

Kristiansen as mechanic. I. K. Olsen and J. Laustrup worked as base personnel while J. Bojesen-Koefoed, J. Halskov, G. S. Nielsen, P. Schiøler and K. Zinck Jørgensen assisted in the field and at base camp. H. Olsen's sedimentological studies in the Devonian are supported by the Carlsberg Foundation. M. Larsen and B. Sikker Hansen helped to prepare the manuscript.

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Upper Devonian and Upper Permian vertebrates collected in 1987 around Kejser Franz Joseph Fjord, central East Greenland

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In July and August 1987 a five-man British/Danish vertebrate palaeontological expedition carried out field work on Gauss Halvø and eastern Ymer Ø to collect fossil vertebrates from exposures of the Upper Devonian continental and Upper Permian marine deposits. In the context of sampling for vertebrates the Upper

Devonian deposits were last visited in 1955 when one of the writers (SEB-A) assisted the late Dr Eigil Nielsen with field work while the Upper Permian marine deposits have not been examined since Bendix-Almgreen's field work in the Kap Stosch area in the summer of 1967.

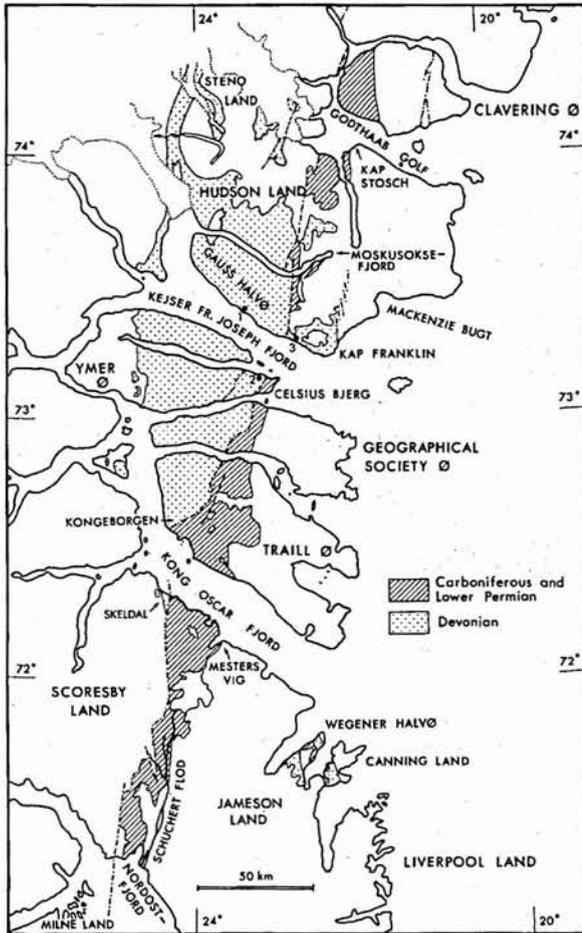


Fig. 1. Continental Devonian deposits in central East Greenland range from the Givetian to the Fammenian-Strunian. Vertebrate fossils, including tetrapods, were collected from deposits of the latter age-bracket, exposed on Stensjö Bjerg and Wiman Bjerg (1) and on Celsius Bjerg (2). At Margrethedal (3) elasmobranchs and actinopterygians were collected from outcrops of the marine Upper Permian. Map from Bendix-Almgreen (1976).

The project was supported from various funds. After flying to Mesters Vig on 5 July the team joined the GGU East Greenland project which provided equipment, provisions and logistic support. On 6 July the team was lifted by helicopter to the first camp site situated at the south-east corner of Stensjö Bjerg. For the subsequent 28 days the team worked from this camp, collecting exclusively from the Upper Devonian deposits cropping out on Stensjö Bjerg and Wiman Bjerg (fig. 1). On 4 August the expedition split into two: one team was transported by helicopter to eastern Ymer Ø where they camped close to the West Circus Valley and the other team proceeded on foot along the

north coast of Kejser Franz Joseph Fjord towards Margrethedal, on the east side of which a camp site was chosen for the remaining days of the field season. Both teams were evacuated by helicopter to the GGU Stordal base camp on 16 August.

Upper Devonian vertebrates

The Fammenian-Strunian continental deposits of central East Greenland have yielded a rich fossil vertebrate fauna which in addition to representatives of the cladodontids, acanthodians, arthrodiroids, antiarchs, dipnoans, porolepiformes, osteolepiformes and struniiformes, also comprises the much celebrated ichthyostegid stegocephalians which until recently were the only known tetrapods of undisputed Devonian age (see e.g. Bendix-Almgreen, 1976; Jarvik, 1980; Clack, in press).

In the summers of 1968–70 expeditions from Cambridge University, under the leadership of Dr Peter Friend, carried out extensive sedimentological field studies of the Devonian deposits of central East Greenland (Friend *et al.*, 1976a,b; Alexander-Marrack & Friend, 1976; Nicholson & Friend, 1976; Yeats & Friend, 1978; Friend *et al.*, 1983). During the field work J. Nicholson succeeded in collecting various tetrapod fossils among which several more or less fragmentary skulls and some postcranial bones came from scree located about 800 m up and close to the south-eastern ridge of Stensjö Bjerg (fig. 2). The material was recently investigated by one of the present writers (JAC) who found that three skulls, preserved juxtaposed to each other in one block of very fine-grained sandstone, all belonged to *Acanthostega gunnari* which had been erected by Jarvik in 1952 (Clack, in press).

Until this discovery *Acanthostega gunnari* was known only from a couple of incomplete skull roofs and the additional material greatly extended the knowledge of the species' skull morphology. The fact that the material from Nicholson's locality also contained other tetrapod remains indicated that this locality had great potential for yielding significant collections of these fossils. Accordingly, the locality was revisited for further collecting during the 1987 field season when not only the rich scree locality was refound, but also the actual horizon of fossiliferous deposits that had yielded the fossils in the scree was located. The deposits belong to the upper part of the Britta Dal Formation (Friend *et al.*, 1983) which in general corresponds to what has earlier been referred to as the Upper Division of the *Remigolepis* series (Jarvik, 1961; Bendix-Almgreen, 1976).

Sedimentology. The Britta Dal Formation (Friend *et al.*, 1983) in which the fossils were found is composed of

Fig. 2. Outcrop of the beds from which tetrapod fossils were collected *in situ* at the south-east crest of Stensiö Bjerg. The sequence, consisting of about 1 m thick channel fill deposits partially laid down on point bars, indicates that deposition took place in shallow meandering channels which apparently formed part of a highly ephemeral low gradient stream system. Tetrapod remains predominate in both number and preservation in the fossil assemblage which also includes plant macrofossils, disarticulated skeletal elements of *dipnoans* and *Holoptychius* but only a single plate of *Remigolepis*. Photo: H.O. 21.7.1987.



alternating siltstone and very fine to fine-grained sandstone. However, detailed sedimentological investigations are not possible due to pronounced weathering and scree development. The siltstone occupies c. 80% and is mainly reddish with some greyish beds. In the upper half of the formation greenish beds also occur. Cross-lamination is the dominant primary structure. Desiccation cracks are common and bioturbation occurs in several intervals. The siltstone is usually highly brecciated either due to frequent desiccation or disruption by rootlets. The sandstone mainly occurs as channel-shaped bodies, 0.5–1 m thick. Individual sandstone-bodies are commonly multistorey. The storeys very often exhibit lateral accretion bedding and fining-upwards lithology. Parallel lamination, cross-lamination and trough cross-bedding dominate the sandstone. Internal mud partings are common, sometimes associated with desiccation cracks. The sandstone was deposited as point bars in shallow meandering fluvial channels. The discharge was highly fluctuating to ephemeral. The depositional environment is accordingly an (ephemeral) meandering channel belt with extensive muddy flood basins.

Tetrapods. Most of the new tetrapod fossils were collected on Stensiö Bjerg from the point bar deposits, forming the outcrop at the 772 m locality and yielding the scree material just below. In addition to a large variety of detached skull and postcranial bones, these comprise a number of articulated skulls of varying degrees of completeness, preservation and size. Some could be identified immediately as belonging to *Acan-*

thostega and probably pertain to the species *A. gunnari*. However, the bulk of the skull material, which may even comprise *Ichthyostega* specimens, awaits determination. It seems that some of the specimens, preserving skull remains in association with postcranial skeleton parts (including elements of the vertebral column), actually pertain to the genus *Acanthostega*. A specimen showing a sizeable, articulated portion of a body squamation preserved in association with pelvic girdle elements may also belong to this genus (fig. 3). A similar partially preserved body squamation was collected from a locality on Wiman Bjerg where a much weathered and entirely flattened skull of *Acanthostega* (skull length c. 9 cm) (fig. 4) was also found preserved in association with articulated parts of the shoulder girdle.

New specimens of the genus *Ichthyostega* were collected from scree derived from the upper part of the Aina Dal Formation (Friend *et al.*, 1983) as exposed just west of Aina Dal. These include part of a skull and associated lower jaw and parts of the pelvic girdle, hind limb (fig. 5) and tail. Yet another partially preserved, but so far unidentified tetrapod specimen showing remains of skull and shoulder girdle in association, was found at the same scree locality. This specimen may derive either from the Wiman Bjerg Formation's lowermost part or perhaps from the Aina Dal Formation.

Ichthyostega skull parts and jaws and other tetrapod remains were also collected from localities on the north side of Celsius Bjerg on eastern Ymer Ø.

Osteolepiformes, Porolepiformes and Stuniiformes. New specimens of the large osteolepiform *Eusthenodon*

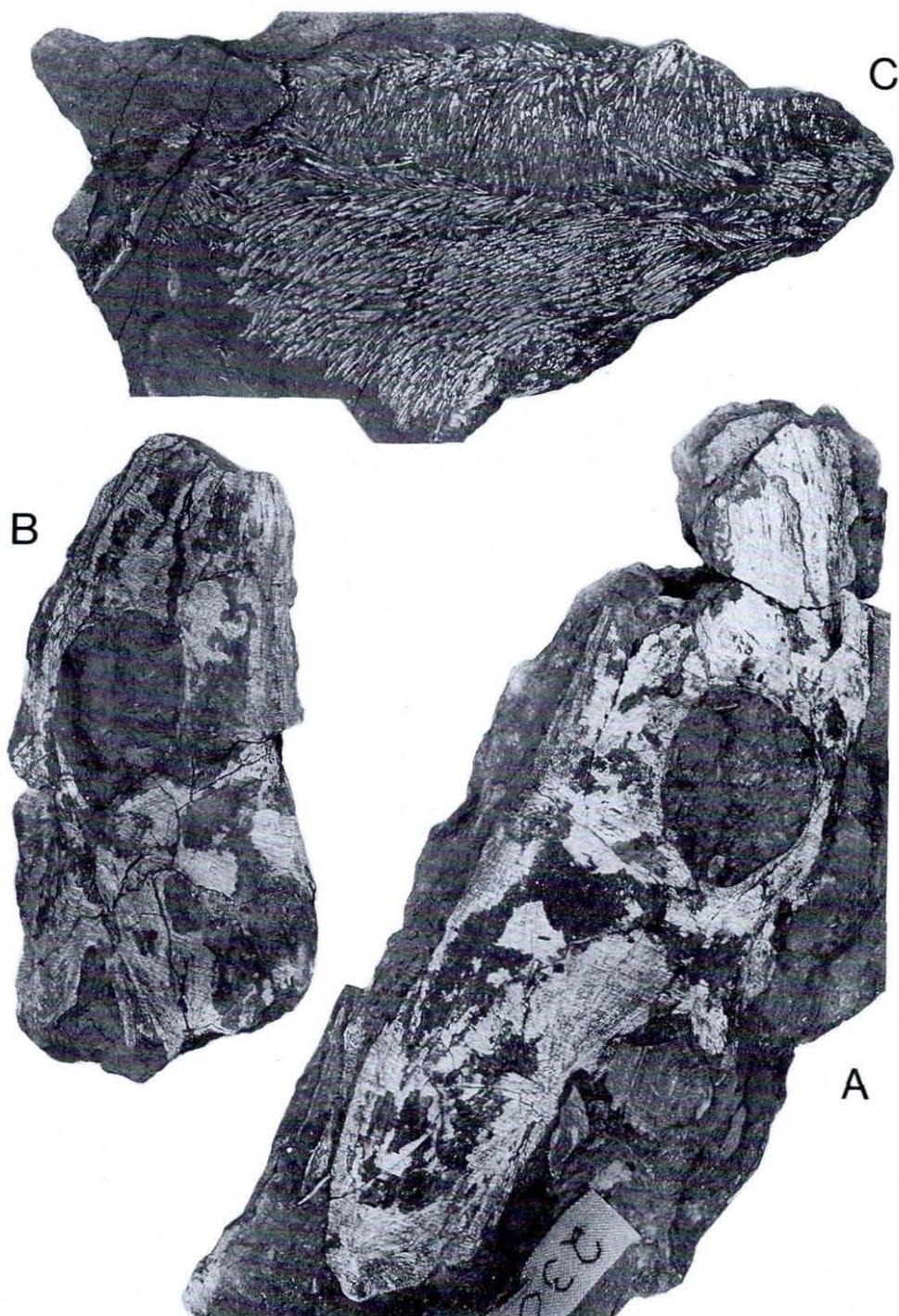


Fig. 3. Tetrapod fossils collected from scree just below the fossiliferous point bar deposits shown on fig. 2. A & B: Incomplete skull roofs of *Acanthostega* cf. *gunnari*. C: Part of articulated body squamation associated with limb endoskeleton elements. Specimens shown in approx. nat. size. A-C: Geological Museum Copenhagen field nos 230a, 251 and 252a, respectively.

Fig. 4. *Acanthostega* sp.; flattened, much weathered skull roof of a small individual collected on Wiman Bjerg. Approx. nat. size. Geological Museum Copenhagen field no. 1400a-b.



Fig. 5. *Ichthyostega* sp.; partially exposed articulated hind-limb and foot endoskeleton. Aina Dal Formation, Stensiö Bjerg. Approx. nat. size. Geological Museum Copenhagen field no. 1384a⁹.



(Jarvik, 1952; Bendix-Almgreen, 1976) were collected at localities both on Stensiö Bjerg and on the north side of Celsius Bjerg. Most of the collected rhipidistian material pertains, however, to the porolepiform genus *Holoptychius* (Jarvik, 1972) and includes specimens displaying skull roof, cheek and lower jaw bones, which may provide new information concerning the entire skull bone pattern. Other specimens may give new information regarding the fin endoskeleton. The material derives from localities on Stensiö Bjerg and on the north side of Celsius Bjerg. One locality discovered on Stensiö Bjerg showed an *in situ* concentration of a considerable number of *Holoptychius* individuals preserved articulated, but totally compacted.

A single *Onychodus* parasymphysial tooth whorl deserves mention because its occurrence on Stensiö Bjerg, in scree derived either from the top of the Wiman Bjerg Formation or from the Britta Dal Formation above, establishes the presence of this struniiform genus at higher stratigraphical levels in the East Greenland Upper Devonian than hitherto recorded (Stensiö, 1936).

Dipnoi. New skull material of the genus *Soederberghia* (Lehman, 1959; see also Bendix-Almgreen, 1976) was collected. Other specimens show a partial skull roof, and the palate, ribs, vertebral centra, anal fin and other associated parts possibly from the same genus. This material from localities on the north side of Celsius Bjerg supplements that found on Stensiö Bjerg which probably derives from deposits of the Aina Dal Formation and includes specimens showing parts of vertebral columns. Specimens from deposits of the Britta Dal Formation comprise detached skull roof bones and parts of the palate; among them a pterygoid and associated tooth plate possibly representing the genus *Oervigia* (Lehman, 1959). Significant dipnoan remains also occur in the richly fossiliferous point bar deposits which yielded a large part of the considered tetrapod fossils.

Arthrodires and Antiarchs. A few exoskeletal bones of unidentified arthrodires were collected from scree on Stensiö Bjerg (? Britta Dal Formation) and an arthrodire jaw was found in scree on the north side of Celsius Bjerg. A few specimens of the very common antiarch *Remigolepis* (Stensiö, 1931; Jarvik, 1985, p. 4) preserved articulated, were taken from scree localities on both Stensiö Bjerg and on the north side of Celsius Bjerg.

Plant fossils and palynological samples. Some stem sections derived from the point bar deposits of the 772 m locality on Stensiö Bjerg were considered worth laboratory inspection but it has turned out that only one of

these might be identifiable (Dianne Edwards, personal communication 1987). Samples for palynological inspection were also brought back from this locality but processing in the laboratory gave no identifiable spores (Stefan Piasecki, personal communication 1987).

Notes on tetrapods and habitat. The fact that the large number of *in situ* tetrapod fossils from the point bar deposits exposed at the 772 m locality on Stensiö Bjerg comprises fairly complete crania and larger associated parts of skeletons indicates that the tetrapod carcasses had not been subject to any long transport before they became embedded in the deposits. Accordingly it seems reasonable to assume that the deposition site was located within the very area in which the tetrapods lived. This area was characterised by shallow, meandering fluvial channels.

The tetrapods may have searched for their prey mainly in the meandering and intertwining streams where mating and breeding also took place. However, the habitat for these early tetrapods may have included the land immediately around the stream banks. Direct evidence for this in the form of fossil trackways like those known from the Upper Devonian of Australia (Warren & Wakefield, 1972) has not yet been found in East Greenland. However, the structure of the postcranial endoskeleton of *Ichthyostega* indicates that this had the functional prerequisites for body support and locomotion also out of the water and this may have been the case also with *Acanthostega*. There are features suggesting that *Ichthyostega* physiologically was dependent on cutaneous respiration (Jarvik, 1980, p. 226) and *Acanthostega* may have had similar requirements. It should be noted therefore, from finds of fossil plants including impressions of large-size trunks, and from other evidence such as brecciation of siltstone due to disruption by rootlets, that a fairly diversified flora existed in the area during the late Devonian. This can only mean that on the moist ground adjacent to the streams there was enough vegetation to give the early tetrapods which ventured out of the water, adequate shelter also against the desiccating effect of the wind upon their skin.

The habitats and mode of life of such early tetrapods as *Acanthostega* and *Ichthyostega* may to some extent have differed from each other though hardly radically so. Bjerring (1985, p. 44) suggests that "*Ichthyostega*... could hardly walk", since in his interpretation of its pelvic appendicular endoskeleton, *Ichthyostega* lacks the articulation *cruropedalis* (see also Jarvik, 1980, figs 163-164). This may be so, but the suggestion that *Ichthyostega* could not walk seems to disagree with almost all the structural features characteristic of the postcranial endoskeleton of this genus. According to Jarvik

(1980), the entire thoracic, abdominal and sacral portion of the vertebral column forms an arched and probably fairly rigid structure apparently capable of supporting the body. The articulation between humerus, ulna and radius is generally like that in other early tetrapods. There are well developed articular connections between sacral vertebrae and the pelvic girdle. This latter forms a large supporting structure and the shape of its two halves suggests that the attaching leg musculature was strongly developed. The compact femur abuts proximally against the well developed acetabulum and has distally articular areas which, judging from their position and shape, suggest that the articulation formed an angle as in other early tetrapods generally considered capable of walking.

Although the articulation *cruropedalis* may be lacking in *Ichthyostega*, the shape and other features of the articulations between the middle and distal tarsals, and between the distal tarsals and the metatarsals suggest that the hind feet with their muscle-clad, skin-covered metatarsals and phalanges resting on the ground were fully capable of walking when this tetrapod emerged on land.

Upper Permian marine vertebrates

Collections were made from Upper Permian marine deposits (the Foldvik Creek Formation: Maync, 1942; Birkelund & Perch-Nielsen, 1976) exposed in the deep ravines located on Vestreplateau and Østreplateau on both sides of Margrethedal. Fossil fish remains from the deposits in this area have been reported previously by Maync (1942) and some few palaeoniscoid specimens were collected by Bütler in the late 1940s and early 1950s.

The new fish fossils were, like those just referred to, collected exclusively from the *Posidonia* Shale Member (Birkelund & Perch-Nielsen, 1976). They occur here both in the shale proper and in the often very large concretions forming horizontal bands in the shale. The shale locally attains a considerable thickness on Østreplateau, as shown by the exposures around and between rivers F and G (for geographical details see Bütler, 1954, Pl. 6). In general the occurrence and preservation of the vertebrate fossils correspond closely to those encountered in the Kap Stosch area towards the north (Nielsen, 1935; Bendix-Almgreen, 1976) and, as a whole, the fossil content of the *Posidonia* Shale and its concretions is also similar.

The bivalve *Posidonia permica* frequently occurs in large concentrations on slabs of the shale in which there are also concentrations of cephalopod prehensile arm-hooks representing no doubt distorted natural assem-

blages from single individuals. A specimen of *Macrotheca almgreeni* (Peel & Yochelson, 1984) was also found. This hyolithid mollusc has hitherto been reported only from the Kap Stosch exposures where it also occurs in the *Productus* Limestone Member of the Foldvik Creek Formation which here is intercalated with the *Martinia* Limestone Member (Maync, 1942; fig. 17 & Pl. 6; Birkelund & Perch-Nielsen, 1976).

Elasmobranchii. Among these the edestid *Fadenia crenulata* is represented by specimens showing articulated large parts of skulls and the associated dentition, and a single specimen preserving a part of an articulated caudal fin endoskeleton and the associated scale covering. Another of the edestids, *Erikodus gröenlandicus*, is represented by large parts of a skull and the dentition. The petalodontid *Janassa*, either the species *J. kochi* or *J. unguicula*, can now also be recorded as part of the elasmobranch fauna of this area as in that of the Kap Stosch area (Bendix-Almgreen, 1976).

Actinopterygii. The palaeoniscoids, represented by both incomplete specimens, detached bones and several virtually complete specimens, include apparently also some juveniles. According to preliminary inspection in the field, the material appears to comprise species referable to the genera *Elonichthys*, *Pygopterus*, *Palaeoniscus*, *Boreolepis* and *Platysomus*.

The new material suggests a faunal composition similar to that of the Kap Stosch area (Bendix-Almgreen, 1976). There is also similarity with the elasmobranch-palaeoniscoid assemblage from localities in Jameson Land and Wegener Halvø, towards the south, known from collections made during GGU's field survey and inspected by one of us (SEB-A).

During the field work in the Margrethedal area several specimens of the actinopterygians *Bobasatrania*, *Pteronisculus* and *Boreosomus*, as well as a single selachian (? *Polyacrodus*), were collected. All these derive from the concretions characteristic of the marine early Triassic (Lower Scythian) deposits which are quite extensively developed within the area.

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Glacier velocities from aerial photographs in North and North-East Greenland

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General descriptions of the glaciers of North and North-East Greenland have been given by Koch (1928), Davies & Krinsley (1962) and Weidick (1975). These

descriptions, however, provide little in the way of quantitative data on glacier velocities, although Davies & Krinsley concluded that a large number of glaciers and