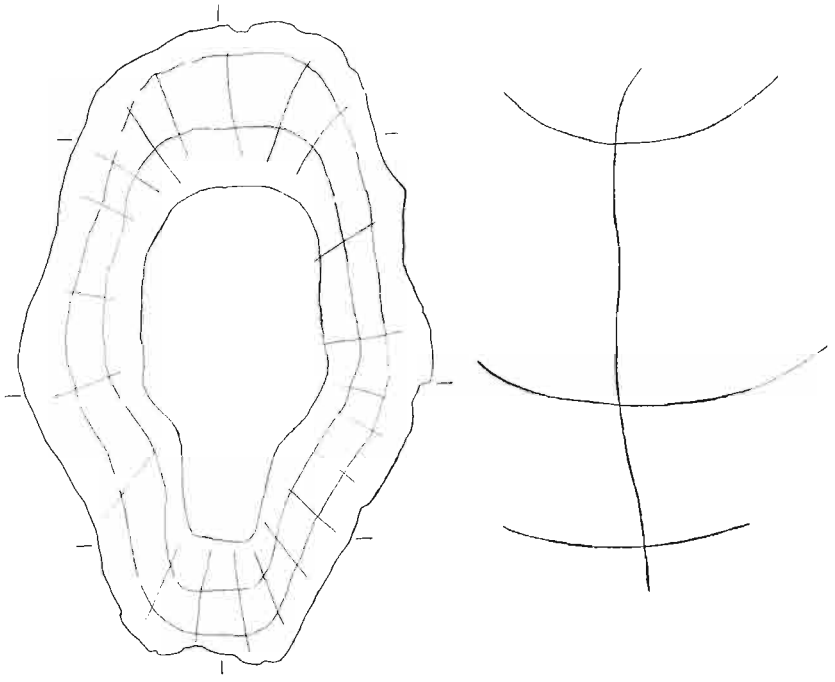

Fig. 39

Psammosteus praecursor OBRUCHEV — adult ventral median plate with schematic sections (G.P.M.L. 4680), × 0.25.

terior margin. In longitudinal section the anterior margin curves upwards in the same way as it does in the smaller plate. At first glance the outlines of the two plates appear dissimilar, but when the internal surface of the larger one is examined, zones of growth can be seen on the basal lamellar aspidin layer, and these show that in the younger stages, the outline was identical to that of the smaller specimen. The difference in the outlines can therefore be attributed to the differential growth of the posterior part of the plate. The larger specimen was originally identified and labelled as a dorsal plate, but from the above description it is evident that both plates are the same. In cross-section the ventral plates of the psammosteids are normally convex anteriorly and the dorsal plates convex posteriorly, but they differ in longitudinal section because in the ventral plates the anterior border is turned upwards whereas the posterior border of the dorsals is flat. In both instances the plates flatten out from the convex part, i. e. the ventrals flatten out posteriorly and the dorsals anteriorly. In the dorsal plates, however, the margins also get wider away from the convexity (i. e. anteriorly) whereas in the ventrals they get narrower away from the convexity (i. e. posteriorly). For this reason

therefore, it is clear that the two plates concerned are ventrals. At the same time it is now apparent that the orientation of the ventral median plate in OBRUCHEV's reconstruction (1947*a*) must be reversed so that the broad convex part faces anteriorly, and the narrow part posteriorly. It should be noted that these plates are similar in outline to the two ventral plates of *Psammolepis undulata* known from Scotland, and the one known from Latvia.

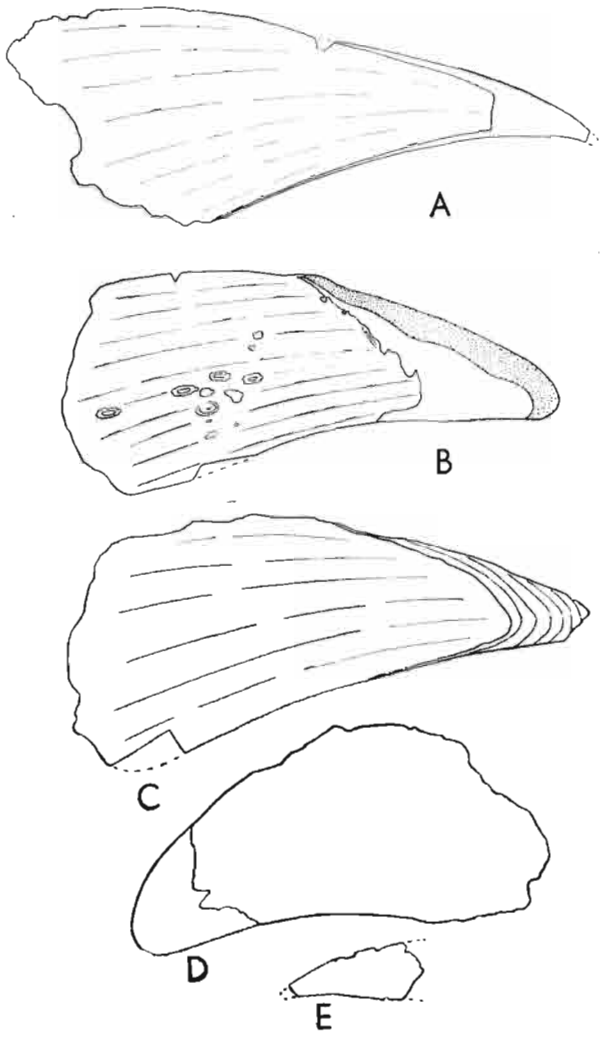

Fig. 40

Psammosteus praecursor OBRUCHEV — *A* holotype, right branchial plate (P.I.M. 220/384, Yam-Tesov), × 0·33; *B* left branchial plate in ventral view showing wide abraded margin and oval tesserae scattered over proximal part of plate (G.P.M.L. 4680, Yam-Tesov), × 0·33; *C* right branchial plate (G.P.M.L. 567/3356, Yam-Tesov); × 0·33; *D* left branchial (P.I.M. plate colln.), × 0·33; *E* immature branchial plate (P.I.M. colln.), × 0·33.

Branchial plate. The holotype of *Psammosteus praecursor* is branchial plate 220/384 P.I.M. (Text-fig. 40*A*). The plate is flat and thin, very wide, and rather short, and its free distal end forms a very sharp acute angled triangle, from which the anterior and posterior margins diverge. Towards the proximal end of the plate the distance between these margins is considerable, being approximately one half that of the total width of the plate measured along its major

axis. The free distal end is ornamented on all surfaces by small dentine tubercles with finely crenulated margins. In dorsal view the entire posterior margin is ornamented by a very narrow border of tubercles with somewhat longer basal crenulations, which are elongated parallel to the margin, whereas only the distal half of the anterior margin is so ornamented. This suggests that in *Psammosteus praecursor*, the greater part of the posterior margins of the branchials must have been free, forming the bulk of the posterior margin of the carapace, while only the distal half of the anterior margins of the plates could have been free, forming the posterior part of the lateral margin of the carapace. The edge of the distal half of the anterior margin of the branchial plate 220/384 P.I.M. is somewhat abraded, suggesting that this came into contact with the substratum.

A somewhat similar specimen (567/3356 G.P.M.L.) was figured by OBRUCHEV (1947*a*) although this plate does not taper so much from the proximal end to the distal end, the angle formed at the distal end being greater than that of the holotype (Text-fig. 40*C*). Again, unlike the position in the holotype, the proximal margin of the free ornamented distal end is clearly complete, and is arcuate in outline. The ornamentation therefore appears to be produced proximally into two limbs, of which the posterior is very narrow, while the anterior limb is somewhat broader.

A specimen similar in outline to the previous one, is P. 4680 G.P.M.L., although this time the distal tip of the plate is more rounded in outline (Text-fig. 40*B*). In addition the anterior margin of the ventral surface is abraded, and there is a considerable area of abrasion on the ventral side of the distal tip itself.

In the Palaeontological Institute, Moscow, there are a number of branchial plates belonging to both mature and immature individuals. One of the mature specimens (Text-fig. 40*D*) has anterior and posterior margins which diverge even more sharply than those in the holotype, and in this specimen the free distal ornamented region is very large, extending almost halfway down the plate. Another fairly mature specimen has a very well rounded distal end, and the anterior and posterior margins do not diverge very markedly. Although the distal tip is broken off an immature branchial plate (Text-fig. 46*C*), nevertheless it is clear that it would have formed a very acute angle. The anterior margin is slightly convex, while the posterior is quite strongly concave, and there is a narrow zone of abrasion along the edge of the anterior margin. Of interest is the circular puncture near the distal end of the plate, which could only have been caused by the tooth of a predator such as a crossopterygian. A second immature specimen (Text-fig. 40*E*) also has a narrow pointed distal end, but this time both the anterior and posterior margins show the same degree of curvature, which is similar to that of the anterior margin of the immature branchial described above.

Although the branchial plates of *Psammosteus praecursor* clearly belong to *Psammosteus*, nevertheless they have characters which indicate the derivation of the genus from *Psammolepis*. For example, unlike the condition in the normal species of *Psammosteus*, the free distal end of the plate is very large, and in the median part of the plate the distance between the anterior and posterior margins is considerable.

Tesserae. The ventral median plates are covered by superficial polygonal tesserae similar to those seen in the dorsal median plate of *Psammosteus megalopteryx*, although in *P. praecursor* the tubercles are more nearly round in shape, and are not so strongly crenulated. Tesserae are also known in branchial plate P. 4680 G.P.M.L., ten isolated tesserae being visible on the ventral surface of the unornamented proximal portion, aligned along the major axis of the plate (Text-fig. 40*B*). Although these tesserae are oval in shape, their rounded tubercles are arranged concentrically like those in the superficial polygonal tesserae, and it is likely that

if they were not isolated, but instead had grown against one another, they too would have become polygonal in outline.

Discussion. — Two specimens of branchial plates were described and figured by ROHON (1899) under the name *Psammosteus arenatus*, and these are now housed in the Palaeontological Institute, Moscow. One specimen (220/836) is almost complete, while the other (220/814) is just a fragment which shows the ornamentation very well. It is not possible to identify these remains from the original description, but recent examination of the specimens themselves show they belong in fact to *Psammosteus praecursor* OBRUCHEV. This species was erected on a branchial plate and a ventral median plate (OBRUCHEV, 1947*a*), and the ventral plate was used in the first reconstruction of *Psammosteus* to be attempted which appeared in the same work. The species comes from the Amata horizon, where *Psammosteus* makes its first appearance and where the last representative of *Psammolepis* — *Psl. undulata* also occurs. It is therefore of interest to note that the ventral median plate of *Psammosteus praecursor* is similar in outline to that of *Psammolepis undulata* (see TARLO, 1961*a*). It should be noted, however, that the plates should be orientated with the narrow end pointing posteriorly, and not as shown in OBRUCHEV'S reconstruction.

The species *P. praecursor* can be recognized by the details of the ornamentation of the branchial plate. In general the tubercles are smaller and have finer crenulations than in *P. megalopteryx*, although the crenulations are still rather short. Unlike those of *P. megalopteryx*, the dentine tubercles along the anterior and posterior margins of the branchial of *P. praecursor* are often fused into rows aligned parallel to the margins. This is rather like the condition seen in *P. maeandrinus*, but the fused rows are much shorter than those known in this latter species.

A new reconstruction of *P. praecursor* is given in the General Part of this work (TARLO, 1964*b*, Text-fig. 10*D*).

Psammosteus markae TARLO, 1961

(Text-figs. 41, 42)

1895. *Psammosteus paradoxus* AGASSIZ; A. S. WOODWARD, The Problem of..., pp. 38-39, text-fig. 1.
1911. *Dyptychosteus tessellatus* n. sp.; I. A. PREOBRAJENSKY, On some representatives..., p. 35, pl. 2, fig. 10-12.
1911. *Psammosteus paradoxus* AGASSIZ; A. S. WOODWARD, On the Upper Devonian..., p. 649.
1917. *Psammosteus tesselatus* (PREOBRAJENSKY); C. R. EASTMAN, Fossil Fishes..., pp. 241-242, text-fig. 1.
1917. *Psammosteus paradoxus* AGASSIZ; C. R. EASTMAN, *Ibid*, pp. 241-242, text-fig. 1.
1930. *Dyptychosteus tesselatus* PREOBRAJENSKY; D. OBRUCHEV, The significance of..., p. 94.
1933*a*. *Dyptychosteus tesselatus* PREOBRAJENSKY; W. GROSS, Die Fische des..., p. 8.
1933*a*. *Psammolepis undulata* (AGASSIZ); W. GROSS, *Ibid.*, p. 8.
1942. *Dyptychosteus tesselatus* PREOBRAJENSKY; W. GROSS, Die Fischfaunen..., p. 410.
1942. *Psammolepis undulata* (AGASSIZ); W. GROSS, *Ibid.*, p. 410.
1950. *Dyptychosteus tesselatus* PREOBRAJENSKY; W. GROSS, Die paläontologische..., p. 31.
1955. *Psammosteus tessellatus* (PREOBRAJENSKY); E. MARK, Psammosteids..., pp. 4, 6.
1958. *Psammosteus tesselatus* (PREOBRAJENSKY); D. OBRUCHEV, On the biostratigraphy..., p. 48.
1961*a*. *Psammosteus tessellatus* (PREOBRAJENSKY); L. B. TARLO, Psammosteids from the..., pp. 193, 203.
1961*a*. *Psammosteus markae* n. sp.; L. B. TARLO, *Ibid.*, pp. 193, 203.

Holotype: Dorsal median plate, 150, housed in the Geological Institute, Tallinn, figured by WOODWARD (1895, text-fig. 1). PREOBRAJENSKY (1911, Pl. 2, fig. 12), and in the present work (Text-fig. 41).

Type horizon and locality: Upper Devonian (Frasnian), Amata Horizon (*Psammolepis undulata* zone); Vastseliina, Latvia.

Diagnosis. — Dorsal median plate broad and convex; superficially divided into polygonal tesserae with closely packed, rounded, crenulated tubercles.

Material. — Two dorsal median plates together with fragments of median plates showing ornamentation of superficial tesserae, from Latvia.

Description. — *Dorsal median plate.* The holotype, 150 G.I.T., was first described and figured by WOODWARD (1895) and later by PREOBRAJENSKY (1911). This plate is complete with the exception of the anterior part, which has been reconstructed to give a straight transverse anterior margin (Text-fig. 41). As preserved the plate measures 18·5 cm. at its maximum width, and 19·5 cm. at its maximum length. For the mid-third of their length the lateral margins run parallel; posterior to this they converge sharply until they near the posterior margin, where they again commence to run parallel. The posterior margin itself forms a very

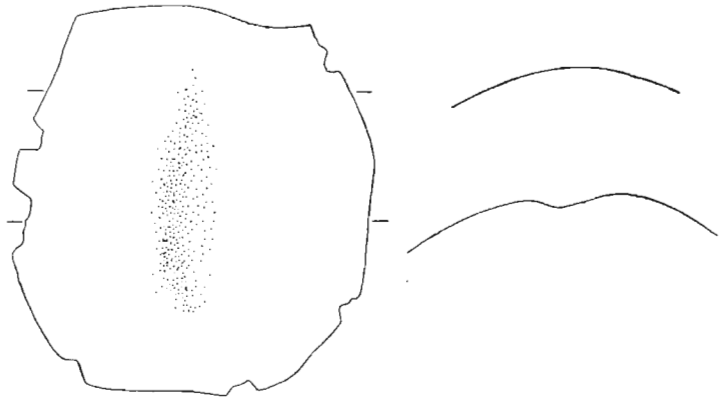

Fig. 41

Psammosteus markae TARLO — holotype, dorsal median plate (G.I.T. 150, Vastseliina), × 0·25.

blunt angle. In the anterior part of the plate the lateral margins again converge, but this time they form a gentle curve until the anterior margin is reached. Although the full margin has been reconstructed, only part is preserved at each side, and there is no evidence that the central part of the margin should be straight. Towards the posterior margin, the plate is moderately arched from side to side, but in the central part, although the plate remains convex, a wide groove develops in the mid-line, which gradually becomes shallower towards the anterior margin where the plate as a whole flattens out.

A further dorsal median plate, 164 G.I.T., is known from the type locality. Although its margins are again not complete, it seems to be more oval in outline than the holotype (Text-fig. 42). It is also rather less convex from side to side, and the median longitudinal groove is not so well marked. In this specimen however, the superficial tesserae are well preserved. These are polygonal in outline, with an ornamentation of rounded, crenulated dentine tubercles which are closely packed; at first glance these appear to have a random arrangement, but on closer inspection it can be seen that in fact they tend to be arranged concentrically. Part of the sensory canal system is clearly visible in the central part of the plate, and consists of a transverse commissure posterior to the longitudinal groove, from which two branches run anteriorly on either side of the groove.

Discussion. — In 1842 MURCHISON presented a papier-maché copy of what is now the holotype to the British Museum (Nat. Hist.), but it was not identified until 1892 when WOODWARD visited the University Museum of Dorpat (Tartu) and there examined the psammosteid remains among which was the original specimen. This he described (1895) and identified as *Psammosteus paradoxus*, but before this work was published he showed the papier-maché

cast to TRAQUAIR, and by means of it TRAQUAIR (1894) was able to identify some Scottish remains as belonging to *Psammosteus*. In 1911, PREOBRAJENSKY, being unaware of WOODWARD's work of 1895, described and figured the same specimen, together with a fragment which showed the ornamentation, under the name *Dyptychosteus tessellatus*. Subsequently, EASTMAN (1917) pointed out that both authors had described the same specimen under different names. He showed further that *Dyptychosteus* was a synonym of *Psammosteus*, and hence that PREOBRAJENSKY's specific name *P. tessellatus* was invalid, since TRAQUAIR (1897) had previously described a different species under the name *P. tessellatus*. EASTMAN suggested therefore that if further work should establish that the specimen did not belong to *P. paradoxus*,

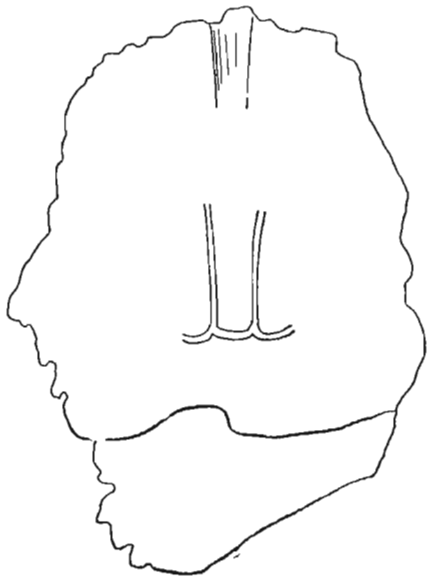

Fig. 42

Psammosteus markae TARLO — dorsal median plate showing anterior median groove, and part of sensory canal system (G.I.T. 164, Vastseliina), × 0·25.

then it would be necessary to propose a new name for the species. OBRUCHEV (1931) retained PREOBRAJENSKY's name *Dyptychosteus tessellatus*, while GROSS (1933*a*) tentatively included it in the synonymy of *Psammolepis undulata*. MARK (1955) and OBRUCHEV (1958) later placed the species in the genus *Psammosteus* in the restricted sense of GROSS (1933*a*), who had transferred TRAQUAIR'S *Psammosteus tesselatus* to *Psammolepis*. However, as both WOODWARD and GROSS realized, PREOBRAJENSKY'S species was close to what is now recognized as *Psammolepis*, and as it comes from the same horizon as TRAQUAIR'S species (now referred to *Psammolepis undulata*), the only way to avoid confusion has been to follow EASTMAN'S advice. The new name *Psammosteus markae* was therefore proposed (TARLO, 1961*a*).

The arrangement of the tubercles of the superficial tesserae in *Psammosteus markae* is very similar to that seen in species of *Psammolepis*, but since the outline of the tesserae is like that known in *Psammosteus*, and the tubercles tend to be arranged concentrically as they are in this latter genus, it seems reasonable to place *P. markae* in that genus. It should be noted, however, that this is a purely arbitrary procedure, as *P. markae* is found in the Amata horizon together with the last species of *Psammolepis (Psl. undulata)*, and the first species of *Psammosteus (P. praecursor)*. It is evident that *Psammolepis* grades into *Psammosteus*.

Since no branchial plates are known in *P. markae*, and no dorsal plate is known in *P. praecursor*, it is not possible to say how close these two species are to one another. They are obviously closely related, and it may well be that with the discovery of further material they may turn out to be conspecific. Until such time however the name *Psammosteus markae* must be retained.

Psammosteus falcatus GROSS, 1942

(Pl. XVIII, fig. 6; Pl. XIX, figs. 2, 4; Text-fig. 43)

1896*b*. *Psammosteus* sp.; R. H. TRAQUAIR, The extinct vertebrata..., p. 263, pl. 6, figs. 4, 5.
1933*a*. *Psammosteus maeandrinus* AGASSIZ; W. GROSS, Die Fische des..., p. 14, pl. 1, fig. 9.
1942. *Psammosteus falcatus* OBRUCHEV M. S.; W. GROSS, Die Fischfaunen..., pp. 411-412, text-fig. 3.
1942. *Psammosteus grossi* OBRUCHEV M. S.; W. GROSS, Die Fischfaunen..., p. 411, text-fig. 3A.
1947*a*. *Psammosteus falcatus* n. sp.; D. OBRUCHEV, On the genus..., p. 520, text-fig. 2d.
1948. *Psammosteus falcatus* OBRUCHEV; S. V. TICHOMIROV, The Devonian... p. 53.
1950. *Psammosteus falcatus* OBRUCHEV; W. GROSS, Die paläontologische und..., pp. 30, 34.
1950. *Psammosteus maeandrinus* AGASSIZ; Z. GORIZDRO-KULCZYCKA, Les Dipneustes..., p. 103.
1958. *Psammosteus falcatus* OBRUCHEV; D. OBRUCHEV, On the biostratigraphy..., p. 49.
1961*a*. *Psammosteus falcatus* OBRUCHEV; L. B. TARLO, Psammosteids from..., pp. 201-202, pl. 7, fig. 6.
1964*b*. *Psammosteus falcatus* OBRUCHEV; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 15, 19-22, 39, 86-91, 102, 107; pl. 2, fig. 4.
1964. *Psammosteus falcatus* GROSS; D. OBRUCHEV, Subclass Heterostraci..., p. 75, pl. 7, fig. 5, text-fig. 58b.

Lectotype: Branchial plate, f. 117, housed in the Geological and Palaeontological Museum, Berlin, figured by GROSS (1933*a*, Pl. 1, fig. 9).

Type horizon and locality: Upper Devonian (Frasnian), *e* horizon, *Psammosteus falcatus* zone; Jurenski, River Pededze, Latvia.

Diagnosis. — Branchial plate short and wide, with anterior and posterior margins nearly parallel; ornamented by well separated tubercles with basal crenulations elongated posteriorly, the crenulations themselves being characterised by fine re-branching. Frequently the tubercles fuse into rows aligned transverse to the major axis of the plate.

Material. — Numerous branchial plates from NW Russia, Latvia, and Scotland, together with fragments from the Timan.

Description. — *Branchial plate.* The lectotype (f. 117 G-P M.B.) is part of an immature branchial of which the distal extremity is missing. The anterior and posterior margins of the plate are roughly parallel, although they converge slightly distally. The anterior margin is gently convex and the posterior gently concave. The tubercles of the ornamentation are well separated from one another, and are irregular in shape being notable for the complexity of their basal crenulations, which re-branch in an irregular manner. On the same block, specimen f. 118 is a fragment of another branchial. This shows tubercles fused into rows aligned transversly to the major axis of the plate, these fused rows having very short crenulations along their distal borders, and long fine fairly parallel crenulations along their proximal borders. These latter have very fine irregular secondary crenulations.

An extremely large branchial (2425/467 P.I.M.) has a maximum width of 25 cm. The distal extremity is broken off, and it is therefore not possible to ascertain the shape of the tip. (Text-fig. 43*A*). The anterior margin of the remainder of the plate is convex and the posterior concave, the margins are parallel for their full length, and the plate measures some 3 cm. between them. A further adult specimen (220/324 P.I.M.) shows the very great width of the plate compared with its extremely short length. The anterior and posterior margins are again

roughly parallel for much of their length; they gradually converge distally, and the distal end is abraded to form a rounded tip. Specimen 220/327 P.I.M. is the branchial plate of another adult individual (Text-fig. 43*B*). In this case the ornamentation is present over more than half of the plate. The proximal unornamented portion has more or less parallel anterior and posterior margins, whereas in the ornamented part the margins gradually converge, although the distal tip is lost. A very immature specimen (Text-fig. 43*C*) has rather similar proportions to the adult specimen, with the anterior and posterior margins more or less parallel, but even though they converge distally, this is so gradual that they give the impression that the plate as a whole is less curved than in the adults. The distal tip of a branchial plate (P. 33990 B.M.) differs from all other examples of this species. It has a very well rounded distal end, its anterior margin is convex and the posterior fairly straight, and the two diverge considerably to give an outline reminiscent of that seen in the adult worn branchials of *Psammosteus megalopteryx*. However, the ornamentation is typical of *P. falcatus*, and even though most of the branchials of the species have an outline like those described earlier, the existence of this second type of branchial shows that there is a considerable degree of variability in the branchials. In *P. megalopteryx* the branchial plates are in the main like the one just described in *P. falcatus*, whilst occasionally examples are found in which the anterior and posterior margins are more or less parallel as in the normal branchials of *P. falcatus*. As has been shown, in *P. falcatus* parallel-sided plates are normal, while plates in which the posterior and anterior margins markedly diverge are found occasionally — the reverse of the position in *P. megalopteryx*. A small fragment of the distal end of a branchial plate (1904.2.12. R.S.M.) was described and figured although not named by TRAQUAIR (1896) and although this specimen is abraded, it clearly belongs to *P. falcatus*.

Tesserae. A small fragment of a dorsal median plate (220/321 P.I.M.) is known, which from its tubercles clearly belongs to *Psammosteus falcatus*. The fragment is rather worn, and tesserae seem to have been lost, but the faint «honeycomb» appearance is present. However, there has been a certain degree of regeneration, secondary tubercles of a very intricate irregular nature having been formed entirely of dendritic crenulations (Text-fig. 43*E*).

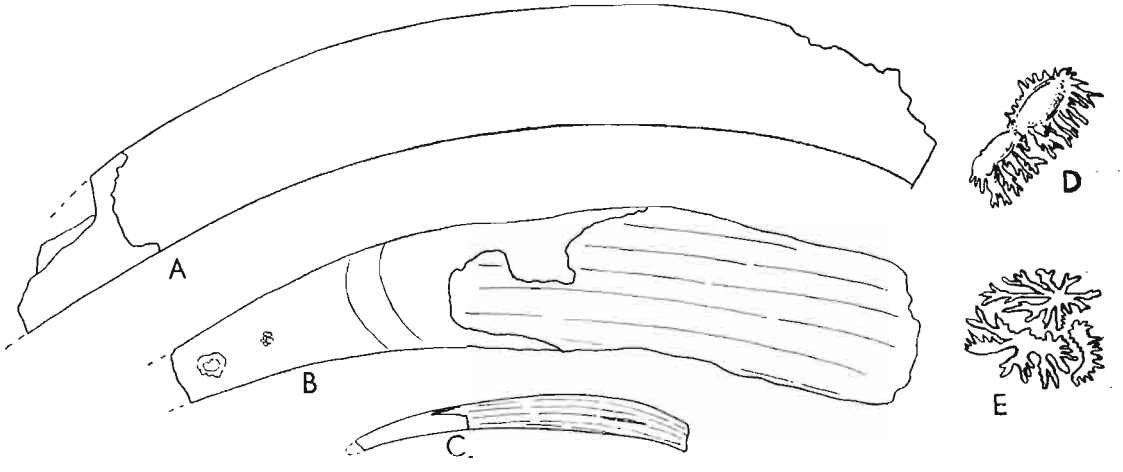

Fig. 43

Psammosteus falcatus GROSS — *A* branchial plate (P. I. M. 2425/467), × 0·5; *B* branchial plate (P.I.M. 220/327), ×0·5; *C* immature branchial plate (P.I.M. Obr. Colln.), ×1; *D* branchial plate, detail of ornamentation (P.I.M. 220/322); × 6; *E* fragment of median plate, detail of ornamentation (P.I.M. 220/321), × 6.

Discussion. — TRAQUAIR (1896*b*) described and figured a branchial plate from Scotland, which has since been included by TARLO (1961*a*) in *P. falcatus*. GROSS (1933*a*) described and figured two branchial plates under the name *Psammosteus maeandrinus*, although these were not in fact conspecific with the species originally described under this name by AGASSIZ. In 1942, GROSS, on information supplied by OBRUCHEV, corrected this, and pointed out that OBRUCHEV intended naming this material *Psammosteus falcatus*, and also intended introducing a further new species — *P. grossi*. GROSS considered that these two species differed only in the outline of their respective branchials, while according to OBRUCHEV (personal communication) the two specimens figured by GROSS were in fact conspecific. Unfortunately these specimens have since been lost. Subsequently OBRUCHEV (1947*a*) described the new species *Psammosteus falcatus* and included within it the material described by GROSS (1933*a*) under the name *Psammosteus maeandrinus*. OBRUCHEV (Text-fig. 2*d*) refigured the specimen figured by GROSS (1942, Text-fig. 3*B*) which was formerly housed in the Geological Institute, Riga, but which unfortunately is now lost. OBRUCHEV'S diagnosis appeared to establish *Psammosteus falcatus* for the first time, and TARLO (1961*a*) selected one of the branchials (f. 117 G-P. M.B.) figured by GROSS (1933*a*) as the lectotype, since OBRUCHEV had omitted to nominate a holotype. However, OBRUCHEV (1964) now claims that as GROSS (1942) figured and described material of this species under the name *Psammosteus falcatus*, then strictly GROSS must be considered the author of the species. Following from this, the specimen described and figured as *Psammosteus grossi* by GROSS belongs in fact to what is now known as *P. falcatus*, and *P. grossi* GROSS becomes a subjective synonym of *P. falcatus* GROSS. The result of this confusion is that the name *P. grossi* is no longer available, as had previously been thought to be the case (see below).

In 1915, KIAER figured a branchial plate under the name *Psammosteus arcticus* which was ornamented by rows of fused tubercles aligned transverse to the major axis of the plate, with well developed proximal crenulations. This was included in the synonymy of *P. falcatus* by TARLO (1961*a*), but a comparison of KIAER'S material with the material available of *P. falcatus* now shows that in fact it represents a distinct species, which is described below under the name *Psammosteus kiaeri*.

Psammosteus waltergrossi nom. nov.

(Pl. XIX, fig. 1; Text-figs. 44 *C*, *D*)

1947*a*. *Psammosteus grossi* n. sp.; D. OBRUCHEV, On the genus..., p. 520, text-fig. 2e.
1950. *Psammosteus grossi* OBRUCHEV; W. GROSS, Die paläontologische..., pp. 30, 34.
1958. *Psammosteus grossi* OBRUCHEV; D. OBRUCHEV, On the biostratigraphy..., p. 49.
1964. *Psammosteus falcatus* GROSS; D. OBRUCHEV, Subclass Heterostraci..., pl. 6, fig. 5.

Lectotype (here selected): Branchial plate, 220/353, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1947*a*, Text-fig. 2e), and in the present work, Pl. XIX, fig. 1.

Type horizon and locality: Upper Devonian (Frasnian), *e/f* horizon, *Psammosteus falcatus* zone; River Misti, NW Russia.

Derivation of the name: waltergrossi — in honour of Professor W. GROSS of the Palaeontological Institute, Tübingen (formerly of Humboldt University, Berlin).

Diagnosis. — Branchial plate short and wide, ornamented by tubercles with extremely coarse prolongations drawn out proximally, and short secondary crenulations forming fine ridges on the primary crenulations.

Material. — Numerous branchial plates, together with three tesserae from NW Russia.

Description. — *Branchial plate.* The lectotype (220/353 P.I.M.) is the major part of a small branchial plate, of which the distal and proximal extremities are missing. The anterior

margin is convex and the posterior concave, and these converge gradually towards the distal extremity. The ornamentation consists of large tubercles which are drawn out into thick finger-like prolongations produced proximally along the major axis of the plate. In some instances the tubercles are elongated in this direction and bifurcate so that the two branches run more or less parallel. These can branch again. The thick branches or prolongations have minor short crenulations along their length, and these form fine ridges, which are usually aligned diagonally, and are drawn out slightly, proximally. The tubercles in the proximal part of the ornamented portion of the plate have a considerable spread, with several finger-like proximal prolongations running more or less parallel, whereas distally the tubercles appear as short

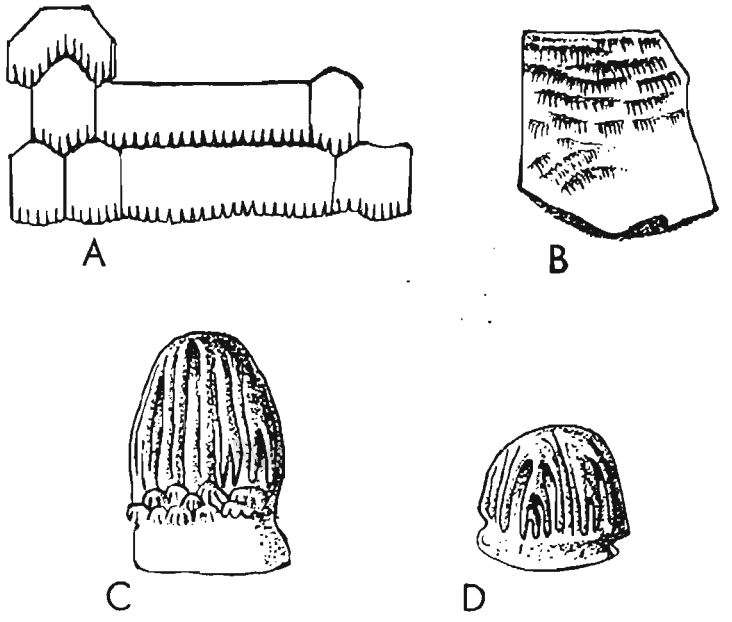

Fig. 44

A Crenosteus levis (OBRUCHEV) — holotype, detail of ornamentation (P.I.M. 220/635), × 8; *B Psammosteus pectinatus* OBRUCHEV — holotype, fragment of branchial plate (P.I.M. 220/259), × 1.33; *C-D Psammosteus waltergrossi* nom. nov. — high crowned tesserae (P.I.M. colln.), × 8.

dentine ridges each of which is equivalent to one of the prolongations of the proximal tubercles. The change from one type of tubercle to the other is gradual along the plate.

Tesserae. In the Palaeontological Institute, Moscow, there are three small tesserae each of which consists of a very large high-crowned tubercle made up of radially arranged prolongations, some of which repeatedly bifurcate (Text-fig. 44 *D*).

Around the base of the tubercle may be numerous minute crenulated tubercles (Text-fig. 44 *C*). There is no indication of how frequent this type of tessera is, nor in which part of the carapace it occurred, but the ornamentation of the high-crowned tubercle is exactly the same as that of the very characteristic tubercles on the branchial plate.

Discussion. — GROSS (1942) on information received from OBRUCHEV, used the name *Psammosteus grossi* OBRUCHEV M.S., but from his description there is no evidence that what he described differed in any way from the material he mentioned under *Psammosteus falcatus*, and it was not until OBRUCHEV (1947*a*) described the species *P. grossi*, that a separate species was clearly shown to exist. It was distinguished from *P. falcatus* on its characteristic orna-

mentation, and not as GROSS supposed on the outline of its branchials. Unfortunately OBRUCHEV did not select a holotype, but the specimen on which his Text-fig. 2*e* was based is here selected as the lectotype.

As noted under *Psammosteus falcatus* (above), since the name *P. grossi* was used for material conspecific with *P. falcatus*, it is now no longer available to be used for another species. It is therefore necessary to propose a new name for the species described as *P. grossi* by OBRUCHEV (1947*a*). In order to keep as near as possible to Prof. OBRUCHEV's original intention, the species in question is here renamed *Psammosteus waltergrossi*.

Psammosteus pectinatus OBRUCHEV, 1965

(Text-fig. 44*B*)

1965. *Psammosteus pectinatus* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).

Holotype: Branchial plate, 220/259, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1965, in the press), and in the present work (Text-fig. 44*B*).

Type horizon and locality: Upper Devonian (Frasnian), Shelon horizon, *Psammosteus megalopteryx* zone, Leningrad district.

Diagnosis. — Branchial plate short and wide, ornamented by narrow rows of fused tubercles aligned transverse to the major axis of the plate, with exceedingly fine comb-like crenulations along the proximal border of the tubercles.

Material. — Unique holotype.

Description. — *Branchial plate.* The holotype is part of the ornamented portion of a branchial plate (220/259 P.I.M.). The ornamentation consists of very narrow rows of fused dentine tubercles which are aligned at right angles to the margins of the plate, and which have exceedingly fine crenulations along their proximal borders (Text-fig. 44*B*). These crenulations are parallel and lie close together, to give a characteristic fine comb-like appearance. This type of ornamentation distinguishes the species from others of the genus, and is somewhat suggestive of the rather less regular comb-like ornamentation seen in the later species *Psammosteus falcatus*.

Psammosteus asper OBRUCHEV, 1965

1965. *Psammosteus asper* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).

Holotype: Branchial plate, 220/771, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1965, in the press).

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon, *Psammolepis undulata* zone; Leningrad district.

Diagnosis. — Branchial plate very short and wide with ornamentation of large stellate tubercles well separated from one another, which may be fused into rows aligned transverse to the major axis of the plate. Dorsal median plate superficially divided into polygonal tesserae, with well separated crenulated tubercles.

Material. — Fragments of branchial plates and dorsal median plates showing characteristic ornamentation, from NW Russia.

Description. — *Dorsal median plate.* A fragment of a dorsal median plate, (220/751 P.I.M.) shows small superficial polygonal tesserae, which are ornamented by well separated

dentine tubercles with comparatively long crenulations, which are generally arranged concentrically. This species is one of the few examples in which the same characteristic ornamentation is found on both the dorsal median plate and the branchial plate.

Branchial plate. The holotype (220/771 P.I.M.) is a fragment of a branchial plate ornamented by well separated tubercles with crenulations measuring more than half the radius of the tubercle as a whole. The tubercles are sometimes fused into rows aligned transverse to the major axis of the plate. In these, the distal crenulations are very short, and the proximal ones are approximately four times as long. These latter are fairly straight and are parallel, giving the tubercles a comb-like appearance. This species which is one of the earliest species of *Psammosteus*, is very distinctive, and its characteristic ornamentation allows it to be readily identified.

Psammosteus tchernovi OBRUCHEV, 1965

(Text-fig. 45)

1899. *Psammosteus* sp. indet.; J. V. ROHON, Die devonischen..., p. 16.
1965. *Psammosteus tchernovi* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).

Holotype: Branchial plate, 220/830, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1965, in the press), and in the present work (Text-fig. 45).

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon, *Psammolepis undulata* zone; River Zylma, Timan.

Diagnosis. — Branchial plate short and wide, ornamented by high-crowned closely packed crenulated tubercles aligned transverse to the major axis of the plate, generally rectangular in shape, but on dorsal surface roof-like.

Material. — Unique holotype.

Description. — *Branchial plate.* The anterior and posterior margins of the plate appear to be more or less parallel, and the distal tip well rounded (Text-fig. 45). The entire ventral surface is ornamented by arcuate rows of tubercles aligned transverse to the

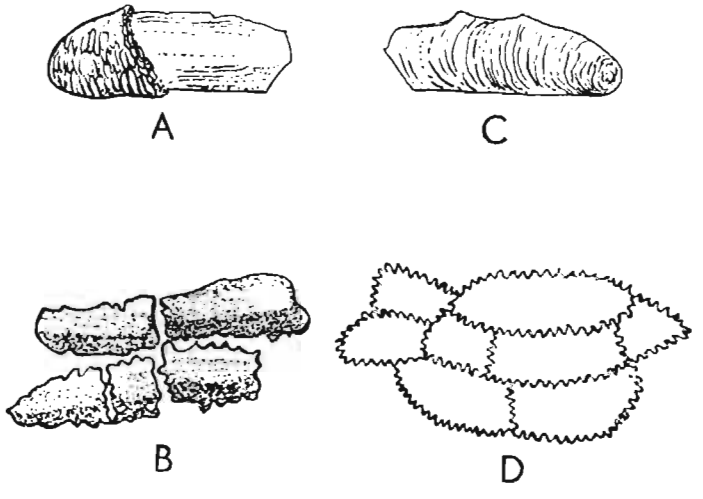

Fig. 45

Psammosteus tchernovi OBRUCHEV — holotype, immature left branchial plate (P.I.M. 220/830, Timan); *A* dorsal view, *C* ventral view, × 1.33; *B*, *D* detail of ornamentation, *B* dorsal view, *D* ventral view, × 8.

major axis of the plate, pointing proximally. These tubercles are fairly flat, closely packed, and have rather fine short crenulations round their entire margins. On the dorsal surface the tubercles appear to be a little more widely spaced and have rather uneven margins with slightly fewer crenulations around them. These dorsal tubercles are very high crowned, and in oblique view are reminiscent of the ridge of a roof. Although this specimen is of a very immature individual it appears to be a very advanced species of *Psammosteus*, because of its extremely short and broad outline even though it is found at the horizon where *Psammosteus* makes its first appearance. It is distinguished from other species of the genus by its characteristic ornamentation.

Psammosteus kiaeri TARLO, 1964

1915. *Psammosteus arcticus* n. sp.; J. KIAER, Upper Devonian Fish..., p. 25, pl. 5, figs. 4, 5.
1950. *Psammosteus arcticus* KIAER; W. GROSS, Die paläontologische und..., p. 46.
1961*a*. *Psammosteus arcticus* KIAER; L. B. TARLO, Psammosteids from the..., p. 201.
1961*a*. *Psammosteus falcatus* OBRUCHEV; L. B. TARLO, *Ibid.*, pp. 202, 213.
1961*a*. *Psammosteus arcticus* KIAER; D. OBRUCHEV, *Ibid.*, p. 212.
1964*b*. *Psammosteus kiaeri* n. sp.; L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 17, 90, 107, 117; pl. 2, fig. 2.

Holotype: Branchial plate, A. 13196-A. 13197, housed in the Palaeontological Museum, Oslo, figured by KIAER (1915, Pl. 5, figs. 4, 5) and TARLO (1964*b*, Pl. 2, fig. 2).

Type horizon and locality: Upper Devonian (Frasnian), Series E; Skrap Valley, Ellesmereland, Arctic Canada.

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.

Material. — Unique holotype.

Description. — *Branchial plate.* The holotype (A. 13196-A.13197, P.M.O.) is part of the distal end of the ventral surface of a branchial plate. The anterior and posterior margins are fairly straight, and gradually converge distally. The ornamentation consists of rows of fused dentine tubercles arranged in a somewhat «v»-shaped manner, pointing proximally. These fused rows of tubercles form slightly concave strips, the concavity being natural and clearly not due to wear. The distal margins of the strips have crenulations giving a scalloped edge, while the proximal margins of the strips have more and longer processes which terminate in fine crenulations.

Discussion. — This specimen was originally described under the name *Psammosteus arcticus* by KIAER (1915) but it differs from the other fragments he included under this name, which are here referred to *Psammolepis*. TARLO (1961*a*) suggested that this specimen might well belong to *Psammosteus falcatus*, but this was not agreed by OBRUCHEV, on account of the arrangement of the rows of fused tubercles. However, the fact that the dentine strips «v» proximally is not considered significant, because such an arrangement occurs on the ventral surface of immature individuals in many species. The ornamentation is somewhat similar to that seen in *P. falcatus*, but as the rows of tubercles in the species from Ellesmereland are either flat or have a natural concavity, and also differ in the form of the proximal crenulations from those of *P. falcatus* it was necessary to propose a new species for its reception, since the name *P. arcticus* is no longer available, being used for the other fragments described by KIAER. The new name *Psammosteus kiaeri* was therefore proposed for the species represented by the branchial plate described above.

Genus **CRENOSTEUS** TARLO, 1964

Type species: *Crenosteus levis* (OBRUCHEV *in* TARLO, 1964)

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

Occurrence. — Upper Devonian (Frasnian), Amata horizon, zone of *Psammolepis undulata*; NW Russia.

Crenosteus levis (OBRUCHEV *in* TARLO, 1964)

(Text-figs. 44*A*, 46*A*)

1964*b*. *Crenosteus levis* (OBRUCHEV); L. B. H. TARLO, Psammosteiformes (Agnatha)... (in the press).
1965. *Psammosteus levis* n. sp.; D. OBRUCHEV, Psammosteids of the... (in the press).

Holotype: Branchial plate 220/635, housed in the Palaeontological Institute, Moscow, figured by OBRUCHEV (1965, in the press), and in the present work, Text-fig. 44*A*.

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon, *Psammolepis undulata* zone; Leningrad district, NW Russia.

Diagnosis. — As for genus, only species.

Material. — Fragments of branchial plates showing characteristic ornamentation, from NW Russia.

Description. — *Branchial plate.* The holotype (220/635 P.I.M.) is the distal tip of a branchial plate which is ornamented by large flat rectangular dentine tubercles many of which are fused into rows, aligned transverse to the major axis of the plate (Text-fig. 44*A*). On the ventral surface these rows are arcuate, curving proximally. All the tubercles have a delicate fringe of short crenulations along their proximal margins. A further branchial plate (Text-fig. 46*A*) has similar ornamentation to that seen in the holotype and hence can be included in the same species. Its shape however seems quite unlike the normal branchial of *Psammosteus*. The distal tip faces posteriorly, and the posterior margin of the plate is strongly concave. The anterior margin is straight, and is almost at right-angles to the posterior margin. The lineation of the proximal portion of the plate is at right-angles to the anterior margin, whereas in the normal species of *Psammosteus* it is parallel to it.

Discussion. — The branchial plate described above is reminiscent of that seen in *Ganosteus stellatus*, but the ornamentation shows that it is not related to it. Although the ornamentation is distinct, it is nevertheless close to that of *Psammosteus*, although the outline of the branchial plate excludes it from this genus, as the anterior margin is at right-angles to the posterior margin, and not almost parallel to it as in *Psammosteus*. In view of this it seems reasonable to erect a new genus to receive it, and the name *Crenosteus* was proposed. It seems likely that *Crenosteus levis* could have been derived from *Psammolepis*, by the drawing out of the distal extremity in a posterior direction. This means however that if the distal ends alone are found, they cannot be generically distinguished from *Psammosteus* unless a more complete specimen exists with which to compare the characteristic ornament. Fortunately although the holotype is just the distal extremity of a branchial plate, a more complete specimen is available for comparison, enabling the generic characters of the species to be established.

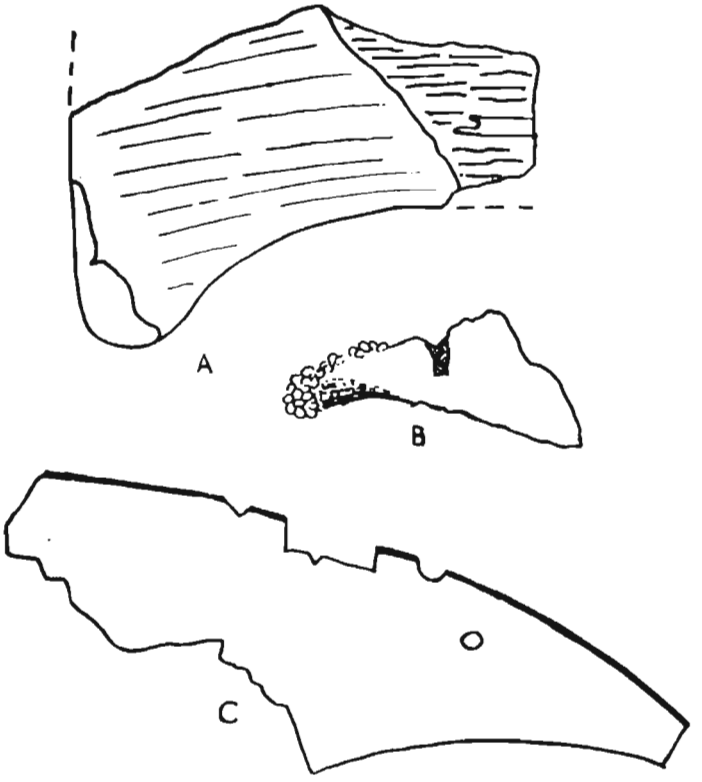

Fig. 46

A Crenosteus levis (OBRUCHEV) — posterior part of left branchial plate (P.I.M. colln.), × 1; *B Ganosteus stellatus* ROHON — tip of postero-lateral corner of branchial plate covered with globular eruptive dentine (G.I.T. 1491-10, Lejeji), × 1; *C Psammosteus praecursor* OBRUCHEV — distal tip of branchial plate showing hole made by bite of predator (P.I.M. colln.), × 1.

Genus **ROHONOSTEUS** TARLO, 1964

Type species: *Rohonosteus ornatus* (ROHON, 1899)

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.

Occurrence. — Upper Devonian (Frasnian), Amata horizon, zone of *Psammolepis undulata*; Timan, and Upper Devonian, Series E; Ellesmereland, Arctic Canada.

Discussion. — The genus *Rohonosteus* includes two species with branchial plates ornamented by closely packed lozenge-shaped dentine tubercles. Although the outline of the plate of one of them — *Rohonosteus ornatus* — is somewhat similar to that of the pycnosteid *Tartuosteus luhai* (see OBRUCHEV, 1961), nevertheless the genus seems more likely to have been derived from the psammolepids because of the ornamentation, although until a ventral median plate is known in *Rohonosteus* it will not be possible to be completely certain to which line it belongs. However, the branchial plates of this genus also appear to be intermediate between those of *Psammolepis* and *Psammosteus*, although they are not sufficiently close to either to be included in one of these genera. The new genus *Rohonosteus* was therefore

proposed for the species *P. ornatus* ROHON and *P. complicatus* KIAER, and because of the ornamentation, and the fact that their branchials appear to be approaching the condition seen in *Psammosteus*, the new genus was provisionally included in the family Psammosteidae.

Rohonosteus ornatus (ROHON, 1899)

(Text-fig. 47*A*)

1899. *Psammosteus ornatus* n. sp.; J. V. ROHON, Die devonischen Fische..., pp. 15-16, text-fig. 6.
1933*a*. *Psammolepis ornata* (ROHON); W. GROSS, Die Fische des..., p. 69.
1958. *Psammosteus ornatus* ROHON; D. OBRUCHEV, On the biostratigraphy..., p. 48.
1961. *Tartuosteus(?) ornatus* (ROHON); D. OBRUCHEV, The genus Tartuosteus..., pp. 110-111, text-fig. 4.
1964*b*. *Rohonosteus ornatus* (ROHON); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 88, 90, 102, 103, 106, 107.

Holotype: Branchial plate, 220/818, housed in the Palaeontological Institute, Moscow, figured by ROHON (1899, Text-fig. 6), OBRUCHEV (1961, Text-fig. 4) and in the present work Text-fig. 47*A*.

Type horizon and locality: Upper Devonian (Frasnian), Amata horizon, *Psammolepis undulata* zone; River Zylma, Timan, NW Russia.

Diagnosis. — Branchial plate fairly short and wide, ornamented by closely packed, small, lozenge-shaped dentine tubercles aligned proximo-distally.

Material. — Unique holotype.

Description. — *Branchial plate.* The holotype (220/818 P.I.M.) is an almost entire branchial plate of which only the distal tip is missing (Text-fig. 47*A*). The plate is considerably longer than those found in *Psammosteus* and wider than those of *Psammolepis*. The posterior margin is almost straight, with the suggestion of a concavity and the anterior margin makes an angle of some 50° with the posterior margin, and is slightly convex. Almost the entire width of the exposed surface of the plate is ornamented, and the normal ornamentation consists of very characteristic lozenge-shaped tubercles which are closely packed with their major axes aligned proximo-distally. The proximal border of the ornamentation is more or less straight, and is at right angles to the posterior margin, and on the ornamented part of the plate zones of growth can be seen parallel to this margin. Among the normal ornamentation

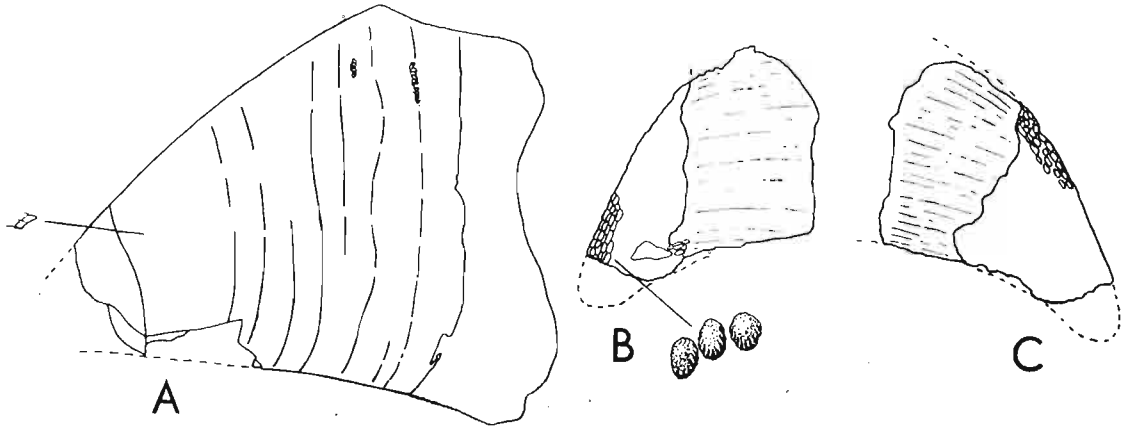

Fig. 47

A Rohonosteus ornatus (ROHON) — holotype, right branchial plate in ventral view (P.I.M. 220/818, Timan), × 0·5; *B, C Karelosteus weberi* OBRUCHEV — holotype, left branchial plate, *B* dorsal view with detail of ornamentation, *C* ventral view (G.P.M.L. 4014/6), × 0·5.

in the proximal part of the plate, there is a short row of irregular rounded tubercles which ROHON figured diagrammatically. These tubercles represent small areas of eruptive dentine.

When ROHON described and figured this branchial plate it was difficult to assess the importance of the specimen, or show its relationship to other psammosteids, as there was insufficient knowledge of the group at that time. It is now known that it comes from a horizon in which are found the last species of *Psammolepis* and the first of *Psammosteus*, and as at this period there was a considerable degree of radiation, it is not surprising to find a form that in some features appears to be intermediate between these two genera.

Rohonosteus complicatus (KIAER, 1915)

1915. *Psammosteus complicatus* n. sp.; J. KIAER, Upper Devonian Fish..., pp. 26-29, pl. 5, fig. 1-3; pl. 6, fig. 1-3; text-fig. 5.

1950. *Psammosteus complicatus* KIAER; W. GROSS, Die paläontologische..., p. 46.

1964*b*. *Rohonosteus complicatus* (KIAER); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 90, 107; pl. 2, fig. 3.

Lectotype (here selected): Branchial plate, A.13189-A.13193, housed in the Palaeontological Museum, Oslo, figured by KIAER (1915, Pl. 5, figs. 1, 2) and TARLO (1964 *b*, Pl. 2, fig. 3).

Type horizon and locality: Upper Devonian (Frasnian), Series E; Skrap Valley, Ellesmereland, Arctic Canada.

Diagnosis. — Branchial plate short and wide, ornamentation of lozenge-shaped closely packed tubercles somewhat larger than those in *Rohonosteus ornatus*.

Material. — Branchial plate, and fragments of median plate from Ellesmereland, Arctic Canada.

Description. — *Branchial plate*. The lectotype (A. 13189-A.13193 P.M.O.) is the distal portion of a branchial plate. The fragment A. 13190 is ornamented on the dorsal and ventral surfaces. The dorsal surface is fairly flat, and is ornamented by short rows of fused tubercles aligned along the axis of the plate, which break up at the posterior margin into shorter more rectangular tubercles. On the ventral surface, which is convex antero-posteriorly, the ornamentation consists of closely packed lozenge-shaped tubercles which are characteristic of the species. Although similar to those seen in *R. ornatus*, they are considerably larger. The posterior margin of the plate is probably fairly straight, and the anterior may well have met it at a marked angle. This specimen was originally described by KIAER (1915) as *Psammosteus complicatus*, but from its ornamentation it is very close to *R. ornatus*, and although it cannot be placed in the same species, it is clearly congeneric.

Genus **KARELOSTEUS** OBRUCHEV, 1933

Type species: *Karelosteus weberi* OBRUCHEV, 1933

Diagnosis. — Branchial plate short and wide, but narrower and longer than in species of *Psammosteus*; ornamented by very large, prominent, oval dentine tubercles with ribbed bases.

Occurrence. — Upper Devonian (Frasnian), *e* horizon, zone of *Psammosteus falcatus*; Leningrad district, NW Russia.

Karelosteus weberi OBRUCHEV, 1933

(Text-fig. 47 *B*, *C*)

1930. *Karelosteus weberi* n. sp.; D. OBRUCHEV, The significance..., p. 94 (nomen nudum).

1933*a*. *Karelosteus weberi* n. sp.; D. OBRUCHEV, Description of four new..., p. 12, 14, pl. 1, fig. 1.

1933*a*. *Karelosteus weberi* OBRUCHEV; W. GROSS, Die Fische des..., p. 17.

1942. *Karelosteus weberi* OBRUCHEV; W. GROSS, Die Fischfaunen..., p. 405.
1950. *Karelosteus weberi* OBRUCHEV; W. GROSS, Die paläontologische und..., p. 31.
1957. *Karelosteus [weberi]* OBRUCHEV; L. B. TARLO, A preliminary..., p. 229.
1964. *Karelosteus weberi* OBRUCHEV; D. OBRUCHEV, Subclass Heterostraci..., p. 74, pl. 6, fig. 6.

Holotype: Branchial plate 4014/6, housed in the Geological and Prospecting Museum, Leningrad, figured by OBRUCHEV (1933, Pl. 1, fig. 1) and in the present work Text-figs. 47 *B, C*.

Type horizon and locality: Upper Devonian (Frasnian), *e/f* horizon, probably *Psammosteus falcatus* zone, River Sviatukha, left-hand tributary of R. Svir, NW Russia.

Diagnosis. — As for genus, only species.

Material. — The holotype together with fragments of other branchial plates from NW Russia.

Description. — *Branchial plate.* The holotype (4014/6 G.P.M.L.) is an almost entire branchial plate (Text-figs. 47 *B, C*). The anterior margin of the free distal end is fairly straight, but the continuation of this margin on the unornamented proximal part of the plate forms a well marked curve. The posterior margin of the free end would also appear to be fairly straight, and the two margins tend to converge gradually distalwards. The unornamented portion of the posterior margin is fairly straight, but is at an angle to the ornamented part of the margin. The lineation of the spongy aspidin of the proximal part of the plate is at a considerable angle to the alignment of the tubercles of the ornament, unlike the condition seen in *Psammosteus*. In *Karelosteus weberi* the ornamented part of the plate turns posteriorly and in this respect is reminiscent of the condition seen in some species of *Psammolepis*. The narrow free distal part of the plate in *K. weberi*, however, is drawn out, to give a similar appearance to the normal branchials of *Psammosteus*.

The ornamentation consists of remarkably large dentine tubercles which are up to 5 mm. in length and 2 mm. in width. They are oval in outline and very prominent and they possess short coarse crenulations which give a characteristic ribbed effect to the base of the tubercles. The tubercles themselves are fairly closely packed together and are aligned in rows more or less parallel to the anterior margin, although those centrally placed have a more random arrangement. The proximal limit of the ornamentation on the dorsal surface is a straight line at right angles to the lineation on the proximal portion of the plate, while on the ventral surface the ornamentation extends more proximally, and ends with an irregular edge. This reaches the anterior margin at a similar point to the edge on the dorsal surface, but has a greater extent proximally on the posterior margin.

Discussion. — *Karelosteus weberi* is one of the last members of the psammosteids, and indicates that even towards the end of the Frasnian there was considerable variety within the group. Although only the branchial plate is known, it is quite unlike those of *Psammosteus* and its contemporary *Obruchevia [Aspidosteus]* and with regard to its tubercles, there is no indication of any reduction of the dentine layer as in *Obruchevia*. It may be a separate development from the *Psammolepis* stock, as its branchial plate shows certain affinities to those of the psammolepids, but nevertheless it is also clearly an advanced form, in some respects close to *Psammosteus*.

OBRUCHEV (1931) listed the name *Karelosteus weberi*, but this remained a *nomen nudum* until he described the specimen in 1933. This genus has been listed by various authors (GROSS, 1942, 1950, and TARLO, 1957), but there has until now been no discussion of its systematic position with regard to the other psammosteid genera.

PSAMMOSTEIDAE gen. et sp. indet.

WOODWARD (1921*b*) described fish remains from the Beacon Sandstone, of Granite Harbour, Victoria Land, Ross Dependency, Antarctica, including what he identified as selachian dermal tubercles. In his description, however, he said that they were referable "to primitive ostracoderms or to elasmobranchs". GROSS (1950) suggested that these remains were likely to be psammosteid, and a re-examination of the original material clearly shows that they are not selachian in nature, but are either thelodont scales or isolated tubercles of a member of the Psammosteidae. Since thelodonts are not known later than the Eifelian (TARLO, 1966*b*), whereas the Antarctic remains are of Frasnian age, there seems every likelihood that these are psammosteid in nature. This record is of some significance therefore, since these tubercles are the sole evidence of the presence of heterostracans in the Southern Hemisphere.

Suborder **OBRUCHEVIIDA** nov.

Diagnosis. — Branchial plates long and narrow, strongly arched from side to side. Dermal armour showing marked reduction or loss of dentine tubercles, but with general strengthening of pleromic dentine in superficial layer of aspidin.

Discussion. — The highly specialized nature of this group shows that it represents a major sidebranch of the Psammosteiformes, and for this reason the Obrucheviidae are here raised to the rank of an independent suborder — the Obrucheviida.

Family OBRUCHEVIIDAE TARLO, 1964

Diagnosis. — As for suborder, only family.

Discussion. — The family Aspidosteidae was erected by BERG (1955) to include *Aspidosteus* OBRUCHEV (= *Obruchevia* WHITLEY, 1940). This genus was characterized by the absence of superficial dentine tubercles, with instead the strengthening of the outer spongy aspidin by pleromic dentine. The recently discovered branchial plates show that this genus belongs to a family quite distinct from the Psammosteidae, with the latest members of which it is contemporary. Although the specialized features of *Obruchevia* were used to erect a new family, until the recent discovery they seemed only to be specializations within the Psammosteidae, and *Obruchevia* could thus have been considered as a highly specialized end member of this family. However, the branchial plates clearly demonstrate that *Obruchevia* cannot belong to the Psammosteidae, and BERG's family Aspidosteidae was therefore fully justified, although it had to be renamed the Obrucheviidae.

The branchial plates in question are very long and narrow — in fact much longer and narrower than those in the psammolepids. In addition they are very unusual as they are strongly bent, so that the median and lateral parts of the plate are at right angles to one another. In this way the lateral margins form narrow runners upon which the animal rested on the substratum, somewhat comparable to the runners in the central part of the median plate of *Pycnosteus*.

Besides *Obruchevia* the new genus *Traquairosteus* is provisionally included in the family Obrucheviidae on account of the reduction of its dentine tubercles, and the incipient development of pleromic dentine.

Genus **OBRUCHEVIA** WHITLEY, 1940

Type species: *Obruchevia heckeri* (OBRUCHEV, 1936)

Diagnosis. — Dorsal median plate thick with wide, shallow re-entrant angle at anterior margin, and marked notch in posterior part of each lateral margin. Ornamentation of smooth radial grooves and shallow circular pits. Histological structure of spongy aspidin reinforced by pleromic dentine towards external surface. Branchial plates thin, long and narrow, and bent at right-angles so that the lateral half is orientated vertically.

Occurrence. — Upper Devonian (Frasnian), *e* horizon, zone of *Psammosteus falcatus*; NW Russia.

Obruchevia heckeri (OBRUCHEV, 1936)

(Text-fig. 48)

1935. *Aspidophorus heckeri* OBRUCHEV M. S.; R. F. HECKER & M. F. PHILIPPOVA, Section along the Lovat..., p. 52 (nomen nudum).
1936. *Aspidophorus heckeri* n. sp.; D. OBRUCHEV, Two new..., p. 118, text-fig. 1.
1940. *Obruchevia heckeri* [OBRUCHEV]; G. WHITLEY, The Nomenclator..., p. 242.
1941. *Aspidosteus heckeri* n. sp.; D. OBRUCHEV, Remains of Aspidosteus..., pp. 7-22, pl. 1, figs. 1-3; pl. 2, fig. 1-3; text-fig. 1.
1942. *Aspidophorus heckeri* OBRUCHEV; W. Gross, Die Fischfaunen..., p. 405.
1955. *Aspidosteus heckeri* OBRUCHEV; A. P. BYSTROW, On the microstructure..., pp. 509-510, text-figs. 36, 37.
1956. *Aspidosteus heckeri* OBRUCHEV; A. P. BYSTROW, On the destruction..., pp. 38-40, text-fig. 8.
1958. *Aspidosteus heckeri* OBRUCHEV; E. A. STENSIÖ, Les Cyclostomes..., pp. 332-333, text-figs. 185 *A*, *B*.
1963. *Obruchevia (Aspidosteus) [heckeri* (OBRUCHEV)]; L. B. H. TARLO, Aspidin..., p. 47, text-fig. 3.
1964. *Obruchevia [Aspidosteus] heckeri* (OBRUCHEV; L. B. H. TARLO, The origin..., p. 00, text-fig. 6.
1964. *Aspidosteus heckeri* OBRUCHEV; D. OBRUCHEV, On the branchials... in the press.
1964*b*. Obruchevia heckeri (OBRUCHEV); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 20, 34, 87, 102, 108; pl. 7, figs. 1, 2, 4; pl. 12, fig. 4, text-fig. 11.
1964. *Aspidosteus heckeri* OBRUCHEV; E. A. STENSIÖ, Les Cyclostomes..., pp. 269, 270, text-figs. 88 A, B.
1964. *Aspidosteus heckeri* OBRUCHEV; D. OBRUCHEV, Subclass Heterostraci..., p. 75, fig. 3.

Holotype: Dorsal median plate, 4680-1, housed in the Geological and Prospecting Museum, Leningrad, figured by OBRUCHEV (1936, Text-fig. 1; 1941, Pl. 1, fig. 1).

Type horizon and locality: Upper Devonian (Frasnian), *Psammosteus falcatus* zone; River Lovat, NW Russia.

Diagnosis. — As for genus, only species.

Material. — Numerous dorsal median plates and several branchial plates from the Upper Devonian of the River Lovat, NW Russia.

Description. — *Dorsal median plate.* The holotype (4680-1 G.P.M.L.) is almost trefoil-shaped in outline. There is a shallow re-entrant angle forming almost the whole of the anterior margin, and from it the lateral margins form a gentle outward curve. About half way down the plate the margins converge sharply and then flare out again to end in an almost semi-circular posterior margin. The central part of the plate is ornamented by smooth shallow rounded pits about 3 mm. wide and about 20 mm. long, but some continue through from one zone to another and may measure as much as 45 mm. in length.

A further dorsal median plate (87/6 P.I.M.) lacks the anterior margin and differs from the holotype, as almost the entire plate is ornamented by rounded pits, with just a single wide surrounding flange, at a level lower than the central part of the plate, ornamented by radial grooves.

Branchial plate. In the Palaeontological Institute, Moscow, there are a number of branchial plates collected by Professor D. OBRUCHEV in 1958. Three representative examples are here figured (Text-fig. 48). These show the changes in outline occurring during ontogeny. The immature specimen has an almost straight lateral margin, and a fairly straight posterior margin sloping posteriorly from it (Text-fig. 48*B*). The anterior margin is gently rounded, while the median margin is rather sinuous and diverges slightly from the lateral margin. In outline the plate is somewhat reminiscent of the branchials of *Guerichosteus* and *Drepanaspis*, except that it is bent so that the free lateral part must have been orientated in the carapace

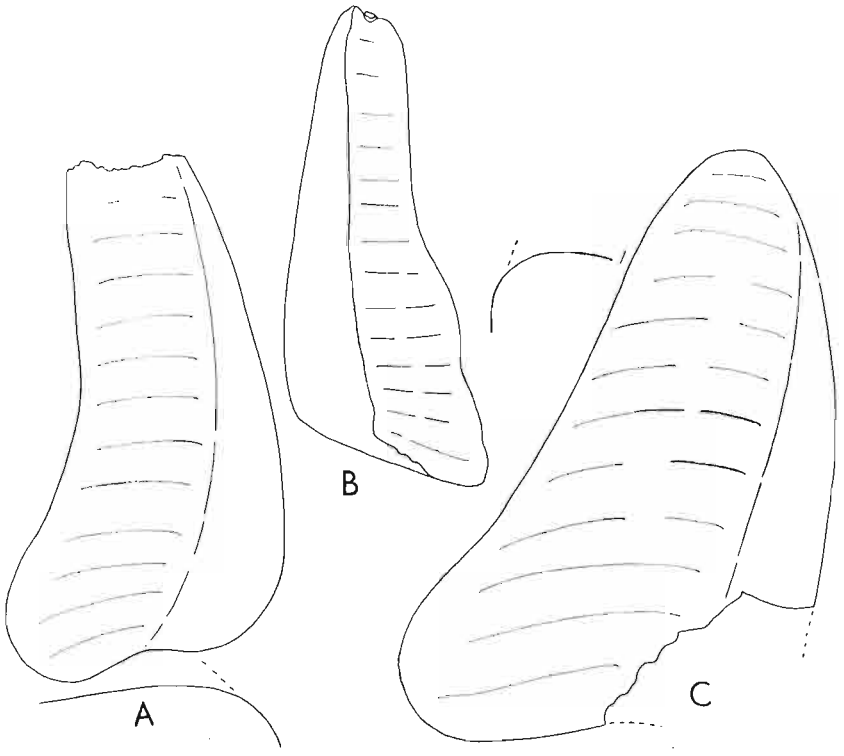

Fig. 48

Obruchevia [Aspidosteus] heckeri (OBRUCHEV) — *A* right branchial plate with cross-section, *B* immature left branchial plate with cross-section, *C* mature right branchial plate (P.I.M. Obr. colln. 1958), × 0·33.

in a vertical position, and would have acted as a runner. The median part of the plate on the dorsal surface must have been covered by other elements of the carapace, except at the posterior margin, as the "ornamented" lateral part of the plate gradually widens posteriorly and ends in a median flange at the posterior margin.

A more mature specimen has a gently curving lateral margin which becomes more rounded towards the posterior margin (Text-fig. 48*A*). In the central part of the posterior margin there is a slight concavity, and a rounded postero-medial flange is developed leading into a slightly concave median margin. This median margin converges very gradually anteriorly with the lateral margin, but in this specimen the anterior margin itself is missing. The "ornamented" lateral part of the plate is still much the same size as that of the younger specimen, the main growth having taken place in the median part of the plate. In section the orna-

mented part is again strongly downturned, and the median part of the plate is almost horizontal.

The very mature specimen again has a gently convex lateral margin, and its ornamented part gradually increases in width posteriorly (Text-fig. 48 *C*). Unfortunately the posterior lateral corner is missing, but the posterior median flange is very well developed and continues as a straight median margin to join the rounded anterior margin. In this mature specimen therefore the plate is very wide along the posterior margin, as the whole of the unornamented median part has increased considerably in width, in particular in the postero-medial corner. The «ornamented» part, however, has again remained virtually unchanged. The markedly concave ventral surface of these plates formed a large part of the ventral surface of the carapace, and was not covered by any other plates or soft tissue.

Histological structure. The plates of *Obruchevia [Aspidosteus] heckeri* are composed of the normal spongy aspidin with a basal lamellar aspidin layer. The outer part of the spongy aspidin is infilled with pleromic dentine, and as this dentine infilling is present over the entire external surface of the dorsal median plate, its existence cannot be explained as a direct response to damage or abrasion, as is the case in the ventral and branchial plates of other genera. The ability to produce pleromic dentine as a response to continued abrasion has clearly been transmitted to *Obruchevia [Aspidosteus]* by ancestral forms, and this ability has been used for overall strengthening and sealing of its dermal armour. In the forms with dentine tubercles, epidermis must have existed on the outer surface of the animal between the tubercles, but in *Obruchevia [Aspidosteus]*, clearly such tissue was not present for very long.

Discussion. — The name *Aspidophorus heckeri* OBRUCHEV M. S. first appeared in the literature in 1935 (HECKER & PHILIPPOVA), and made its last appearance in 1942 (GROSS). In these works, however, it was a *nomen nudum*, It was also described by OBRUCHEV in 1936, as *Aspidophorus heckeri* but the generic name was preoccupied, and WHITLEY (1940) proposed the name *Obruchevia*. Thus although OBRUCHEV (1941) gave a detailed description under the name *Aspidosteus*, WHITLEY'S name had priority. OBRUCHEV recognized that this new genus was a psammosteid, and he included it in the family Cardipeltidae which was erected by BRYANT (1933). OBRUCHEV agreed with BRYANT in considering the lateral notches of *Cardipeltis* to be branchial notches, and not orbital notches as was originally thought by BRANSON and MEHL (1931). However, he considered that *Cardipeltis* had been wrongly orientated and that the broad notched end should be placed anteriorly. Subsequent work on *Cardipeltis* by DENISON (1953) has shown that the original orientation was correct, and that there was no real similarity between it and *Obruchevia [Aspidosteus]*. Unfortunately, the confusion with regard to these two genera has been reintroduced by STENSIÖ (1958) who included *Aspidosteus* (= *Obruchevia*) in the order Cardipeltida, and reversed it so that the narrow portion of its median plate faced anteriorly and the broad re-entrant angle faced posteriorly. In fact *Cardipeltis* and *Obruchevia [Aspidosteus]* were both originally described the right way round, and are not comparable.

From the outline of the dorsal median plates and the normal histology of *Obruchevia [Aspidosteus]*, it is quite clearly a psammosteid, although by virtue of its lack of dentine tubercles and the development of pleromic dentine, it is clearly a highly specialized form. Its branchials show that it is on a separate line from *Psammosteus*. An attempted reconstruction of *Obruchevia [Aspidosteus]* is given in the General Part of this work (TARLO, 1964*b*, Text-fig. 11).

Genus **TRAQUAIROSTEUS** TARLO, 1964

Type species: *Traquairosteus pustulatus* (TRAQUAIR, 1897)

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

Occurrence. — Upper Devonian (Frasnian), Scaat Craig Beds, zone of *Psammosteus falcatus*; Scotland.

Traquairosteus pustulatus (TRAQUAIR, 1897)

(Pl. XVII, fig. 1)

1897. *Psammosteus pustulatus* n. sp.; R. H. TRAQUAIR, Additional notes on..., pp. 379-380, pl. 11, figs. 3, 4.
1923. *Psammosteus pustulatus* TRAQUAIR; J. HORNE, The Geology of the...
1931. *Psammosteus pustulatus* TRAQUAIR; D. OBRUCHEV, The significance..., p. 98.
1948. *Psammosteus pustulatus* TRAQUAIR; H. H. READ, The Grampian..., p. 65.
1950. *Psammosteus pustulatus* TRAQUAIR; W. GROSS, Die paläontologische..., p. 19.
1961*a*. *Psammosteus pustulatus* TRAQUAIR; L. B. TARLO, Psammosteids from the..., pp. 200-201, pl. 7, fig. 7, text-figs. 3c, 6.
1964*b*. *Traquairosteus pustulatus* (TRAQUAIR); L. B. H. TARLO, Psammosteiformes (Agnatha)..., pp. 89, 108, 117.

Holotype: Fragment of median plate, P. 8297, housed in the British Museum (Natural History), London, figured by TRAQUAIR (1897, Pl. 11, fig. 3, 4), TARLO (1961*a*, Pl. 7, fig. 7) and in the present work, Pl. XVII, fig. 1.

Type horizon and locality: Upper Devonian (Frasnian), Scaat Craig Beds; Scaat Craig, Elgin, Scotland.

Diagnosis. — As for genus, only species.

Material. — Single dorsal median plate and numerous fragments of the same from Scotland.

Description. — *Dorsal median plate.* A single dorsal median plate (110 E.M.) has a more or less oval outline with a shallow re-entrant angle at the anterior margin. The characteristic ornamentation is missing, but with oblique lighting the rippling is seen which is produced when the conical mounds of spongy aspidin usually found, are worn away. In several places there are clusters of large rounded tubercles, which are not part of the normal ornamentation, but are areas of eruptive dentine. The plate is preserved as a natural mould, and is slightly convex posteriorly from side to side, gradually flattening out anteriorly. The holotype (P. 8297 B.M.) which is a fragment of a dorsal median plate, shows the ornamentation very well, since many of the pustules still retain their apical dentine tubercles. These have short thick rounded crenulations which give a lobate appearance to the tubercles. This species shows a considerable reduction in the amount of dentine present on the external surface of the plate, as it has far fewer tubercles than any other psammosteid, with the exception of *Obruchevia [Aspidosteus]*.

In vertical section, the tubercles show the typical psammosteid development of dentine tubules, but instead of appearing to radiate from a single pulp cavity these appear to arise within the vascular spaces of the spongy aspidin reminiscent of pleromic dentine. This feature would therefore appear to represent an intermediate stage between the condition seen in *Obruchevia [Aspidosteus]*, where the outer layer of the aspidin of the dorsal median plate is strengthened by pleromic dentine and there are no dentine tubercles present at all, and the

condition in psammosteids and psammolepids where well formed dentine tubercles are present on the outer surface, and pleromic dentine is confined to those parts of the carapace which suffer continued abrasion.

In *Traquairosteus pustulatus* branchial plates are unknown, but the very great reduction of the dentine tubercles together with the incipient development of pleromic dentine, would seem to suggest that it has close affinities to *Obruchevia [Aspidosteus]* and hence *Traquairosteus* is here provisionally included in the family Obrucheviidae.

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

PLATE I

Page

Tesseraspis tessellata WILLS 3

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

Fig. 1. Associated tesserae, lectotype, specimen figured by WILLS (1935, pl. 4, fig. 5); (113. B.U.); × 1.
Photo: L. J. Wills

Fig. 2. Associated tesserae showing ridge plates of lateral margin and those of central area (540. B.U.); × 1.
Photo: P. R. Gurr

Fig. 3. Tesserae showing segments of sensory canal system, specimen figured by WILLS (1935, pl. 4, fig. 6); (110. B.U.) × 2.
Photo: L. J. Wills

Fig. 4. Associated tesserae (541. B.U.); × 0·75.
Photo: P. R. Gurr

Fig. 5. Detail of ornamentation, specimen figured by WILLS (1935, pl. 4, fig. 3); (111. B.U.); × 2.

Fig. 6. Lateral ridge plates with adjoining thin tesserae (114. B.U.); × 2.
Photo: L. J. Wills

Tesseraspis toombsi TARLO 6

Associated tesserae, holotype. Mad Bay, Skokholm, Pembrokeshire; Lower Devonian, Lower Gedinnian

Fig. 7. Lateral ridge plates (P. 29621. B.M.); × 1.

Fig. 8. Body scales (P. 29622. B.M.); × 1.

Fig. 9. Associated tesserae with associated median scales (P. 29683. B.M.); × 1.

Fig. 10. Associated tesserae (P. 29624. B. M.); × 1.
Photo: N. Tanti

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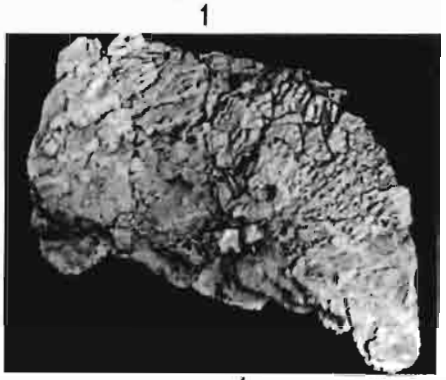

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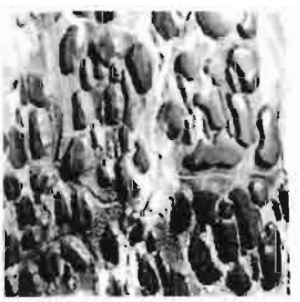

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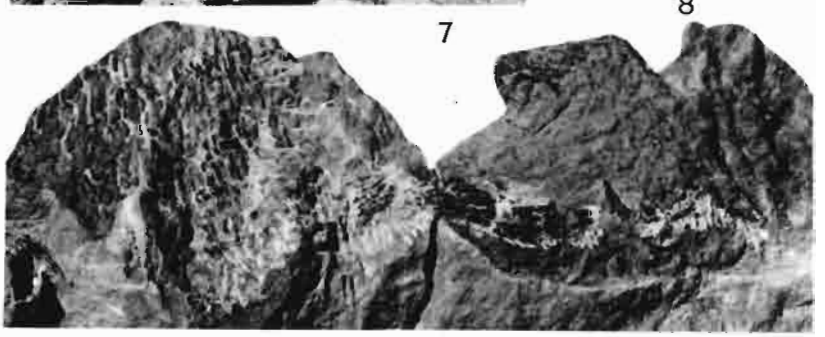

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE II

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Kallostrakon grindrodi TARLO 14

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

Fig. 1. Tessera, holotype (P. 88896. B.M.); × 2·5.
Fig. 2. Tessera (D. 84. O.U.M.); × 2·5.

Kallostrakon macanuffi TARLO 11

Bush Pitch, near Ledbury, Herefordshire; Silurian, Upper Ludlovian, Downtonian. × 2·5 (except fig. 4).

Fig. 3. (D. 88. O.U.M.).
Fig. 4. (D. 235. O.U.M.); × 2.
Fig. 5. (P. 41946. B.M).
Fig. 6. (P. 5372. B.M.).
Fig. 7. (P. 41944. B.M.).
Fig. 8. (P. 41945. B.M.).
Fig. 9. (P. 1652. B.M.).
Fig. 10. (P. 41947. B.M.).
Fig. 11. (P. 1654. B.M.).
Fig. 12. (P. 1653. B.M.).
Fig. 13. (P. 30189. B.M.).
Fig. 14. (P. 41948. B.M.).
Fig. 15. (P. 24756. B.M.).
Fig. 16. (P. 41949 B.M.).

Photo: P. F. Green


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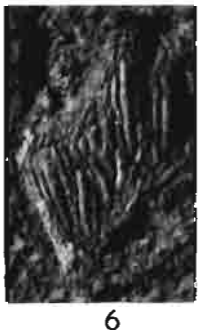
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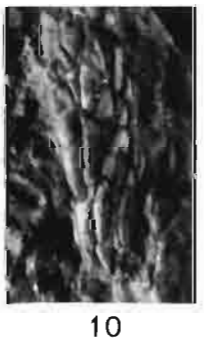
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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE III

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Corvaspis kingi WOODWARD 16

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

Fig. 1. Fragment of median plate, holotype, specimen figured by WOODWARD (1934, pl. 19, fig. 1), (P. 16446. B. M.); × 1.

Photo: L. J. Wills

Fig. 2. Orbital plate, specimen figured by TARLO (1960*b*, pl. 37, fig. 2), (P. 42841. B. M.); × 3.

Photo: G. S. Bryant

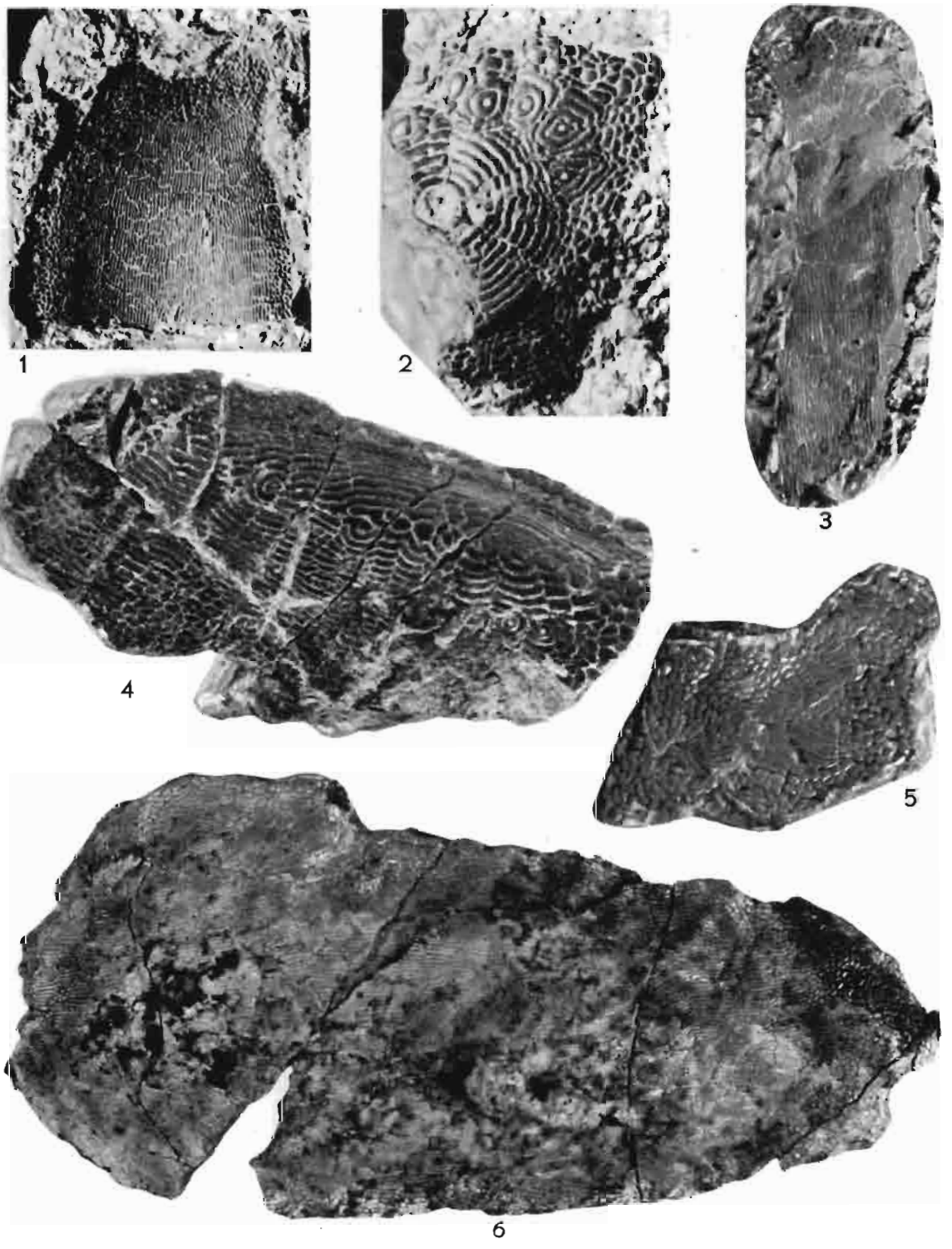
Fig. 3. Median plate with no evidence of superficial tesserae, specimen figured by TARLO (1960*b*, pl. 38, fig. 5), (717. B. U.); × 00.

Fig. 4. Branchial plate, specimen figured by DINELEY (1953, pl. 2, fig. 2), (653. B. U.); × 3.

Fig. 5. Pineal plate, specimen figured by TARLO (1960*b*, pl. 37, fig. 5), (P. 42843. B. M.); × 3.

Fig. 6. Complete median plate showing gradation into squamation at posterior part (P. 40575. B. M.); × 1·5.

Photo: W. Brackenbury



L. B. H. Tarlo: Psammosteiformes (Agnatha)

PLATE IV

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Weigeltaspis heintzi TARLO 25

Fig. 1. Associated carapace in ventral view. Ben Nevis, Spitsbergen; Lower Devonian, Upper Gedinnian, Red Bay Series, Ben Nevis Division (E.N.S. Exp., Fld. no. 88, P.M.O.); × 0·5.

Fig. 2. Dorsal median plate, holotype. Ben Nevis, Spitsbergen; Lower Devonian, Upper Gedinnian, Red Bay Series, Ben Nevis Division (D. 2440-2441. P.M.O.); × 1.

Weigeltaspis alta BROTZEN 21

Fig. 3. Natural cast of dorsal median plate, lectotype, specimen figured by BROTZEN (1933*a*, text-fig. 1). Uscieczko, Dnjestr, Podolia, Ukraine; Lower Devonian, Upper Gedinnian, Stage I of BROTZEN (G.P.I.H.); × 1.

Fig. 4. Fragment of plate showing detail of ornamentation, preserved as natural mould, specimen figured by BROTZEN (1933*a*, text-fig. 2). Uscieczko, Dnjestr, Podolia, Ukraine; Lower Devonian, Upper Gedinnian, Stage I of BROTZEN (G.P.I.H.); × 2·5.

Photo: K. Taylor

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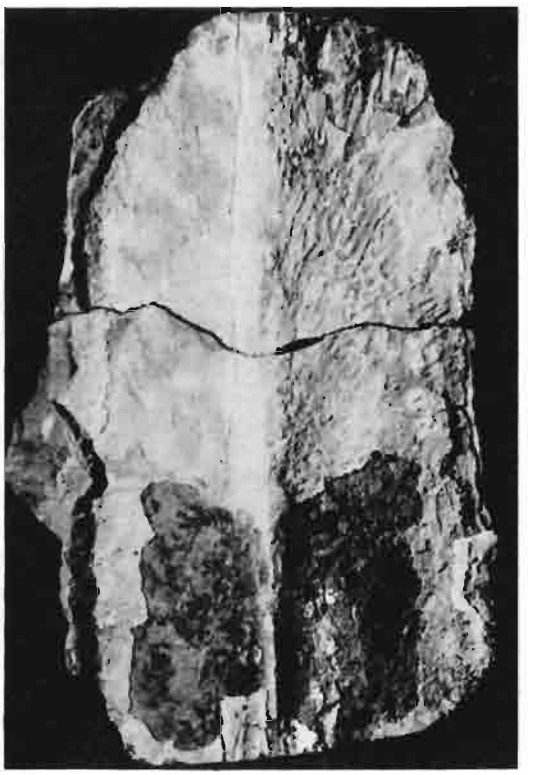

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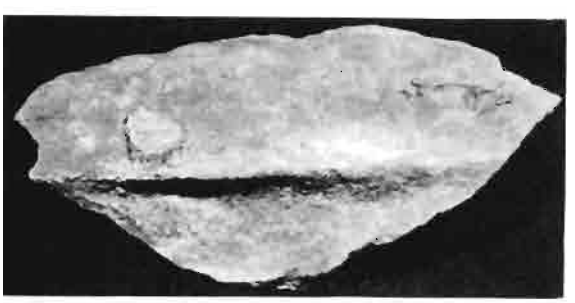

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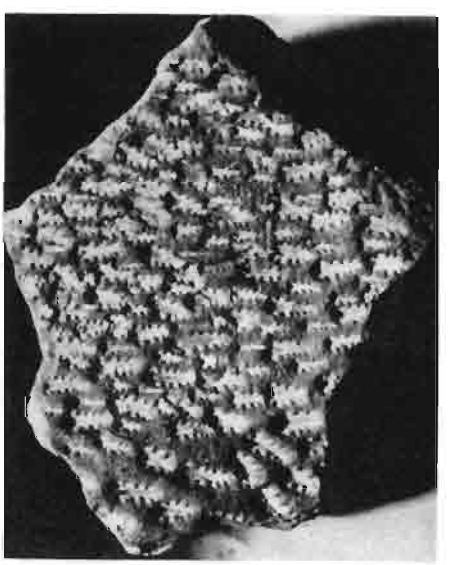

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE V

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Weigeltaspis alta BROTZEN 21

Fig. 1. Dorsal median plate, preserved as natural mould. N. Burakowska, Podolia, Ukraine; Lower Devonian, Upper Gedinnian, Stage I of BROTZEN (P. 18221, counterpart P. 18222. B.M.); × 1.

Weigeltaspis brotzeni TARLO 23

Fig. 2. Orbital plate, *A* counterpart, *B* natural mould. Uscieczko, 200-210 m., Podolia, Ukraine; Lower Devonian, Upper Gedinnian, Stage I of BROTZEN (P. 20605-4. B.M.); × 2.

Fig. 3. Fragment of plate, preserved as natural mould, holotype. 163 m. W. Uscieczko, Podolia, Ukraine; Lower Devonian, Upper Gedinnian, Stage I of BROTZEN (P. 18266. B.M.); × 1.

Weigeltaspis godmani TARLO 24

Fig. 4. Posterior part of ?post-orbital plate, preserved as natural mould. Grove Quarry, by mill at Pont-yr-Ynys, near Longtown, Herefordshire; Lower Devonian, Upper Gedinnian, *Pteraspis crouchi* zone (P. 20200, counterpart 20201. B.M.); × 1.

Fig. 5. Branchial plate, preserved as natural mould. Castle Mattock Quarry, near Clodock, Herefordshire; Lower Devonian, Upper Gedinnian, *Pteraspis crouchi* zone (P. 19166, counterpart P. 19165. B.M.); × 1.

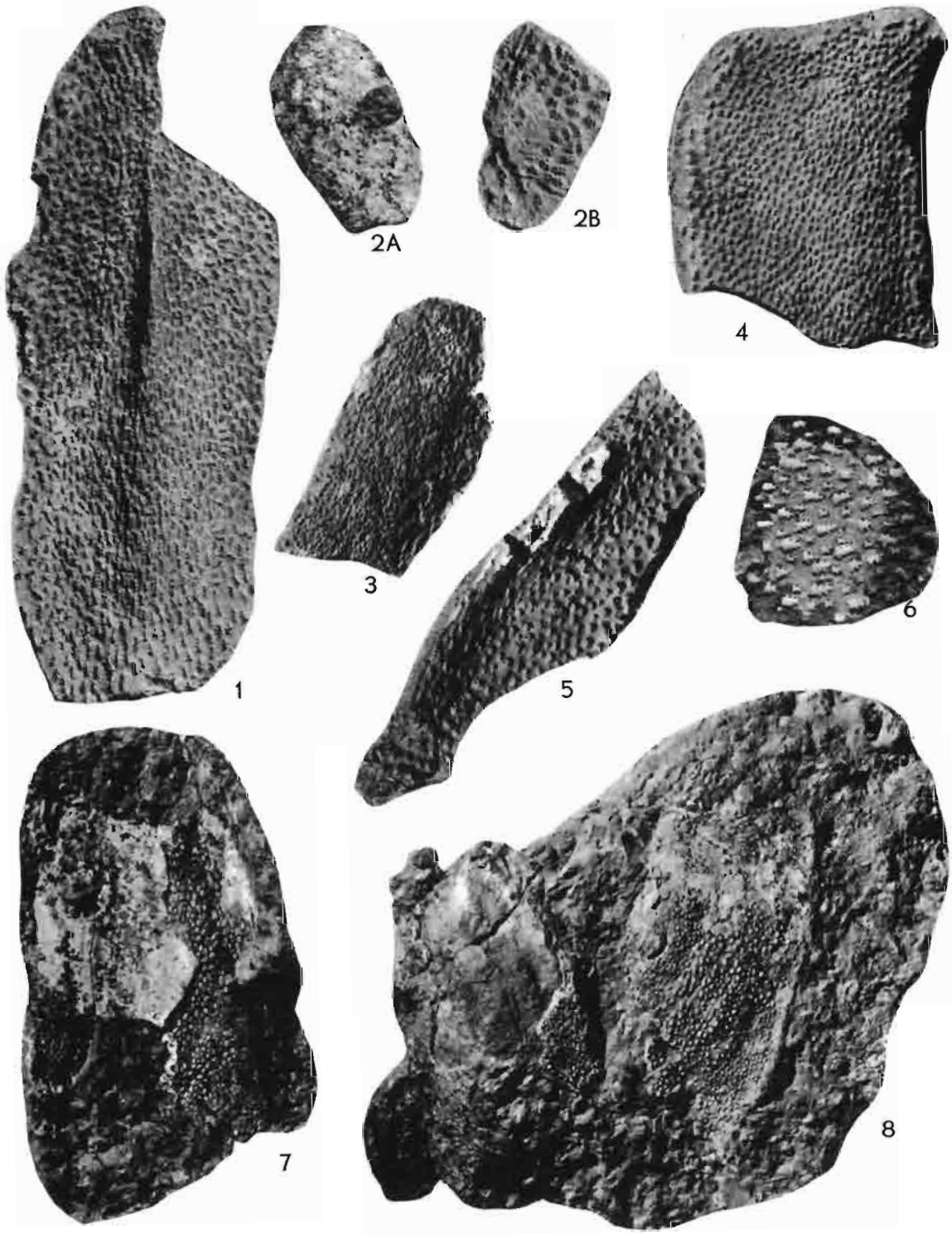
Fig. 6. Fragment showing ornamentation. Castle Mattock Quarry, near Clodock, Herefordshire; Lower Devonian, Upper Gedinnian, *Pteraspis crouchi* zone (P. 33149. B.M.) × 1·5.

Fig. 7. Ventral median plate, internal view, showing pattern of ornamentation. Castle Mattock Quarry, near Clodock, Herefordshire; Lower Devonian, Upper Gedinnian, *Pteraspis crouchi* zone (P. 23748. B.M.); × 0·5.

Fig. 8. Major portion of ventral median shield with associated branchial plate, showing external ornamentation and tesserae, holotype. Counterpart of P. 23748 seen on left of figure. Castle Mattock Quarry, near Clodock, Herefordshire; Lower Devonan, Upper Gediinnian, *Pteraspis crouchi* zone (P. 23747. B.M.); × 0·5.

Photo: J. V. Brown

Note: Specimens preserved as natural moulds are here figured with reversed lighting



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

PLATE VI

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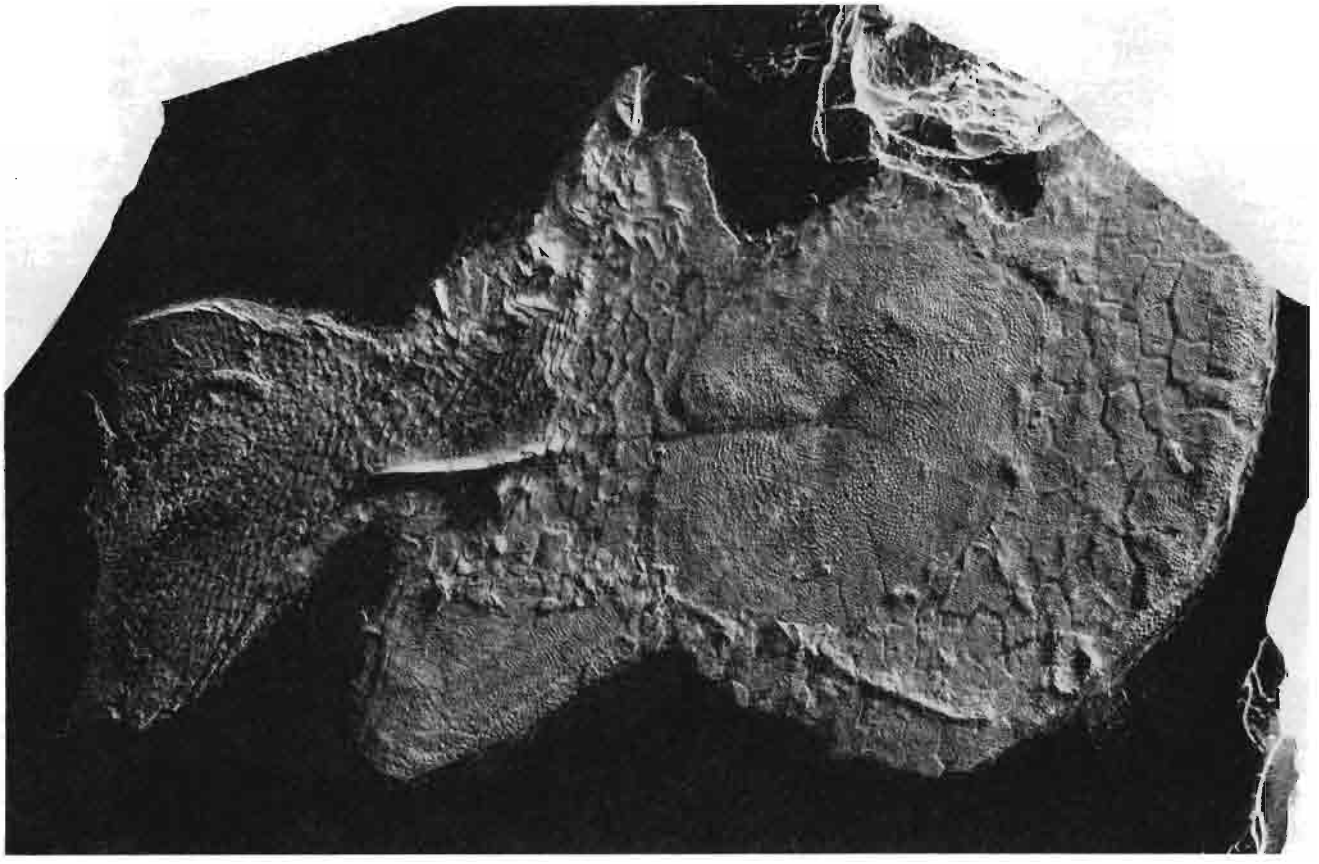
Drepanaspis gemuendenensis SCHLÜTER 29

Fig. 1. Complete carapace in ventral view, specimen figured by BOTTLEY (1961, text-fig. 1). Gemünden, Rhineland; Lower Devonian, Siegenian-Emsian, Hunsruckschiefer (Univ. Newcastle Colln.); × approx. 0·5.

Photo from E. P. Bottley

Fig. 2. Cast of fragment of dorsal median plate with associated left branchial plate, holotype. Gemünden, Rhineland, Lower Devonian, Siegenian-Emsian, Hunsruckschiefer (G.I.U.B.); × 1. (Cast: D. 79 U.W.).

Photo: K. Taylor



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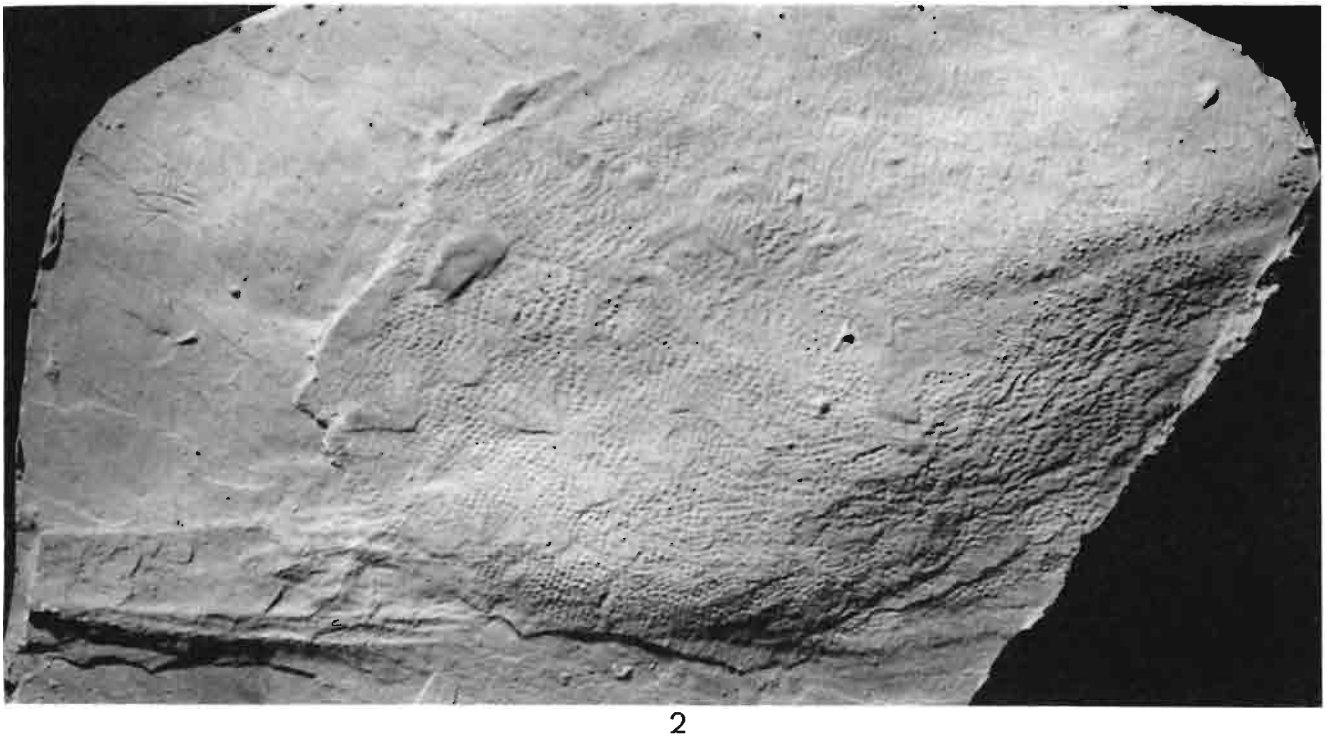

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

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

PLATE VII

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Drepanaspis jaegeri TARLO 35

Fig. 1. Fragment of median plate, holotype. Sud Wald, Altenahr, Rhineland; Lower Devonian, Siegenian-Emsian. Herdorfer Schichten, Effelsberger Schichten (G-P.M.B.); × 1.

Fig. 2. Fragment of median plate. Stephanshausen, Pressburg, Rhineland; Lower Devonian, Siegenian. Taunusquartzit (81. Rose Colln. G-P.M.B.); × 1.

Fig. 5. Body scale. Steinbruck, Bendorf, Rhineland; Lower Devonian, Emsian, Singhofener Schichten (G-P. M.B.); × 1·5.

Photo: N. Tanti

Figs. 6-9. Stephanshausen, Pressburg, Rhineland; Lower Devonian, Siegenian, Taunusquartzit.

Fig. 6. Fragment of eroded ornamentation (85. Rose colln. G-P.M.B.); × 2.

Fig. 7. Fragment of branchial plate (102. Rose colln. G-P.M.B); × 4.

Fig. 8. Body scale (609 Rose colln. G-P.M.B.); × 3.

Fig. 9. Fulcral scale (90. Rose colln. G-P.M.B.); × 4.

Photo: P. R. Gaur

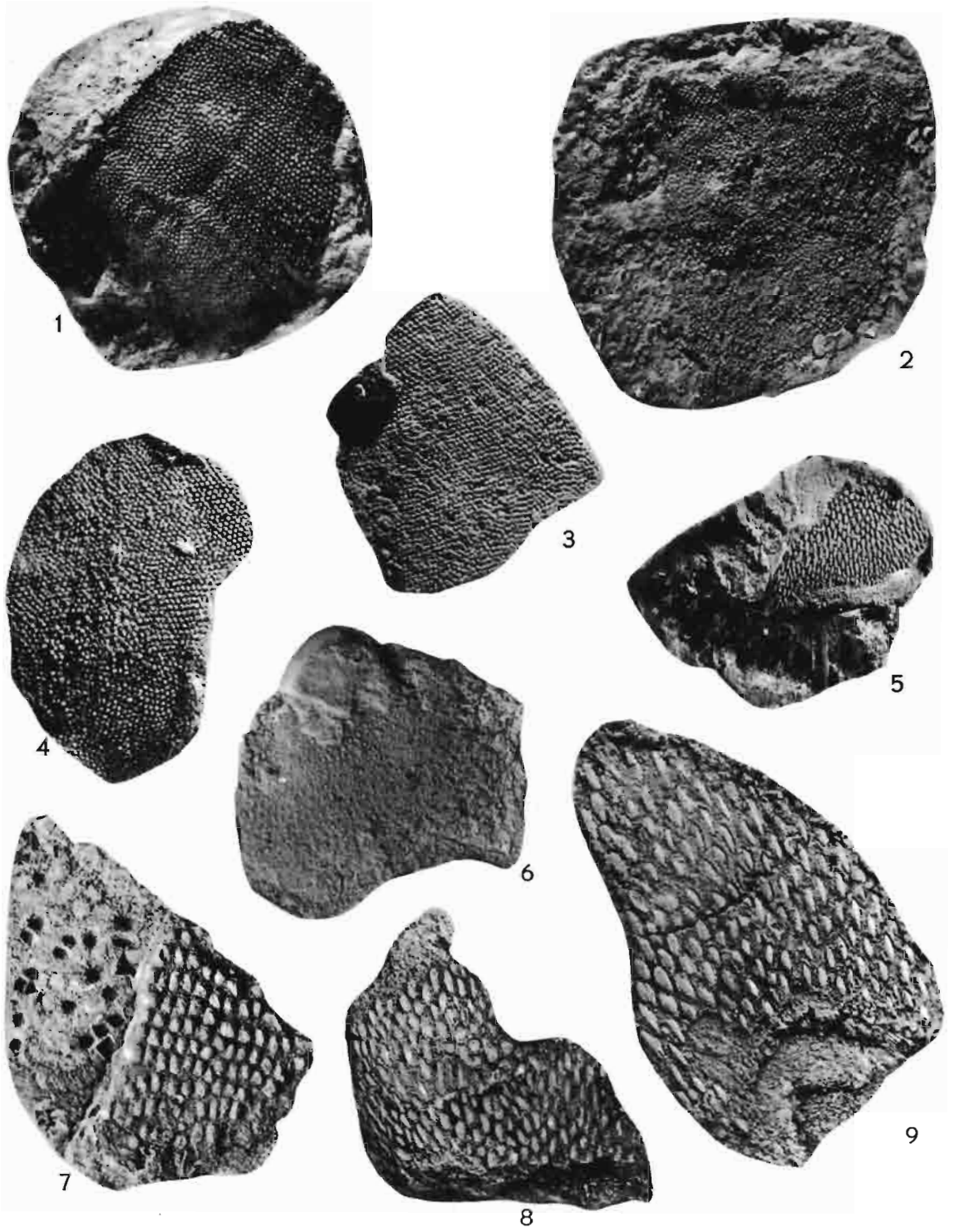
Guerichosteus kulczyckii TARLO 50

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

Fig. 3. Fragment (D. 42. U.W.); × 1·5.

Fig. 4. Fragment, holotype (D. 41. U.W.); × 1·5.

Photo: N. Tanti



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

PLATE VIII

Page

Drepanaspis carteri (McCoy) 36

Fig. 1. Fragment of median plate, holotype, specimen figured by McCoy (1855, pl. 2A, figs. 4, 4a) as *Steganodictyum carteri*. Lantivit (Lantivett) Bay, Cornwall; Lower Devonian, Dartmouth Slates (A. 3466. S.M.); × 1.

Fig. 2. Isolated tessera with ornamentation of elongated tubercles. Watergate Bay, near Creepinghole Point, SW of Tregurrian, Cornwall; Lower Devonian, Dartmouth Slates (102472 (1072) G.M.S.); × 1·5.

Fig. 3. Fragment of median plate. Cornwall; Lower Devonian, Dartmouth Slates (5690. G.S.M.); × 1·5.

Fig. 4. Fragment of median plate. Watergate Bay, near Creepinghole Point, SW of Tregurrian, Cornwall; Lower Devonian, Dartmouth Slates (82833 (1055). G. S. M.); × 1·5.

Fig. 5. Fragment of median plate. Cornwall; Lower Devonian, Dartmouth Slates (5691. G.S.M.); × 1·5.

Fig. 6. Fragment showing regular arrangement of ornament. Cornwall; Lower Devonian, Dartmouth Slates (5715. G.S.M.); × 1·5.

Fig. 7. Fragment of orbital plate. Watergate Bay, near Creepinghole Point, SW of Tregurrian, Cornwall; Lower Devonian, Dartmouth Slates (102473 (1068) G.S.M.); × 1·5.

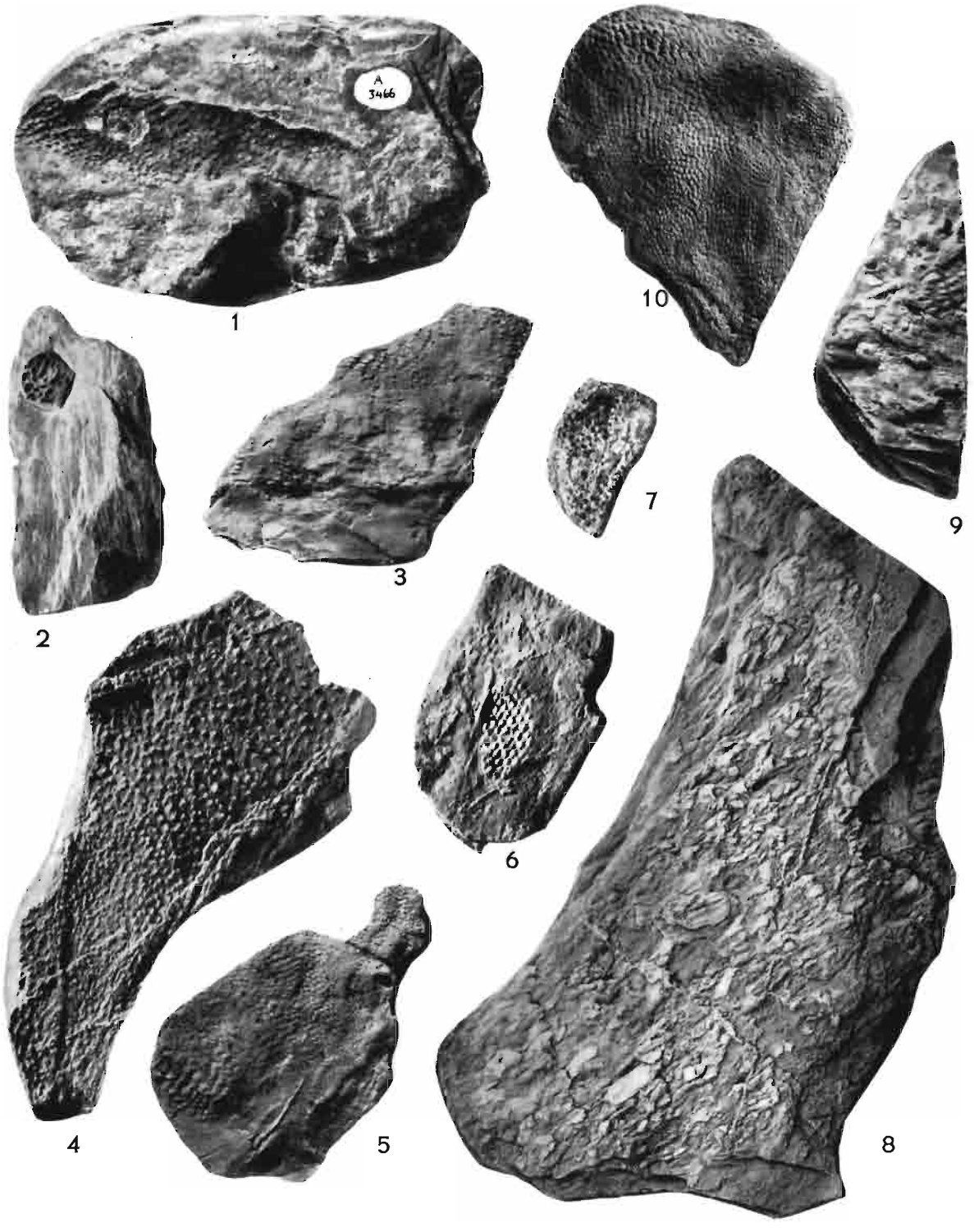
Fig. 8. Fragment of median plate with part of field of tesserae. St. Colomb Porth, Cornwall; Lower Devonian. Dartmouth Slates (8476. G.S.M.); × 1.

Fig. 9. Fragment of median plate (8476. G.S.M.); × 1·5.

Drepanaspis edwardsi Tarlo 37

Fig. 10. Part of ?post-orbital plate ornamented by closely-packed, large rounded tubercles, holotype. Lantivit Bay, Cornwall; Lower Devonian, Dartmouth Slates (P. 13750. B.M.); × 1·5.

Photo: N. Tanti



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

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

PLATE IX

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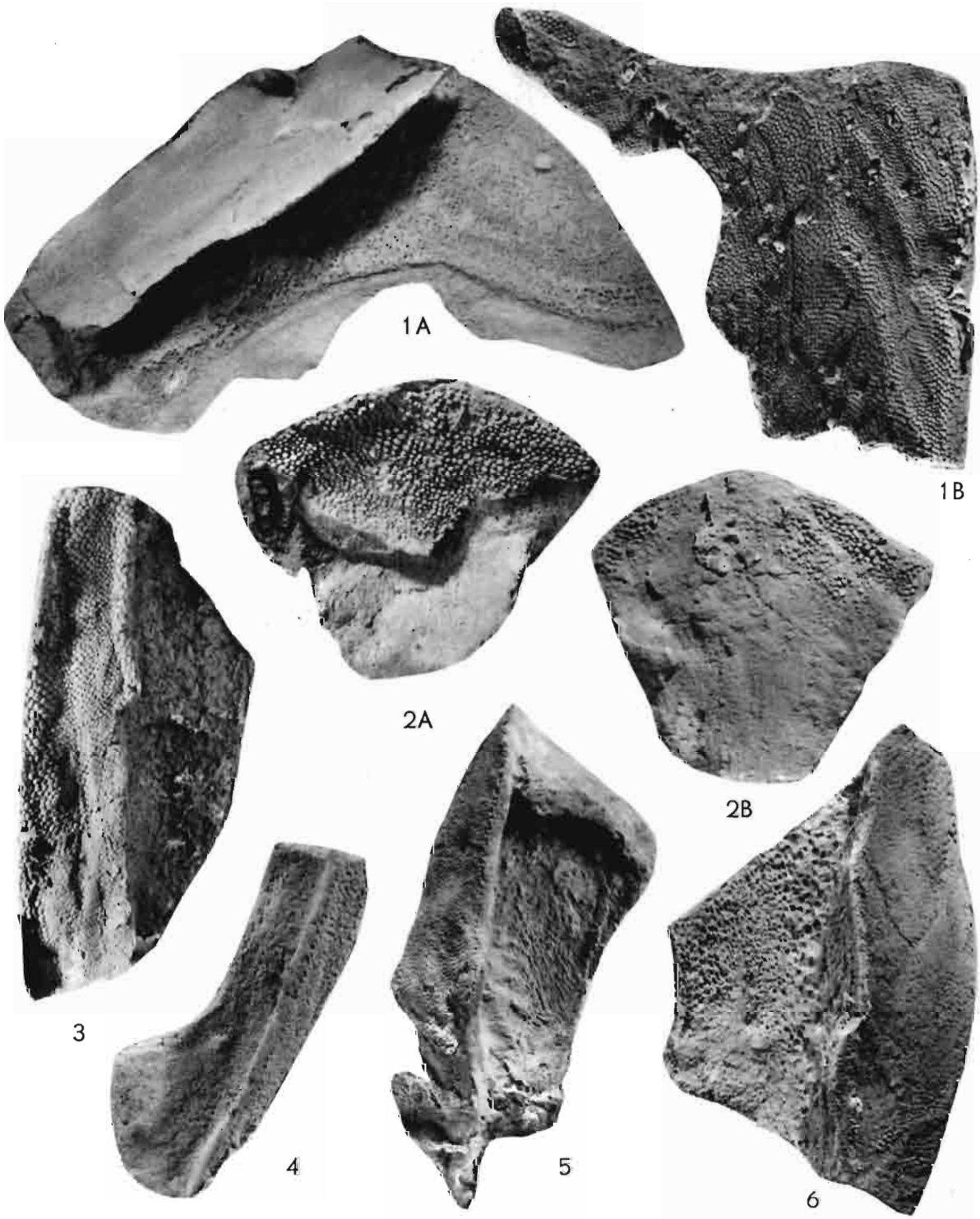
Guerichosteus kozlowskii TARLO 41

Branchial plates. Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone: × 1

Fig. 1. (D. 9. U.W.). *A* in dorsal view, *B* in ventral view.
Fig. 2. (D. 17. U.W.). *A* in dorsal view, *B* in ventral view.
Fig. 3. (D. 8. U.W.).
Fig. 4. (D. 16. U.W.).
Fig. 5. (D. 15. U.W.).
Fig. 6. Holotype (D. 7. U.W.).

Photo: N. Tanti



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

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

PLATE X

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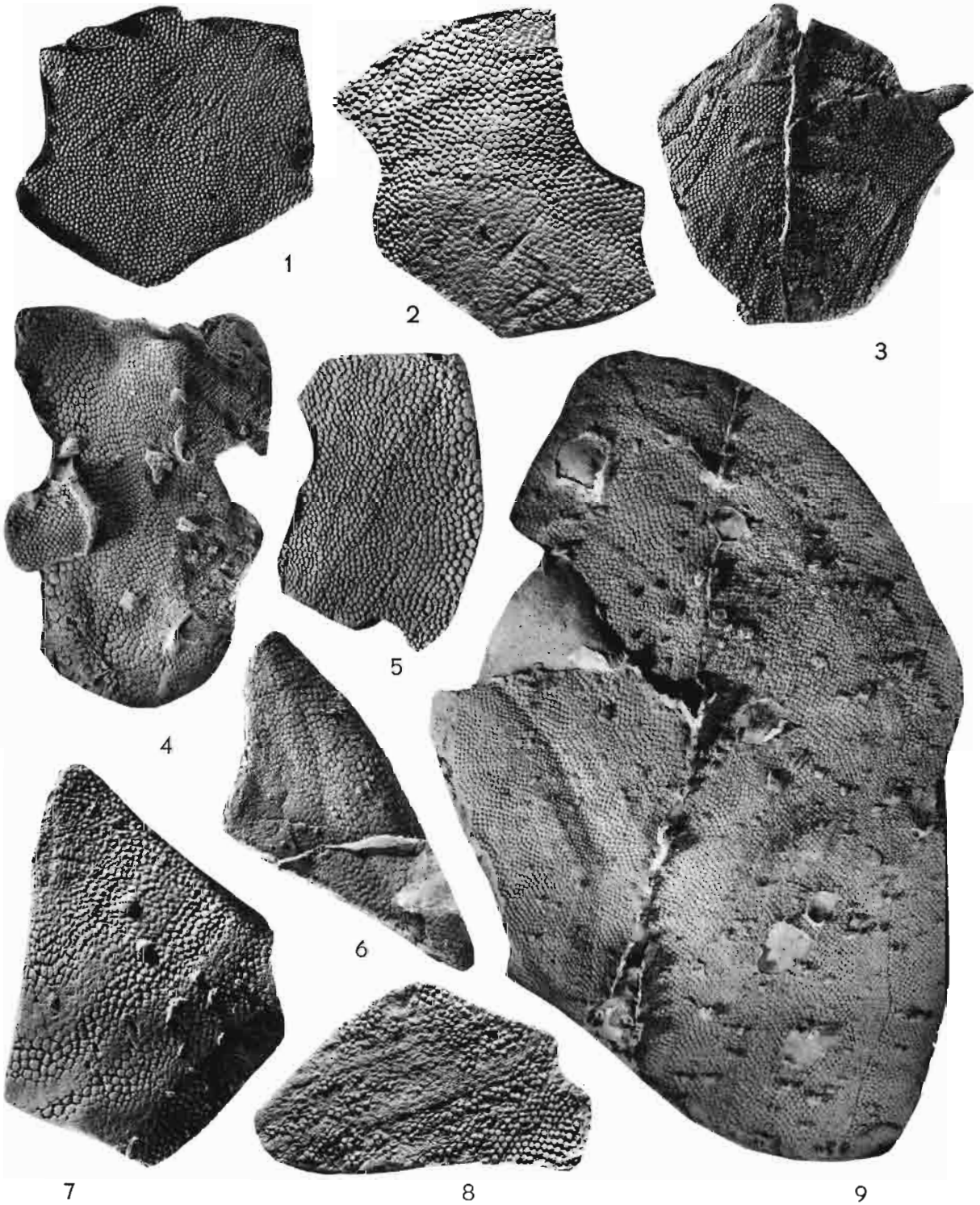
Guerichosteus kozlowskii TARLO 41

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

Fig. 1. Fragment of dorsal median plate (D. 2. U.W.); × 1.
Fig. 2. Fragment of ventral median plate (D. 5. U.W.); × 1·5.
Fig. 3. Cornual plate (D. 19. U.W.); × 1.
Fig. 4. Branchial plate (D. 11. U.W.); × 1·5.
Fig. 5. Fragment of branchial plate (D. 12. U.W.); × 1·5.
Fig. 6. Distal tip of branchial plate (D. 14. U.W.); × 1·5.
Fig. 7. Fragment of ventral median plate (D. 6. U.W.); × 1·5.
Fig. 8. Fragment of plate (D. 82. U.W.); × 1·5.
Fig. 9. Dorsal median plate (D. 1. U.W.); × 1.

Photo: N. Tanti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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE XI

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Guerichosteus kozlowskii TARLO 41

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

Fig. 1. Fulcral scale in external view (D. 25. U.W.); × 1·5.
Fig. 2. Fulcral scale in external view (D. 26. U.W.); × 1·5.
Fig. 3. Fragment of plate of lateral margin (D. 83. U.W.); × 1·5.
Fig. 4. Branchial plate (D. 13. U.W.); × 1·5.
Fig. 5. Fulcral scale in internal view (D. 28. U.W.); × 1·5.
Fig. 6. Body scale (D. 32. U.W.); × 1·5.
Fig. 7. Body scale (D. 33. U.W.); × 1·5.
Fig. 8. Body scale (D. 31. U.W.); × 1·5.
Fig. 9. Body scale (D. 34. U.W.); × 1·5.
Fig. 10. Oral plate in dorsal view (D. 23. U.W.); × 2·5.
Fig. 11. Fulcral scale in internal view (D. 30. U.W.); × 1·5.
Fig. 12. Fulcral scale in internal view (D. 29. U.W.); × 1·5.
Fig. 13. Fulcral scale in internal view (D. 27. U.W.); × 1.

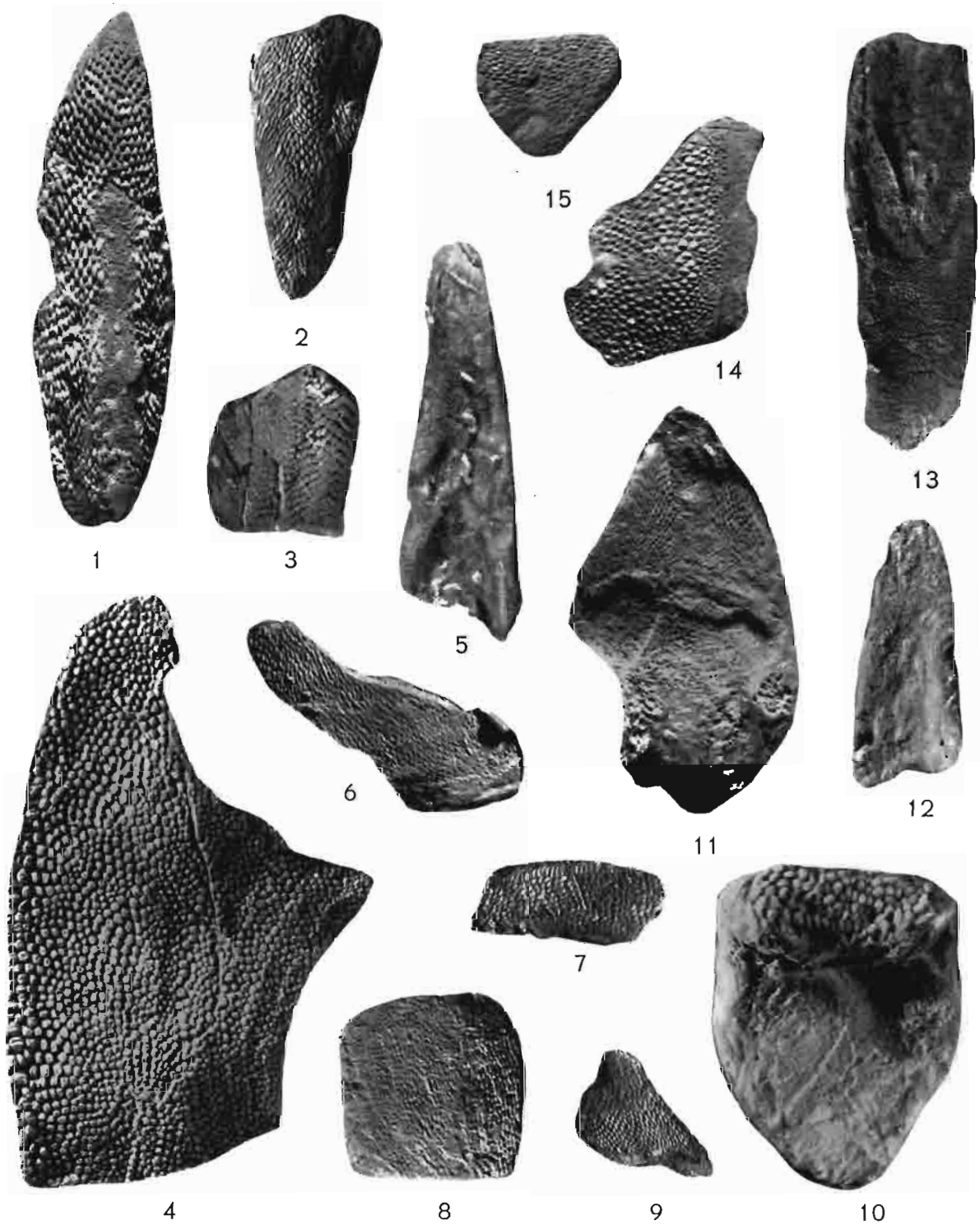
Hariosteus kielanae TARLO 52

Fig. 14. Body scale. Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone (D. 58. U.W.); × 1·5.

Guerichosteus kulczyckii TARLO 50

Fig. 15. Body scale. Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone (D. 44. U.W.); × 1·5.

Photo: S. Tanti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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE XII

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Guerichosteus kozlowskii TARLO 41

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

Fig. 1. Pineal plate (D. 22. U.W.); × 2.
Fig. 2. Fragment of plate of lateral margin (D. 84. U.W.); × 1·5.
Fig. 3. Ventral median plate in external view (D. 4. U.W.); × 1.
Fig. 4. Ventral median plate in internal view (D. 4. U.W.); × 1.

Photo: K. Taylor

Guerichosteus kotanskii TARLO 50

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

Fig. 5. Fragment, holotype, (D. 37. U.W.); × 1·5.
Fig. 6. Fragment (D. 40. U.W.); × 1·5.
Fig. 7. Fragment (D. 38. U.W.); × 1·5.

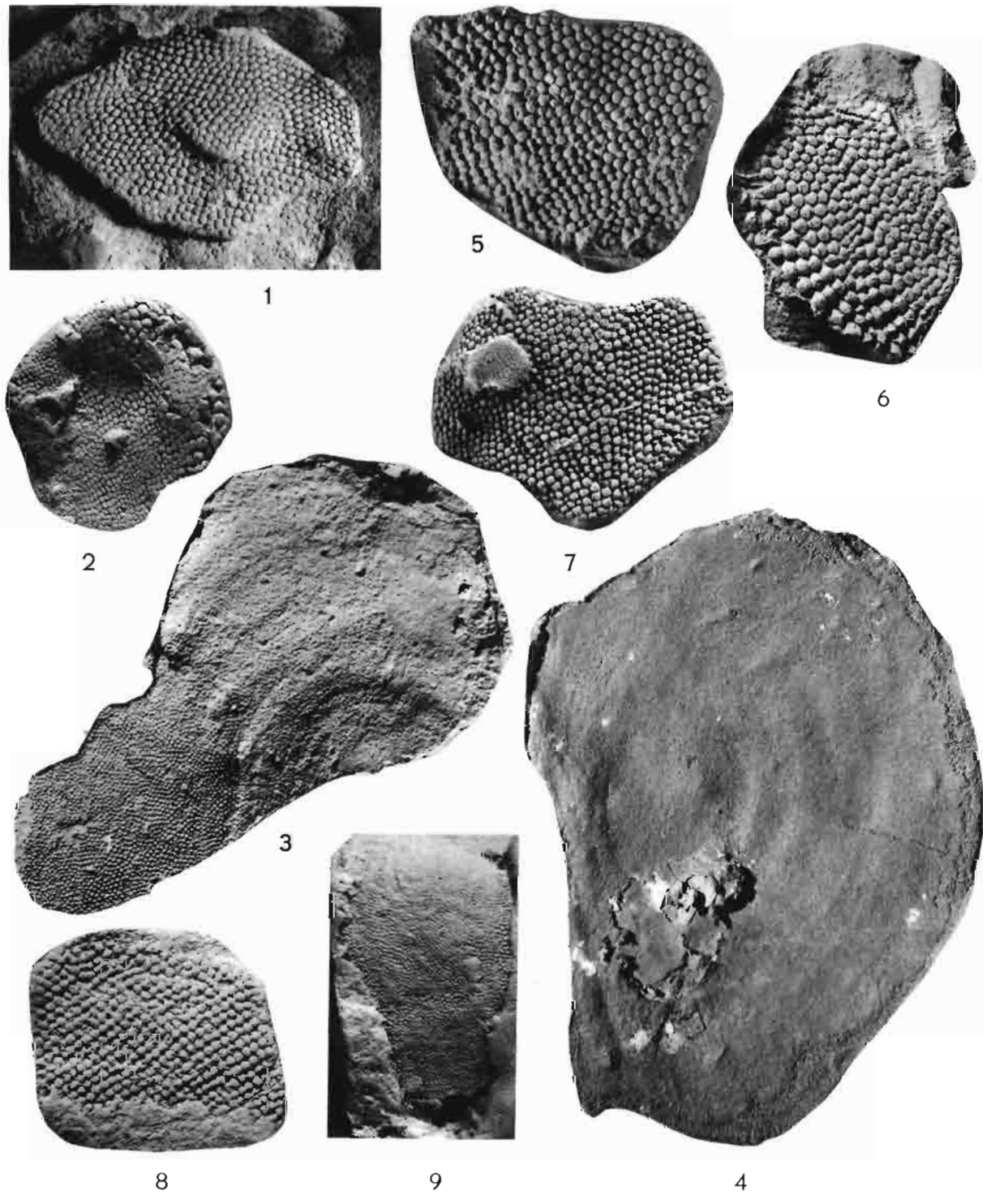
Photo: N. Tanti

Guerichosteus lefeldi TARLO 51

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

Fig. 8. Body scale (D. 47. U.W.); × 3.
Fig. 9. Fragment of ventral median plate, holotype (D. 45. U.W.); × 1·33.

Photo: W. Brackenbury



L. B. H. Tarlo: Psammosteiformes (Agnatha)

PLATE XIII

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Hariosteus kielanae TARLO 52

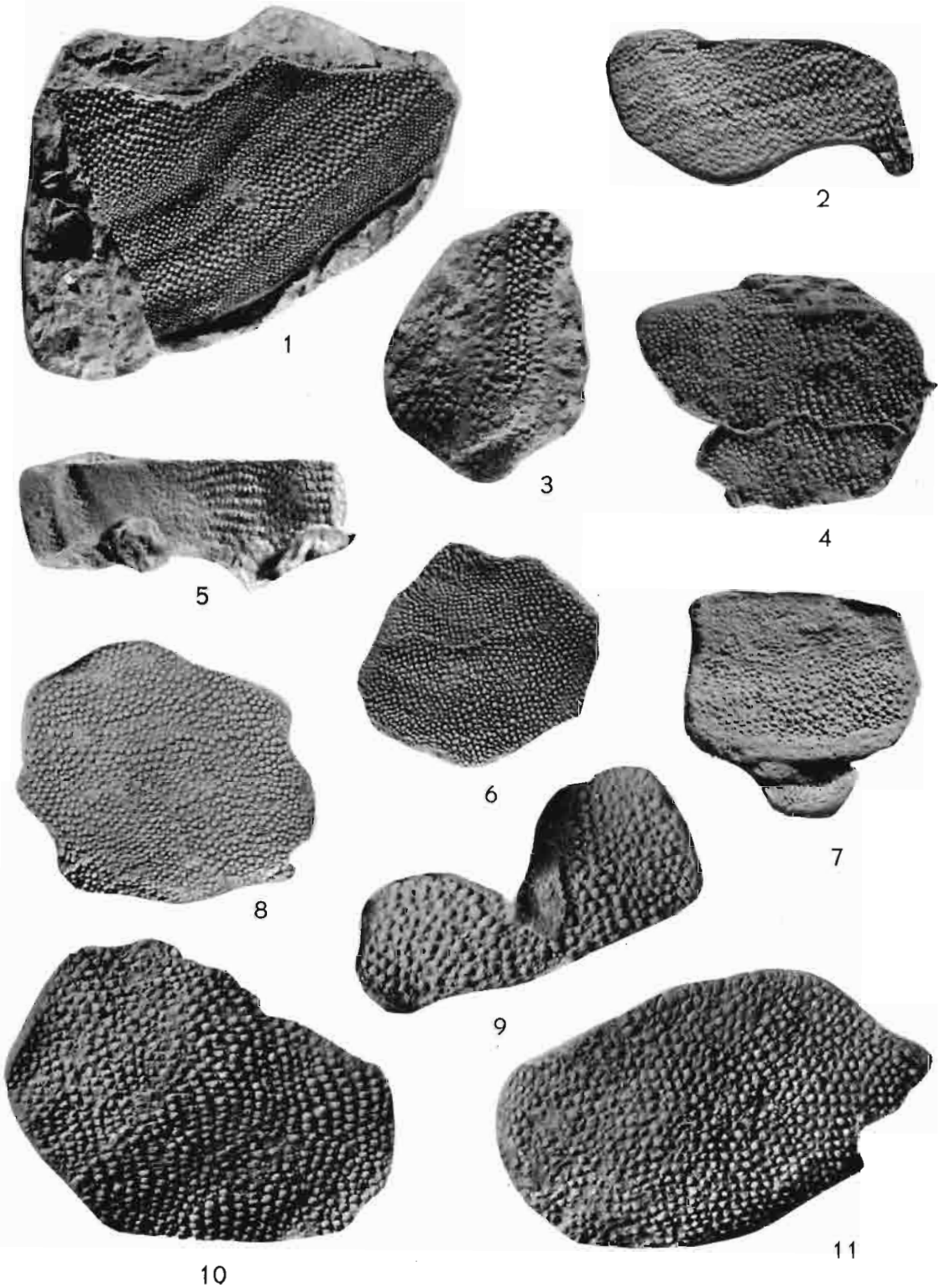
Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone

Fig. 1. Fragment of dorsal median plate, holotype (D. 48. U.W.); × 1.
Fig. 2. Fragment (D. 50. U.W.); × 1·5.
Fig. 3. Body scale (D. 85. U.W.); × 1·5.
Fig. 4. Fragment (D. 51. U.W.); × 1·5.
Fig. 6. Fragment of branchial plate (D. 55. U.W.); × 1.
Fig. 7. Body scale (D. 59. U.W.); × 1·5.
Fig. 8. Fragment (D. 54. U.W.); × 1·5.
Fig. 9. Fragment (D. 53. U.W.); × 1·5.
Fig. 10. Fragment (D. 52. U.W.); × 1·5.
Fig. 11. Branchial plate (D. 56. U.W.); × 1·5.

Hariosteus lobanowskii TARLO 55

Fig. 5. Branchial plate, holotype. Daleszyce, near Kielce, Holy Cross Mountains, central Poland; Lower Devonian, Emsian, Placoderm Sandstone (D. 60. U.W.); × 1.

Photo: N. Tanti



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

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

PLATE XIV

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Schizosteus perneri (RŮŽIČKA) 63

Fig. 1. Cast of left branchial plate, holotype. Holin, Hlubočepy, Prague, Bohemia; Middle Devonian, Givetian, Chotek limestones. Horizon gγ (G-g_3) (B.R./123-60. N.M.P.); × 1. (cast D. 78. U.W.). (N.M.D.); × 1.

?*Psammolepis granulata* (MCCOY) 112

Fig. 2. Fragment of plate, holotype. Kesh, River Banagh, County Fermanagh, Ireland; Yellow Sandstone (N.M.D.); × 1.

Psephaspis williamsi ØRVIG 38

Fig. 3. Fragment of plate showing superficial tesserae. Idaho, United States; Lower Devonian, ?Siegenian, Water Canyon Formation (D. 76. U.W.); × 1.

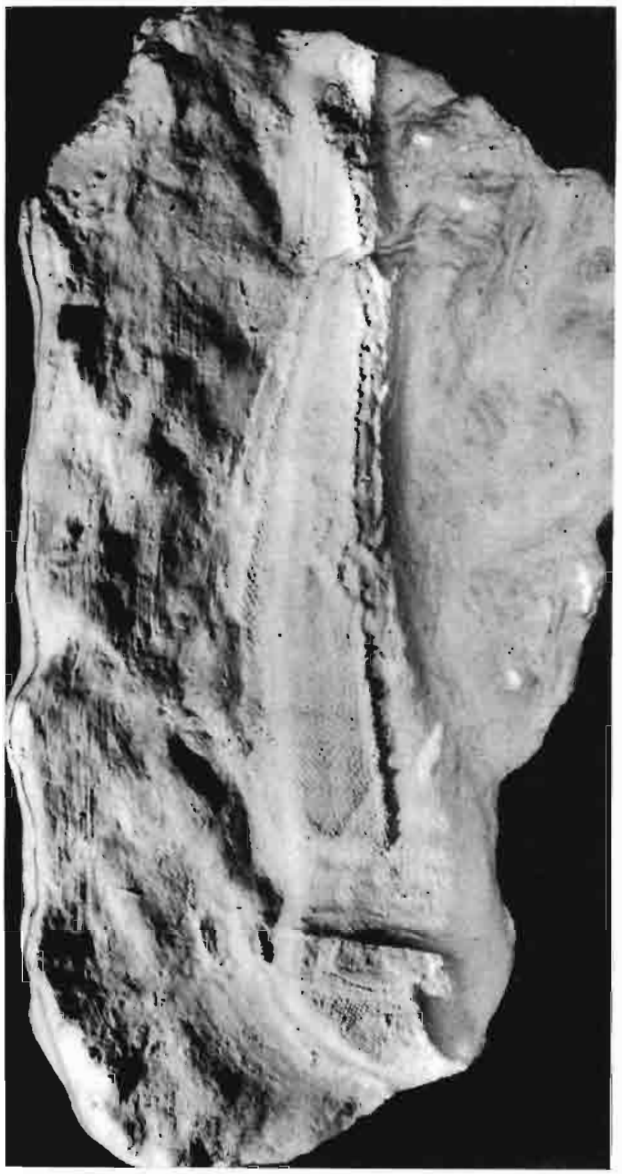
Schizosteus heterolepis (PREOBRAJENSKY) 57

Fig. 4. Branchial plate. Tori, Estonia; Middle Devonian, Givetian, Pernau horizon (A. 28130 a-d. P.M.O.); × 1.

Schizosteus wellsi TARLO 63

Fig. 5. Fragment of dorsal median plate. Idaho, United States; Middle Devonian, Eifelian (D. 77. U.W.); × 1.

Photo: K. Taylor



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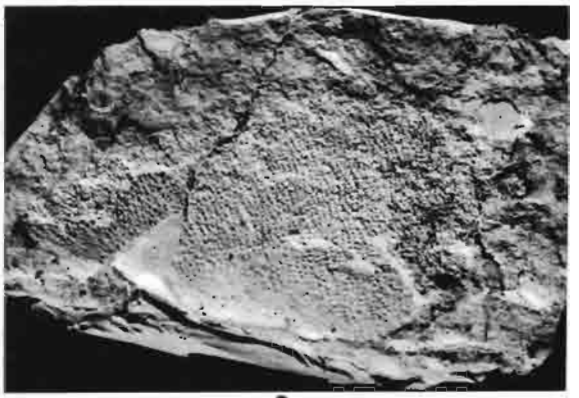

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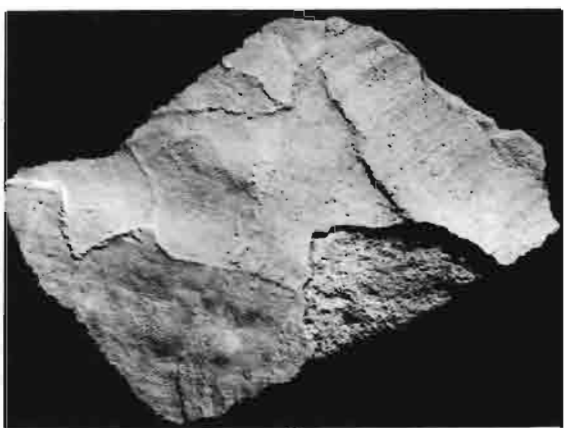

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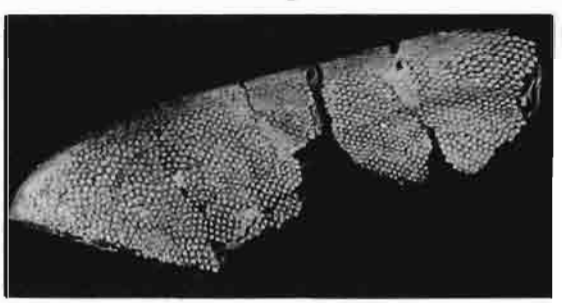

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L. B. H. TARLO: PSAMMOSTEIFORMES (AGNATHA)

PLATE XV

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Schizosteus striatus (GROSS) 60

Fig. 1. Left side of rostral plate with tesserae. Gorodenko, Estonia; Middle Devonian, Givetian, Narowa horizon (446. G.I.T.); × 1.

Fig. 2. Left branchial plate in dorsal view. Gorodenko, Estonia; Middle Devonian, Givetian, Narowa horizon (443. G.I.T.); × 1.

Psammolepis groenlandica TARLO 112

Fig. 3. Fragment showing ornamentation, holotype. Sydryggen, Canning Land, East Greenland; Middle Devonian, Givetian, Series with *Asterolepis save-soderberghi* (905. G.M.U.K.); × 2·5.

Psammosteus megalopteryx (TRAUTSCHOLD) 115

Figs. 4, 5. Right branchial plate, fig. 4 in ventral view, fig. 5 in dorsal view. Stolbovo, river Sjass, NW Russia; Upper Devonian, Frasnian, Shelon horizon (D. 80. U.W.); × 1.

Photo: K. Taylor

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

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

PLATE XVI

Page

Psammosteus megalopteryx (TRAUTSCHOLD) 115

Associated carapace, specimen figured by WOODWARD (1911, pl. 9, figs. 1-6) as *Psammosteus taylori* — Newton Quarry, Alves, Scotland; Upper Devonian, *Pst. megalopteryx* zone (P. 10956. B.M.); × 0·25.

Fig. 1. Dorsal median plate seen in internal view, showing distal portion of right branchial and traces of left post-orbital, branchial and cornual plates.

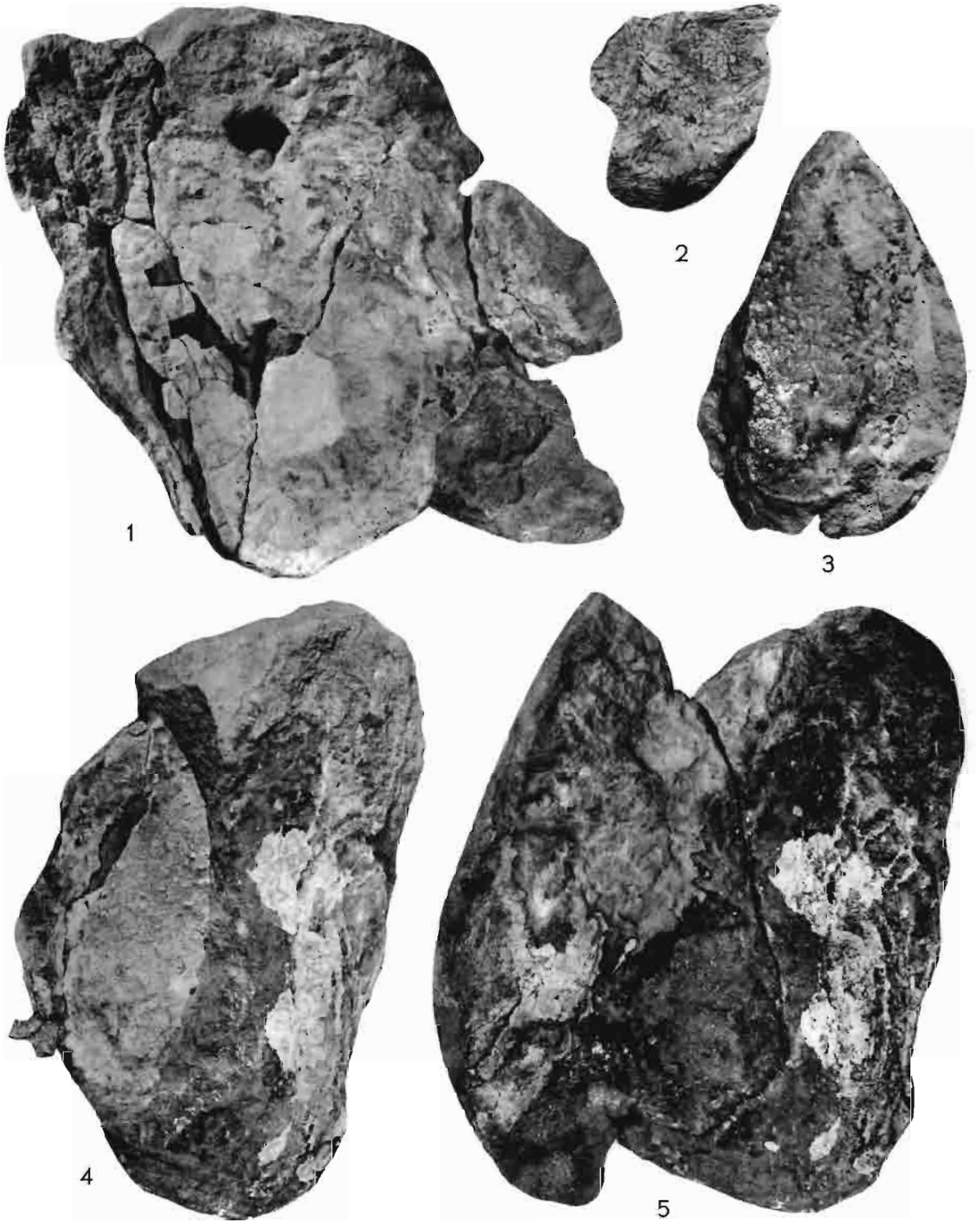
Fig. 2. Part of field of tesserae from area between ventral median plate and right lateral margin of carapace.

Fig. 3. Impression of internal surface of ventral median plate, showing on left side part of adjoining field of tesserae curving towards lateral margins.

Fig. 4. Ventral median plate seen in internal view with adjoining field of tesserae on the left side. The remains of the basal layer of the right half of dorsal median plate are seen in dorsal view.

Fig. 5. Same view of dorsal median plate as in Fig. 4 but with the addition of the left side. The lateral margin of the carapace is formed bythe post-orbital and branchial plates, and in places the field of tesserae between the dorsal median plate and the post-orbital is preserved together with traces of the cornual plate and squamation.

Photo: N. Tanti



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

PLATE XVII

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Traquairosteus pustulatus (TRAQUAIR) 150

Fig. 1. Fragment of median plate, holotype, specimen figured by TRAQUAIR (1897, pl. 11, fig. 3, 4) as *Psammosteus pustulatus*. Scaat Craig, Elgin, Scotland; Upper Devonian, *Pst. falcatus* zone (P. 8297. B. M.); × 1·5.

Psammolepis undulata (AGASSIZ) 103

Fig. 2. Part of ventral median plate, specimen figured by TRAQUAIR (1897, pl. 11, fig. 1, 2) as holotype of *Psammosteus tessellatus*. Kingsteps, Nairn, Scotland; Upper Devonian, *Psl. undulata* zone (1897.56.1 R.S.M.); × 1.

Psammosteus megalopteryx (TRAUTSCHOLD) 115

Fig. 3. Posterior part of dorsal median plate, showing sensory canal system, specimen figured by TARLO (1961, pl. 7, fig. 1). Newton Quarry, Alves, Scotland; Upper Devonian, *Pst. megalopteryx* zone (1960.9 R.S.M.); × 0·5.

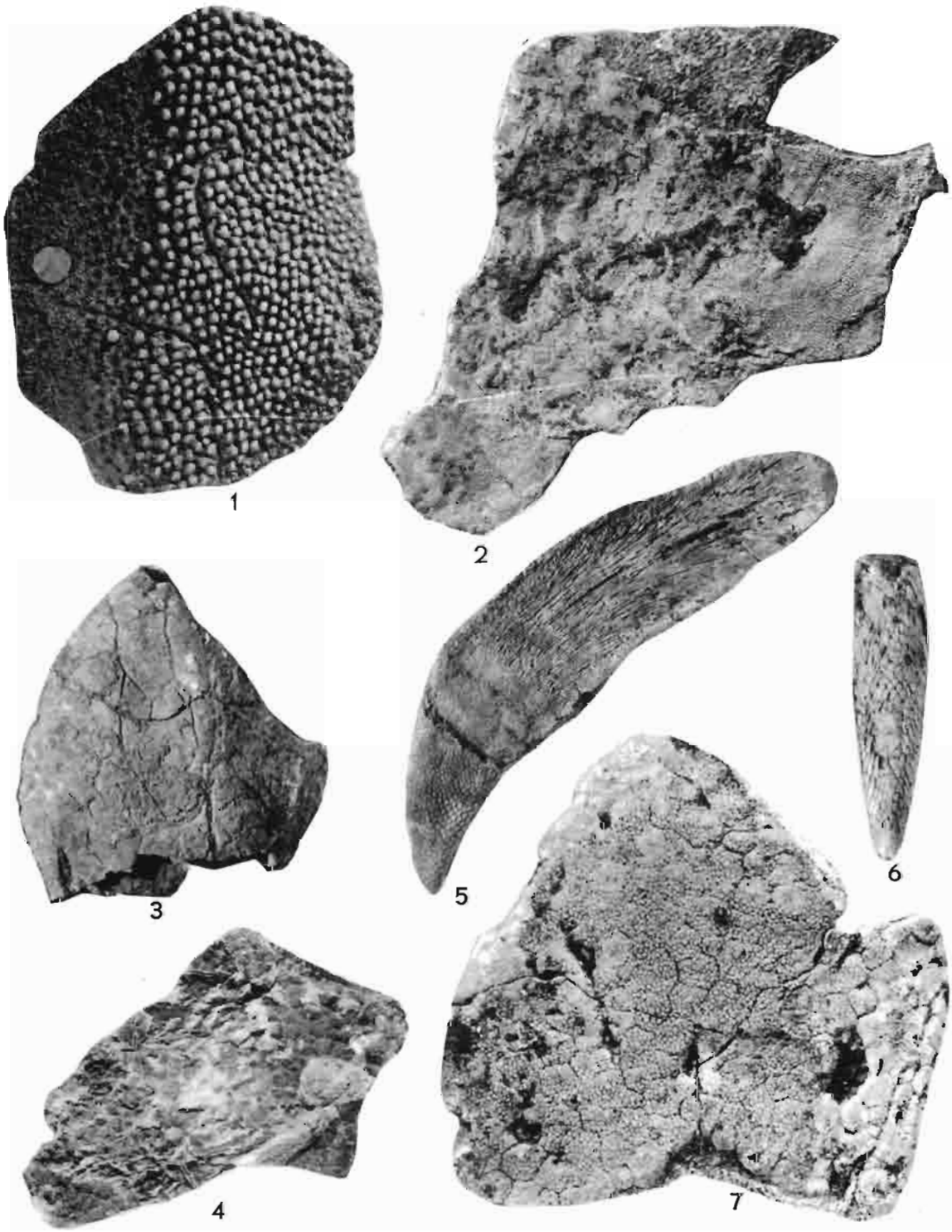
Fig. 4. Fragment of dorsal median plate, showing sensory canal system. Newton Quarry, Alves, Scotland; Upper Devonian, *Pst. megalopteryx* zone (1894.169.3. R.S.M.); × 0·5.

Fig. 5. Branchial plate, specimen figured by TARLO (1961, text-fig. 2). Whitemire, Scotland; Upper Devonian, *Pst. megalopteryx* zone (1904.2.10. R.S.M.); × 1.

Fig. 6. Fulcral scale. Findhorn, Scotland; Upper Devonian, *Pst.* megalopteryx zone (1904.2.11. R.S.M.); × 1·5.

Fig. 7. Fragment of dorsal median plate, showing superficial tesserae, specimen figured by TRAQUAIR (1897, pl. 11, fig. 5) as *Psammosteus taylori*. Newton Quarry, Alves, Scotland; Upper Devonian, *Pst. megalopteryx* zone (1900. 60.30. R. S. M.); × 1·5.

Photo: P. F. Green



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

PLATE XVIII

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Psammolepis paradoxa (AGASSIZ) 96

Fig. 1. Right branchial plate, *A* ventral view, *B* dorsal view. Wenden, Latvia; Upper Devonian, Frasnian, Gauja horizon (P. 7465. B. M.); × 0·5.

Pycnosteus palaeformis PREOBRAJENSKY 69

Fig. 2. Right branchial plate in dorsal view. Arukula, Estonia; Middle Devonian, Givetian, Arukula horizon (1894. 61.22. R.S.M.); × 0·5.

Psammosteus maeandrinus AGASSIZ 124

Fig. 3. Distal tip of immature branchial plate. Kokenhusen, near Riga, Latvia; Upper Devonian, Frasnian, Snetogor horizon (P. 17792. B.M.); × 2.

Fig. 4. Distal tip of immature branchial plate. Kokenhusen, near Riga, Latvia; Upper Devonian, Frasnian, Snetogor horizon (P. 17793. B.M.); × 2.

Psammosteus megalopteryx (TRAUTSCHOLD) 115

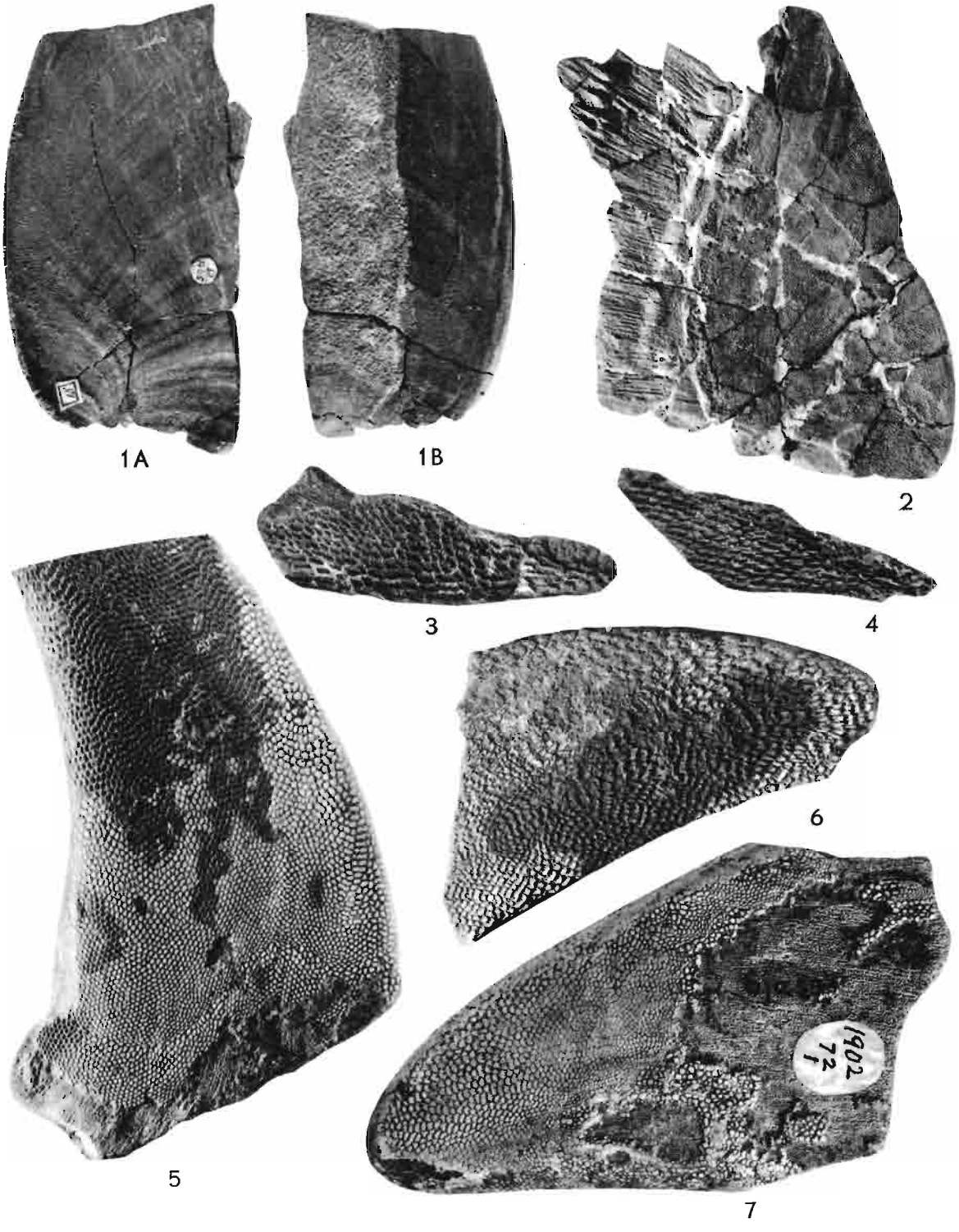
Fig. 5. Left branchial plate in dorsal view, showing well marked growth zone at proximal edge. River Sjass, NW Russia: Upper Devonian, Frasnian, Shelon horizon (P. 4493. B.M.); × 1·5.

Fig. 7. Right branchial plate in ventral view, showing branchial tesserae. River Sjass, NW Russia; Upper Devonian, Frasnian, Shelon horizon (1902.72.1. R.S.M.); × 1·5.

Psammosteus falcatus GROSS 134

Fig. 6. Right branchial plate in dorsal view, showing ornamentation. No locality details; Upper Devonian, Frasnian (P. 33990. B.M.); × 1·5.

Photo: P. F. Green



L. B. H. Tarlo: Psammosteiformes (Agnatha)

PLATE XIX

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Psammosteus waltergrossi nom. nov. 136

Fig. 1. Branchial plate showing ornamentation, lectotype. River Misti, Luga, NW Russia; Upper Devonian, Frasnian, *e* horizon (220/353. P.I.M.); × 3.

Psammosteus falcatus GROSS 134

Fig. 2. Distal tip of branchial plate showing ornamentation. River Luga, NW Russia; Upper Devonian, Frasnian, *e* horizon (P.I.M. colln.); × 3.

Fig. 4. Left branchial plate. River Luga, NW Russia; Upper Devonian, Frasnian, *e* horizon (220/327. P.I.M.); × 0·3.

Psammosteus praecursor OBRUCHEV 127

Fig. 3. Left branchial plate. NW Russia; Upper Devonian, Frasnian, Amata horizon (P.I.M. colln.); × 0·5.

Psammosteus maeandrinus AGASSIZ 124

Fig. 5. Right branchial plate, neotype, specimen figured by OBRUCHEV (1947*b*, pl. 51, figs. 3, 4). Andoma, NW Russia; Upper Devonian, Frasnian, Snetogor horizon (220/684. P.I.M.); × 0·5.

Psammosteus megalopteryx (TRAUTSCHOLD) 115

Stolbovo, NW Russia; Upper Devonian, Frasnian, Shelon horizon

Fig. 6. Superficial polygonal tesserae showing secondary healing of cavity due to loss of tessera (220/546. P.I.M.); × 3.

Fig. 7. Branchial plate showing ornamentation (P.I.M. colln); × 3.

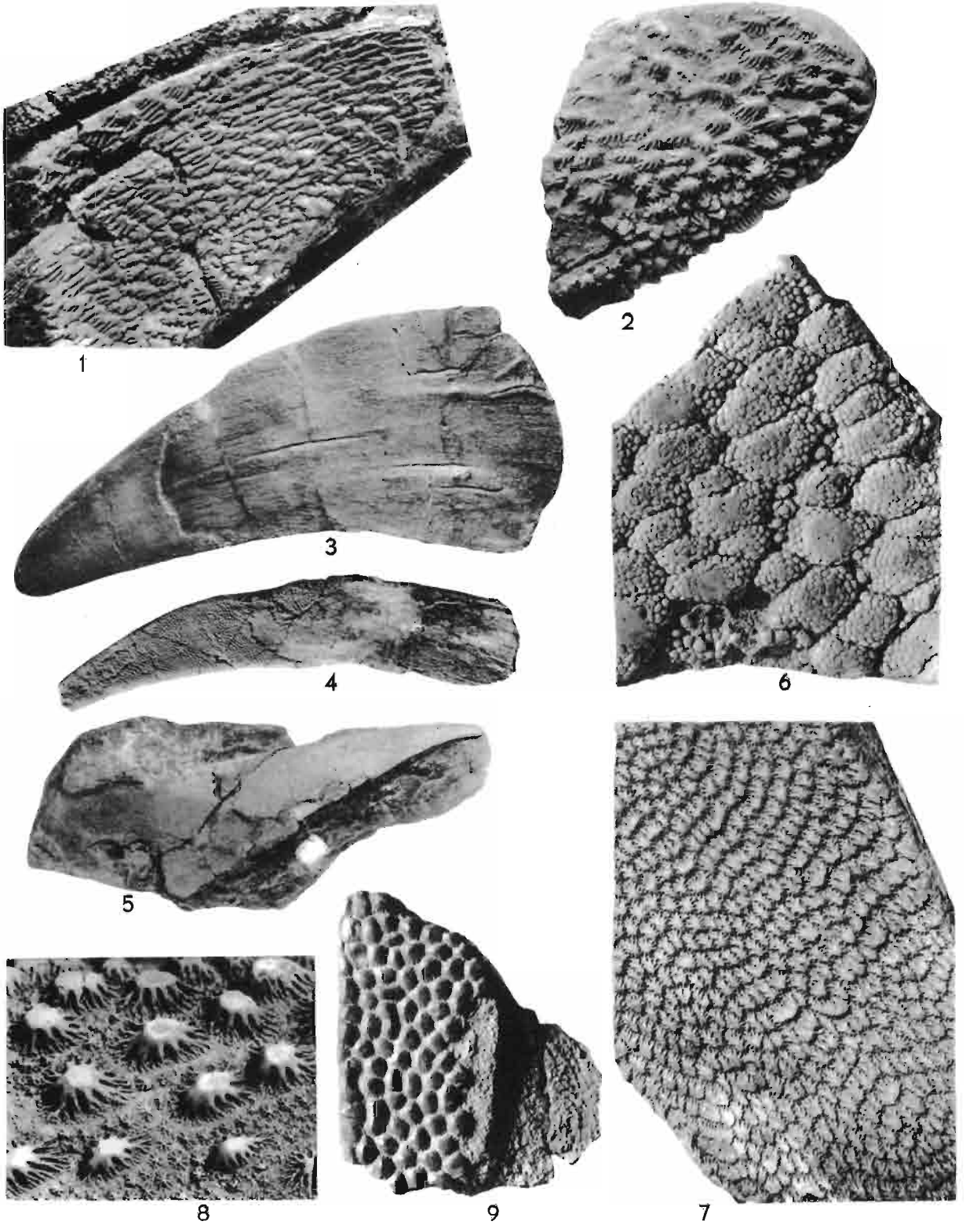
Ganosteus stellatus ROHON 79

Fig. 8. Branchial plate showing ornamentation, specimen figured by TARLO (1962*b*, text-fig. 2). Lejeji, Latvia; Upper Devonian, Frasnian, Gauja horizon (176. G.I.T.); × 3.

Psammolepis aerata OBRUCHEV 111

Fig. 9. Branchial plate showing ornamentation, holotype. Milodej, NW Russia; Upper Devonian, Frasnian, Amata horizon (220/527. O.I.M.); × 3.

Photos: from D. Obruchev



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

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