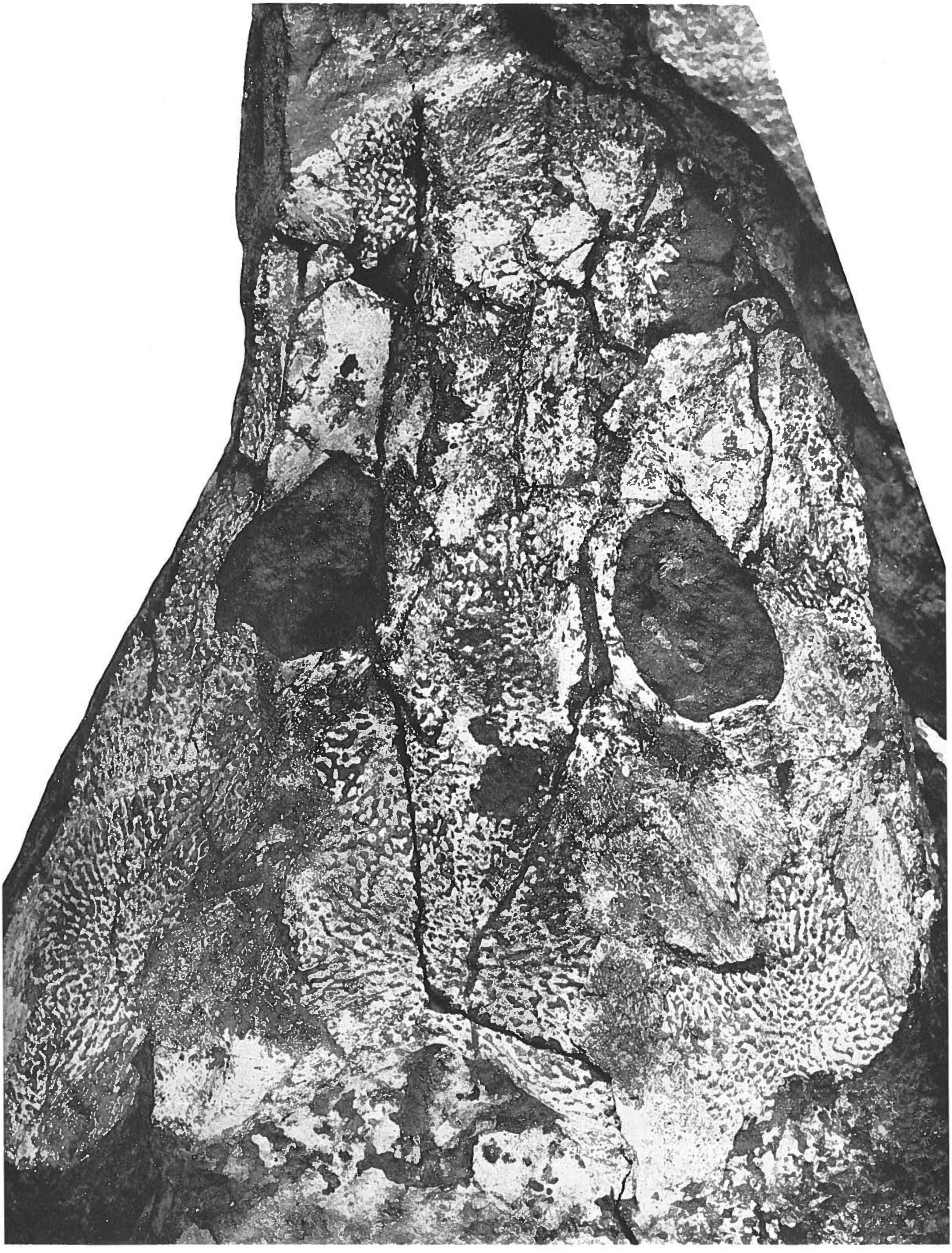


Palaeovertebrate faunas of Greenland

Svend Erik Bendix-Almgreen

Introduction

Palaeontology has a tradition in Greenland reaching back to the eighteenth century (Cranz, 1765; Stauning, 1775; see also Giesecke, 1910) and serious research and collecting work, primarily in the field of palaeobotany, started around 1850. Vertebrate palaeontology, however, manifested itself comparatively late due to the fact that most of the important vertebrate yielding deposits are located on the east coast of Greenland north of latitude 70° in a region where access is extremely difficult and depends on large-scale, well organised expeditions. Such prerequisites became available in the 1920s when Danish expeditions started scientific work in central East Greenland under the leadership of the late Dr Lauge Koch. Teams headed by vertebrate palaeontologists were established at an early date as part of these expeditions, and were rewarded with the discovery of well preserved fossil vertebrates, in some cases whole faunas, ranging in age from Middle Devonian to Quaternary. These finds included, as the highlight, the discovery of the World's oldest known amphibians – the Upper Devonian ichthyostegalians – which perhaps represents the most important advance in the field of vertebrate palaeontology in our century. Greenland may still be regarded as a potential source area for new and important discoveries of fossil vertebrates. This has been exemplified in recent years by finds of Lower Silurian agnathans in North Greenland.

Fig. 439. *Ichthyostega*, the World's oldest known tetrapod, so far found only in the Upper Devonian Old Red deposits (*Remigolepis* series) of central East Greenland, is illustrated here by a well preserved skull roof (A. 64; Mineralogical Mus. Coll., Copenhagen) reproduced in approx. nat. size. Photo: E. Jarvik 1974.

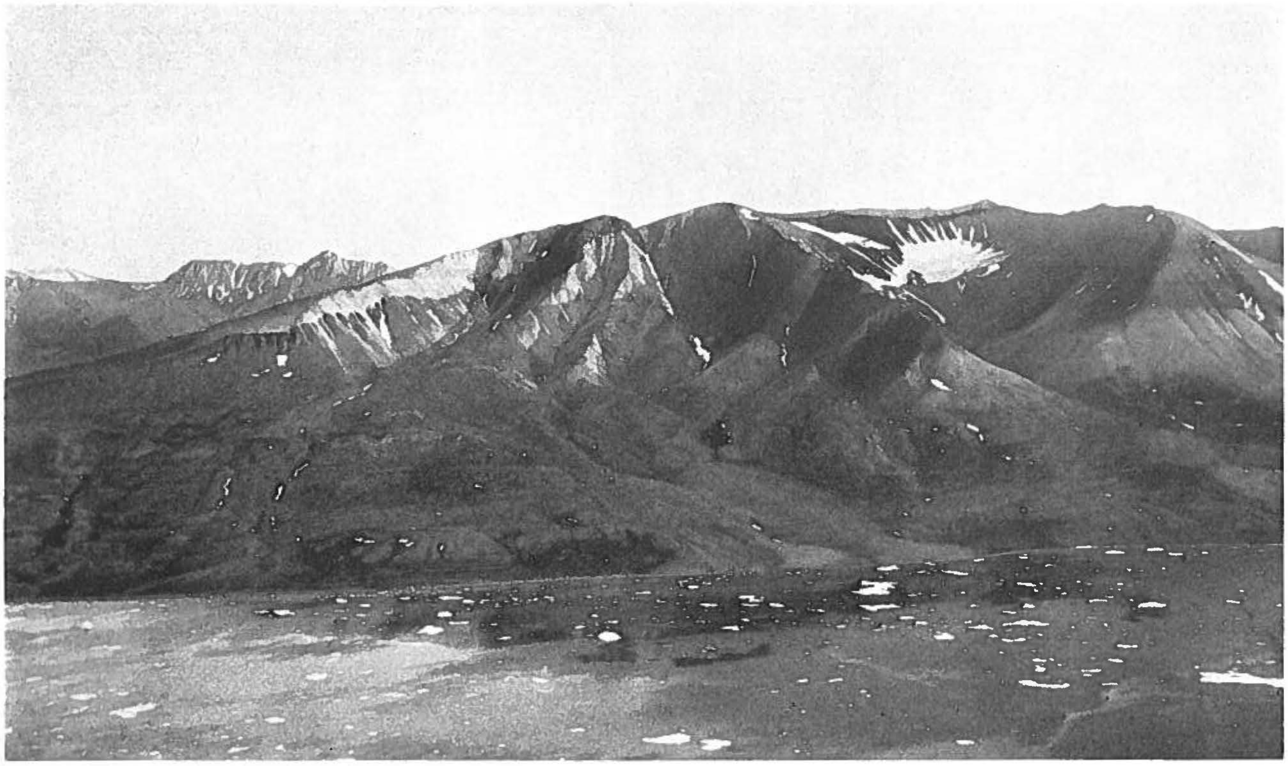


Fig. 440. Celsius Bjerg seen from the north. It was from here that Nathorst, in 1899, brought home those few vertebrate fossils which established the presence of Devonian rocks in East Greenland. Here also lie the localities that yielded the first determinable ichthyostegalian remains. Photo: J. Fabricius 1974.

Silurian

The recent discovery of anaspid remains in Llandoverian (*Monograptus spiralis* Zone) or early Wenlockian deposits described by Norford (1972) east of Kap Tyson in Hall Land, North Greenland has considerably extended the history of vertebrates in Greenland back in time. According to Norford the vertebrate yielding deposits are equivalent in age to the Cape Phillips Formation (Thorsteinsson, 1958) found from Cornwallis Island to eastern Ellesmere Island in the Arctic Archipelago. The occurrence of anaspid agnathans in these marine deposits in Greenland is in good agreement with Norford's correlation since abundant remains of large anaspids have also been found in the Cape Phillips Formation on Cornwallis Island. Here they occur somewhat above the *Monograptus spiralis* Zone (Thorsteinsson, 1958, p. 99), i. e. roughly at the same stratigraphic level as those from Hall Land.

Devonian

The first Devonian vertebrates from Greenland were discovered by the Swedish palaeobotanist and geologist A. G. Nathorst who led an expedition along the East Greenland coast in search for possible survivors of the ill-fated 'Andrée expedition' in the summer of 1899. The Nathorst expedition visited the Kap Graah area and Celsius Bjerg in the eastern part of Ymer Ø (figs 440, 441), where a few fossils were found (Nathorst, 1900). According to Woodward (1900) these fossils included *Asterolepis incisa* and *Holoptychius nobilissimus* and indicated an Upper Devonian age for the deposits.

In 1929 and 1930 Norwegian and Danish expeditions independently explored the Devonian deposits in various places along Kejser Franz Josephs Fjord, Dusén Fjord and Kong Oscars Fjord and found them to be very rich in vertebrate fossils.

Since then collections of Devonian fossil vertebrates comprising more than 10 000 specimens have been brought together by teams of vertebrate palaeontologists and geologists.

The Devonian strata of East Greenland attain a thickness of more than 7000 m and comprise both volcanic rocks and continental sediments of limnic-fluviatile origin (Henriksen & Higgins, this volume). They are exposed in an almost 250 km long zone extending from about 72°20′N in Scoresby Land to approximately 74°25′N in Steno Land. The zone has its greatest east-west width (about 90 km) in the area around Kejser Franz Josephs Fjord and covers approximately 5600 km². Outside this main area a small inlier occurs in the Canning Land – Wegener Halvø area (figs 441, 442).

In addition to vertebrates the fossil fauna includes only *Estheria* (found in the Middle Devonian Vilddal series; Table 29). Fossil plants are relatively abundant at certain horizons but they are, as a whole, poorly preserved (Raunsgaard Pedersen, this volume). Age determination of the deposits rests therefore exclusively on the vertebrate material which indicates that the strata range from the upper Middle Devonian to the upper Upper Devonian. There are, on the other hand, gaps in the sequence, and considerable parts, such as the Lower Sandstone Complex (Table 29), are poor in fossils or even unfossiliferous.

To the now classical vertebrate fauna from the Devonian of East Greenland has recently been added one of early Devonian age, which was discovered in samples from Hall Land, North Greenland (Bendix-

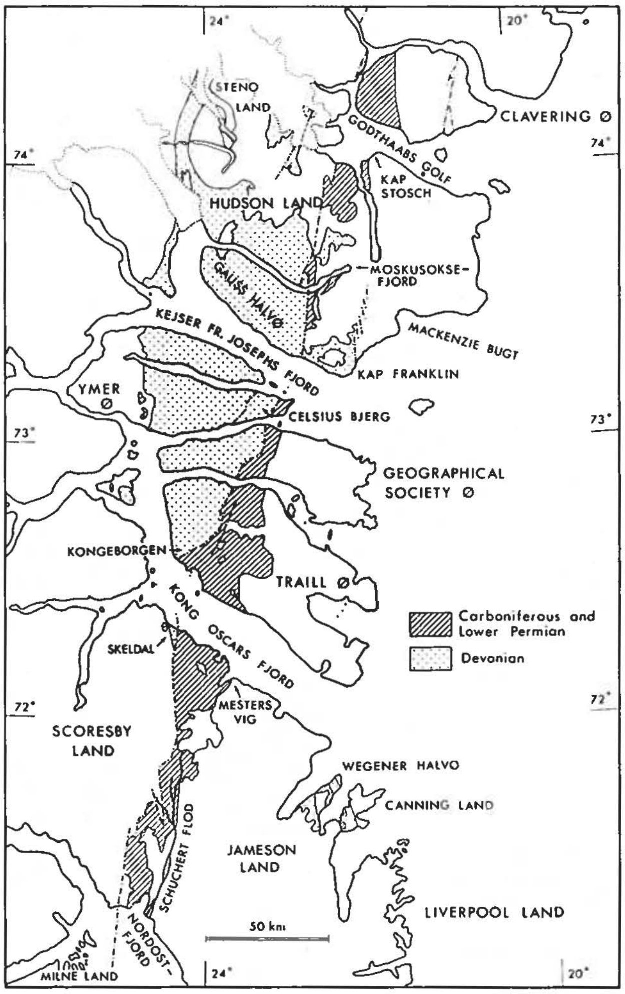
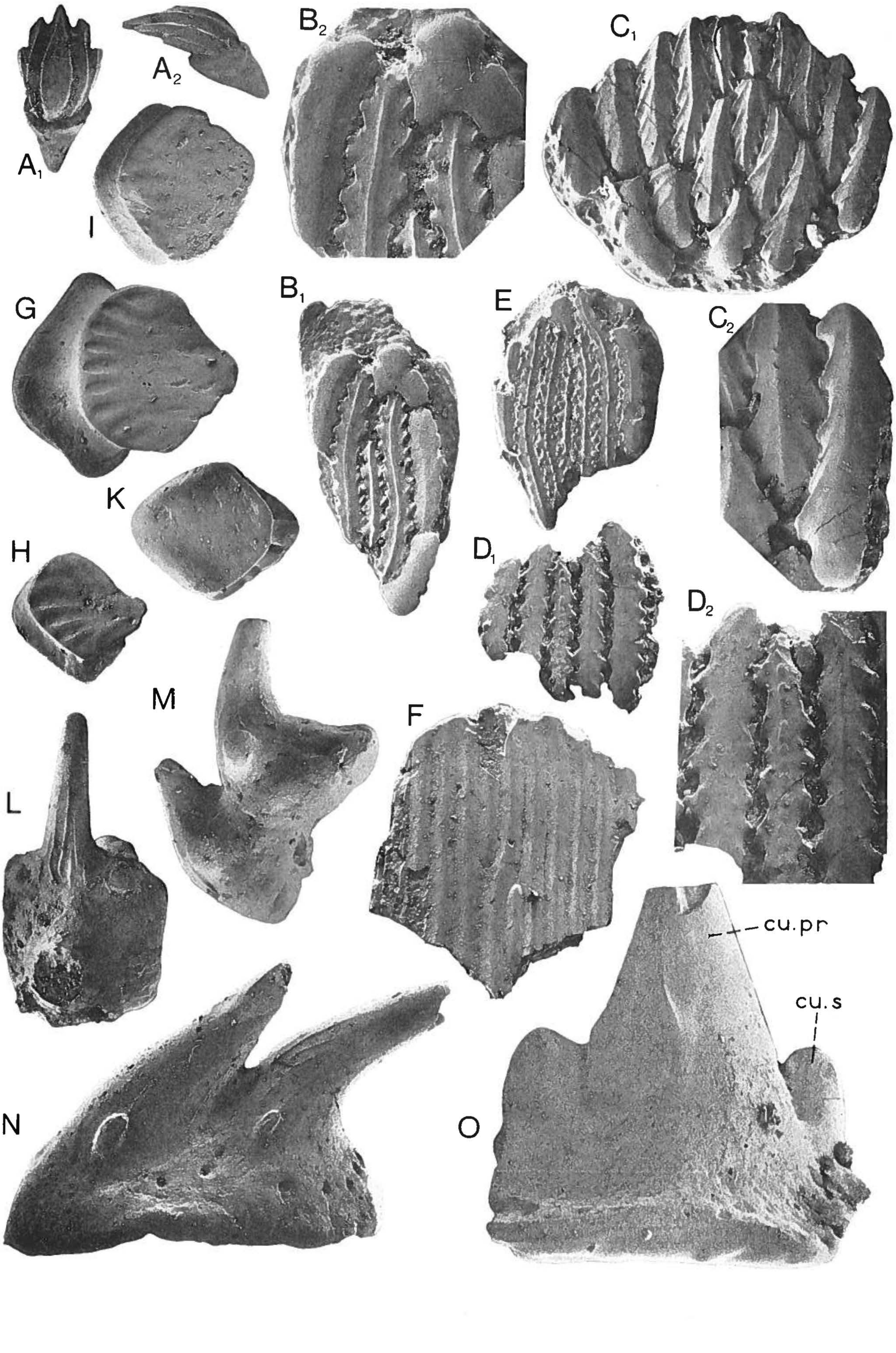


Fig. 441. Distribution in central East Greenland of Middle and Upper Devonian, Carboniferous and Lower Permian deposits. Map redrawn and modified from Bütler (1961).

Fig. 442. View eastwards from the summit of Kollen showing the Middle Devonian strata on Hesteskoen and Sydryggen on Canning Land. Photo: S. E. Bendix-Almgreen 1956.



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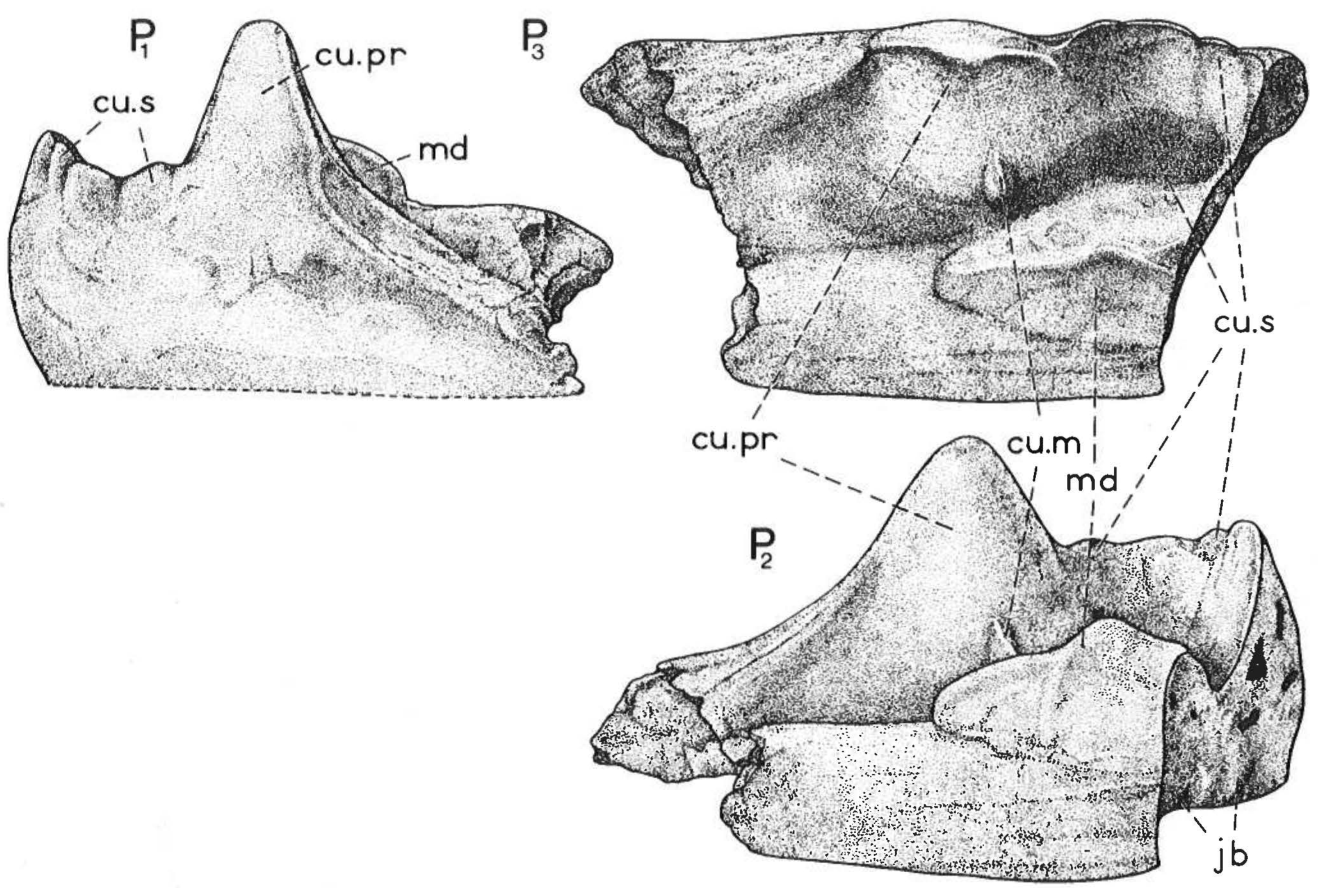

Fig. 443. SEM-micrographs and drawings of detached dermo-skeletal elements of some lower vertebrates from early Devonian deposits in Hall Land, North Greenland. Thelodonti. A: Scale of thelodontid, reminiscent of *Thelodus trilobatus*, shown in superficial (A_1) and lateral (A_2) view; *c.* × 70. Heterostraci. B-E: *Oniscolepis* ? sp., scutes (partly fragmentary) in superficial view, displaying a dentine ridge pattern (B_1, C_1, D_1, E; *c.* × 33) and a variation in the shape and ornamentation of the individual dentine ridges (shown in *c.* 66 × magnification on B_2, C_2 and D_2) which are very similar to that of *Oniscolepis* sp. indt., figured by Gross (1961). F: *Poraspis* sp.; *c.* × 33. Acanthodii. G-K: Scales of the *'Gomphodus'* and *'Poracanthodes'* types, orientated with their anterior part pointing to the left and shown in superficial (G-I; *c.* × 62) and basal (K; *c.* × 60) view. L-N: Tooth-whorls of the *'Gomphodus'* (*'Plectrodus'*) type shown in superficial (L) and lateral (M-N) view; *c.* × 63. O-P: *Nostolepis* sp., fragments of dentigerous jawbones shown in medial (O, P_2), oblique lateral (P_1), and superficial (P_3) view; *c.* × 66.

Specimens from GGU 82737 (E, G-L, N) and 82738 (A-D, F, M, O-P). *cu.m*, *cu.pr*, *cu.s*, medial side cusp, and principal tooth-cusp and side cusps; *jb*, dentigerous jaw-bone; *md*, small tooth anchylosed to jaw-bone.

Almgreen & Peel, 1974). The fossiliferous deposits are of *marine* origin and contain also a variety of invertebrate fossils.

Early Devonian vertebrates from North Greenland

A preliminary examination of the newly discovered fauna, yielded by samples treated with acetic acid, revealed the presence of thelodonts, heterostracans and acanthodians which were all represented by detached dermal elements such as scales, scutes and tooth-bearing bones. Heterostracan remains were found in lesser quantities than those of both thelodonts and acanthodians.

Thelodonts. Several types of scales belonging to this still insufficiently known group have been detected in the Hall Land material and so far constitute the only occurrence of thelodonts in Greenland. Among the scale types may be mentioned some that are reminiscent, by and large, of species described and referred to such genera as *Thelodus* (e. g. *Thelodus trilobatus*, fig. 443 A_{1-2}) and *Logania* (e. g. *Logania kummerowi* and *Logania scotia* = in part *'Thelodus scoticus'* Gross, 1967; references are given by Bendix-Almgreen & Peel, 1974).

Heterostracans. The samples have yielded some fragments of shields and/or scutes belonging to representatives of the Heterostraci. This group has hitherto been known in Greenland only from a single fragment of a drepanaspid detected in Middle Devonian material from East Greenland. Among the new early Devonian material are fragments of cyathaspids which almost certainly belong to *Poraspis* (fig. 443 F). There are also some small, more or less fragmentary, scutes which in the distribution pattern and size of their dentine-ridges are very suggestive of plates or scutes of the so-called *Oniscolepis* (*Strosipherus*) as described and figured by Gross (1961). The dentine-ridges show a most distinctive marginal crenulation and surface ornamentation (fig. 443 B_1–E). With due regard to the limited information available about *Oniscolepis* (no articulated specimen has so far been found of this form) the writer prefers to designate the scutes under consideration as *Oniscolepis* ? sp., as did Ørvig (1969) for somewhat similar material from the Frænkelryggen Formation (Vestspitsbergen).

Acanthodians. Ischnacanthid remains such as scales of the '*Gomphodus*' and '*Poracanthodes*' types (fig. 443 G–K) and tooth-whorls of the '*Gomphodus*' (or '*Plectrodus*') type (fig. 443 L–N) are abundant in the Hall Land material. It is, therefore, surprising to find that those fragments which could be identified as parts of dentigerous jaw-bones show the distinctive feature (i. e. the more or less triangular cross-sections of the principal tooth cusps; fig. 443 O–P) of the *Nostolepis*-type of such elements (Gross, 1957; Ørvig, 1967). A variety of *Nostolepis* scales are present in the material, resembling in shape and ornamentation of their crowns and in their thick, rounded bases, those generally referred to as *Nostolepis striata* and *Nostolepis gracilis.* Finspine fragments that may perhaps belong to *Nostolepis* are also present. However, none of the several tooth-whorls in the material have the 'blattförmig' tooth cusps which Gross (1957) considered to be diagnostic for such elements in *Nostolepis.* The limited quantity of material available at present may, on the other hand, easily be responsible for this peculiar circumstance.

Concluding remarks. The new vertebrate fauna from Hall Land is still insufficiently known for biostratigraphic purposes. No osteostracan or anaspid remains have so far been detected in the material and the current yield of heterostracans is poor. There is no reason to suggest that the apparent poverty of the fauna will reflect the actual situation when more material becomes available for investigation. With due regard to its present limitations, the Hall Land vertebrate fauna agrees in its general composition with late Silurian – early Devonian vertebrate faunas occuring elsewhere (Vestspitsbergen, the Anglo-Welsh borderland, the Baltic area). In particular, one may suspect that increasing knowledge of the new fauna from Greenland will show this to be closely related to the large and varied vertebrate fauna discovered in recent years in the lower member of the Peel Sound Formation in the Canadian Arctic Archipelago (Thorsteinsson, 1958, 1967; Thorsteinsson & Tozer, 1963; Broad, 1973; Broad & Dineley, 1973).

In conclusion, the new fauna under consideration has yielded no evidence to prevent acceptance of the early Devonian age indicated by monograptids (*Monograptus* sp. of *M. transgrediens* type and *Monograptus* cf. *M. aequabilis*) found in strata *below* the vertebrate-bearing beds in the Hall Land sequence.

Devonian vertebrates from East Greenland

The vertebrate fauna comprises all the principal groups of lower vertebrates, many of which are represented in the collections by comprehensive material. The faunal list of all vertebrate forms known at present from the Middle and Upper Devonian of East Greenland is considerable.

Drepanaspida
- *Psammolepis groenlandica* Tarlo

Euarthrodira
- *Heterostius groenlandicus* Stensiö
- *Homostius kochi* Stensiö
- *Phyllolepis orvini* Heintz
- *Phyllolepis nielseni* Stensiö
- *Grönlandaspis mirabilis* Heintz
- Coccosteomorph cf. *Clarkeosteus halmodeus* (Clarke)

Antiarchi
- *Asterolepis säve-söderberghi* Stensiö
- *Asterolepis* sp.
- *Bothriolepis grönlandica* Heintz
- *Bothriolepis jarviki* Stensiö
- *Bothriolepis nielseni* Stensiö
- *Remigolepis incisa* (Woodward)
- *Remigolepis cristata* Stensiö
- *Remigolepis acuta* Stensiö
- *Remigolepis kochi* Stensiö
- *Remigolepis kullingi* Stensiö
- *Remigolepis* spp.

Elasmobranchii
- *Cladodus* sp.

Ichthyodorulites
- *Onchus* sp.

Acanthodii
- Acanthodii g. et sp. indet.

Dipnoi
- *Oervigia nordica* Lehman
- *Jarvikia arctica* Lehman
- *Soederberghia groenlandica* Lehman
- *Nielsenia nordica* Lehman
- ? *Soederberghia*
- ? *Dipterus*

Actinopterygii
- Palaeonisciformes g. et sp. indet.

Porolepiformes
- *Glyptolepis groenlandica* Jarvik
- *Holoptychius* sp.

Osteolepiformes
- *Gyroptychius groenlandicus* (Säve-Söderbergh)
- Osteolepiform cf. *Thursius macrolepidotus* (Sedgwick & Murchison)
- *Eusthenodon wängsjöi* Jarvik
- Osteolepiform cf. *Eusthenopteron*

Tetrapoda
- *Ichthyostega stensiöi* Säve-Söderbergh
- *Ichthyostega watsoni* Säve-Söderbergh
- *Ichthyostega eigili* Säve-Söderbergh
- ? *Ichthyostega kochi* Säve-Söderbergh
- *Ichthyostega* spp.
- *Ichthyostegopsis wimani* Säve-Söderbergh
- *Acanthostega gunnari* Jarvik

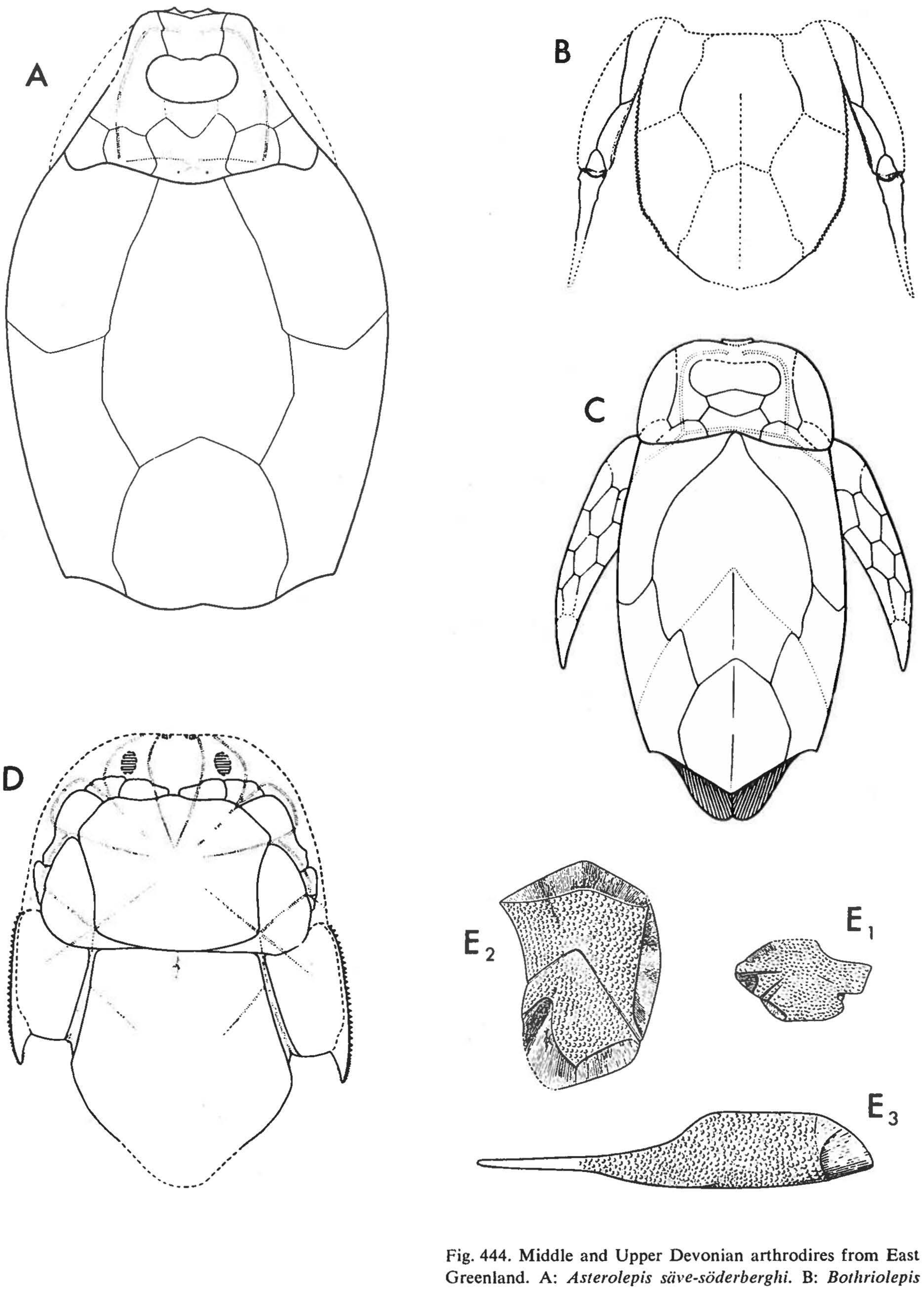

Fig. 444. Middle and Upper Devonian arthrodires from East Greenland. A: *Asterolepis säve-söderberghi*. B: *Bothriolepis nielseni*. C: *Remigolepis* sp. D: *Phyllolepis orvini*. E_{1-3}: *Grönlandaspis mirabilis* (E_1: Central plate, upper view; E_2: Posterior dorsolateral plate, lateral view; E_3: Posterior ventrolateral plate, lateral view). All figs *c.* × 0.5. Reproduced from: Stensiö (1936, 1939, 1948); Stensiö & Säve-Söderbergh (1938); Miles (1964).

Fig. 445. *Cratoselache pruvosti*, Lower Viséan, Mabre noir de Denée. Cast of type specimen, cat. no. 233, Coll. Abbaye de Maredsous; *c.* × 0.5.

Mk, Meckel's cartilage; *Sc. co*, scapulocoracoid; *a. pr. pq*, articular area for palatoquadrate; *fa*, facet on postorbital process; *f. bhy*, bucco-hypophysial foramen; *ot-oc*, ventral side of otoccipital part of the compressed, fractured and somewhat distorted braincase; *pq*, palatoquadrate; *pr.po*, postorbital process seen from the ventral side; *ra*, pectoral fin radials; *sb.sh*, ventral side of orbital region of braincase possessing, on both sides, a strongly developed suborbital shelf (*Cratoselache* is in this particular feature, as incidentially in several other cranial features, very reminiscent of *'Cladodus' wildungensis*, cf. Gross, 1937); *t*, teeth enveloped in matrix.

Ostracoderms, elasmobranchs, acanthodians and palaeonisciforms are rare. A single dermal bone fragment of the drepanaspid *Psammolepis* has been found in the *Asterolepis säve-söderberghi* series in Canning Land (Ørvig, 1961; Tarlo, 1965) which has also yielded detached acanthodian scales (Jarvik, 1961) and a single ichthydorulit *Onchus* sp. (Stensiö & Säve-Söderbergh, 1938). Acanthodian scales occur also in the lower part of the *Phyllolepis* series on Ymer Ø, as do elasmobranch remains, i. e. a single *Cladodus*-like tooth and a fragmentary elasmobranch fin-spine (Stensiö, 1948). Palaeonisciforms, suggestive of *Rhadinichthys,* have been found only in the upper-most part of the Devonian (*Grönlandaspis* series) near the summit of Celsius Bjerg on Ymer Ø (Jarvik, 1961).

Euarthrodira as well as Antiarchi occur in the Middle and in the Upper Devonian strata. Euarthrodires are rare and generally their remains are incompletely preserved. *Heterostius groenlandicus* and *Homostius kochi* (order Pachyosteomorphi) are found in the lowermost part of the Middle Devonian strata in Canning Land (Stensiö & Säve-Söderbergh, 1938) and the latter form occurs also in the overlying *Asterolepis säve-söderberghi* series. The Middle Devonian Randbøl series (Kap Franklin area) has yielded specimens of a coccosteomorph resembling, according to Ørvig (1960, footnote p. 309), *Clarkeosteus halmodeus* from the lower Middle Devonian Marcellus Shale in the USA. The order Phyllolepida is represented in the Upper Devonian strata by *Phyllolepis orvini* (fig. 444 D) and *Phyllolepis nielseni.* The former is a large form, occurring rather abundantly in certain localities in the upper part of the *Phyllolepis* series, while the smaller *Phyllolepis nielseni* seems to be restricted to the lower part of the *Remigolepis* series (see Jarvik, 1950b). The Greenland *Phyllolepis* material collected before 1935 was described by Stensiö (1934, 1936, 1939) who demonstrated (incidentially, simultaneously with Gross, 1934) that the phyllolepids are highly specialised euarthrodires. From the very top of the Devonian sequence comes the dolichothoracid *Grönlandaspis mirabilis* (fig. 444 E_{1-3}), first described by Heintz (1932). Additional but still limited and imperfect material was described by Stensiö (1934, 1939) and Miles (1964). This particular arthrodire is of considerable interest both phyletically and stratigraphically. It is the last known survivor of the predominantly Lower Devonian dolichothoracids and may even be the youngest known representative of the arthrodires.

It is possible that parts of the *Grönlandaspis* series, in fact, belong to the lowermost Carboniferous (Bütler, 1959, 1961). If this should prove correct then *Grönlandaspis* is the only arthrodire known to have survived into the Carboniferous. All other reports of arthrodires from beds of this age rest either on reworked material, such as *Ptyctodus* teeth and *'Dinichthys'* remains from the Lower Carboniferous Bushberg Formation of Missouri and Louisiana (see Branson, 1938a, p. 181; 1938b, pp. 109–110), or are due to misinterpretation of the fossils, as is the case of *Cratoselache pruvosti* from the Lower Carboniferous of Belgium.

Cratoselache pruvosti has been reinvestigated by

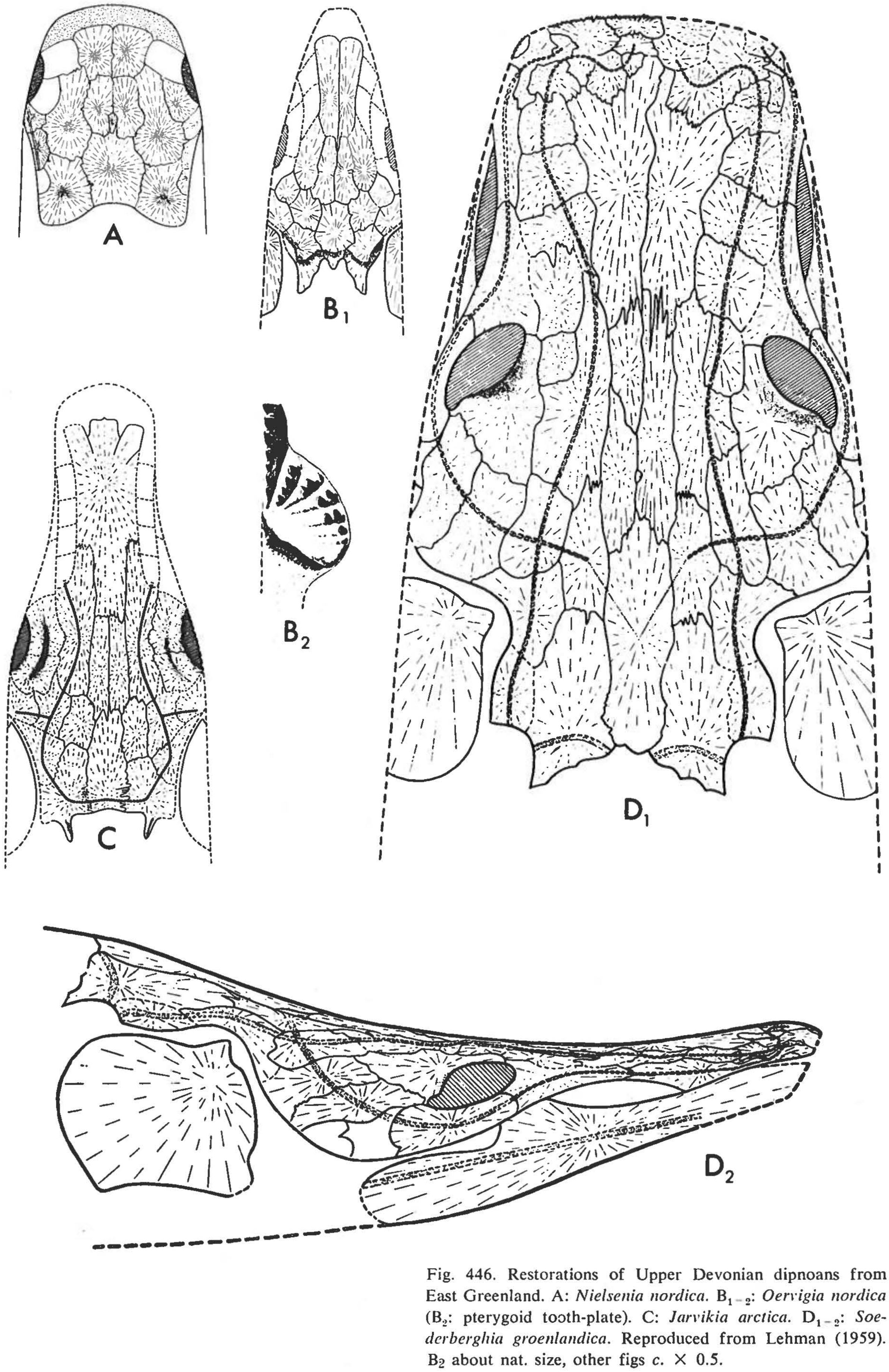

Fig. 446. Restorations of Upper Devonian dipnoans from East Greenland. A: *Nielsenia nordica*. B_{1-2}: *Oervigia nordica* (B_2: pterygoid tooth-plate). C: *Jarvikia arctica*. D_{1-2}: *Soederberghia groenlandica*. Reproduced from Lehman (1959). B_2 about nat. size, other figs *c.* × 0.5.

the writer. It was found that those elements, which Woodward (1924) interpreted as dermal bones (and designated: *anterior dorso-median, occipital, pineal* and *preorbital plates*), have a surface structure very different from that of dermal bone. It is, however, exactly like the surface structure of the jaws, the shoulder girdle and fin-endoskeleton (see fig. 445; *Mk, pq, Sc.co, ra*). In fact, all these skeletal elements possess that characteristic granulated surface structure which is so typical of fossilised calcified cartilage. The alleged 'dermal bones' in *Cratoselache,* consequently, constitute the broken parts of the heavily calcified endocranium (see fig. 445). Even the dentition can be traced on the specimen. A series of small elongate or conical impressions (the specimen is preserved in negative) are spread out on the slab anterior to the jaws, these impressions being caused by the matrix enveloped teeth (fig. 445; *t*). *Cratoselache pruvosti* is thus a genuine selachian and belongs, in the writer's opinion, to that particular group of early selachians which also includes *'Cladodus' wildungensis* (Gross, 1937) among others.

The most common vertebrates in the East Greenland Devonian are the antiarchs. In the Middle Devonian of Canning Land and Wegener Halvø *Asterolepis säve-söderberghi* (fig. 444 A) is abundant in the series to which it gives its name (Säve-Söderbergh, 1937) but other species are probably also present in the collection which now includes new material from Canning Land and from the Kap Franklin area. The Upper Devonian antiarchs were described by Heintz (1930) and Stensiö (1931, 1948) who recognised several species of *Bothriolepis* (fig. 444 B) and a new genus *Remigolepis* (fig. 444 C). Stensiö's (1931) investigations of the East Greenland Antiarchi, in conjunction with material from Canada (*Bothriolepis canadensis*), proved that the antiarchs were true gnathostomes. His later studies of *Bothriolepis* from Greenland led ultimately to a thorough revision of the family Bothriolepinae, including an extremely detailed anatomical description of the Antiarchi in general and of the genus *Bothriolepis* in particular (Stensiö, 1948).

Dipnoans are rare in the Middle Devonian of East Greenland. So far only a single imperfect dermal skull-roof of a *Dipterus*-like form has been found in the *Asterolepis säve-söderberghi* series in Canning Land (Jarvik, 1961). In Upper Devonian deposits, however, dipnoans are fairly common. They have been investigated by Lehman (1959) who found them to represent four new genera and species, namely *Nielsenia nordica, Jarvikia arctica, Oervigia nordica* (fig. 446 A-C) and the big, long-snouted form *Soederberghia groenlandica* (fig. 446 D; length of skull-roof *c.* 30 cm) which seems to be related to other long-snouted dipnoans of the Upper Devonian, i. e. the Scottish *Rhynchodipterus* and *Griphognathus* from Germany. The vertebral column of *Jarvikia* and ? *Soederberghia* (and other early dipnoans) was investigated by Jarvik (1952) and Schultze (1970) who, discussing the morphology and histological structure of dipnoan vertebral centra, arrived at strongly diverging opinions on the relationship of dipnoans to other lower vertebrate groups.

Osteolepiforms and porolepiforms are abundantly represented in the collections and include some really outstanding finds. From the Middle Devonian *Asterolepis säve-söderberghi* series in Canning Land about twenty extremely well preserved specimens of the porolepiform *Glyptolepis groenlandica* (fig. 447 A-C) were obtained from a single sandstone lens during the expedition of 1956. This material has recently been described in detail by Jarvik (1972) and has even been used on various occasions for reference and comparison by Jarvik and others (cf. Jarvik, 1972, p. 13). It has widened considerably the knowledge of porolepiform structure and has played an important role in Jarvik's argumentation for his view of a porolepiform ancestry of the Urodela.

The Upper Devonian porolepiform material comprises large numbers of detached scales, bones, teeth and parts of endocrania (fig. 448 A-B) of *Holoptychius*-like forms (cf. Jarvik, 1972, pp. 12–13). Parts of this material have been used for palaeohistological studies (Ørvig, 1957; Schultze, 1969).

Middle Devonian osteolepiforms comprise *Gyroptychius groenlandicus* (fig. 449 A) found in the Kap Franklin area (Vilddal series), in Canning Land (*Gyroptychius* series and from the underlying *Asterolepis säve-söderberghi* series; see Table 29) and Wegener Halvø, and a form resembling *Thursius macrolepidotus* from the Randbøl series of the Kap Franklin area. *Gyroptychius groenlandicus* is mainly known from detached cranial bones and scales, only few specimens show articulated remains. Generally, however, the bone-substance of this material is extraordinarily well preserved and the bone surface frequently exhibits resorption areas and blisters, the study of which has yielded information on the mode of growth of cosmine in osteolepids (Jarvik, 1950a).

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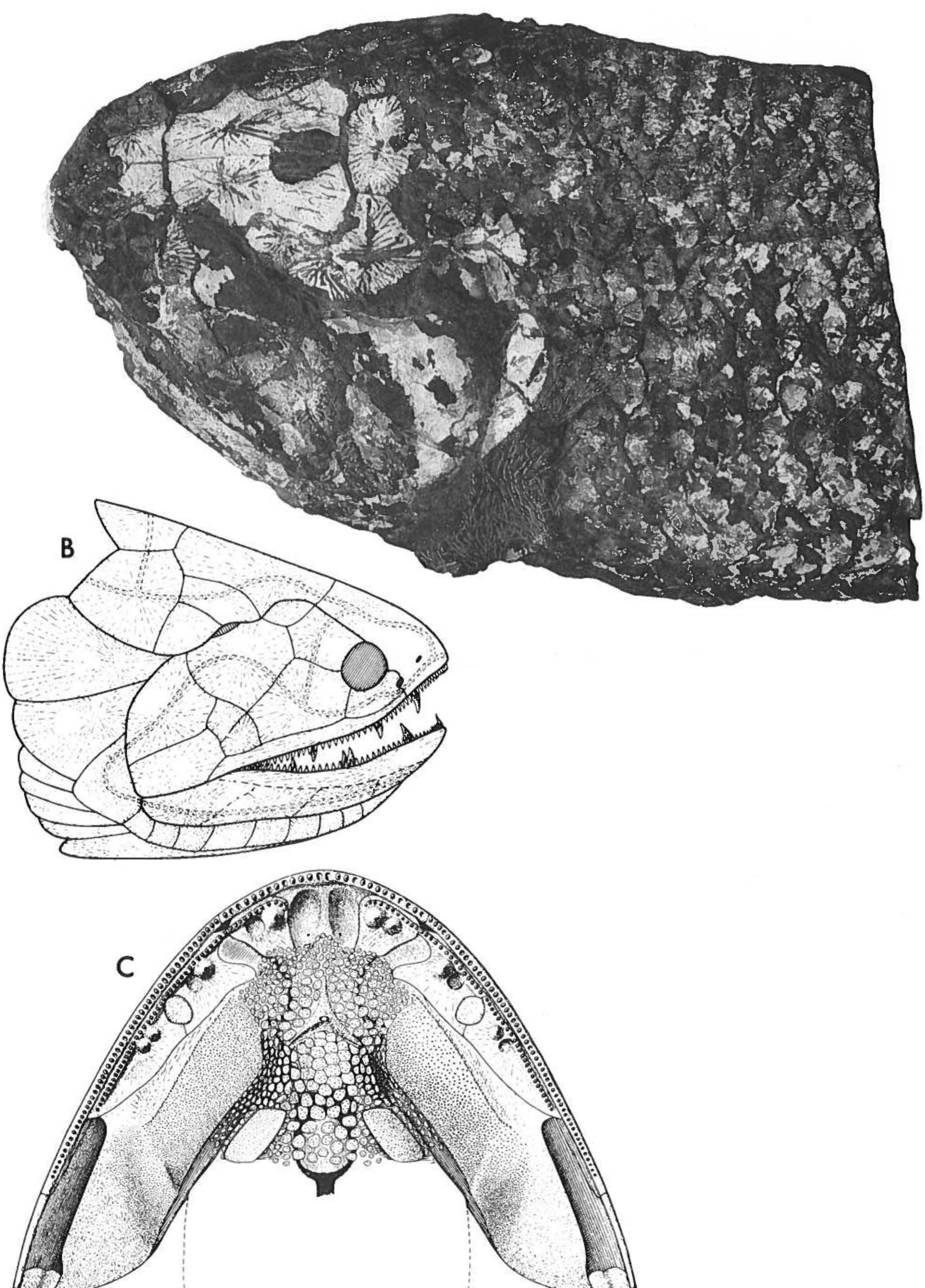
Fig. 447. *Glyptolepis groenlandica,* Middle Devonian, Canning Land, East Greenland. A: Flattened specimen showing skull roof, left cheek and parts of body squamation in dorsal aspect (P. 1523; Mineralogical Mus. Coll., Copenhagen). B-C: Restorations showing the head in lateral view and the palate in ventral aspect. B-C: Reproduced from Jarvik (1972).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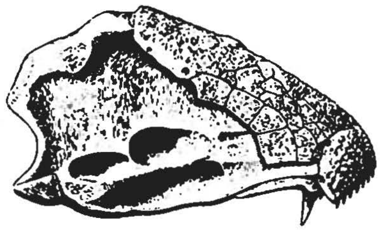
C

A



B

Fig. 448. *Holoptychius* sp. from the Upper Devonian of East Greenland. A: Large scale (P. 1530; Mineralogical Mus. Coll., Copenhagen) from a fish whose total length may have exceeded 2 m. B: Restoration of ethmosphenoidal ossification of braincase with dermal skull roof bones, lateral view (from Jarvik, 1961). Both figs nat. size.

The Kap Kolthoff series (the lower part of which appears to be transitional between the Middle and Upper Devonian; Bütler, 1959) has yielded various osteolepiform remains among which should be mentioned the neural endocranium of a small form which is suggestive, according to Jarvik (1961), of *Eusthenopteron*. Other osteolepiforms include the large *Eusthenodon wängsjöi* (fig. 449 B), a fairly common form in the Upper Devonian *Remigolepis* series (Jarvik, 1952).

The most important contribution to vertebrate palaeontology yielded by the Greenland Devonian is unquestionably the discovery of the ichthyostegalians – so far the oldest known true tetrapods in the World. Remains of these stegocephalians, which come from the *Remigolepis* series of Ymer Ø and Gauss Halvø (figs 440, 441, Table 29), were first discovered in 1929. The true nature of these finds, however, was not disclosed until further material, comprising a number of incomplete skulls, was found during the expedition in 1931 and described by Säve-Söderbergh (1932) who erected the family Ichthyostegidae including two genera: *Ichthyostega* and *Ichthyostegopsis*.

Up to 1955, the last year in which collecting of ichthyostegids took place, some 250 specimens had been recovered, comprising several fine skulls (fig. 439) and remarkably well preserved remains of the postcranial skeleton. An exhaustive description of this important material by Professor Jarvik in Stockholm is in progress, but he has, on various occasions mainly in conjunction with discussions of particular fundamental problems related to tetrapod structure and phylogeny, unveiled many structural details of the ichthyostegalians (for complete references see Jarvik, 1964). It is now known that they comprise two distinct families, the Ichthyostegidae (*Ichthyostega, Ichthyostegopsis;* fig. 449 C-G) and the Acanthostegidae (*Acanthostega*; fig. 449 H-I). These diverge considerably from each other in the development of the posterior part of the skull. The Ichthyostegidae and the Acanthostegidae may therefore represent two different evolutionary lines which had probably been separate for a long time. This interesting fact may further indicate, as emphasised repeatedly by Jarvik, that the emergence of tetrapods from osteolepiform ancestors took place far back in the Devonian.

The primitive nature of the ichthyostegalians manifests itself in the large number of piscine features retained in their skeleton. The ichthyostegids, being the best known of the two families, exhibit features

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Fig. 449. Devonian osteolepiforms and tetrapods from East Greenland. A: *Gyroptychius groenlandicus*, Middle Devonian, Canning Land. B: *Eusthenodon wängsjöi*, Upper Devonian, *Remigolepis* series. C-G: Restorations of *Ichthyostega* sp., Upper Devonian, *Remigolepis* series. H-I: *Acanthostega gunnari*, Upper Devonian, *Remigolepis* series. A: *c*. nat. size; B-I: *c*. × 0.25. Reproduced from Jarvik (1950a, 1952, 1955).

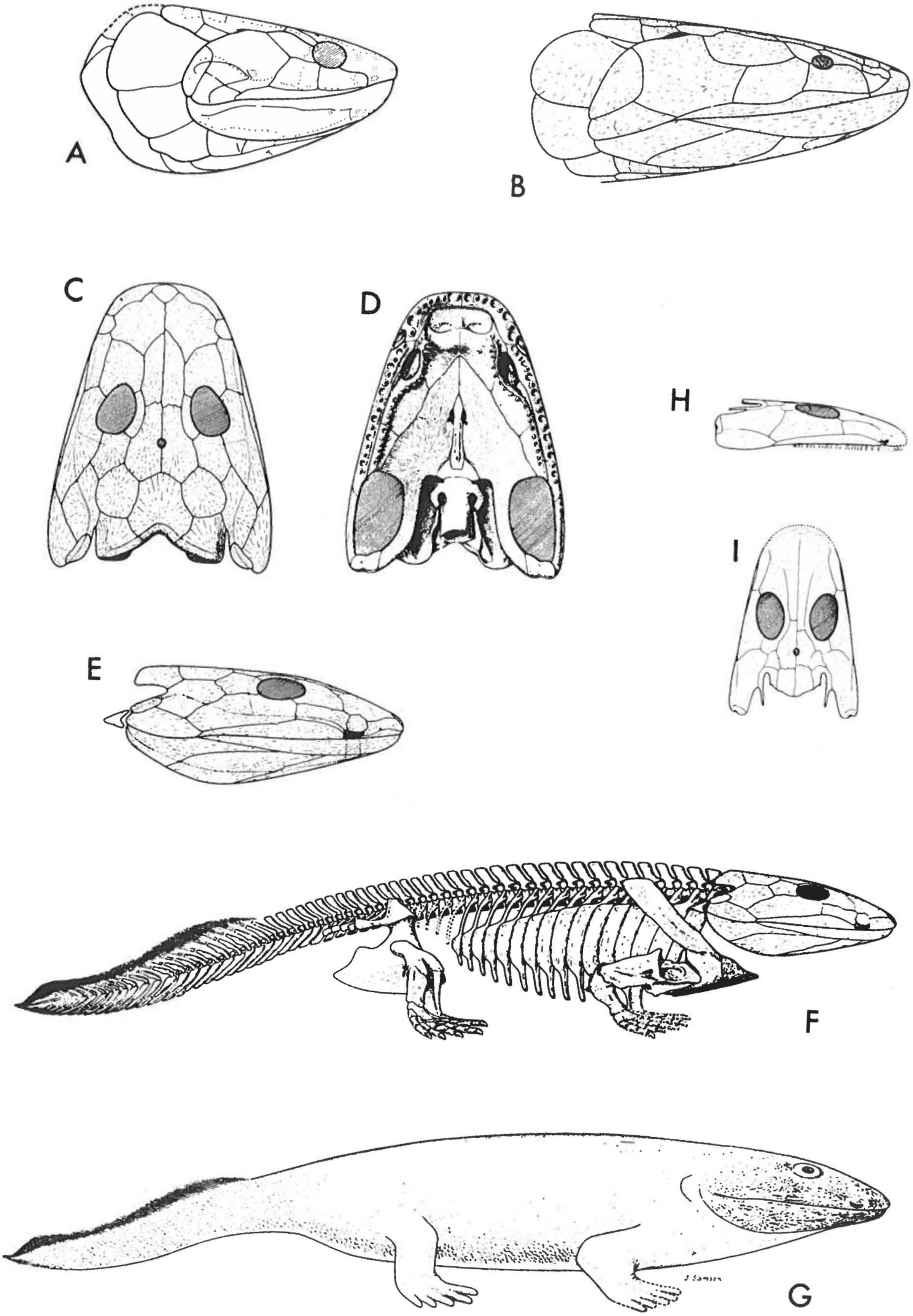
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Table 29. Biostratigraphy of the East Greenland Devonian

CARBONIFEROUS	Tournaisian		Ymer Ø (Celsius Bjerg, Kap Graah area); Gauss Halvø (Nathorst Fjeld, Wimans Bjerg, Stensiö Bjerg, Smith Woodward Bjerg, Sederholm Bjerg and Remigolepisryg)
UPPER UPPER DEVONIAN	Strunian		*Grönlandaspis* series. *Grönlandaspis mirabilis*, indet. Arthrodira, indet. Palaeonisciformes, *Holoptychius* sp., plants (indet. Calamariaceae, ? *Knorria*)
	Strunian	*Remigolepis* series (c. 800 m)	Upper Division (*c.* 520 m) *Remigolepis* spp., *Oervigia nordica*, *Jarvikia arctica*, *Holoptychius* sp., *Eusthenodon wängsjöi*, *Ichthyostega* spp., *Ichthyostegopsis wimani*, *Acanthostega gunnari*
			Middle Division (*c.* 200 m) Unfossiliferous
			Lower Division (*c.* 80 m) *Remigolepis* spp., *Bothriolepis nielseni*, *Phyllolepis nielseni*, *Soederberghia groenlandica*, *Holoptychius* sp., *Ichthyostega* spp.
	Famennian	*Phyllolepis* series	Upper part *Phyllolepis orvini*, *Bothriolepis grönlandica*, indet. Acanthodii, *Nielsenia nordica*, ? *Soederberghia*, *Holoptychius* sp.
			Lower part *Bothriolepis jarviki*, indet. Selachii, *Cladodus* sp., *Holoptychius* sp.
			Lower Sandstone Complex. Poor in fossils. Indet. Arthrodira, *Holoptychius* sp., Osteolepiform (cf. *Eusthenopteron* sp.)

			Canning Land	Kap Franklin area (subdivision according to Bütler; correlation uncertain)
UPPER MIDDLE DEVONIAN	Givetian	Upper part	*Gyroptychius groenlandicus* series (*c.* 350 m). Indet. Porolepiformes, *Gyroptychius groenlandicus*, plants	Randbøl series (*c.* 800 m). *Asterolepis* cf. *säve-söderberghi*, cf. *Clarkeosteus halmodeus*, Osteolepiformes cf. *Thursius macrolepidotus*
		Lower part	Plant-bearing series (*c.* 500 m)	
			Asterolepis säve-söderberghi series (*c.* 400 m). *Psammolepis groenlandica*, indet. Acanthodii, *Homostius kochi*, *Asterolepis säve-söderberghi*, indet. Dipnoi, *Glyptolepis groenlandica*, *Gyroptychius* cf. *groenlandicus*, plants (*Psilophyton* sp.)	Unfossiliferous beds (*c.* 1000 m)
			Heterostius series (*c.* 50 m). *Heterostius groenlandicus*, *Homostius kochi*, plants (*Thursophyton* sp.)	Vilddal series (*c.* 1500 m). *Estheria*, indet. Porolepiformes, *Gyroptychius* cf. *groenlandicus*

Table from Jarvik (1961).

such as: suboperculum, preoperculum (known also in the acanthostegids), lateral rostrals, neural endocranium divided into ethmosphenoidal and otoccipital ossifications (the latter having a persisting wide notochordal canal), cephalic sensory canals enclosed in the dermal bones, endoskeletal radials and dermal fin-rays supporting the median fins, etc.

In spite, however, of their clear intermediate position between osteolepiforms and later tetrapods both the ichthyostegids and the acanthostegids possess certain specialisations which, as pointed out repeatedly by Jarvik, disqualify them as ancestors of any known post-Devonian tetrapods. Most probably the ichthyostegids and acanthostegids represent blind offshoots amongst the early tetrapods, the evolutionary differentiation of which, judging from the above facts and from the rich diversification of the post-Devonian tetrapod fauna, apparently had progressed much further already in the Devonian than reflected in the fossil record as known at present.

Biostratigraphical correlation

The biostratigraphical subdivision of the East Greenland Devonian is shown in Table 29 reproduced from Jarvik (1961). Correlation with other areas has been attempted by Säve-Söderbergh and, more recently, by Jarvik (for complete references see Jarvik, 1961), who, on the basis of the great similarity between *Gyroptychius groenlandicus* and *Gyroptychius milleri,* correlates the Middle Devonian *Gyroptychius* series of Canning Land and Wegener Halvø with the Thurso Flagstone Group and the Rousay beds in Scotland. Jarvik also found that the *Heterostius* series, yielding the arthrodires *Heterostius* and *Homostius,* is broadly contemporaneous with the Stromness beds in Scotland and the Pernau and Narowa beds in the Baltic area.

Concerning the age of the Upper Devonian of Greenland Jarvik (1950b, pp. 17–18) concludes that "the lower division of the ... *Remigolepis* series ... is probably broadly contemporaneous with the Evieux beds in Belgium and that the beds with *Phyllolepis orvini* and *Bothriolepis grönlandica* correspond approximately to the beds with *Bothriolepis ornata* and *Phyllolepis* sp. in the Russian – Baltic Devonian. Thence it follows that the lower division of the *Remigolepis* series in East Greenland is probably Upper Famennien in age . . ." and " . . . the middle and upper division of the *Remigolepis* series and the overlying *Grönlandaspis* series may very well correspond to the part of the Famennien overlying the Evieux beds, and to the Etroeungt beds, which form the top of the Devonian in the marine sequence."

Carboniferous

Carboniferous vertebrate yielding strata are located in two areas in East Greenland; a northern one, the Holm Land – Amdrup Land area (80°–81°N; fig. 450) where the fossiliferous strata are of marine origin, and a southern area around Kong Oscars Fjord in central East Greenland (fig. 441) with freshwater deposits. The vertebrate assemblages of the two areas are confined to fishes and seem to be broadly contemporaneous. For detailed information on the marine fauna and parts of the freshwater

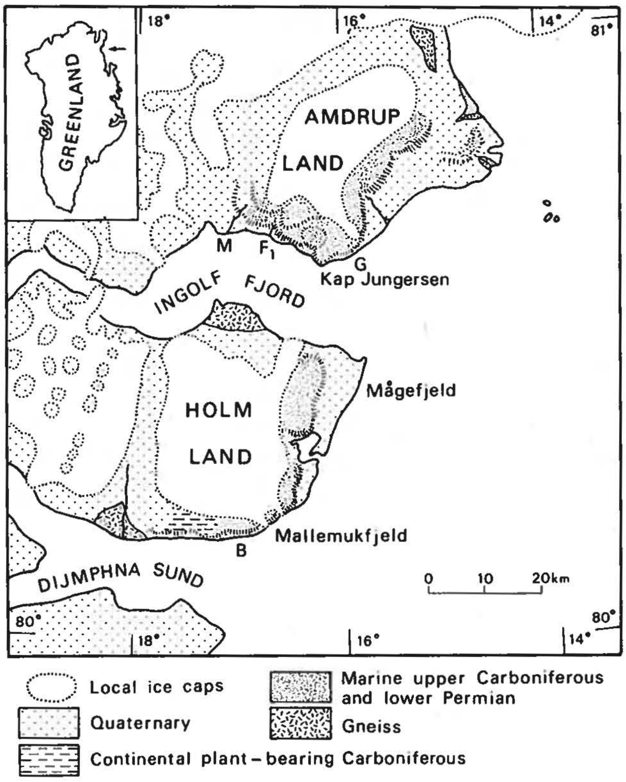

Fig. 450. Map of Holm Land and Amdrup Land showing the distribution of Carboniferous and Lower Permian sedimentary deposits and the location of vertebrate yielding sections (B, F_1, G and M).

fauna the reader is referred to Bendix-Almgreen (1975) and Jensen (in press).

Upper Carboniferous marine fish assemblage

This comprises *Ctenacanthus* sp. (fin-spine), tooth plates of *Petalodus* sp., *Lagarodus* sp., a cochliodontid (or menaspid) and detached scales of *Acrolepis?* sp. which originate from various horizons in the lower part (i. e. the Lower Marine Group) of the Permo-Carboniferous deposits exposed in Holm Land – Amdrup Land (figs 450, 451). The invertebrates (foraminifera, bryozoans, brachiopods) from the Lower Marine Group indicate a Moscovian age and show close affinity to faunas of the Kashira and Podolsk stages of the Moscow Basin (Dunbar *et al.,* 1962). The fish assemblage under consideration is, therefore, roughly contemporaneous with marine ichthyofaunas known from various localities south and south-east of Moscow (e. g. Myachkovo) and from the Donets Basin on the Russian platform (for references see Bendix-Almgreen, 1975). Comparisons reveal similarity between the Greenland fish assemblage and the Russian ichthyofaunas in their general composition and even at genus level (*Ctena-*

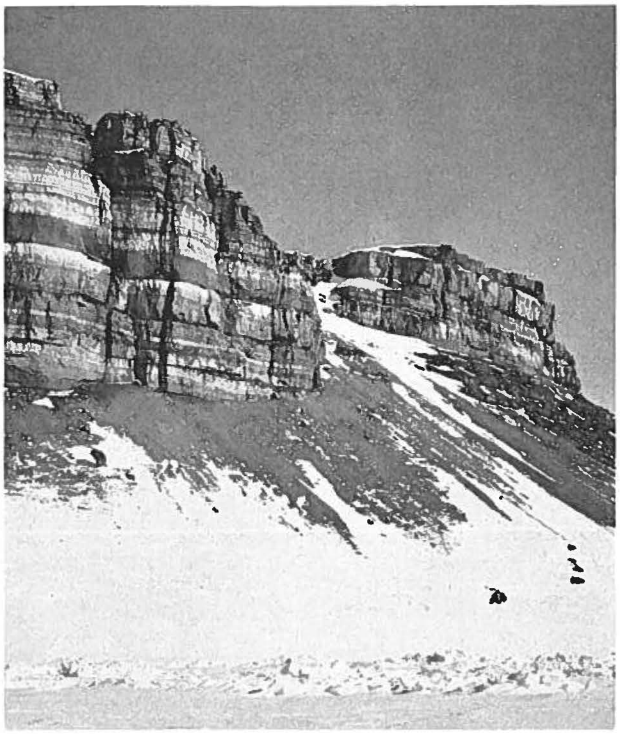

Fig. 451. Strata of the Lower Marine Group (Upper Carboniferous) exposed at Mallemukfjeld. Photo: E. Nielsen 1939.

canthus, Petalodus and, possibly, *Lagarodus*) but the poor preservation state of the small number of specimens from Greenland excludes comparison at species level. For the same reasons close comparison cannot be made with Upper Carboniferous marine ichthyofaunas from western Europe and North America. For biostratigraphical purposes, therefore, the Greenland material is insignificant. This small fish assemblage represents the most northerly known occurrence of Upper Carboniferous vertebrates.

Upper Carboniferous freshwater fish assemblage

Acanthodians (*Acanthodes* and *Traquairichthys*; Nielsen, 1932; Jensen, in press) and palaeonisciforms (*Aldingeria biertheri, Whiteichthys greenlandicus* and some indeterminable fragmentary forms; Moy-Thomas, 1943) comprise the Upper Carboniferous freshwater fish assemblage (fig. 452 A-C). The acanthodian genus *Traquairichthys* has hitherto only been known from Czechoslovakia where it is restricted to deposits dated by their fossil flora to the Westphalian D and Stephanian (Bendix-Almgreen, 1975). There are reasons to believe that the Greenland and the Czechoslovakian species of *Traquairichthys* are broadly contemporaneous even though they differ in certain features (Jensen, in press). This indicates an upper Westphalian-Stephanian age for the Greenland *Traquairichthys*-bearing strata which are confined to the Skeldal Member, the lowermost lithostratigraphic unit of the Permo-Carboniferous Mesters Vig Formation (Perch-Nielsen *et al.*, 1972). The presence of *Traquairichthys* enables the Skeldal Member to be traced from northern Scoresby Land to the south-western part of Traill Ø (fig. 441).

Acanthodes and the two palaeonisciforms *Aldingeria biertheri* and *Whiteichthys greenlandicus,* in contradistinction to *Traquairichthys,* occur also at a higher level in the Mesters Vig Formation in strata which seem to reach into the lowermost Permian (Profilbjerg Member = *Lebachia* series of Witzig, 1954).

Permian

The oldest Permian vertebrates from Greenland are apparently those constituting the small vertebrate assemblage derived from parts of the continental freshwater Profilbjerg Member of the Mesters Vig Formation supposed to be of Autunian age (fig. 453; Witzig, 1954; Kempter, 1961). The marine vertebrate faunas yielded by deposits of Lower Permian (Sakmarian and Artinskian) and Upper Permian (Araksian) ages are, for both palaeozoological and biostratigraphical studies, of the utmost importance.

Lower Permian freshwater vertebrate assemblage

As known at present the fauna consists of pleuracanthid selachians, acanthodians, palaeonisciforms and stegocephalians. The first two of these groups have not previously been recorded in deposits of this age in Greenland, and the stegocephalians have hitherto only been known from trails referred to that group (fig. 452 D). The latter are now represented by

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Fig. 452. Upper Carboniferous and Lower Permian vertebrates from central East Greenland. A: Fin-spine of *Acanthodes* sp. B: *Whiteichthys greenlandicus* Moy-Thomas. C: *Aldingeria biertheri* Moy-Thomas. A-C: *c.* nat. size. D: Sandstone slab showing casts of tetrapod (? stegocephalian) trails. E-F: Nuchal spine of *Pleuracanthus* sp. (MMH. VP. 1014; Lower Permian, Profilbjerg Member, Profilfjeldet, Mesters Vig area) showing the lateral serrated edges (*s* in E; *c.* × 3), more clearly discernible at higher magnification in F (*c.* × 15), which corresponds to the rectangular area marked off on E. G-M: Stegocephalian (?anthracosaurian) femur, slightly compressed dorso-ventrally (MMH. VP. 1015; Lower Permian, Profilbjerg Member, Mesters Vig area; *c.* × 2.6). Presented in ventral (G), dorsal (H), fibial side (I), tibial side (K), proximal (L) and distal (M) aspects. A-D: Reproduced from Nielsen (1932); Moy-Thomas (1943); Witzig (1954). E-M: originals.

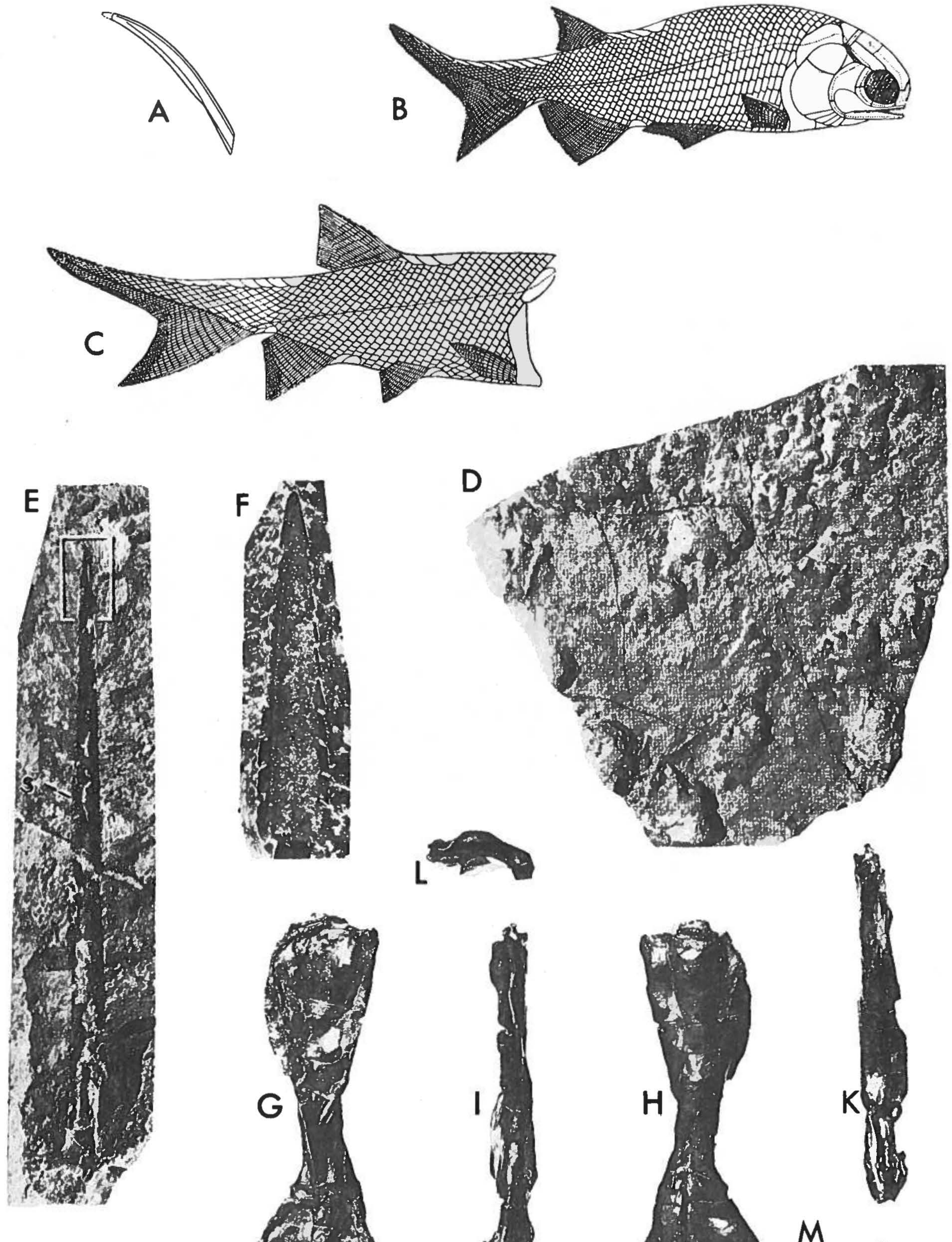
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Fig. 453. Profilfjeldet, the type locality for the Profilbjerg Member (Lower Permian), one of the lithostratigraphical units within the Mesters Vig Formation. View from south. Photo: Bente Soltau Bang 1959.

some bones of which the best preserved is a femur (fig. 452 G-M), but the material hardly permits closer determination.

The single specimen of a pleuracanthid selachian, showing a nuchal spine and remains of calcified cartilage, was collected from exposures on Profilfjeldet (fig. 453), in the Mesters Vig region. The saw-tooth shape of the denticles forming a serrated edge on both sides of the spine indicates, along with other features, that this specimen belongs to the genus *Pleuracanthus* (fig. 452 E-F).

The few acanthodian remains appear to represent the genus *Acanthodes*. The palaeonisciforms include *Aldingeria biertheri* and *Whiteichthys greenlandicus* (fig. 452 B-C) as the best known forms which seem to have lingered in Greenland from late Carboniferous time. According to Moy-Thomas (1943), they are unlike any other palaeonisciforms so far known. There is, however, very little doubt as to the affiliation of *Whiteichthys* with the canobiids.

In its general composition this vertebrate assemblage is comparable to late Palaeozoic freshwater vertebrate faunas occurring elsewhere. However, none of the forms represented are significant for biostratigraphic evaluation and close age determination of the Profilbjerg Member. On the other hand, the presence of genuine pleuracanthids and acanthodians, the late Carboniferous and early Permian representatives of which are exclusively freshwater, invalidates the assumption based on the fish fossils and maintained by Stauber (1940) and Bierther (1941; see also Bütler, 1961) of marine influence on the deposits of the Profilbjerg Member.

Fig. 454. Section through part of the vertebrate-bearing *Posidonia* Shale Member (Upper Permian; Foldvik Creek Formation) exposed in the low coastal cliff at River 6, Kap Stosch. Photo: Bente Soltau Bang 1959.

Lower Permian marine fish assemblage

This assemblage is confined to a few elasmobranch teeth of the *Helodus* and *Cladodus* types (Bendix-Almgreen, 1975) which are derived from the top part (i. e. the *Athyris amdrupi* zone) of the marine series, known as the Upper Marine Group and exposed in Holm Land – Amdrup Land (northern East Greenland; fig. 450). This small fish assemblage, in addition to being so far the northernmost occurrence of its kind and age, is also of interest due to the close similarity between its *Cladodus* type teeth and those reported under the name *'Cladodus occidentalis'* from beds of the Meade Peak Member in south-west Wyoming, considered to be of late Artinskinan (Roadian) age (*sensu* Furnish, 1973; for references see Bendix-Almgreen, 1975). The vertebrate fauna from the Wyoming beds also includes teeth of the *Helodus* type but none of these show much similarity to those in the Greenland material.

The similarity between the Greenland and the Wyoming *Cladodus* specimens could perhaps indicate contemporaneity of the *Athyris amdrupi* zone in Greenland and the *'Cladodus occidentalis'* yielding beds from south-west Wyoming. This suggestion is, at any rate, not incompatible with indications offered by some of the invertebrates from the *Athyris amdrupi* zone which also point towards an Artinskian age (*sensu* Furnish, 1973) for the top part of the Upper Marine Group in Holm Land – Amdrup Land (Dunbar *et al.*, 1962).

Upper Permian vertebrates

Upper Permian marine deposits (i. e. the Foldvik Creek Formation) are widely distributed in central East Greenland (Birkelund & Perch-Nielsen, this

Fig. 455. Large nodule excavated from the *Posidonia* shale at River 14, Kap Stosch. It contains articulated skeletal parts (neuro- and viscerocranial parts, pectoral girdle and fins, parts of dentition and scale-covering) from a single specimen of *Erikodus groenlandicus*. Hammer length 46 cm. Photo: Bente Soltau Bang 1959.

volume). These sediments were deposited in a shallow transgressive sea and are characterised by rapid and complex changes of facies (Maync, 1942; Birkelund & Perch-Nielsen, this volume, fig. 272). One of these facies, the *Posidonia* Shale Member (figs 454, 455), has yielded abundant well-preserved fossil vertebrates. Fragmentary remains have also been obtained in small numbers from the *Martinia* Limestone Member and the *Productus* Limestone Member (Nielsen, 1935).

The vertebrate fauna comprises the following:

Elasmobranchii
- *Cladodus* sp.
- *Arctacanthus uncinatus* Nielsen
- *Erikodus groenlandicus* Nielsen
- *Fadenia crenulata* Nielsen
- *Sarcoprion edax* Nielsen
- *Janassa kochi* Nielsen
- *Janassa unguicula* (Eastman)
- Petalodontid g. et sp. nov.
- Three new elasmobranchs

Ichthyodorulites
- Indeterminable fin-spines

Actinopterygii
- *Elonichthys punctatus* Aldinger
- *Pygopterus nielseni* Aldinger
- *Pygopterus gleerupi* Aldinger
- *Palaeoniscus freieslebeni* Blainville
- *Palaeoniscus freieslebeni*?
- *Boreolepis jenseni* Aldinger
- *Acropholis stensioei* Aldinger
- *Plegmolepis kochi* Aldinger
- *Plegmolepis groenlandica* Aldinger
- *Platysomus* sp.

Tetrapoda
- Reptilia g. et sp. nov.

Elasmobranchs play a prominent role comprising more than 50 per cent of the vertebrate specimens found. The large forms *Fadenia* and *Erikodus* predominate (their close relative *Sarcoprion* is known only from a couple of specimens) and both the exoskeleton and endoskeleton are often well-preserved (fig. 456 A–G; fig. 457 A, C). The study of this material, especially that of *Fadenia* and *Sarcoprion*, has yielded much information on skull structure, jaws and branchial skeleton, and fins, as well as on dentition and scale-covering (see Nielsen, 1932, 1952; Ørvig, 1951; Stensiö, 1961; Bendix-Almgreen, 1962, 1967, 1968; Kjellström, 1971) but much remains unpublished.

Fadenia, Erikodus and *Sarcoprion* will not be dealt with at length but it may be appropriate to give some comments on their phyletic position which is at present under discussion. As is well known, these three genera are characterised by their specialised symphysial dentition and by their teeth having crowns consisting of the so-called 'tubular dentine'. On the basis of these two features the three Greenland genera (which are close relatives as clearly shown by neurocranial features shared by them) were referred originally to the edestid family, assumed also to comprise such forms as *Edestus, Agassizodus, Helicoprion* and *Parahelicoprion* (Nielsen, 1932, 1952). Subsequent research has, however, seriously impaired the significance of the two features for phyletic evaluation (Bendix-Almgreen, 1968). Other evidence has indicated rather conclusively that *Fadenia, Erikodus* and *Sarcoprion* are not akin to *Helicoprion* (Bendix-Almgreen, 1966). Likewise, close kinship to the Upper Carboniferous forms *Ornithoprion* and *Agassizodus* seems very doubtful judging from comparisons of cranial features. At any rate, Zangerl's (1966) line of argumentation for a close relationship between these Upper Carboniferous forms on the one hand, and *Fadenia, Erikodus* and *Sarcoprion* on the other, may be rejected (Bendix-Almgreen, 1968). On the basis of unpublished observations the writer tends to believe that the Greenland forms are descendants of an early selachian group which also gave rise to the various pleuropterygian lineages comprising, among others, the one to which *Ornithoprion* and *Agassizodus* belong. This would of course suggest that the Upper Permian forms *Fadenia* (reported also from the Marl Slate of England; Westoll, 1941), *Erikodus* and *Sarcoprion* (known only from Greenland) constitute a group of their own and occupy a phyletically isolated position. It may, therefore, be of some interest to mention that the symphysial tooth-arch described under the name *Parahelicoprion clerci*, originating from the Lower Permian (Artinskian) deposits of the USSR (Karpinsky, 1924), is in most features remarkably similar to the symphysial tooth-arch of *Sarcoprion edax* (fig. 457 A–B). However, all we have of *Parahelicoprion* is the symphysial tooth-arch and some tooth fragments, and there is, consequently, no means of deciding if, as the writer tends to believe, the similarities have some bearings on close kinship between *Parahelicoprion* and the three Greenland forms. The same applies to the teeth from the Lower Pennsylvanian of Missouri that Eaton (1962) described and referred to *Fadenia* under the specific name *Fadenia gigas*.

The petalodontids comprise two genera and three species, viz. *Janassa kochi, Janassa unguicula* and one representing a new genus and species. No complete skeletons of these forms have so far been recovered. Judging, however, from available remains (squamations, parts of dentitions and various endoskeletal parts) these petalodontids are medium size elasmobranchs.

Forms with *Cladodus*-like teeth are represented by a few specimens which, among other things, are characterised by *genuine placoid scales*.

Amongst the new elasmobranchs in the fauna, one in particular deserves to be mentioned here, namely a form where the teeth, like those in pleuracanthids (e. g. *Dittodus*), have two prominent lateral cusps and a single median smaller one. All the cusps are situated on the labial side of the thick base which, when viewed from above, varies in shape from rectangular with gently rounded corners, to elliptical or broadly obovate. These teeth diverge from known pleuracanthid teeth only in various minor features. However, in contrast to all genuine pleuracanthids so far described, the form under consideration possesses a remarkably well-developed, dense squamation. The comparatively large scales have thick basal plates which are to some extent suggestive of the basal plates in *Holmesella?* sp. (Ørvig, 1966; Zangerl, 1968). The scale crowns, on the other hand, are made up of clusters of massive 'denticles' irregularly arranged somewhat like those on the anteriormost part of *Orodus* scales (Zangerl, 1968, fig. 1b). The specimen includes calcified cartilage, presumably from the cranial skeleton, but the deficient state of preservation excludes identification.

As far as the elasmobranchs are concerned, new finds of *Arctacanthus uncinatus* (Nielsen, 1932) show this spine (fig. 456 H) to have the inserted base asymmetrically shaped. This feature shows rather conclusively the correctness of Woodward's (1934) assumption that this spine-type was originally carried on the head of some selachian, in a position comparable to that of the postorbital spines in certain hybodontids (e.g. *Hybodus, Lissodus*). There is at present little evidence to indicate with which of the other elasmobranchs (with the exception of *Fadenia* and *Erikodus*) the spine is to be associated.

The actinopterygians comprise forms closely related to, or even identical with, some of those occurring in the European marine Upper Permian, e. g. *Palaeoniscus freieslebeni, Platysomus, Pygopterus nielseni* and *Acropholis stensioei* (fig. 458 A–C). The two last mentioned of these are, according to Aldinger (1935a, 1937; see also Westoll, 1941), close relatives respectively of *Pygopterus humboldti* (Kupferschiefer, Germany; Marl Slate, England) and of

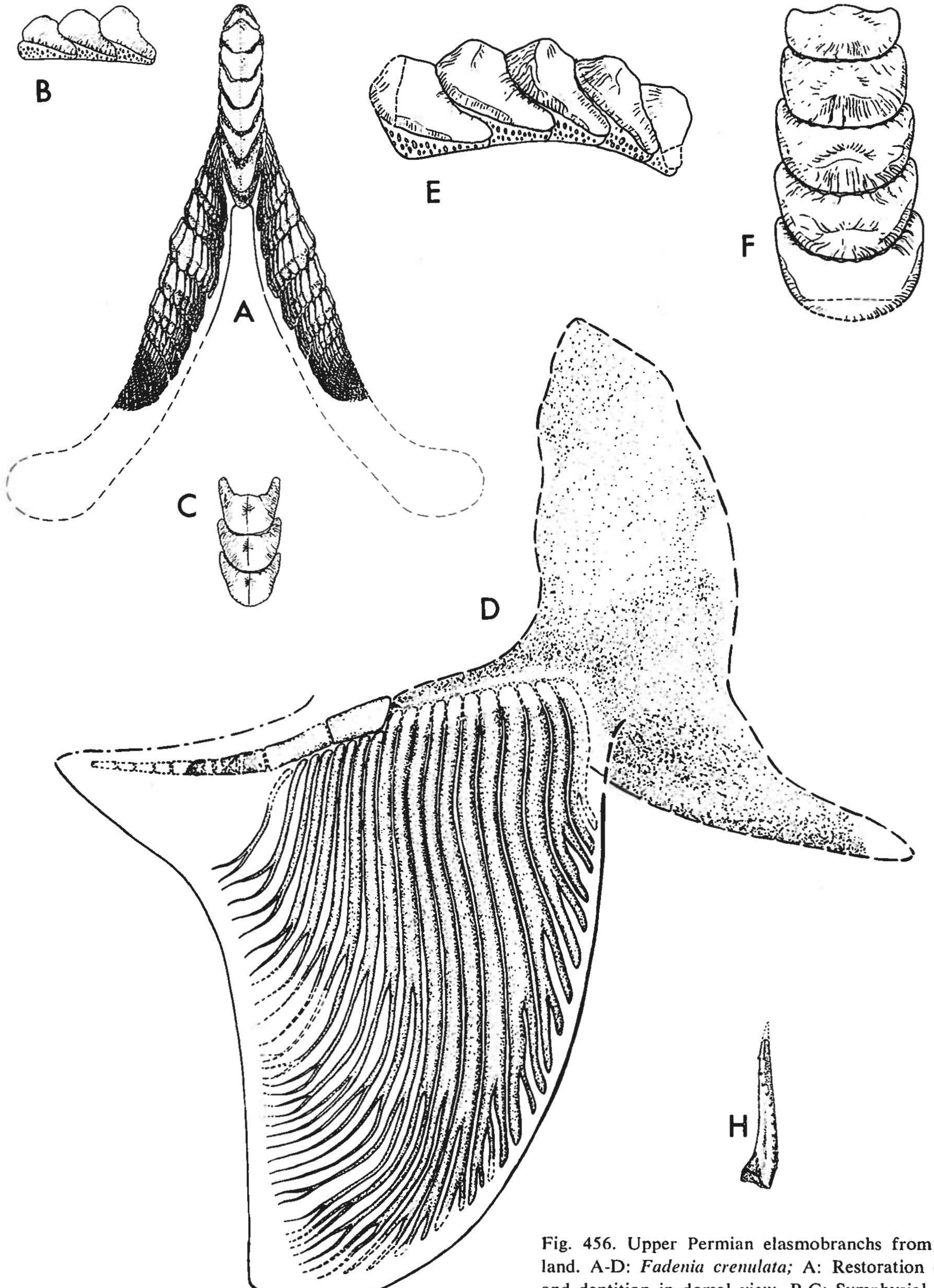

Fig. 456. Upper Permian elasmobranchs from East Greenland. A-D: *Fadenia crenulata;* A: Restoration of lower jaw and dentition in dorsal view. B-C: Symphysial teeth in lateral and dorsal view. D: Pectoral girdle and fin in lateral view. E-F: *Erikodus groenlandicus,* symphysial teeth in lateral and dorsal view. G: *Sarcoprion edax,* restoration showing the anterior part of the cranial capsule, jaws and dentition in lateral view. H: *Arctacanthus uncinatus.* A, D, G: *c.* × 3/8; B, C, E, F: *c.* × 0.5; H: approx. nat. size. A: original; B-H: reproduced from: Nielsen (1932, 1952); Bendix-Almgreen (1967).

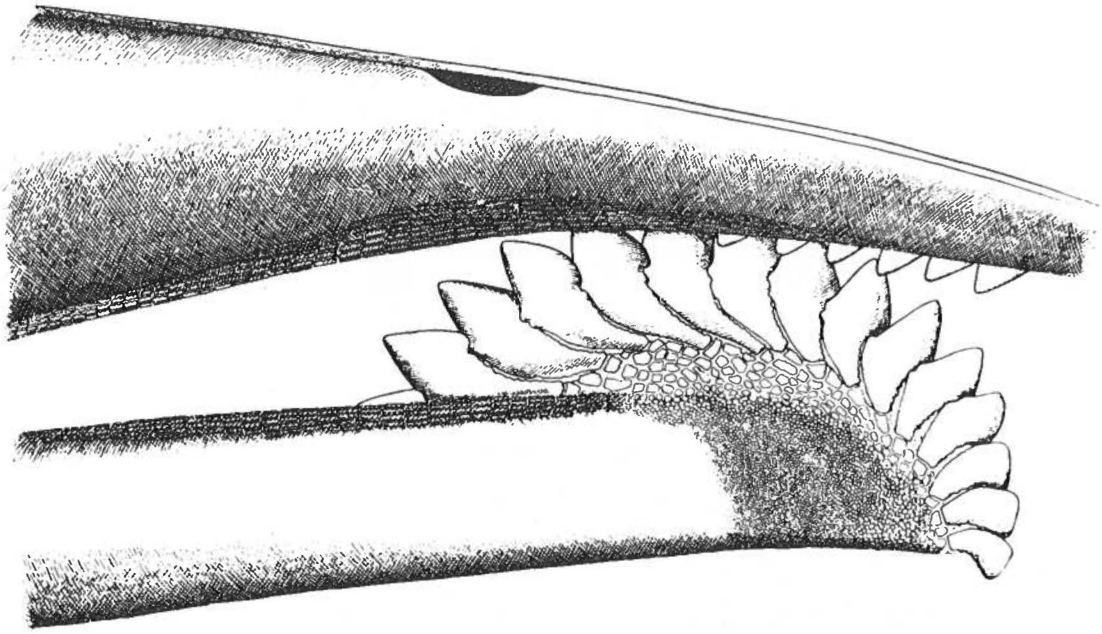

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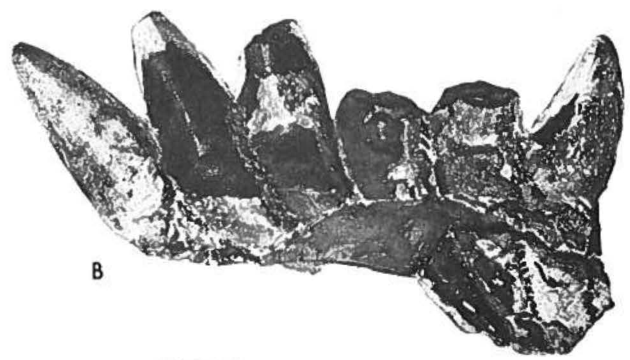
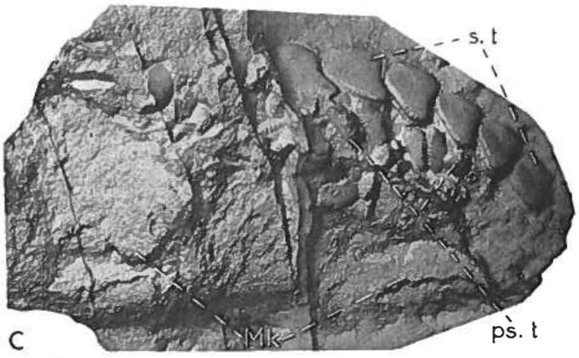
Fig. 456 *cont.*



B

Fig. 457. Symphysial dentitions in lateral aspect. A: *Sarcoprion edax* (detail from MMH. VP. 214, Orig. no. 93; River 14, Kap Stosch, East Greenland). B: *Parahelicoprion clerci* Karpinsky (cast of specimen in the Krasnoufimsk Museum, USSR). C: *Fadenia crenulata* (cast of detail from MMH. VP. 224; River 14, Kap Stosch, East Greenland). A-B: *c.* × 0.24; C: *c.* × 0.4. *Mk*, Meckel's cartilage; *ps.t*, parasymphysial tooth series; *s.t*, symphysial teeth.



C

A

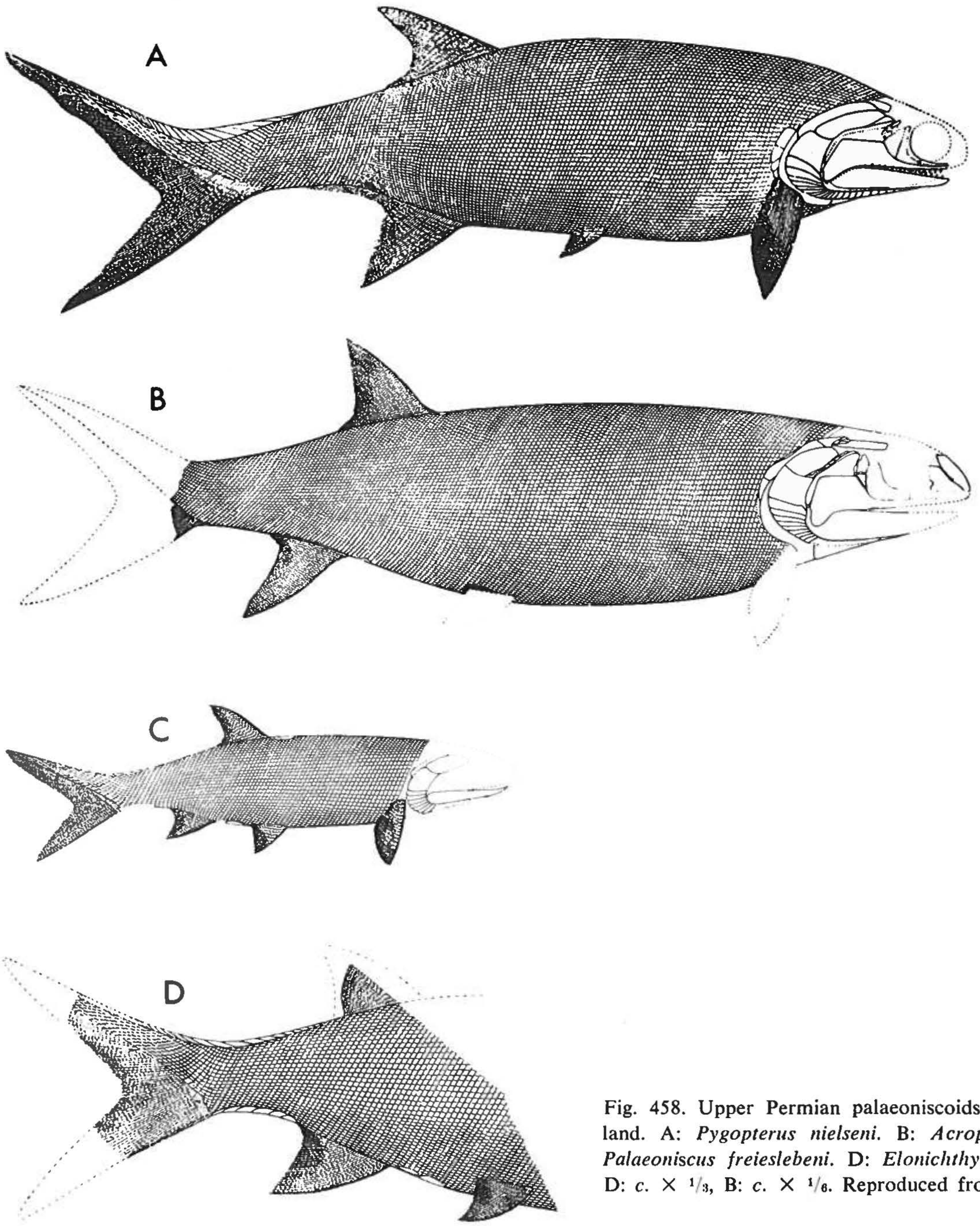


Fig. 458. Upper Permian palaeoniscoids from East Greenland. A: *Pygopterus nielseni.* B: *Acropholis stensioei.* C: *Palaeoniscus freieslebeni.* D: *Elonichthys punctatus.* A, C, D: *c.* × 1/3, B: *c.* × 1/6. Reproduced from Aldinger (1937).

the so-called *Acrolepis* cf. *A. murchisoni* (Kasan beds, USSR). Aldinger's excellent morphological and histological description of this material has produced a considerable increase in our knowledge of lower actinopterygian structure, phylogeny and classification but the new collections call for some revisions to be made.

Biostratigraphical comments
The Araksian age of the vertebrate-bearing Upper Permian deposits in central East Greenland is now also well established by means of ammonoids (for references see Furnish & Glenister, 1970). The first reliable clue to the correct age of these beds was, however, offered by vertebrates of which the actinopterygians gave evidence for correlation with Europe (England, Germany and the USSR) while the elasmobranchs (*Arctacanthus* in particular) permitted correlation with certain deposits in the western USA, more precisely with the Franson Member of the Phosphoria Formation as developed in Wyoming and adjacent states (Branson, 1934; Aldinger, 1935a; Nielsen, 1935, 1952). The occurrence in Greenland of a *Janassa* species, which the writer has com-

pared with and found indistinguishable from Wyoming specimens of *Janassa unguicula* (specimens P. 21037–39 in the British Museum (Natural History), London), is yet another proof of the strong faunal similarity existing between Wyoming and East Greenland in Upper Permian time. A corresponding close similarity has, incidentally, also recently been observed for the conodont faunas of the two areas (Kummel & Teichert, 1970, p. 76).

Triassic

Triassic vertebrate bearing deposits are known from central East Greenland and from Peary Land. The deposits range in age from Lower Scythian to Rhaetic (see Birkelund & Perch-Nielsen, this volume). The bulk of the collections have been obtained from the Lower Scythian marine to brackish beds exposed in several places in central East Greenland (Clavering Ø, Kap Stosch area, Kap Franklin area, Traill Ø, Mesters Vig region, Jameson Land etc; see fig. 441). The vertebrate fauna comprises:

Elasmobranchii
- *Polyacrodus claveringensis* Stensiö
- *Polyacrodus* sp.
- *Parahelicampodus spärcki* Nielsen
- *Nemacanthus*-type fin-spine.
- Various other fin-spines.

Coelacanthiformes
- *Laugia groenlandica* Stensiö
- *Whiteia* sp.
- *Sassenia* sp.
- Coelacanthiform aff. *Wimania*
- Coelacanthiform aff. *Laugia*

Actinopterygii
- *Boreosomus piveteaui* Nielsen
- *Pteronisculus arctica* Stensiö
- *Pteronisculus aldingeria* Nielsen
- *Pteronisculus gunnari* Nielsen
- *Pteronisculus magna* Nielsen
- *Pteronisculus stensiöi* Nielsen
- *Australosomus kochi* Stensiö
- *Australosomus simplex* Nielsen
- *Australosomus pholidopleuroides* Nielsen
- *Australosomus* aff. *A. simplex* Nielsen
- *Saurichthys* sp.
- *Birgeria groenlandica* Stensiö
- *Errolichthys* sp.
- *Bobasatrania groenlandica* Stensiö
- *Bobasatrania* sp.
- *Perleidus stoschiensis* Stensiö
- *Perleidus* sp.
- *Helmolepis gracilis* Stensiö
- *Ospia whitei* Stensiö
- *Ospia* sp.
- *Broughia perleididoides* Stensiö
- *Parasemionotus* sp.
- *Watsonia* sp.

Fig. 459. Exposures of the vertebrate-bearing Lower Scythian Wordie Creek Formation, Falkeryg at Kap Stosch. Photo: E. Nielsen 1947.

Tetrapoda
- *Wetlugasaurus groenlandicus* Säve-Söderbergh
- *Stoschiosaurus nielseni* Säve-Söderbergh
- *Stoschiosaurus nielseni* ?
- *Stoschiosaurus* sp.
- *Lyrocephalus kochi* Säve-Söderbergh
- *Lyrocephalus johanssoni* Säve-Söderbergh
- *Lyrocephalus rapax* Säve-Söderbergh
- *Lyrocephalus* sp.
- *Tupilakosaurus heilmani* Nielsen

In addition to proper Mesozoic forms such as *Polyacrodus* (fig. 460 B) and others, the elasmobranch fauna also includes 'archaic' types, such as *Parahelicampodus* (fig. 460 A) and one other so far undescribed 'tooth-arch' shark, which are survivors of some of those elasmobranch lines where specialised symphysial dentitions evolved during the late Palaeozoic. The undescribed specimen shows, in impression, the left side of a symphysial tooth-arch fragment. It displays features which clearly reveal that it represents a new form, although there is some slight similarity to *Helicoprion* in characters such as the relation between successive tooth crowns and the apparently fused bases.

The preservation of the East Greenland Lower Scythian vertebrates is ideal, and the actinopterygians (fig. 460 C–L) are in that particular respect hardly superseded by any other known material of this group, as descriptions given by Stensiö (1932) and by Nielsen (1942, 1949) prove beyond doubt. Nielsen in his monographs treated the structure of *Pteronisculus, Boreosomus, Australosomus* and *Birgeria* (fig. 460 D, G–L) to such an extent that these forms are in certain respects better known than many extant fishes. It is, therefore, not surprising

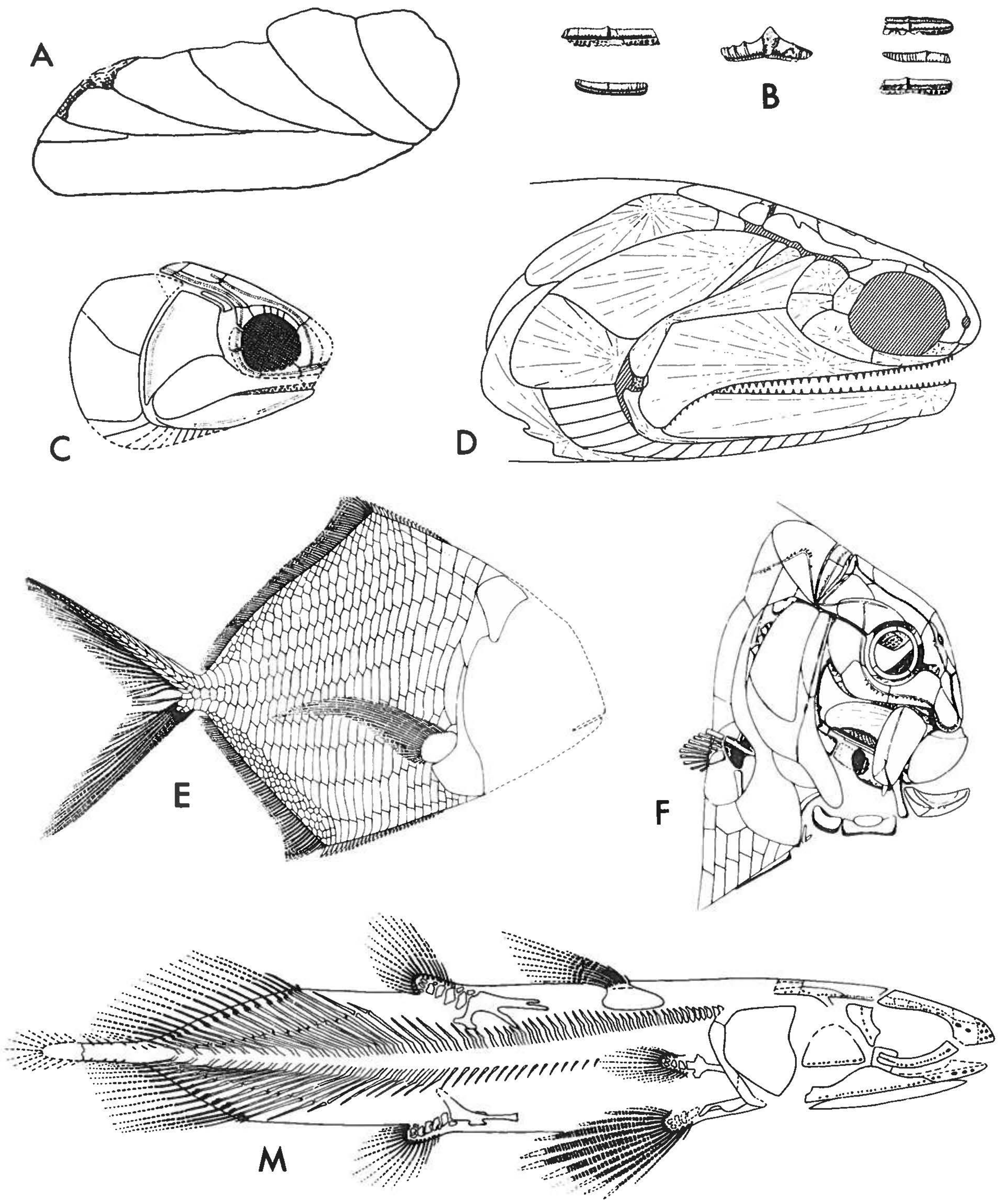
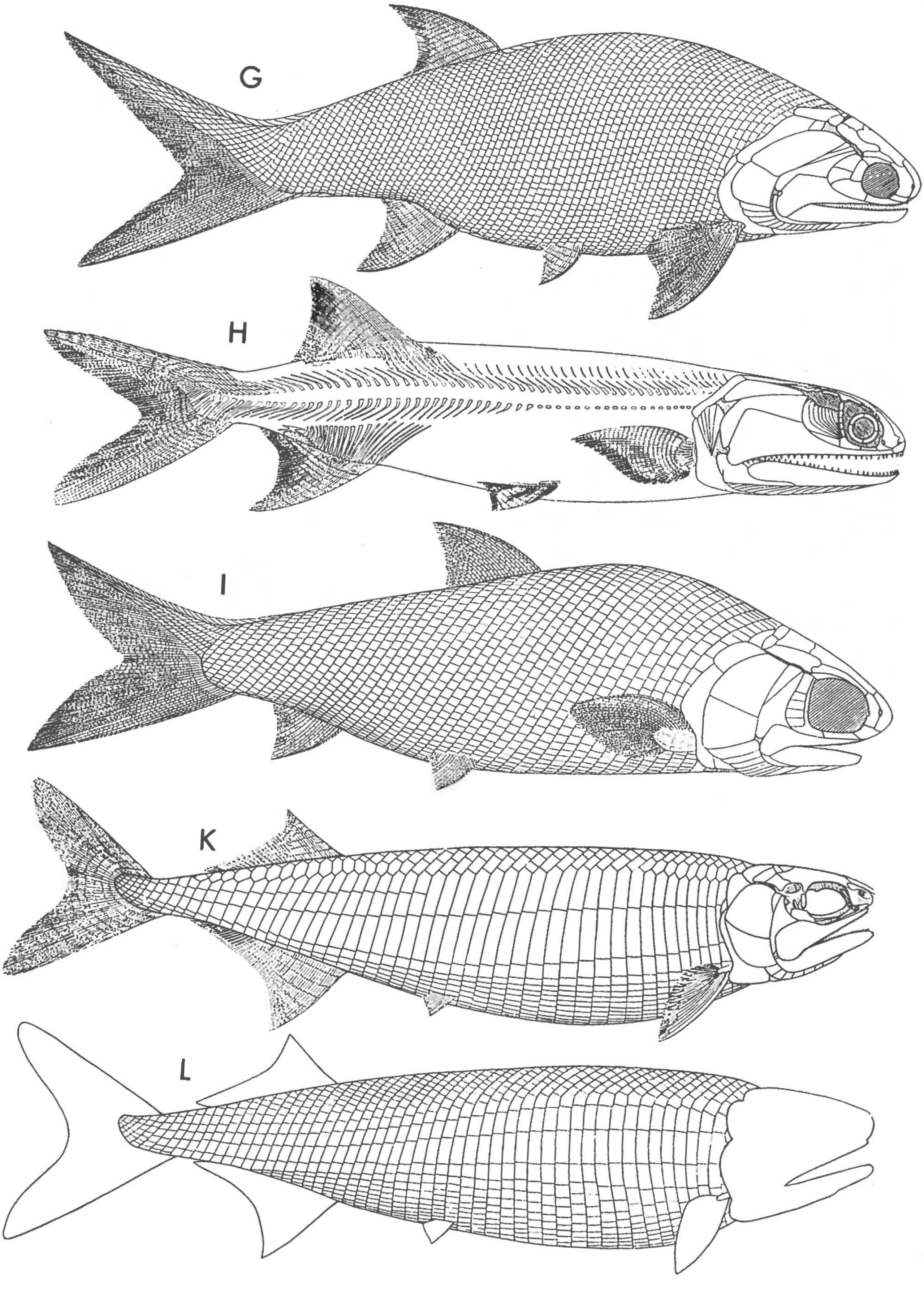


Fig. 460. Triassic (Lower Scythian) elasmobranchs, actinopterygians and coelacanthid from East Greenland. A: *Parahelicampodus spärcki*. B: *Polyacrodus claveringensis*. C: *Perleidus stoschiensis*. D & G: *Pteronisculus magna* (head) and *Pteronisculus stensiöi*. E-F: *Bobasatrania groenlandica*. H: *Birgeria groenlandica*. I: *Boreosomus piveteaui*. K-L: *Australosomus kochi* and *Australosomus simplex*. M: *Laugia groenlandica*. A, C, D: nat. size; B: *c.* × 2.5; E: *c.* × 0.5; F-M: each of these restorations is based on several specimens. Reproduced from: Stensiö (1932); Nielsen (1942, 1949, 1952, 1953).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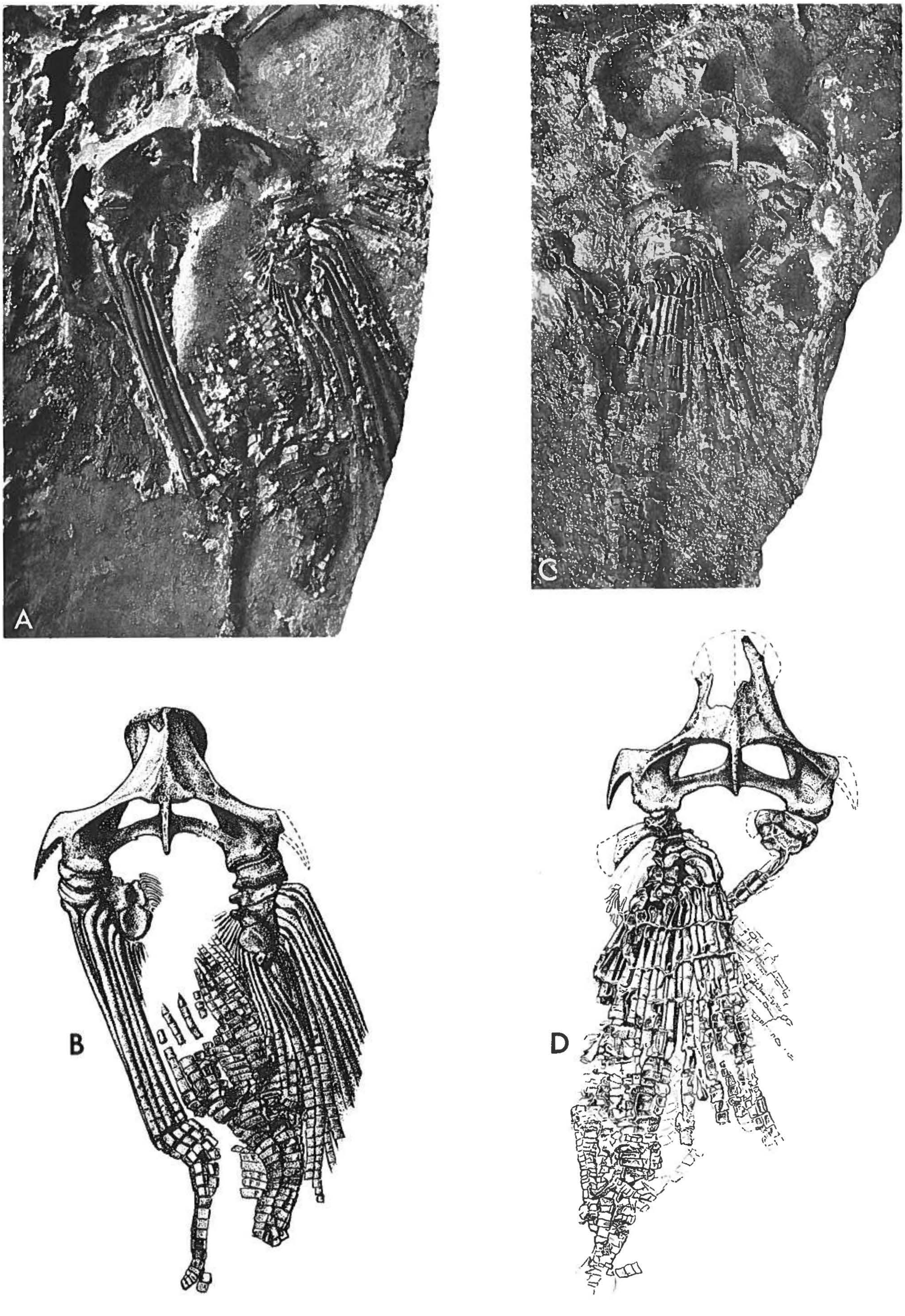
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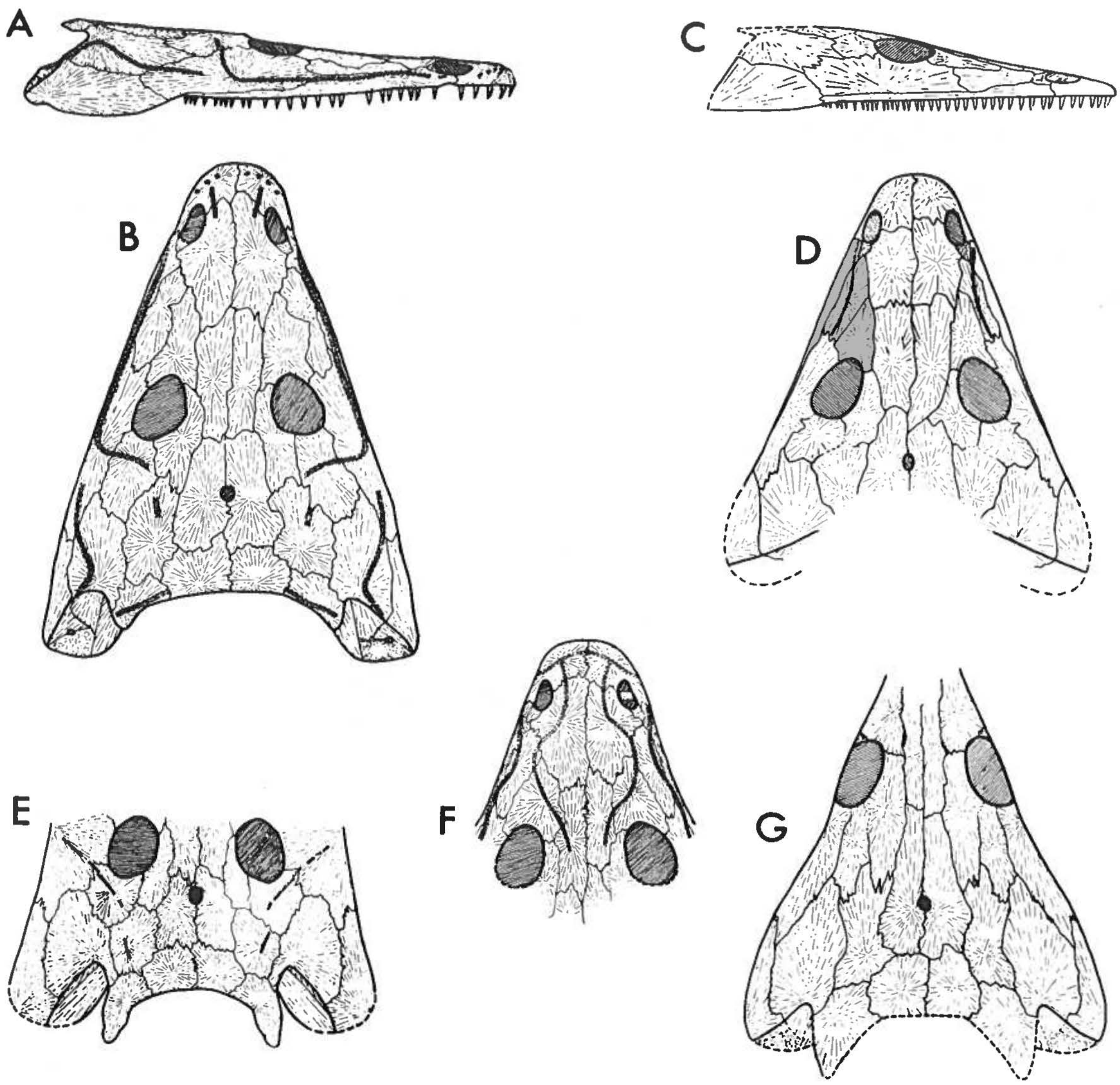


Fig. 462. Restorations of stegocephalian skulls from the Triassic (Lower Scythian) of East Greenland. A-B: *Lyrocephalus kochi*. C-D: *Lyrocephalus rapax*. E: *Wetlugasaurus groenlandicus*. F: *Lyrocephalus johanssoni*. G: *Stoschiosaurus nielseni*. All figs *c.* × 0.5. Reproduced from Säve-Söderbergh (1935).

that in the field of palaeoichthyology these studies have become standard works.

Laugia groenlandica (fig. 460 M), a coelacanth known only from Greenland, was described by Stensiö in 1932, but the fauna includes also forms which according to Nielsen (1936), pertain to or are close relatives of such genera as *Sassenia, Wimania* and *Whiteia* from the early Triassic of Spitsbergen and Malagasy. Nielsen was unfortunately unable to publish this material but there remain photographs and drawings of the pelvic girdle and fins of *Laugia* which he, from acetic acid prepared material, had found to differ radically from the reconstructions published by Stensiö (1932). There is no doubt as to the importance of Nielsen's observations which prove, as he has pointed out in a handwritten note found together with the illustrations (given here as fig. 461 A–D) that *Laugia* is not congeneric with the Jurassic *Coccoderma* as maintained by White (1954).

The stegocephalians (fig. 462 A–G) were described by Säve-Söderbergh (1935) and Nielsen

←

Fig. 461. Pelvic girdle and fins of *Laugia groenlandica* (ventral view) which, as displayed by the figured specimens (A-B: MMH. VP. 1017; C-D: MMH. VP. 1018), differs from all other known coelacanthids in having the halves of its pelvic girdle completely fused so as to form an unique single structure. Photographs and drawings prepared by the late Eigil Nielsen from acetic acid developed specimens. A-B: *c.* × 3; C-D: *c.* × 2.25.

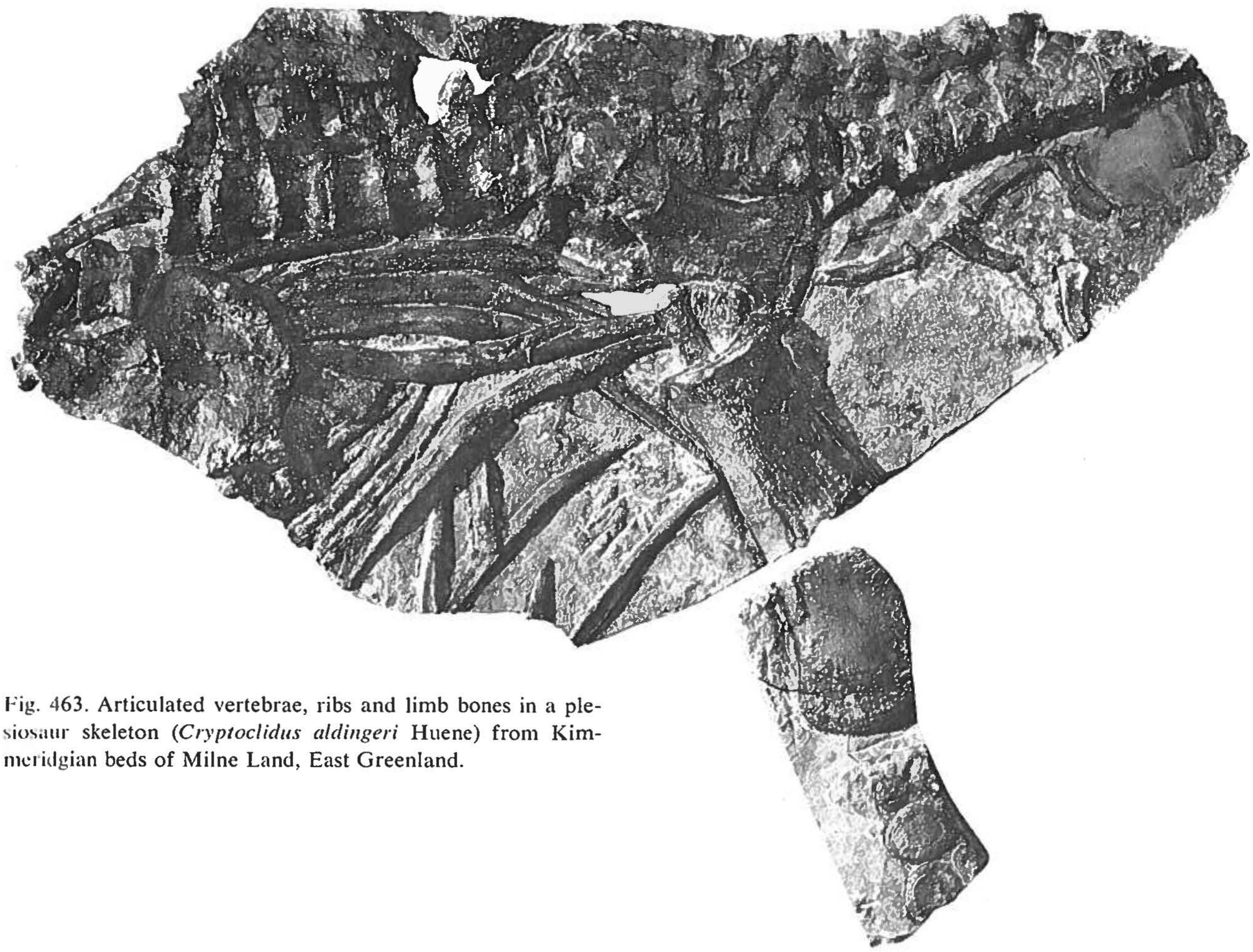


Fig. 463. Articulated vertebrae, ribs and limb bones in a plesiosaur skeleton (*Cryptoclidus aldingeri* Huene) from Kimmeridgian beds of Milne Land, East Greenland.

(1954, 1967). On the basis of their respective studies, both writers advanced various widely discussed new ideas concerning tetrapod phylogeny and classification.

The vertebrate material from later parts of the Triassic sequence is inconsiderable. A small collection of fish-remains from eastern Peary Land contains, according to Nielsen (cf. Kummel, 1953), forms corresponding to those from the Lower Triassic of Spitsbergen.

The Upper Triassic exposures in Jameson Land (fig. 441) have yielded various fish finds (Stauber, 1940; Perch-Nielsen *et al.*, 1972) of which those from the Rhaetic beds collected by Stauber comprise well preserved, fairly large actinopterygians, presumably *Gyrolepis*. Unfortunately, the whole collection of the better preserved fishes, which were to have been studied by Aldinger, was destroyed during a World War II raid on Stuttgart. From Rhaetic beds came also a hybodontid fin-spine found, together with a few undeterminable large bone fragments, by Harris in the Kap Stewart Formation (Rosenkrantz, 1934; Harris, 1937). The occurrence of this particular fin-spine in an otherwise typical limnic-fluviatile formation prompted Harris to conclude that the area where the sedimentation took place "was liable to be temporarily flooded by the sea and that it was normally just above sea level". However, hybodontids are now known to include, in addition to their marine representatives, also numerous forms adapted to purely freshwater environments (Patterson, 1966). Harris' conclusion, consequently, receives no definite support from the hybodontid specimen and may be abandoned.

Jurassic

Jurassic vertebrates occur at several localities in Jameson Land and Milne Land (fig. 441), within the Scoresby Sund area, where marine deposits of this age are widespread (see Birkelund & Perch-Nielsen, this volume). The first find, made in 1900 by the Danish geologist N. Hartz (1902), was an ichthyosaur vertebra which, according to Fraas (1909), belongs to *Ophthalmosaurus*. Hartz also brought home a sandstone slab showing imprints arranged in a pattern recalling that of dinosaur trails (Hartz, 1902) and it was described as such by Fraas (1909). However, Rosenkrantz (1934) has found this interpretation untenable.

As known at present, the vertebrate fauna of the Greenland Jurassic comprises fish and marine reptiles but so far only a little has been published.

Fish are apparently not rare but most finds consist of detached scales or badly preserved specimens (Aldinger, 1935b). From beds of Middle Jurassic age, a single elasmobranch tooth provides the only known indication of the presence of this group (Stauber, 1940). Among the actinopterygian material from Upper Jurassic beds, Aldinger (1935b) identified remains of *Leptolepis*-like forms. However, a well-preserved part of a head of a caturid collected by Rosenkrantz from the uppermost Jurassic exposed near Kap Leslie (Milne Land; fig. 441), and described as *Caturus groenlandicus* by Aldinger (1932), indicates the presence within this area of beds with fish fossils worthy of palaeoanatomical studies.

Ichthyosaurs and plesiosaurs are represented in the collection mostly by fragments, such as vertebrae, teeth and parts of ribs, originating from Liassic and Upper Jurassic (Kimmeridgian) beds in Jameson Land and Milne Land (Rosenkrantz, 1934; Aldinger, 1935b; Håkansson *et al.*, 1971). Some finds, however, are more complete, as is the case with an ichthyosaur skeleton from Milne Land collected in 1970. An apparently complete plesiosaur skeleton, about 4 m long, was found by Stauber (1940) in Liassic beds in upper Klitdal (northern Jameson Land) but, owing to difficult travelling conditions, only a few pieces of this skeleton were brought home. Another specimen (fig. 463), showing parts of an articulated skeleton, was collected by Aldinger (1935b) from Kimmeridgian strata on Milne Land (fig. 441). It was described and named *Cryptoclidus aldingeri* by von Huene (1935). Looking at this specimen, however, one finds various features showing that von Huene apparently erred in his interpretation and redescription of this specimen is therefore needed.

Cretaceous – Tertiary

Sedimentary deposits of this age are encountered both on the west and east coasts of Greenland (see Henderson *et al.,* this volume; Birkelund & Perch-Nielsen, this volume) but vertebrate remains have so far only been found in those from northern West Greenland (fig. 464). These deposits, it may be added, yielded the first non-Quaternary fossil vertebrates to be found in Greenland, namely some teleost

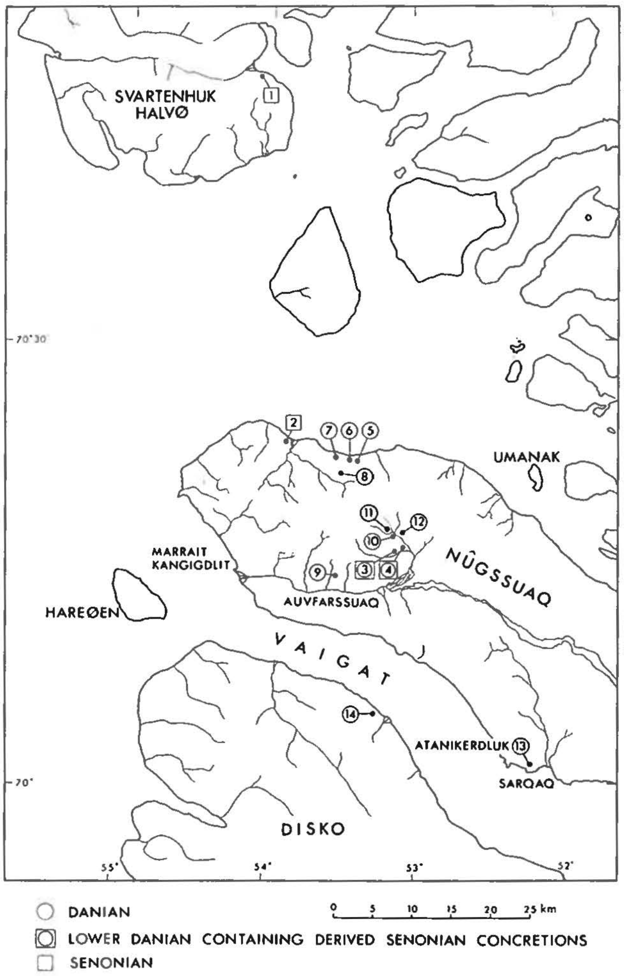


Fig. 464. Map showing the distribution of vertebrate yielding localities in the Upper Cretaceous and lowermost Tertiary (Danian) marine deposits in West Greenland. 1: Umîvik (Coniacian). 2: Tuperssuartâ (Lower Santonian). 3 & 4: Oyster-ammonite conglomerate locality I & III. 5. Igdlorssuaussaq. 6: Kangilia. 7: Vestre Konglomeratkløft by Angnertuneq. 8: Danienkløft. 9: Ilugigsoq. 10: Agatkløft. 11: Turritellakløft. 12: Qaersutjægerdal. 13: Tartunaq. 14: Kugssinikavsak.

remains collected by F. Søltoft in 1862 and 1866 and by K. J. V. Steenstrup in the 1870s and subsequently studied by Ravn (1918).

Fossil vertebrates are not particularly abundant in the otherwise rich marine faunas from West Greenland (Bendix-Almgreen, 1969). They comprise elasmobranchs (detached teeth, spines and vertebrae) secured from reworked Maastrichtian concretions and from Lower and Upper Danian deposits on Nûgssuaq, and actinopterygians from Senonian and Danian deposits on Svartenhuk Halvø (Coniacian), Nûgssuaq (Lower Santonian, Maastrichtian, Lower and Upper Danian) and Disko (Danian?) (fig. 464). For the sake of completeness, one should add here that material not available when the writer published his earlier paper has shown the presence of chimaeroids in the Maastrichtian vertebrate fauna.

Among the actinopterygians a fairly well preserved gadoid deserves to be mentioned which, as it derives from the Lower Danian deposits constituting the Kangilia Formation, is the oldest known representative of the gadoids.

The elasmobranchs from the Danian deposits have been found to represent two different assemblages which proved to be of much interest in relation to stratigraphy (Bendix-Almgreen, 1969). These assemblages are:

Kangilia Formation elasmobranchs (Lower Danian)

Selachoidei
Notidanidae
Notidanus sp.
Squatinidae
? *Squatina* sp.
Squalidae
Squalus sp. aff. *S. (A.) orpiensis* Winkler
Lamnidae
Scapanorhynchus raphiodon Agassiz
Lamna appendiculata Agassiz
Lamna cf. *L. appendiculata* Agassiz
Lamna incurva Davis
Lamna elegans Agassiz
Lamna cf. *L. elegans* Agassiz
Lamna cf. *L. venusta* Leriche
Oxyrhina cf. *O. lundgreni* Davis
Oxyrhina sp.

Agatdal Formation elasmobranchs (Upper Danian)

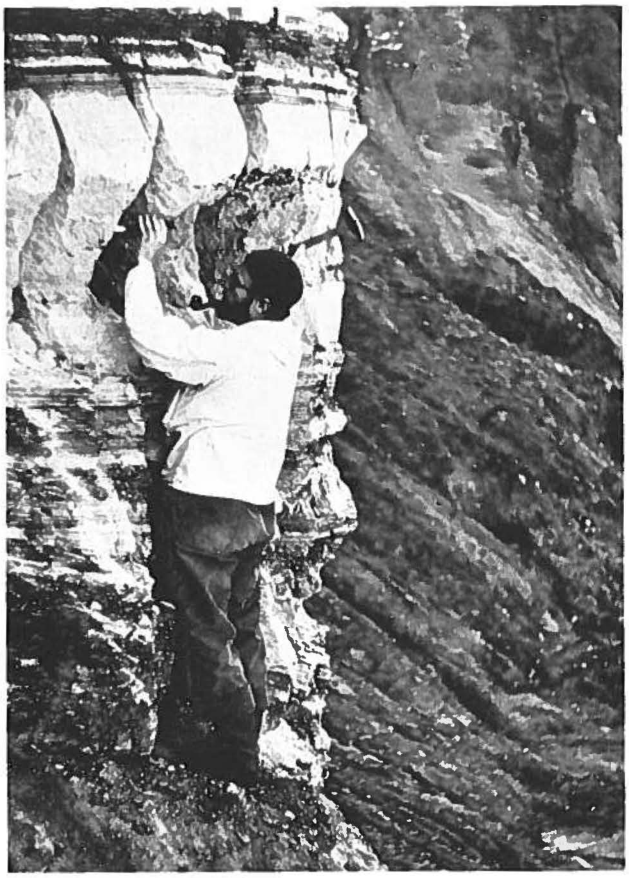
Selachoidei
Heterodontidae
Heterodontus sp. nov.
Synechodus eocænus Leriche
Squantinidae
Squatina prima Winkler
Squalidae
Squalus (Acanthias) orpiensis Winkler
Squalus (Acanthias) minor Daimeries
Scylliidae
Scyllium vincenti Daimeries
Scyllium minutissimum Winkler
Scyliorhinidae
Galeus sp.
Scymnorhinidae
Somniosus crenulatus Arambourg
Lamnidae
Lamna vincenti Winkler
Lamna verticalis Agassiz
Lamna cf. *L. venusta* Leriche (probably derived from eroded older deposits)
Odontaspis (Odontaspis) rutoti Winkler
Odontaspis (Synodontaspis) macrota Agassiz, premut. *striata* Winkler
Odontaspis (Synodontaspis) hopei Agassiz
Odontaspis (Synodontaspis) winkleri Leriche
Odontaspis sp. indet.
Batoidei
Rajidae
? *Raja* sp.

The Kangilia Formation assemblage shows a broad conformity with the elasmobranch fauna described by Davis (1890) from the Lower and Middle Danian type localities in Dano-Scania and has, like the Dano-Scanian fauna, a certain affinity to Cretaceous elasmobranch faunas. This is in good agreement with the invertebrate fauna of the Kangilia Formation which proves a Lower Danian age for this formation.

The close correspondence between the selachoid fauna of the Kangilia Formation and that of the Lower and Middle Danian of Dano-Scania (common genera: *Notidanus, Scapanorhynchus, Lamna, Oxyrhina;* common species: *Lamna appendiculata, Lamna elegans, Lamna incurva, Oxyrhina* cf. *O. lundgreni*) indicates a marine connection between the West Greenland sea and the Dano-Scanian Basin in early Danian time. The selachoids, therefore, support the palaeogeographical hypothesis set forward by Rosenkrantz (1951) on the basis of the invertebrates.

The Agatdal Formation (fig. 465) fish assemblage, which besides the above mentioned elasmo-

Fig. 465. The richly fossiliferous Sonja lens (worked on by the late Kristian Skou) constituting a part of the Sonja Member (Agatdal Formation; Rosenkrantz, 1970) has yielded the main part of the Upper Danian vertebrate fauna collected from Nûgssuaq. Photo: A. Rosenkrantz 1953.



branchs also includes such actinopterygians as *Arius* and *Sphyraenodus*, shows very close affinity in both genera and species to faunas of the marine younger Paleocene in Europe and North Africa. It also shows some remote affinity to the Paleocene Aquia Formation of eastern North America (Bendix-Almgreen, 1969). However, the age of the Agatdal Formation is Upper Danian (Rosenkrantz, 1970) and its fish assemblage is consequently decidedly older than those referred to from Europe and North Africa. It may be inferred, therefore, that the Agatdal Formation fish fauna could represent the earliest hitherto known emergence of that particular faunal assemblage which occurs in Europe at the beginning of the transgression in the Upper Paleocene. This may, in turn, have some bearing on palaeofaunal migrations.

Quaternary

The present review of the Greenland vertebrate palaeofaunas would not be complete without some remarks on the Quaternary vertebrate fossils which are found, sometimes in large numbers, in the raised marine deposits encountered in many places within the ice free coastal region of Greenland (fig. 466). The rich and varied collections of these vertebrate fossils have never been closely investigated; merely some particular specimens have been mentioned in passing in literature concerned with other topics. A closer study of them is also beyond the scope of this review but a short list of forms can be provided:

Actinopterygians
- *Mallotus villosus* Müller
- *Gadus* sp.
- *Sebastes* cf. *S. marinus* Linné

Mammalia
- *Balaena mysticetus* Linné
- *Odobaenus* sp.
- *Phoca vitulina* Linné
- *Pusa hispida* (Schreber)
- *Phoca* sp.
- *Rangifer* sp.

Some of the forms in the list, namely *Sebastes* cf. *S. marinus* and *Pusa hispida*, are reported here for the first time. Among the detached bones which can be referred to *Sebastes* is an incomplete maxillary (fig. 467 D–E) collected by A. Weidick at Qaleragdlit sermia (Weidick, 1972) and identified by the writer. The *Pusa hispida* specimen, an articulated but incomplete skeleton, was found by L. Símonarson at Pátorfik (fig. 466) and identified by U. Möhl and Ella Hoch. The latter find is of particular interest inasmuch as there are reasons to suggest that it belongs to an interglacial fauna (Rosenkrantz, 1968). Other finds (*Rangifer* antlers from Saunders Ø and from the Angmagssalik area, and an *Odobaenus* cranium from Frederikshåbs Isblink (C. Vibe & U. Möhl, personal communication) have been suspected to be of interglacial age but the evidence for this assumption seems inconclusive.

Fig. 466. Map to show the localities mentioned in the text from which interglacial and post-glacial Quaternary vertebrates have been collected.

Most finds, however, derive from raised marine deposits formed during post-glacial time; their absolute age ranges from more than 9000 to about 4000 years (Weidick, 1968). The youngest of these are then about contemporary with the oldest evidence of man's presence in Greenland found by Eigil Knuth in Peary Land (Knuth, 1965, 1967). The fish fossils from these deposits are mainly preserved in clay nodules. *Mallotus villosus* (fig. 467 A–C) is the most common form but several others, including gadids, are represented from Sydostbugten (Orpigsôq, Marraq, Marrait), Godthåb, Frederikshåb, Qôrnoq near Ivigtut etc. (fig. 466). The mammals include whales, seals and even caribou remains. The Greenland Whale or Bowhead (*Balaena mysticetus*) has been reported both from West Greenland (North Star Bugt and Holsteinsborg; fig. 466) and from East Greenland (Hvalsletten, fig. 466), while the Harbour Seal (*Phoca vitulina*) is reported from Orpigsôq at Disko Bugt (fig. 466).

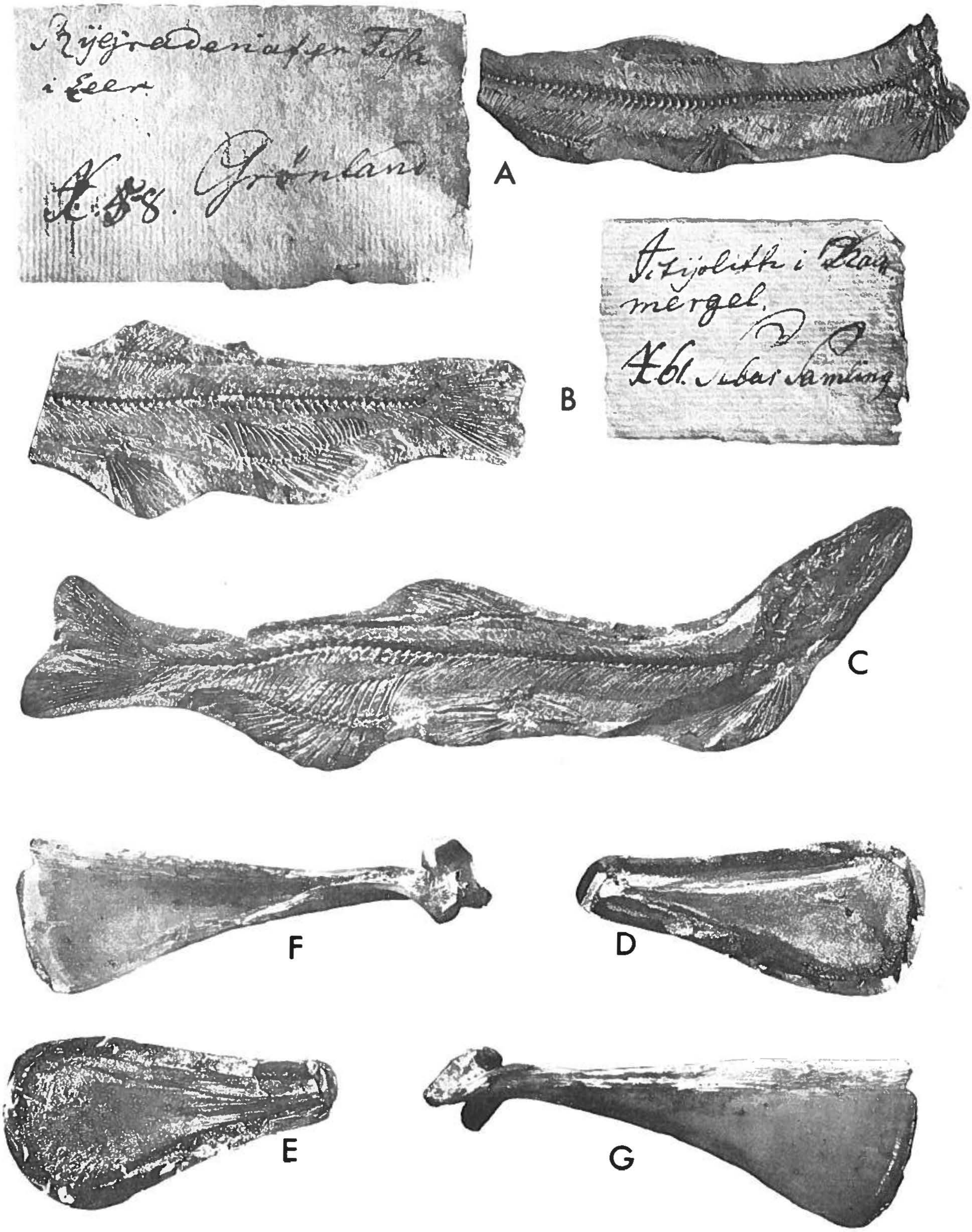


Fig. 467. Some fossil fishes from the Quaternary of Greenland. A-C: *Mallotus villosus* (MMH. VP. 1334, 1335 & 1336; approx. × 1). D-E: *Sebastes* cf. *S. marinus* (MMH. VP. 1337; approx. × 1.5), casts of detached, incomplete maxillary (dexter) in medial (D) and lateral (E) view. Compare with figs F & G displaying, in the same aspects, a somewhat larger maxillary (sinister) of *Sebastes marinus* (from specimen K. 82; Zoological Mus. Coll., Copenhagen; *c.* × 1) caught off Sukkertoppen in Davis Strait.

The *Mallotus* specimens A & B are figured in conjunction with their original eighteenth century labels which show them to originate from the geological section of the Dutch collector Albert Seba's (1665–1736) natural curiosity cabinet. Parts of this were purchased by the Danish Count A. G. Moltke at the general sale in 1752 and sent to Denmark. These two *Mallotus* specimens are, in effect, some of the first fossil vertebrates from Greenland that are known to have been brought to Europe.

One may finally add, as a historical curiosity, that the Quaternary fossil fishes were apparently the first Greenland fossil vertebrates known to European science. Information on these fossils is found in the early literature on Greenland in records by Cranz (1765) and Stauning (1775). The fossils were also brought to Europe (Agassiz, 1833–43), probably by whalers hunting in the Greenland waters. The Dutch collector Albert Seba (1665–1736) possessed specimens of *Mallotus villosus* (fig. 467 A–B) from Greenland in his renowned cabinet of natural curiosities, studied by Carl von Linné and Peter Artedi, and these specimens are now kept in the collections of the Mineralogical Museum of Copenhagen University.

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