Meddelelser om Grønland

Devonian osteolepiform fishes
from East Greenland

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The Middle and Upper Devonian deposits of East Greenland have yielded several osteolepiform fishes, of which only two, the osteolepid *Gyroptychius groenlandicus* Jarvik, 1950 and the rhizodontid *Eusthenodon waengsjoei* Jarvik, 1952 have been described previously. This paper gives new information on the structure of these two species. Three new forms are described, the osteolepids *Gyroptychius dolichotatus* sp. nov. and *Thursius? minor* sp. nov., and a rhizodontid, *Spodichthys buetleri* gen. et sp. nov.

G. dolichotatus is represented mainly by the holotype, which is the only almost complete specimen of an osteolepiform found in East Greenland. In this specimen the squamation is well preserved, exhibiting structural details unknown or imperfectly shown in other osteolepids. The gradual transition from scales into lepidotrichia is thus well documented, and the remarkable change in direction of the scale rows on the tail is displayed. It is demonstrated that the scale rows are directed anteroventrally (not posterodorsally as previously assumed) and meet the next anterodorsally directed row of flank-scales at varying angles, obtuse in *G. dolichotatus,* but almost normal in other osteolepids. This change in direction of the scale rows was first thought to be characteristic of actinopterygians with rhomboid scales. In addition to osteolepids it occurs in brachiopterygians (*Polypterus*) and is shown to occur also in *Eusthenopteron,* which like other rhizodontids has cycloid scales. A specimen of *Gyroptychius groenlandicus* provides information on the change in direction of the scale rows at the ventrolateral ridge, which marks the position of the ventrolateral fin-fold. The transformation of the rhomboid osteolepid scales into the externally very different cycloid rhizodontid scales is analysed and illustrated.

In *Spodichthys* the occipital region of the neural endocranium is proportionally longer and includes more cranial vertebrae than in *Eusthenopteron.* The fissura oticalis ventralis anterior is distinct in several specimens. The ventral arcual plate following in front of that fissura is interpreted as the interventral of cranial vertebra CV 3+4.

The large collections of *Remigolepis* from East Greenland are discussed taxonomically, the importance of knowledge of variation in palaeontological species is emphasised, and the validity of the antiarch genus *Hillsaspis* Stensiö and the osteolepiform genera *Ectosteorhachis* Cope and *Eusthenopteron* Whiteaves is tested.

In order to emphasise the fundamental differences between the Porolepiformes and the Osteolepiformes, the endoskeletal shoulder girdles in the porolepiform *Glyptolepis groenlandica* and the osteolepiform *Eusthenopteron foordi* are illustrated.

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The large collections of fossil vertebrates made from the Middle and Upper Devonian of East Greenland during the Danish expeditions 1929–1956, under the leadership of Dr. Lauge Koch, were assembled at the Palaeozoological Section of the Swedish Museum of Natural History, Stockholm for preliminary identification and documentation (Stensiö 1939a, Jarvik 1961, 1963a, 1969). Much of this material, which belongs to the Geological Museum, University of Copenhagen, has been described or utilised by Stensiö (1931, 1934, 1936, 1939, 1939a, 1948, 1963, 1969), Stensiö & Säve-Söderbergh (1938), Säve-Söderbergh (1932, 1933, 1934, 1935, 1937a), Jarvik (1942, 1948, 1948a, 1950, 1950a, 1952, 1954, 1955, 1955a, 1959, 1959a, 1960, 1962, 1963, 1963a, 1964, 1965, 1966, 1967, 1967a, 1968, 1972, 1980, 1980a, 1981), Lehman (1959), Bjerring (1967, 1971, 1973, 1975, 1977, 1978), Schultze (1969), and others. However, the comprehensive collections of the antiarch *Remigolepis* collected after 1930 and some other placoderm material are still undescribed. Following Säve-Sö-

derbergh's preliminary account (1932), I have discussed the ichthyostegids on various occasions (Jarvik 1942, 1952, 1955, 1955a, 1959, 1959a, 1964, 1965, 1967a, 1980, 1980a, 1981), but since 1952 only a few photographs of specimens have been published. It may be of some interest that this gap in our knowledge of these oldest known tetrapods is currently being filled by work in preparation, including photographs of interesting specimens. The purpose of the present paper is to describe a new species of *Gyroptychius*, *G. dolichotatus,* and two other osteolepiforms, *Spodichthys buetleri* gen. et sp. nov. and *Thursius? minor* sp. nov., which were referred to previously (Bütler 1954:113; 1959:170; 1961:191; Jarvik 1961:202, table 1) as "small *Eusthenopteron*-like rhizodontid" and "osteolepid resembling *Thursius macrolepidotus"*, respectively. In addition, new material of *Gyroptychius groenlandicus* and *Eusthenodon waengsjoei* is described and the endoskeletal shoulder girdles of the porolepiform *Glyptolepis groenlandica* and the osteolepiform *Eusthenopteron foordi* are figured.

Historical and taxonomic remarks

The generic name *Remigolepis* was introduced by Stensiö (1931), who distinguished six species on the basis of material collected on the Danish expeditions in 1929 and 1930: *R. incisa, R. cristata, R. kochi, R. kullingi, R. acuta* and *R? tuberculata*. However, when more material was obtained subsequently it turned out to be difficult to use these specific names, and in the complementary stratigraphical papers (Säve-Söderbergh 1932a, 1933a, 1934a, 1937,1937b, Jarvik 1935) only preliminary identifications (partly made by E. Stensiö) are recorded ("R. of the *kullingi*-type" or "with ornamentation of the *acuta-incisa*-type", etc.; the new species, *R. emarginata,* mentioned by Säve-Söderbergh in 1932a is still a nomen nudum).

The Upper Devonian deposits in East Greenland are generally well exposed. In the central parts of the depositional basin, where most of the collecting was done, the fossiliferous sandstone banks are almost horizontal and can be followed for long distances. The most favourable areas for stratigraphical work are the mountains surrounding the Paralleldal on Gauss Halvø (Fig. 1 C), and in the summer of 1936 Säve-Söderbergh (1937b) measured no less than 18 profiles on the southern side of Sederholm Bjerg through the Remigolepis Group, which in the central parts of the mountain attains a thickness of about 670 m. In all, 22 profiles have been investigated on this slope, and by using a characteristic nomenclature for the various banks Säve-Söderbergh tried to create a solid basis for a detailed biostratigraphy of the Remigolepis Group. Because of his illness from 1937 to his death in 1948 he was unable to fulfil his plans, which also included sedimentological studies, and the large collections of *Remigolepis* made during 11 summer expeditions from 1931 to 1955 are still undescribed.

Before starting a description of this extensive material it is necessary to assess its scope, quality and limitations. *Remigolepis* specimens include isolated plates, more or less complete exoskeletal parts of the head, the shoulder girdle (trunk-carapace) and the pectoral fin, whereas remains of the squamation are rare. The specimens are generally embedded in hard sandstone and it is clear that the preparation (mechanical, or negative preparation with acids) of several thousand individuals requires considerable time and specialist facilities. Then all important specimens must be photographed, countless measurements taken, ratios calculated, etc., before it is possible to undertake a revision of Stensiö's species and to describe the species intimated by Säve-Söderbergh and perhaps other new species. Stensiö permitted considerable variation in the species that he described (e.g. in the shape of the posterior dorsolateral plate, 1931, fig. 85), and the evaluation of these variations (including growth changes and sexual dimorphism) that will certainly be encountered in the large new collec-

tions will certainly cause considerable taxonomic problems. Whether it will then prove possible to establish a detailed biostratigraphy of the Remigolepis Group, which was one of Säve-Söderbergh's goals, or to say anything definitive about the phylogenetic evolution of the genus during the time of deposition of these Caledonian molasse sediments (Bütler 1935) is difficult to say. Under these circumstances, and in view of the many years work involved, it is understandable that nobody has attempted a taxonomic revision of the material of *Remigolepis* from East Greenland. It is of course regrettable that the large collections of this genus, now stored in Copenhagen, and gathered together with great care in the field have not yet been revised; this is particularly emphasised now since material assigned to the genus *Remigolepis* has been recorded recently from such widespread areas as Australia and South China (Ritchie 1974, P'an 1981, Long 1982, 1982a, 1983, Young 1983). Increased knowledge of *Remigolepis* from the type localities in East Greenland would certainly be of a great value for the description of new material from other regions, and for biogeographical considerations. In a view of the great difficulties involved in a complete taxonomic revision, one possibility to satisfy the most urgent needs would perhaps be to select some of the best specimens, and on this basis to elaborate new restorations of *Remigolepis* without bothering about the description of species. This is a method that I have been compelled to use when dealing with material of other forms represented in the Remigolepis Group by isolated skeletal remains.

The best known fossil vertebrates from the Remigolepis Group are undoubtedly the oldest known tetrapods, the ichthyostegalians. After Säve-Söderbergh's death in 1948 the material collected before the Second World War and in 1947, 1948 and 1949 was entrusted to me. When describing the tail (Jarvik 1952) and other postcranial remains it was of course impossible to refer these specimens to any of the four species of *Ichthyostega* or the single species of *Ichthyostegopsis* described by Säve-Söderbergh in his preliminary account (1932), all based on cranial remains from local talus on and above the Eastern Plateau of Celsius Bjerg (Fig. 1 C; cf. Jarvik 1980, fig. 154). Also when preparing the restorations of the skull of *Ichthyostega* published in 1952 I found it impossible to use any of the specific names. In photographs and restorations published later (1955, 1955a, 1959, 1959a,1964, 1980, 1980a), based partly on material collected during the expeditions in 1951, 1954 and 1955, I have also omitted such names.

The most common fossils in the Remigolepis Group are isolated scales of *Holoptychius*, referred tentatively by Stensiö (1931) and in the stratigraphical publications to *H. nobilissimus* Agassiz or, more rarely, to *H. giganteus* Agassiz. The underlying Phyllolepis Group has
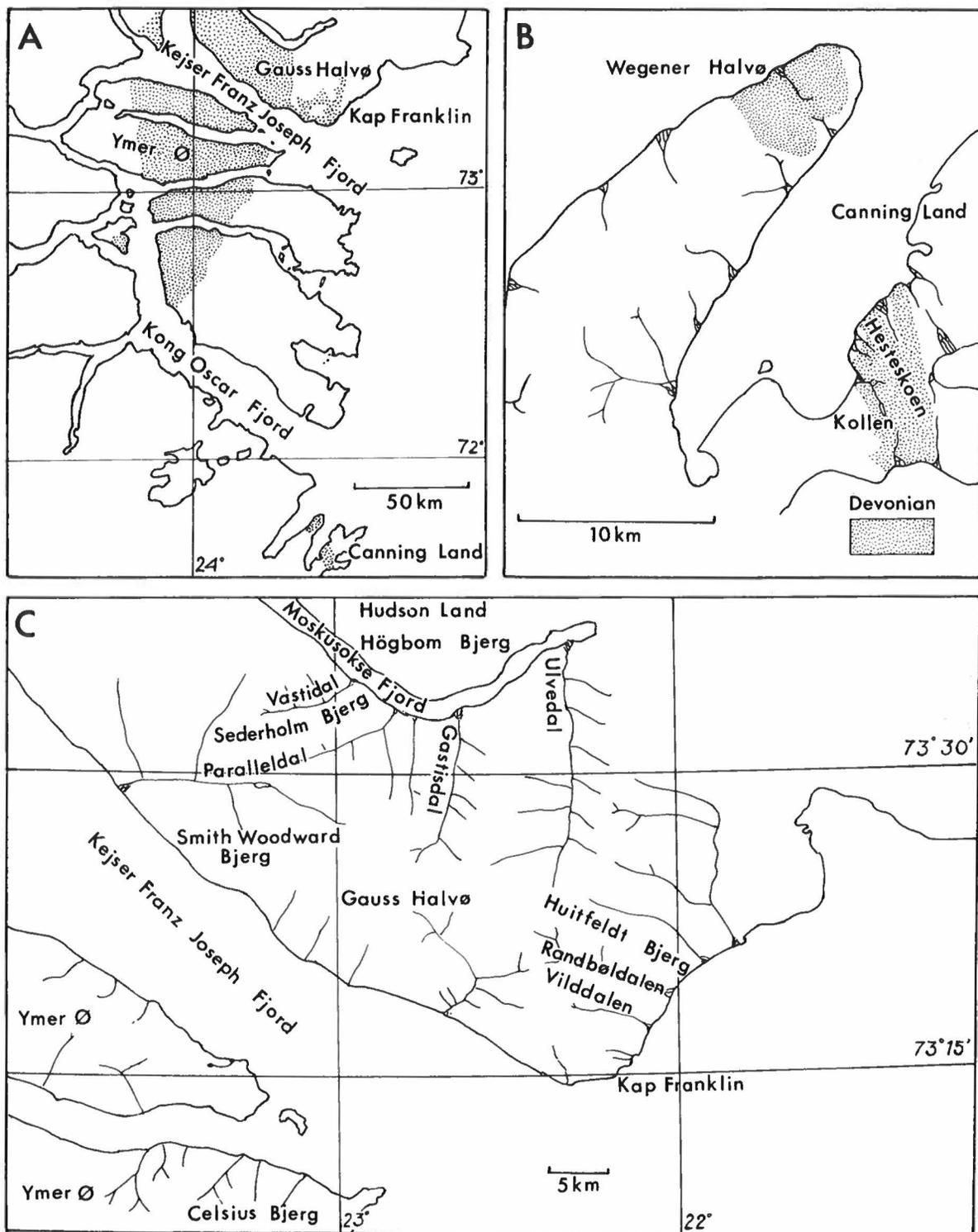
Fig. 1. **A**: key map of the distribution of Devonian rocks in the coastal area of East Greenland, from Canning Land to Gauss Halvø; from Bütler 1959, fig. 1. **B**, **C**: detailed maps of Canning Land and Wegener Halvø and of the eastern parts of Gauss Halvø and Ymer Ø.

also yielded numerous holoptychiids, sometimes with considerable parts of the squamation preserved. The material that I described in 1972 is all from the Remigolepis Group, and disregarding isolated scales it consists of cranial remains and elements of the exoskeletal shoulder girdle. Considerable variations have been found, e.g. in the shape of the cleithrum (Jarvik 1972: 126), and several species are obviously represented. The porolepiform scales are all of the type characteristic of *Holoptychius* (Jarvik 1980: 249). However, identification of species on the basis of isolated scales is hardly possible (Jarvik 1948: 106, 283; 1950: 13, 100, 110–112), and the specific names mentioned by Stensiö could not be used. Of course a new specific name could have been coined on the basis of one of the most complete specimens (no complete skull has been found) but this would hardly serve any sensible purpose and would rather entangle the description. A consequence would be that all, or at any rate most of the other specimens (isolated jaws, gular plates, etc.), would become indeterminate at the species level. When dealing with fossil material, like that of *Holoptychius* from East Greenland or *Porolepis* from Spitsbergen, it is the structure of the genera as a whole that is of interest. The variations that are of course important can be considered without the introduction of a new specific name for each of the more conspicuous morphological variants.

The single osteolepiform described from the Remigolepis Group, *Eusthenodon waengsjoei* Jarvik, 1952, is also represented only by scales and parts of the skull. In order to find more complete osteolepiforms in East Greenland it is necessary to turn to the Middle Devonian deposits in Canning Land and the area of Kap Franklin on Gauss Halvø (Fig. 1).

The osteolepid material collected in Canning Land (and Wegener Halvø) before the Second World War (Säve-Söderbergh 1937) consists mainly of isolated scales and cranial remains. At that time only three genera of Middle Devonian osteolepids were known: *Osteolepis*, *Thursius* and *Gyroptychius* (= *Diplopterus* or *Diplopterax*). These three genera, all based on Scottish material, were distinguished by differences in the shape of the tail and the relative position of the dorsal, anal, and pelvic fins. Because the skull was incompletely known and the various Scottish osteolepid species were defined unsatisfactorily, Säve-Söderbergh found it necessary to undertake a morphological and taxonomic revision of them in order to be able to identify the Greenland material. For that purpose he borrowed a great number of specimens from various British museums. Unfortunately his illness prevented him from fulfilling his plans and in 1945 I had to carry on with the revision (Jarvik 1948). The material at my disposal, including also specimens in Swedish museums, permitted only studies of the external morphology. In order to determine proportional and other differences between the genera and species I had to make numerous measurements and scale counts. Linear measurements with dividers and a millimetre rule on more or less distorted and often small bones or complex units give no precise result, and measurements on photographs are also subject to errors. The values obtained and the ratios calculated on the basis of such measurements are therefore more or less approximate, but nevertheless they give a good idea of the range of variation of the numerous characters that I found it necessary to consider. Instead of diagrams and various statistical representations (see e.g. Mayr 1969: 169–180) I found it more appropriate to compile tables in which a great number of data for each species could be included. On the basis of the information provided by the tables and other characteristics it was possible to present what I consider to be fairly satisfactory diagnoses of the three Scottish genera (a new generic name, *Latvius*, was erected on material from the Soviet Union), and of seven named species (of which two were new, *Thursius moythomasi* and *Gyroptychius milleri*).

After the revision of the Scottish osteolepids I was able to continue with the Middle Devonian material from East Greenland. It could be established that the cranial remains from Canning Land and Wegener Halvø collected in 1934 and 1936 (Säve-Söderbergh 1937) relate to a form very similar to *Gyroptychius milleri*. Rejecting the generic name *Canningius* as used provisionally by Säve-Söderbergh, this form was termed *Gyroptychius groenlandicus* (Jarvik 1950). However, in 1948 H. Bütler (1949) had collected some osteolepid remains in the area of Kap Franklin farther to the north (Fig. 1), and in a preliminary note (Jarvik 1950a) this material was also referred to *G. groenlandicus*. The diphycercal caudal fin is an important characteristic feature of the genus *Gyroptychius*. It is therefore of interest that such a tail, although imperfect, was found in the material from the type locality of *G. groenlandicus* (Jarvik 1950: 93, pl. 23: 4). Moreover, in the summer of 1950 G. Wängsjö found some specimens in the area of Kap Franklin in which considerable parts of the trunk are preserved, including one (Fig. 9B) with parts of the diphycercal caudal fin, and in 1956, when I was assisted by S. Bendix-Almgreen and H. C. Bjerring, an almost complete specimen of *Gyroptychius* (Fig. 11) was found in Canning Land in the beds characterised by *Asterolepis saevesoederberghi* (see Jarvik 1961, table 1). These finds confirm that the osteolepids from East Greenland referred to *Gyroptychius* really belong to that genus. They also demonstrate that it is possible to identify osteolepid genera on the basis of cranial remains.

After the publication of two papers early in 1950 (Jarvik 1950, 1950a), a considerable new material of both osteolepids and rhizodontids was collected from East Greenland. Disregarding the specimens mentioned above and a few specimens showing the anterior part of the fish, this material includes scales and isolated cranial remains. In dealing with this material several taxonomic problems become apparent, one of which concerns variation (see also Jarvik 1948: 20–21).

As far as I know no investigations have been made to establish the variation permitted in the number, size and shape of the external skull bones in species of Recent fish, and this lack of a standard has contributed to the difficulty in evaluating the variations in fossil fish. The safest way to obtain some idea of the permissible variation in the skull bones of a species is to compare the right and left side in one individual, and in doing so considerable differences are often encountered. Some of these differences are due to fusions of elements in various combinations, as in the nasal series of *Eusthenopteron foordi* (Jarvik 1944: 15–16, fig. 3 A), whereas differences in the number and extent of the dermal bones, e.g. in the skull roof of Devonian dipnoans and Recent sturgeons (Jarvik 1948, figs 18, 19; 1980, figs 306, 326) are still difficult to explain. For the study of specific variations one can also turn to what are considered to be well established species. It may then be sufficient to refer to the remarkable variations in the number of the postrostrals and in the shape of the extratemporal and other bones in *Osteolepis macrolepidotus* (Westoll 1936, Jarvik 1948: 20, figs 15, 17, 38) as well as in the extent of the posterior supraorbital in *Eusthenopteron foordi* (Jarvik 1944, fig. 5). There are certainly also many variations due to differential growth (Thomson & Hahn 1968, Schultze 1984), as for example the considerable growth changes in the caudal fin in *Osteolepis, Eusthenopteron,* and other fishes (Jarvik 1948, fig. 31; 1980, fig. 148).

As a consequence of these and other conditions it is often difficult to distinguish and define species in fossil fishes. In many cases specific names should therefore be regarded as local names, rather than names of true biological species (for discussion of paleontological species see Simpson 1961: 163, Mayr 1969: 35, with references). Linnean binomial nomenclature is no doubt the most practical method by which to classify fossil forms (cf. Simpson 1961: 158), and it is of course desirable – not only for museum curators – that fossil material that has been collected is identified and described. This has, however, led to a great number of specific names having been introduced, and for many genera long lists of named species have been presented. Thus, for example, in the antiarch *Bothriolepis,* a genus also represented in East Greenland (Stensiö 1948), more than sixty species have now been described (Long 1983: 312). It may be questioned if this great number of species can be mastered satisfactorily even by specialists. Of these species only twentyfive are known by head- and trunkshields, and only in *B. canadensis* and two Australian species are the squamation and tail known. Of the latter *B. gippslandiensis* Hills deserves some comment.

This Australian species was referred by Stensiö (1969: 508) to the new genus *Hillsaspis,* characterised by a strong median crest of the trunk armour and "certains autres détails". Young & Gorter (1981: 93), in contrast, claim that "Stensiö (1969: 508) erected the new genus *Hillsaspis* on the basis that the Nu plate was ex-

cluded from the orbital margin by the PP" (with regard to this detail Stensiö, 1948: 518, stated that the nuchal plate, "reached forwards to the orbital fenestra only with its very antero-lateral corners"). However, since Young & Gorter, upon reexamination of the holotype, could prove "that this plate participated in the orbital margin ... as in all other species of the genus" (*Bothriolepis*) and "since there are no other features which justify exclusion from the genus, *Hillsaspis* Stensiö becomes redundant". Long (1983) accepts this conclusion, but at the same time he presents (fig. 5 A) a restoration of the Australian species showing that it differs considerably from *B. canadensis* (Stensiö 1948, fig. 38, Long 1983, fig. 5 B; cf. Jarvik 1959: 15–19, Stensiö 1969: 641–642) in the squamation and fins. Long (1983: 302) comments on these remarkable differences as follows: "Although this species and other new species described below differ from *B. canadensis* in the structure of the tail, it would be confusing to alter the generic status of those species on this character alone, as this feature is very rarely preserved on other species. In the relative shapes and sizes of the dermal plates, *B. gippslandiensis* resembled other species and is here retained within the genus". Certainly acceptance of the generic name *Hillsaspis* would make it difficult to decide which of the numerous species that have been assigned to *Bothriolepis* really belong to that genus. On the other hand, we cannot ignore important differences for the reason given by Long. For example, if we disregard the squamation and fins in osteolepids we would be entitled to refer all the Middle Devonian osteolepids, which are certainly very similar in details of the external skull bones, and probably other Devonian osteolepids as well, to *Osteolepis* Agassiz, 1835. This example illustrates the dilemma, when, as is most often the case, one has to deal with incomplete fossil material. For my part I have tried to be conservative in describing new species and sometimes, as in my descriptions of the holoptychiids and ichthyostegids from the Remigolepis Group, I have been compelled to drop specific names altogether.

Turning to a higher category in the taxonomic hierarchy, the genus, it is reasonable to demand that the taxa are more sharply delimited and "separated of other taxa of the same rank (other genera) by a decided gap" (Mayr 1969: 92). However, because of the fragmentary nature of the fossil material, inadequate descriptions, etc. many genera of osteolepiforms and other fossil fishes are still characterised insufficiently. An example is the confusion surrounding the validity of the generic name *Ectosteorhachis.*

The name *Ectosteorhachis* was coined by Cope (1880) for an osteolepid fish, *Ectosteorhachis nitidus,* from the Texas "redbeds." The name was later (1891) rejected by Cope himself in favour of *Megalichthys* Agassiz, and for many years was then regarded as invalid. In 1937 Romer published an excellent description of the braincase of what he then referred to as "The Carboniferous Crossopterygian *Megalichthys nitidus*". However, somewhat later (1941) – impressed by a suggestion by T.

S. Westoll – he became uncertain and placed the generic name within quotation marks. According to the view held by Romer in 1937 (p. 4) those parts of the Texas "redbeds" yielding *M. nitidus* are Carboniferous in age, although close to the Permo-Carboniferous boundary, but it now seems to be generally agreed that they are Permian. More than twenty years later Thomson (1964, 1964a) attempted to re-establish the validity of "*Ectosteorhachis*"; in doing this he possibly believed that a Permian fish should have a different generic name from forms which like *Megalichthys* are known only from the Carboniferous (cf. however, Heintz 1933), or perhaps more likely, as a link in his futile endeavours (1964a: 316) to show that the differences, which I have maintained since 1942 to exist between porolepiforms and osteolepiforms (cf. p. 45, Fig. 34), disappear if a greater number of genera are investigated than I had at my disposal. However, knowing the conditions in *Eusthenopteron* I found reason to suspect that the figures and descriptions given by Thomson were inadequate in several regards, and in order to check his statements I borrowed two specimens of *Megalichthys hibberti*, one from Glasgow and one from Edinburgh. After careful preparatory work, which led to the discovery of numerous structural features, it could be established (Jarvik 1966) that *Megalichthys* agrees fundamentally with *Eusthenopteron* in the structure of the snout and other regards. Moreover, with regard to the validity of the generic name "*Ectosteorhachis*" I stated (1966: 69): "Thus since the differences which according to Thomson (1964b) distinguish *Megalichthys* and *Ectosteorhachis*, do not exist, in all cases I have been able to check them, and since no other reliable distinctive characters of any importance have been presented, his re-establishment of the genus *Ectosteorhachis* cannot be accepted. New researches are therefore necessary in order to decide if one is justified in referring *Megalichthys nitidus* to a genus of its own". However, in spite of these statements practically all students have accepted the validity of "*Ectosteorhachis*" without reservation, and although unimportant in itself this problem has assumed a false status in the debate. Thus in referring to my paper (1966), Romer (1968: 69) accuses me of claiming that *Megalichthys* and "*Ectosteorhachis*" are generically identical, and he declares categorically: "the two are not identical, although closely related." I have certainly not synonymised the two genera. I have only found it legitimate to require that if the Carboniferous and Permian forms belong to different genera, then it should be easy to say what the generic differences are. Apparently not quite satisfied with earlier considerations, Schultze (1974) has made a new attempt to re-establish the validity of "*Ectosteorhachis*", partly with new arguments.

In contrast to Thomson and previous students, Schultze (1974: 42) thus claims that the fenestra exonarina anterior in "*Ectosteorhachis*" is less elongated than in *Megalichthys*, but is oval or sometimes "nahezu rund". However, in the same paper (p. 43) he stated that the opening in *M. macropomus* is much shorter (about half as long) and has a different position than in *M? hibberti*. When I studied the two specimens of *M. hibberti* one of my first tasks was to clean the fenestra exonarina from matrix and to illustrate it photographically, as I had done in *Gyroptychius* and *Eusthenopteron* (Jarvik 1966, fig. 13).

Schultze (1974: 42–43, figs 1–3) also claims that there are differences of diagnostic value in the shape of the brain. However, it seems difficult to make any safe statements as to the shape of the brain in *Megalichthys* on the basis of a specimen which shows only fragments without periosteal lining of the walls of the cranial cavity.

A remarkable statement made by Schultze (1974: 46–48) is that *Megalichthys* is unique among osteolepiforms (and other teleostomes) in having a paired "Interpremaxillare" between the premaxillaries. Such a statement requires strong evidence and until such has been presented I prefer to regard the alleged sutures as fractures which might easily be produced in the thin anterior wall of the fossa apicalis, on each side of the strong toothbearing median process of the premaxillaries (such a process is also present in "*Ectosteorhachis*", Romer 1937: 21).

A widespread opinion (Moy-Thomas 1935, Thomson 1964, Young & Gorter 1981: 116) is that there should be only two extrascapulars – in contrast to other osteolepiforms. However, a median extrascapular has been recognised both in *Megalichthys* (Andrews & Westoll 1970a, fig. 2; see also Bjerring 1972, fig. 7) and in "*E*". *nitidus* (Thomson 1975, fig. 8).

In 1964 (fig. 2) Thomson presented two similar schematic reconstructions of the external cheek plate in "*Ectosteorhachis*" and *Megalichthys*. However, in 1975 (fig. 8) he published a drawing of "*E*". *nitidus*, in which the postorbital and jugal differ considerably from those shown in 1964; the dermosphenotic (fig. 1) also has a very different shape. Compare also the sketches of the anterior part of the palate (Thomson 1964, fig. 3) with my reconstruction (Jarvik 1966, fig. 17) of *Megalichthys hibberti*.

Finally it is claimed (Thomson 1964: 301–302) that the tail in "*Ectosteorhachis*" is "intermediate between the heterocercal and diphycercal conditions" (as it is in *Megalichthys* according to Birks 1916: 324), while in *Megalichthys* it is "heterocercal, tending towards diphycercal". In the two almost complete specimens of "*Ectosteorhachis*" *nitidus* that have been figured (the holotype, Cope & Matthew 1915, pl. 1 and AMNH 5724, Thomson 1975, figs 35, 36) the tail is lacking, and in *Megalichthys* (Traquair 1884, pl. 5: 1, 2, Woodward 1891, pl. 13: 4, Birks 1916, pl. 12: 1) it is incompletely known.

As I hope will be clear from this review, a morphologic and taxonomic revision of the genus *Megalichthys* is urgently needed. There is also need for a reliable and well documented description of Permian species, of which one form is of particular interest, being probably the latest representative of the Osteolepiformes (the contemporaneous? Norwegian form, tentatively placed in *Megalichthys* by Heintz 1934, is currently being studied by U. Borgen and will be referred to a new genus).

The well known genus *Eusthenopteron* (Jarvik 1980: 99–194) presents other problems. This generic name was introduced in 1881 by Whiteaves, who both then and later (1889) presented diagnoses of the genus and the single species, *E. foordi*. However, Whiteaves had some trouble in distinguishing his new genus from *Tristichopterus* Egerton. Of the distinguishing characters given by Whiteaves (1889) two hold good according to Traquair (1890: 17), and the validity of the name *Eusthenopteron* was not doubted. When I published my first paper on *Eusthenopteron* (Jarvik 1937) I had studied the excellent material of *E. foordi* in the Riksmuseum, Stockholm, and I had also (in 1935) examined the material of this form and of *Tristichopterus alatus* in British museums. On the basis of these studies it could be shown that of the two distinguishing features accepted by Traquair, one (the shape of the teeth) is untenable, whereas the other difference (the shape of the tail) was found to be (p. 66) "only one of degree, and of but small value generically". However, a new distinguishing character was discovered that was considered to be of more importance. In *T. alatus* the frontoethmoidal shield is only about 1.4 times longer than the parietal shield, whereas the corresponding ratio (b/a, Jarvik 1948, fig. 12 A) in *E. foordi* is about 1.85 (according to later measurements, Jarvik 1950b: 28, 1.70–1.85). Westoll (1937: 517) was unable to find other distinguishing cranial features (for details of the principal gular see also Jarvik 1950: 87) and the small differences in the postcranial skeleton "are probably only sufficient for specific distinction" (Andrews & Westoll 1970a: 397). *Eusthenopteron* and *Tristichopterus* are no doubt very similar, and since the latter is still known imperfectly hopes have been expressed (Jarvik 1937: 67–68, Andrews & Westoll 1970a: 397) that new investigations will reveal differences of generic importance. Such expectations are irrelevant and the validity of the genus *Eusthenopteron* currently rests entirely on the proportional differences in the skull roof. In agreement with Andrews & Westoll I now doubt that this is a sufficient distinguishing feature. Considering the imperfect knowledge of the range of variation not only in *T. alatus* but also in *E. foordi* (see below), the defects incident to calculated ratios (p. 6), and also the fact that a great difference in the ra-
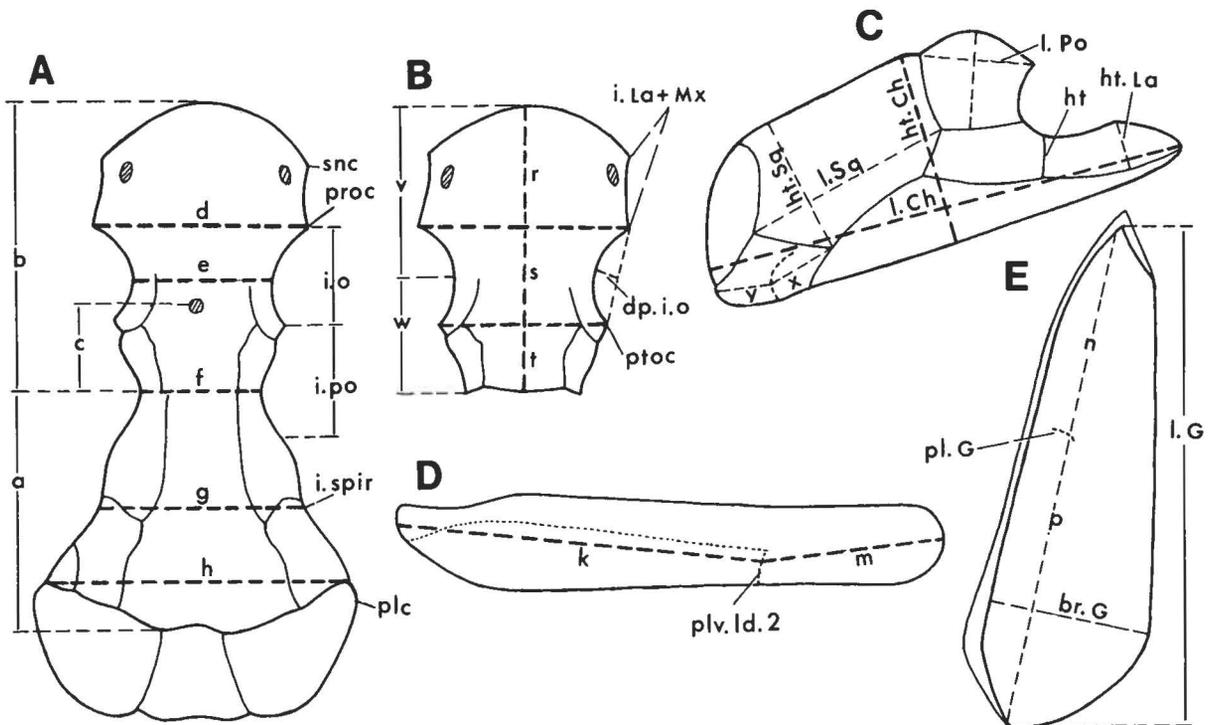
Fig. 2. Diagrammatic explanation of the basis for taking some fundamental measurements. **A**: exoskeletal cranial roof, comprising frontoethmoidal shield (b), parietal shield (a), and extrascapular bone series. **B**: frontoethmoidal shield. **C**: external cheek plate. **D**: lower jaw. **E**: principal gular plate. From Jarvik 1948, fig. 12 (slightly modified).

tio in question has been permitted within the genus *Thursius* (in *Th. moythomasi b/a* is about 1.48–1.50, but only about 1.10–1.14 in *Th. pholidotus,* Jarvik 1948: 42, table 1) it seems clear that the validity of the genus *Eusthenopteron* is dubious. However, *Tristichopterus* is still monotypic, known only from imperfectly preserved material from strata in Scotland and the Orkneys, and there is little hope that better material will be discovered in the foreseeable future. In contrast *Eusthenopteron* includes several species, among them *E. foordi,* which is the most completely known Palaeozoic fish, and in contrast to "*Ectosteorhachis*", the generic name has been used without objection for more than a hundred years, and is well established in the scientific literature. Under these circumstances, and in view of the confusion which, as pointed out by Romer (1968: 4–9, see also Jarvik 1980: 19), has been caused by what he appositely refers to as "priority-seekers", the only reasonable conclusion must be that the generic name *Eusthenopteron* should be retained.

There are also other problems with definitions. In 1937 I promised to give new diagnoses of *Eusthenopteron* in a forthcoming paper, and of *E. foordi* which was then the single known species of the genus. However, *E. foordi* has subsequently become increasingly well known, and it now exhibits numerous characters that are unknown in allied fishes, and will probably remain so for a long time. To give a long diagnosis of *Eusthenopteron* on the basis of these characters seems to be meaningless and it is sufficient here to refer to the exhaustive description presented recently (Jarvik 1980: 99–194). As to the well known species *E. foordi* from Escuminac Bay, it must be admitted that studies of variability in this form have been neglected. Variations in the nasal series, in the shape of the posterior supraorbital (Jarvik 1944), as well as in the shape of the

caudal fin (Jarvik 1948: 105; 1980: 213–214) have been recorded. Moreover, variations due to changes in growth have been mentioned by Thomson & Hahn (1968) and Schultze (1984). However, no thourough analysis has been made of variability in all the large samples taken from Escuminac Bay and now scattered to museums and private collections throughout the world. Therefore it is not possible to present a satisfactory diagnosis of this widely reported fish; and accordingly it is also difficult to define and delimit allied forms.

Several other species have been referred to *Eusthenopteron,* but unfortunately, with the exception of *E? dalgleisiensis* (Jarvik 1950b), the trunk and fins are unknown. In 1937, impressed by the many new structural features discovered in *E. foordi,* I described two new species, *E. wenjukowi* and *E. saevesoederberghi,* from the Baltic States, and in the same year Westoll (1937) added a fourth species, *E. traquairi,* from Scotland. Another Scottish form, *E.* cf. *traquairi,* was later described by Westoll (1940), but this form and *E? dalgleisiensis* are possibly conspecific (Jarvik 1950b: 31). With regard to *E. wenjukowi,* Vorobyeva (1960, 1962) first claimed that it belongs to the genus *Eusthenodon,* but later (1977) assigned it to the new genus *Jarvikina* (for *Eusthenopteron obruchevi,* see Vorobyeva 1977: 176). My description of *E. saevesoederberghi* (1937) was based on incomplete material. When the snout of the holotype was discovered later (in a drawer in Uppsala), it turned out (Jarvik 1942: 481, fig. 62 A; 1944: 47, fig. 19) to be narrower than in *E. foordi,* with considerable differences in the shape of the fossa apicalis. Whether the species from the Baltic area really belongs to *Eusthenopteron* therefore remains uncertain. In fact many of the structures first observed in *E. foordi* and thought to be characteristic of *Eusthenopteron* also occur in other osteolepiforms, and it is always hasardous to make ge-

neric and specific identifications of incomplete fossil material. Thus, when I collected a well preserved parietal shield in East Greenland in 1947 (Jarvik 1952, fig. 24), I was first inclined to refer it to *Eusthenopteron,* but when more material was studied it became evident that it should be assigned to a new genus (*Eusthenodon*). Similarly, the new form described below as *Spodichthys,* was referred to as an *Eusthenopteron*-like rhizodontid in my preliminary identification. Another example is provided by *Gyroptychius dolichotatus* which until recently I was unable to distinguish from *G. groenlandicus* (see p. 20).

Above the genus level numerous categories have been added to the Linnean hierarchy (Simpson 1961: 16–17, Mayr 1969: 89–90). It is of course justifiable to try to classify the fossil vertebrates within these taxa, as is generally done in text books, but this procedure has led to many controversies. The Linnean class Pisces was used by Woodward as late as in 1932, but already in 1909 Goodrich excluded the Cyclostomata, and now the usage of the term Pisces in this restricted sense is also abandoned. Intensive studies of early fossil vertebrates during the last decades have revealed that when they appear in the fossil record, in the Devonian or earlier, they were already divided into a great number of highly specialised groups (Jarvik 1959a, 1960, 1964, 1968, 1980, 1980a). Intermediate forms between these distinct groups have been looked for in vain and their origin, still wrapped in obscurity, can only be hypothesised (Jarvik 1980a, fig. 139). These new facts, and comparisons with recent forms have forced me to present a classification of the vertebrates (1980a, fig. 140) which differs considerably in important respects from those usually found in modern scientific publications and text books. In addition to Pisces, many taxa, such as Agnatha, Osteichthyes, Crossopterygii, Rhipidistia, Amphibia, Lissamphibia, Sarcopterygii, etc. have been rejected; and also – for the sake of simplicity – hierarchial prefixes such as Superclass, Class, Subclass, Infraclass, etc. have been avoided above the family level.

The distinct group of fish which I have termed Osteolepiformes since 1942 is classified by Romer (1966) as a superfamily, Osteolepidoidea, whereas Miles (1971) and Andrews (1973), excluding *Rhizodus* and allied forms, rank it as an order. This order is divided by Miles into three suborders given the unwieldy names Osteolepidoidei, Eusthenopteroidei and Rhizodopsidoidei. Andrews, in contrast, ranks the same units only as families: Osteolepididae, Eusthenopteridae and Rhizodopsidae. I can see no advantage in creating long and clumsy taxonomic terms, difficult to use and handle in scientific descriptions and discussions. With the aim of maintaining clarity and simplicity, and in keeping with most other students, I have found it reasonable to follow Woodward's sensible suggestion (1891: XXII) to omit the duplication of "*id*" in generic names terminating in "*aspis*" or "*lepis*" (e.g. Osteolepidae instead of Osteolepididae; Jarvik 1980: 19). In addition to the three families mentioned above, several other osteole-

piform families (e.g. Gyroptychiidae, Glyptopomidae, Berg 1958), and even numerous subfamilies have been distinguished (Vorobyeva 1975, 1977). However, in view of our still incomplete knowledge, and in agreement with Woodward (1891, 1932), Goodrich (1909), Romer (1966), and others I have distinguished only two families; the Osteolepidae, characterised by cosmine and rhomboid scales, and the Rhizodontidae without cosmine and with cycloid scales. This is not to be regarded as a natural classification and is retained mainly for practical reasons. It may be reasonable to assume that the rhizodontids arose from forms with cosmine and rhomboid scales, that is osteolepids, and in a natural classification we should of course classify the various rhizodontids together with their osteolepid ancestors. This is currently impossible. We cannot, for example, say from which osteolepid *Eusthenopteron* is derived, and because clear definitions of *Eusthenopteron* and
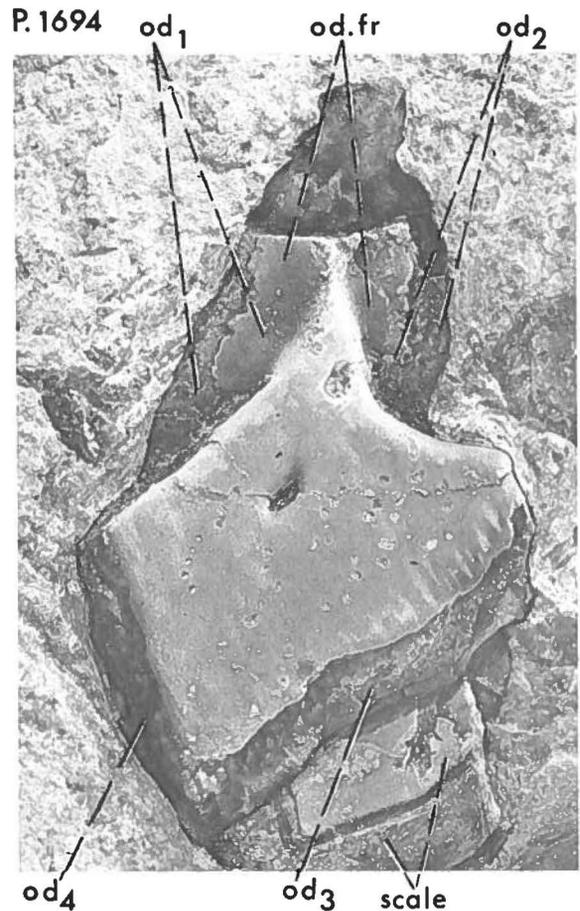
Fig. 3. P. 1694. Unidentified cosmine-covered plate with overlapped areas (od$_1$-od$_4$) along each of the four margins, and two pits of uncertain importance. Total height of plate (as orientated arbitrarily: 21 mm. Total length of adjoining scale 7 mm. From the type locality of *Gyroptychius groenlandicus,* Hesteskoen, 210–234 m. Coll. 1956.

Fig. 4. *Gyroptychius groenlandicus* Jarvik. Imperfect, dorsoventrally compressed skulls in dorsal view. A: P. 1685, Wängsjö's loc. Ec. 1, about 12 km W of Kap Franklin. Coll. 1950. × 1.5. B: P. 1651, Vilddalen. Coll. 1950. × 1.

many other osteolepiforms are still wanting I have found it best to avoid family names such as Eusthenopteridae Berg, 1955 used by several modern writers (more correct is Tristichopteridae Cope, 1889: 355). The use of the well established family name Rhizodontidae (Traquair, 1881: 17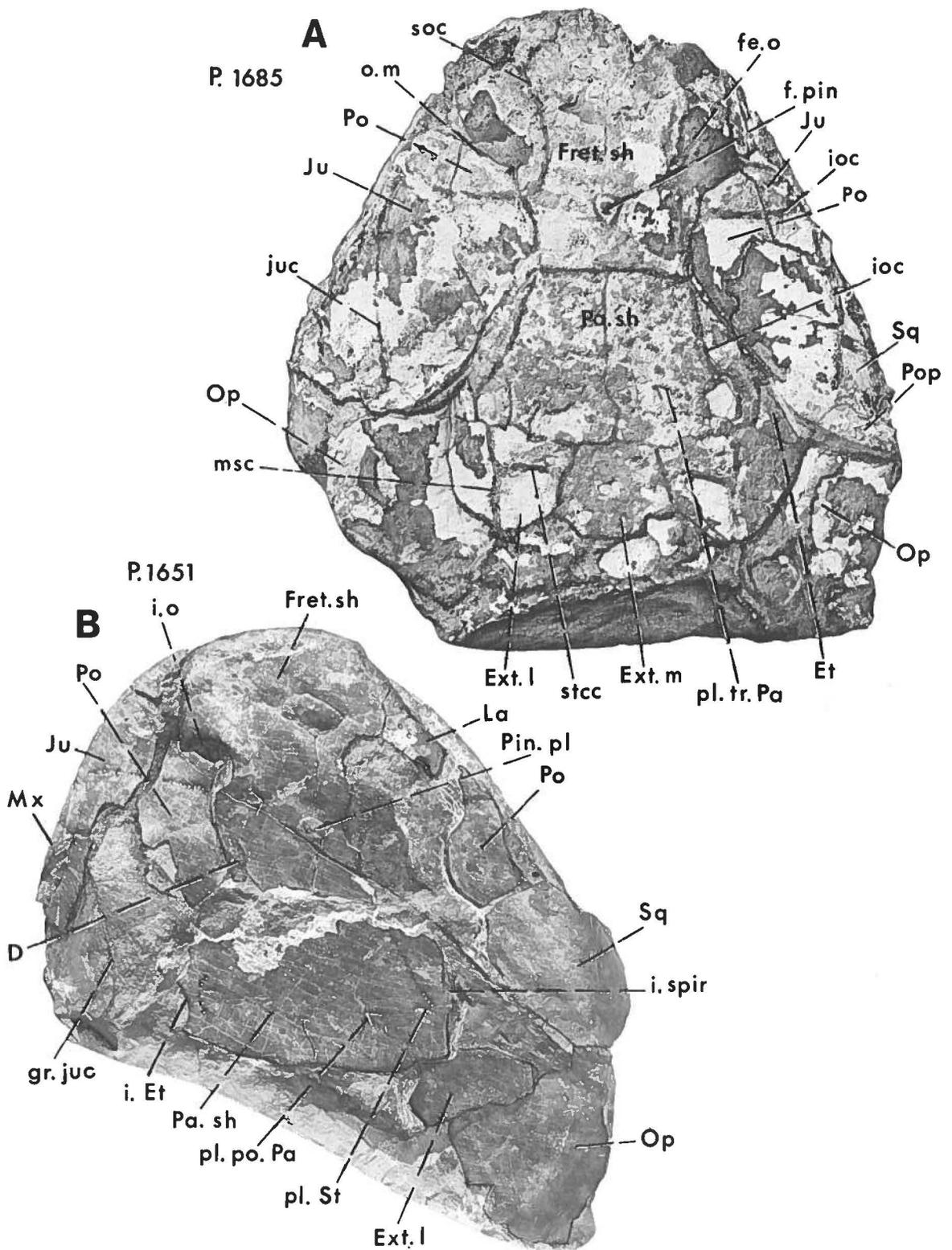9) in a restricted sense, viz. for some incompletely known genera (*Rhizodus, Strepsodus, Sauripterus*) as suggested by Andrews & Westoll (1970a: 462, cf. Berg 1940: 389), is not to be recommended.

Systematic descriptions

In the following taxonomic discussions I use the system developed in my revision of the Scottish osteolepids (1948), and measurements, either directly on the specimens or on photographs, have been made as illustrated in Fig. 2. As pointed out above (p. 6) the values obtained and the ratios calculated should be regarded as only approximate (cf. Young & Gorter 1981: 116). All specimens from East Greenland belong to the Geological Museum, University of Copenhagen.

Family Osteolepidae Woodward, 1891

Several modern writers (Vorobyeva & Obruchev 1964: 291, Andrews & Westoll 1970a: 479, Andrews 1973, Young & Gorter 1981: 116, and others) accept the family name Osteolepididae Cope, 1889. However, this name was introduced by Cope without any definition, and in his "Synopsis" (1889: 856) the family is placed together with the Holoptychiidae Owen in the suborder Taxistia of the superorder Crossopterygii. In another superorder of the subclass Teleostomi, the Rhipidopterygia, Cope (p. 855) included the Rhipidistia with the single family Tristichopteridae. We are indebted to Woodward (1891) for bringing order to the confusion of "crossopterygian" fishes: and since Woodward (1891: 367) was the first to give a definition of the family which he, omitting the *id* (see p. 10), called the Osteolepidae (a spelling immediately accepted by Cope, 1891: 459–460), I find it reasonable to regard him as the author of the family.

Genus *Gyroptychius* McCoy, 1848

The type species of *Gyroptychius* is *G. agassizi* (Traill, 1841) from the Sandwick Fish bed, Orkney (Upper Middle Devonian; Jarvik 1948, 1949, table 5). Other species assigned more or less definitely to the genus have been recorded: from Scotland (*G. milleri*, G. cf. *agassizi*, *G.* sp. inc.1, *G.* sp. inc.2, *G?* sp. Jarvik, 1948, *G.* sp. Thomson, 1964b), Norway (*G? kiaeri* Jarvik, 1949), the Soviet Union (*G. pauli, G. elgae* Vorobyeva, 1977; two other species, *G. grossi* Vorobyeva and *G. latvicus* Vorobyeva are mentioned by Lyarskaya 1978), East Greenland (*G. groenlandicus, G?* cf. *groenlandicus* Jarvik, 1950, 1950a), Canada (*G? taylori* Jessen, 1968a) and Australia (*G? australis* Young & Gorter, 1981).

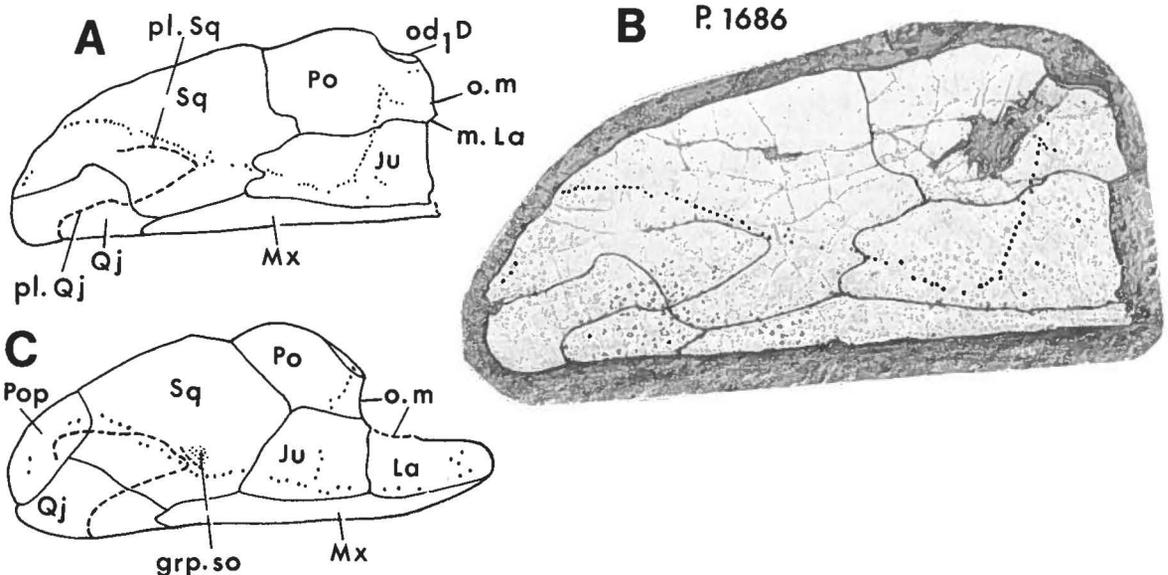Fig. 5. **A, B**: *Gyroptychius groenlandicus?* Incomplete external cheek plate. **B**: P. 1686, Vilddalen. Coll. 1955. × 2. **C**: *Gyroptychius groenlandicus.* Restoration of external cheek plate. Based mainly on holotype. × 2 approx. From Jarvik 1950, fig. 18.

On *Gyroptychius groenlandicus* Jarvik, 1950

Material and localities. – The new material assigned to this species is from the type locality at 210–234 m in the NW part of Hesteskoen, and from Kollen in Canning Land (division with *Gyroptychius groenlandicus*) and from the area of Kap Franklin (Vilddalen Group) farther to the north (Fig. 1). The age is Upper Middle Devonian (Bütler 1959, Jarvik 1961).

The material from Canning Land collected in 1956 consists of isolated cranial remains. Only two examples from Kollen, both showing the median gular plate (unrepresented in the original material) are figured (Fig. 6B, C). These plates are described below (pp. 15–16). In addition may be mentioned the fact that one frontoethmoidal shield from the type locality attains a length of 32 mm and is thus considerably larger than the largest one (25 mm; Jarvik 1950, table 1) from that locality found earlier. An unidentified plate (P. 1694) from the type locality is shown in Figure 3.

The first osteolepid material from the northern district was collected by H. Bütler in 1948 in Randbøldalen, in deposits which he later (1954: 29) called the Vilddalen "Series": Some of the specimens were described in a preliminary note (Jarvik 1950a) and were found to belong to a form indistinguishable from *G. groenlandicus* in the southern district. The new material collected in 1950 by H. Bütler and G. Wängsjö and in 1955 by E. Nielsen, comes from the thick Vilddalen Group, exposed in Randbøldalen, Vilddalen and along the southern shore up to about 12 km to the west of Kap Franklin (Fig. 1). The specimens have thus been collected over a fairly extensive area, and, moreover, from different levels in a series of sandstones about 1500 m thick (Bütler 1959: 169). The possibility can not be excluded therefore that more than one species is represented, and in one case (Fig. 5 A, B) I have found it justified to question the specific name.

Description

Skull and exoskeletal shoulder girdle. – The dorsal side of the skull, including the external cheek plates and the operculars, is fairly well shown in two flattened specimens (Fig. 4), one (P. 1685) from Wängsjö's locality Ec, 12 km to the west of Kap Franklin, and one (P. 1651) from Vilddalen (Fig. 1). In P. 1685, which is strongly weathered, showing most of the sensory canals, the parietal shield is about 19 mm and the frontoethmoidal shield about 30 mm long. This specimen is accordingly about the same size as the large specimens from the southern district (cf. above and Jarvik 1950, table 1). However, as noted earlier (1950a: 9) the specimens from the area of Kap Franklin are comparatively large and in one specimen from a nearby locality (Wängsjö's locality E.1) the length of the frontoethmoidal shield is

about 48 mm, and in another specimen from the same locality no less than about 60 mm. This specimen is larger than any other specimen of *Gyroptychius* and other known Middle Devonian osteolepids. P. 1651 is of moderate size. The parietal shield is about 28 mm and the frontoethmoidal shield about 43 mm long; that is they are about 1.5 times as long as in P. 1685 making the specimens shown in Fig. 4 directly comparable. In both the frontoethmoidal shield is about 1.55 times longer than the parietal shield (the ratio b/a, cf. Fig. 2), and the ratio f/b in both is about 0.60, f/a about 1.00, and g/a about 1.50. In these and other respects (the position of the pineal foramen and the parietal pitlines, and, shown in P. 1651 only, the position of the frontal pitline and the dimensions of the orbital notch) the two specimens agree well in the structure of the dorsal side of the skull with the specimens of *G. groenlandicus* from the southern district. In addition the external cheek plate seems to be much as in the material from Canning Land in its general proportions and in the shape and proportions of the individual dermal bones. These features indicate that these two specimens belong to *G. groenlandicus* as do probably most other osteolepids from the Vilddalen Group in the northern district.

However, as in the material from Canning Land (Jarvik 1950), there is also considerable variation in the material from the area of Kap Franklin. In some cases the specific identifications are uncertain. As an example may be mentioned P. 1686 (Fig. 5 B), which is an incomplete but otherwise well preserved external cheek plate from Vilddalen. The preserved part of the plate (the lachrymal and the anterior part of the maxillary are lacking) is strikingly long and low as compared with the corresponding part of the cheek plate in the holotype (Fig. 5 C). Measured from the anterior end of the jugal it is thus about 2.30 times longer than high in P. 1686, and in the holotype only about 1.90 times longer. This is due mainly to the fact that the jugal, which differs considerably in shape from that in the holotype and other specimens from Canning Land (Jarvik 1950, fig. 19 C–J, pls 2:1, 10: 1–8, see also 1950a, fig. 2 A) is relatively long, its length being about 0.45, and in the holotype about 0.35 of the length of the preserved part of the cheek plate. Also, it is about 2.10 times longer and in the holotype only about 1.40 times longer than it is high (cf. l.Ju/ht.Ju, 1950, table 2). The postorbital in P. 1686 also differs from that in the holotype, but a postorbital similar to that in P. 1686 is found in P. 1651 (Fig. 4 B), and as in that specimen it has a short margin (m.La) that obviously meets the lachrymal and thus excludes the jugal from the orbital fenestra (cf. 1950: 72). The notch in the quadratojugal for the posterior end of the maxillary, which is present in most specimens from Canning Land (1950, i.Mx, pls 11, 12:2, 13:5, 14:3) is lacking. More important is probably the fact that the quadratojugal pitline crosses the bone farther back than in other specimens, the ratio x/y (see Fig. 2) being about 1.90 in P. 1686, whereas this ratio in specimens from Canning
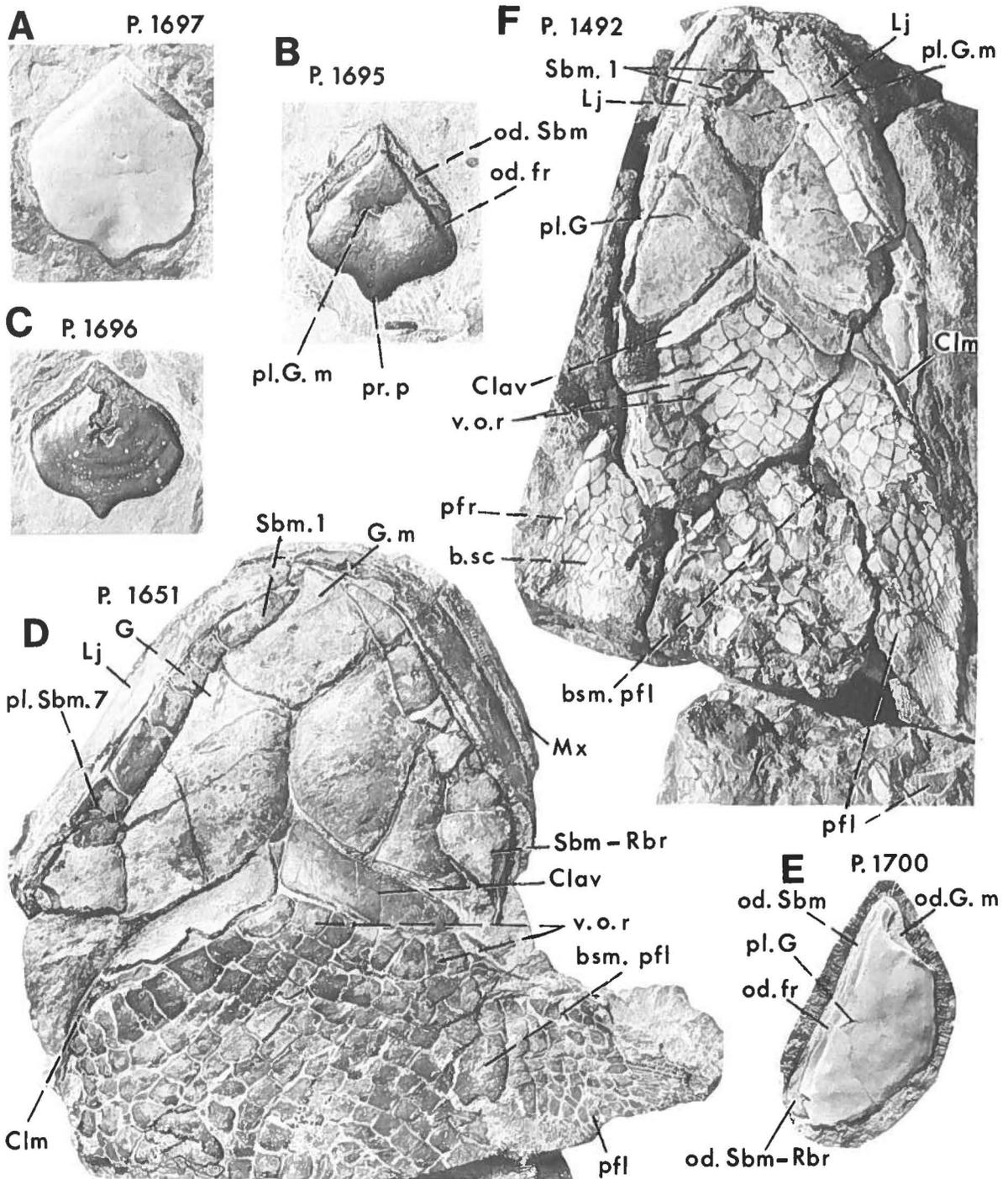
Fig. 6. A–E *Gyroptychius groenlandicus.* A–C: three isolated median gular plates in external view. A: P. 1697, Randbøldalen. Coll. 1948. Total length 28 mm. B, C: P. 1695, P. 1696, Kollen. Coll. 1956. Total length 16 mm and 14 mm. D: compressed skull and anterior part of trunk in ventral view. Same specimen as in Fig. 4 B. × 0.9 approx. E: principal gular plate. P. 1700, Wängsjö's loc. E. 1, about 12 km W of Kap Franklin. Total length 63 mm. F: *Gyroptychius dolichotatus* sp. nov. Dorsoventrally compressed skull and anterior part of trunk in ventral view. P. 1492 (holotype), Hesteskoen (division with *Asterolepis saevesoederberghi*). Coll. 1956. Same specimen as in Figs 11, 12, 14, 18 B, 21. × 1.2 approx.

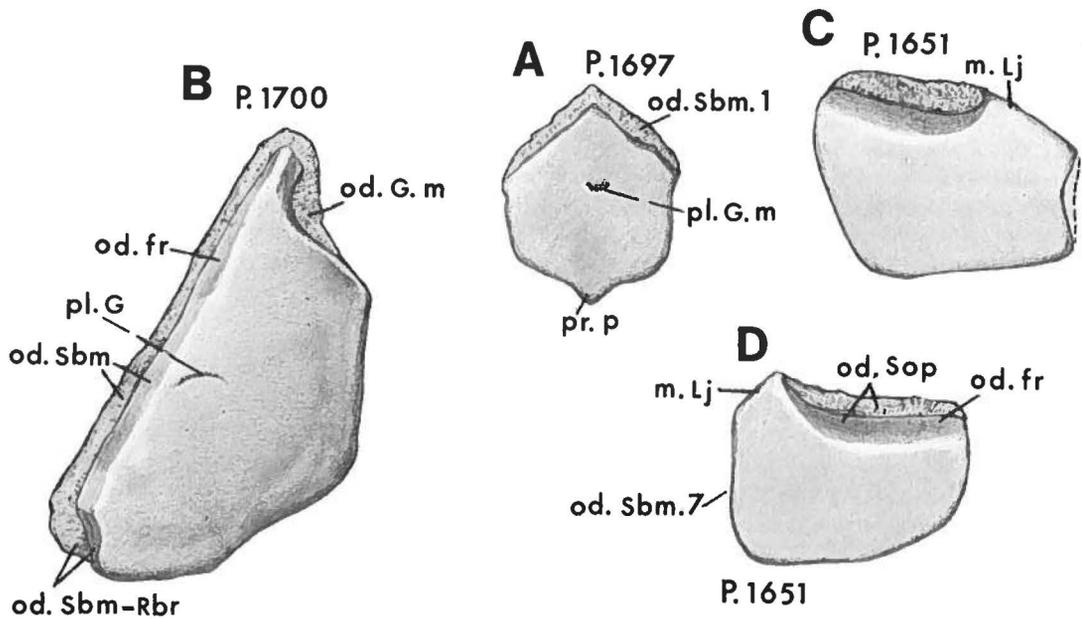Fig. 7. *Gyroptychius groenlandicus.* A, B: drawings of median and principal gular plates shown in Fig. 6 A, E, × 1. C, D: drawings of right and left submandibulo-branchiostegal plates after latex cast of counterpart of P. 1651 (Fig. 6 D). × 3/2.

Land ranges from about 1.00 to about 1.50 (see Jarvik 1950, figs 2, 16; pls 2:1, 12:2, 13, 14:3). Intermediate conditions occur in P. 1472 from Randbøldalen (1950a, fig. 2 C) in which x/y is about 1.70.

P. 1651 also presents the ventral side of the skull together with considerable parts of the squamation and the pectoral fins (Fig. 6 D). The lower jaw, which is too imperfectly preserved to be described, is about 79 mm long and 1.Lj/a about 2.82 (in the holotype about 2.75).

The submandibular series extends forwards almost to the jaw symphysis much as in *G. milleri* (Jarvik 1948, figs 77 C, 80 H). As in osteolepiforms (and porolepiforms) in general (Jarvik 1963: 13) the seventh plate carries a pitline. The hindmost plate in the series, since 1963 (p. 13) termed the submandibulo-branchiostegal plate, is well shown in external view on both sides in the counterpart of P. 1651 (Fig. 7 C, D). It is about 21 mm long, about 1.30 times longer than high, and its length is about 0.75 the length of the parietal shield. In shape it agrees well with those from the type locality and resembles that in other species of the genus (Jarvik 1948, figs 75H–J, 80 H, 83, 84 F; 1949, fig. 8 E, F; 1950, fig. 23 H, J; Young & Gorter 1981, fig. 26 C), and as in them the margin (m.Lj) meeting the lower jaw is relatively long; this is particularly true of the right plate (Fig. 7 C), in which the length of this margin amounts to more than 0.40 of the length of the plate.

The principal gular plate in P. 1651 (Fig. 6 D) is about 48 mm long, about 2.10 times longer than broad, and about 1.80 times longer than the parietal shield, and disregarding its larger size it agrees with those from the

type locality. However, the plate is better shown in P. 1700 (Figs 6 E, 7 B), which is an isolated example from Wängsjö's locality E. 1, about 12 km to the west of Kap Franklin. This plate is 62 mm long, about 2.20 times longer than wide, and the pitline lies a little behind the middle of the bone (p/n about 0.94). It is interesting that the area (od.Sbm) along the lateral margin overlapped by submandibulars 1–7, in its medial part (od.fr) is moderately depressed and covered by cosmine. This area widens posteriorly and forms a delimited depression (od.Sbm-Rbr) for the submandibulo-branchiostegal plate in much the same way as in a specimen of *G. milleri* (Jarvik 1948, pl. 35:5). The medial part of this depression is also covered by cosmine, and most probably the depressed cosmine-covered area (od.fr) was overlapped by a narrow skin-flap in the same way as I have restored in the porolepiform *Holoptychius* (Jarvik 1963: 25, fig. 11 B; 1980, fig. 180). The area (od.G.m) overlapped by the median gular plate is also covered partly by cosmine, as is the area of the submandibulo-branchiostegal plate overlapped by the subopercular, indicating that the median gular and the subopercular were also fringed by soft tissues (see also Young & Gorter 1981, fig. 26 C, pl. 9:4; cf. also the unidentified plate in Fig. 3).

The median gular plate is represented by three well preserved isolated examples, two (P. 1695 and P. 1696) from Kollen, and one larger (P. 1697) from Randbøldalen (Figs 6 A-C, 7 A) and is fairly well shown in P. 1651, too (Fig. 6 D). It is unusually large, being almost as long as the parietal shield in P. 1651 (1.G. m/a about 0.90, in

G. agassizi only about 0.60). In all four specimens it is about as long as it is broad and has a characteristic small posterior median process (pr.p.) As in *G. dolichotatus* (Fig. 6 F), *G. milleri, Thursius pholidotus* (Jarvik 1948, figs 65, 77, 80 H) and *Panderichthys* (Vorobyeva 1975, fig. 1; cf. Vorobyeva 1980, fig. 2), but in contrast to *G. agassizi* and most other Devonian osteolepids (Jarvik 1948, 1950b, Jessen 1973, fig. 1; see also Greiner 1977), it is overlapped by the anterior submandibular (Sbm. 1), as it is also in *Eusthenopteron* (Jarvik 1944, fig. 9). The pitline is a V-shaped, more or less irregular structure.

The cleithrum in P. 1651 is imperfectly preserved, but the ventromedial horizontal lamina of the clavicle (Figs 6 D, 19 A) is well shown on both sides (the dorsolateral lamina with a strong ascending process is shown in P. 1702 from Vilddalen). The ventromedial lamina shows a fairly short posterolateral margin overlapping the cleithrum, a long posteromedial margin which overlaps 5 or 6 scales of the foremost ventral oblique scale row (cf. Jar-

vik 1948: 99), and a medial margin. The latter margin is shorter proportionally than in the holotype (Jarvik 1950, fig. 28 D, pl. 2: 2; cf. *G? australis,* Young & Gorter 1981, fig. 28), its length being about 0.50 the length of the parietal shield as opposed to about 0.70 in the holotype. The medial margin of the left clavicle lies in the median line and it possibly met that of the right side in a median suture (cf. *G. dolichotatus,* Fig. 6 F). However, the right clavicle is slightly displaced and between the diverging medial margins of the two clavicles is exposed a fragmentary dermal bone, which is possibly the interclavicle.

Squamation and fins. – No complete example of *G. groenlandicus* has been found, but considerable parts of the squamation and some of the fins are shown in specimens from the northern district. P. 1651 from Vilddalen (Fig. 6 D) shows the anterior part of the squamation of the ventral side of the fish, and the pectoral fins (Figs 8, 19 A). Some 20 of the foremost ventral oblique scale

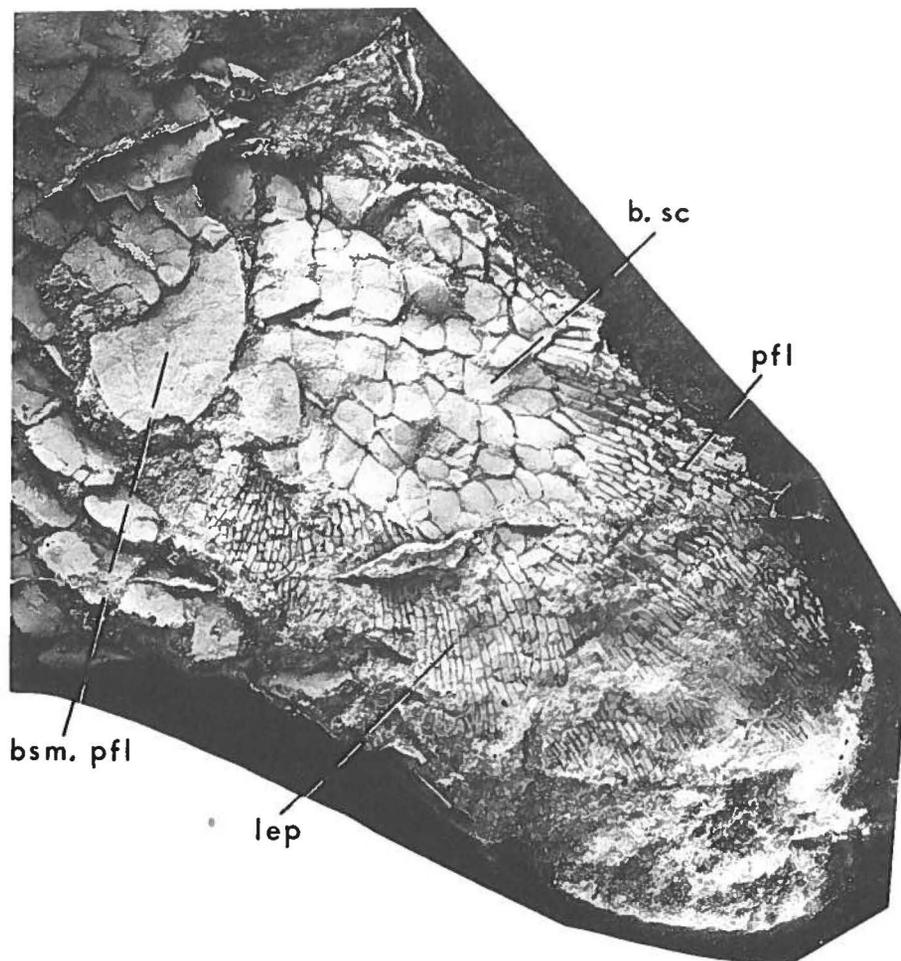Fig. 8. *Gyroptychius groenlandicus*. Left pectoral fin, inner side. Latex cast of counterpart of P. 1651 (Fig. 6 D). × 1.
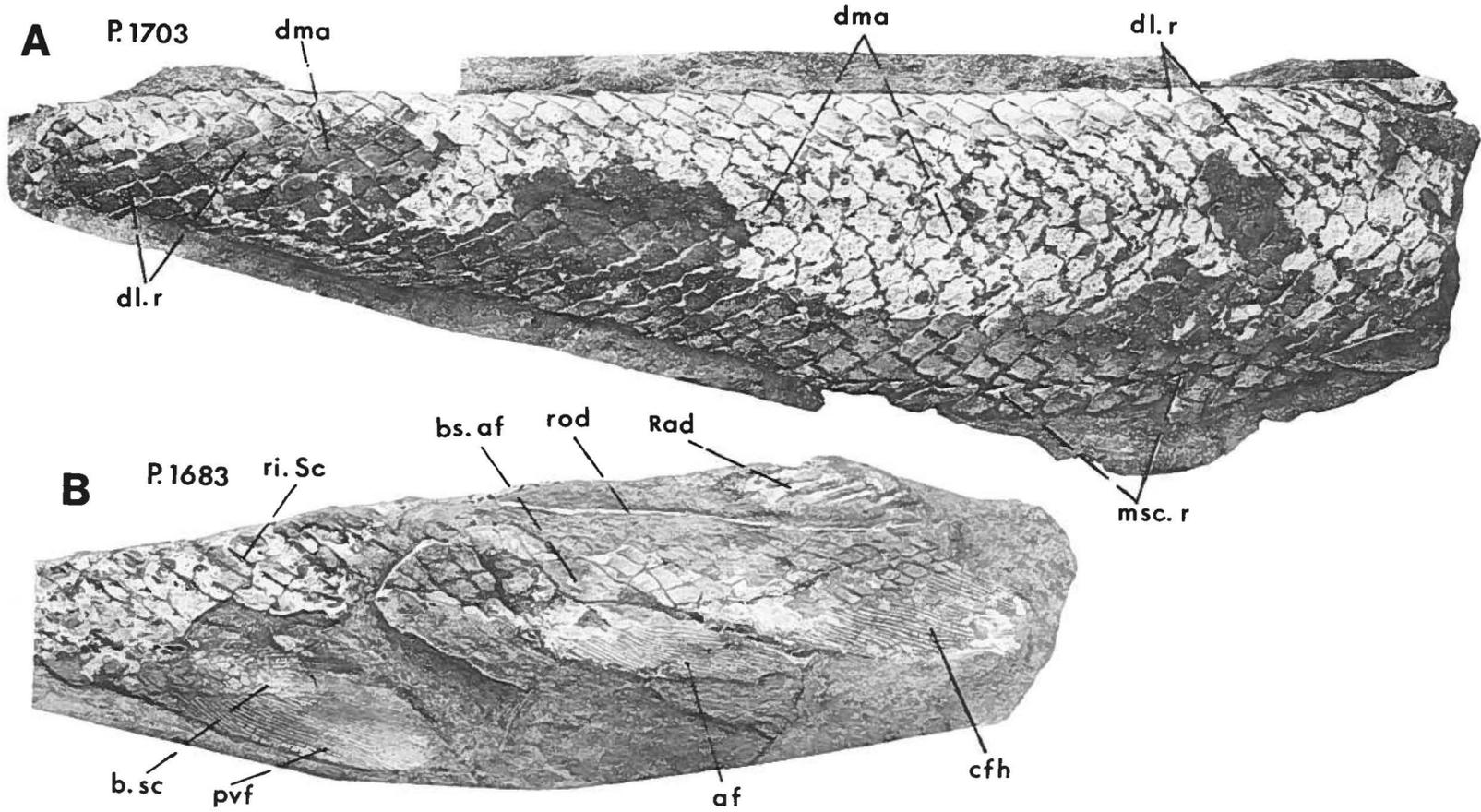
Fig. 9. *Gyroptychius groenlandicus*. **A**: main part of trunk of dorsoventrally compressed specimen in dorsal view. **B**: imperfect posterior part of trunk and part of tail in lateral view. Both specimens, P. 1703, P. 1683, Wängsjö's loc. E. c, about 12 km W of Kap Franklin. Coll. 1950. × 1.

rows are preserved, but due to flattening the scales are somewhat in disorder and the ventral median scale row is only partly discernible behind the foremost oblique row, which meets its adjacent row in an irregular fashion (see also Jessen 1972, fig. 2 D). It is interesting that the medial basal scute of the pectoral fin, which has been unknown previously in Middle Devonian osteolepids (Jarvik 1948: 110), is preserved on both sides. In shape it agrees with that in *Sterropterygion* (Thomson 1972, fig. 2) and *Megalichthys* (Miall 1885: 10, figs 5, 6; Andrews & Westoll 1970a, pl. 4 A). The pectoral fins are exposed in inner view. That of the left side is almost completely preserved and has been restored (Fig. 19 A) partly after the counterpart (Fig. 8). It resembles that in other Middle Devonian osteolepids (Jarvik 1948, Jessen 1973, fig. 2 A, pls 19:1, 21:1; cf *Sterropterygion*, Thomson 1972), and as in them it is about twice as long as the parietal shield.

The squamation of the trunk is more or less well shown in P. 1683, P. 1703, P. 1704, and some other specimens from Wängsjö's locality Ec, that is the same locality that yielded the skull shown in Fig. 4A.

P. 1683 (Fig. 9 B) is of interest in showing some of the fins. The right pelvic fin is displayed in medial view, as are also some of the scales dorsal to it. Farther back are shown a part of the squamation of the left side, the anal fin, and the anterior part of the hypochordal lobe of the caudal fin. Dorsal to the hypochordal lobe there is a long, straight endoskeletal rod, probably formed by fused vertebrae and marking the position of the body axis. Dorsal to that rod are some of the endoskeletal radials (Rad) of the epichordal lobe. The length of these radials and the straight body axis indicate that the caudal fin is diphycercal (cf. also Jarvik 1950: 93, pl. 23: 4), and together with the evidence provided by the skull it can be safely concluded that *G. groenlandicus,* and certainly also the closely allied *G. milleri,* belong to the genus *Gyroptychius.*

P. 1703 (Fig. 9 A), which like the skull in Fig 4 A is compressed dorsoventrally, shows the main part of the anterior division of the dorsal median scale row (dma; cf. Jarvik 1948, fig. 26) and the adjoining parts of the dorsolateral transverse scale rows – on the right side down to the main sensory canal scale row (msc.r.). About 36 transverse rows are shown on the preserved part. Since there are no dorsal fins on this part, this must mean that there are at least 36 transverse rows in front of the first dorsal fin, that is probably about as in *G. agassizi* in which there are 39–40 such rows (Jarvik 1948: 256, table 10; cf. also table 2).

P. 1704 (Fig. 10A, B) shows part of the squamation of the trunk in inner view similar to that in *Latvius* (Fig. 10 C) as shown in external view by Jessen (1972). This specimen is of particular interest in illustrating the mode of articulation between the dorsolateral (dl. r) and the ventral oblique (v.o.r) scale rows at the ventrolateral ridge (ri.vl, Jarvik 1948: 18, 99, fig. 26), a ridge which marks the position of the ventrolateral fin-fold (Jarvik

1948: 19; 1980a: 117, fig. 79). The articular processes (pr. Sc) of the articular ridges (cf. Figs 14, 15, 17, 18, 21) of the scales of the dorsolateral rows are directed anterodorsally – these rows may therefore be referred to as anterodorsally directed (or running) scale rows; cf. below p. 26–27 – whereas the articular processes in the ventral oblique rows are directed anteromedially. The articular ridges of the scales in the ventral oblique rows are wedge-shaped (ri.Scb), which is of some interest as discussed below (p. 27).

Gyroptychius dolichotatus sp. nov.

(Figs 6 F, 11–15, 18 B, 19 B, 20 B, 21)

1950 *Gyroptychius?* cf. *groenlandicus* – Jarvik: 100, pl. 23:1
1959 *Gyroptychius* sp. – Jarvik: 21–24, figs 9 B, 10 A, pl. 2
1961 *Gyroptychius* cf. *groenlandicus* – Jarvik, table 1
1980 *Gyroptychius groenlandicus* – Jarvik, fig. 150 B

Name: *dolichotatus,* superlative of Gr. adj. *dolichos* long, referring to the long and slender shape.

Diagnosis. – Long, slender fish, about 22 times longer than the parietal shield, attaining a length of at least 360 mm. Total body length about 6.5 times longer than the skull which is about 3.4 times longer than the parietal shield. Frontoethmoidal shield longer than the parietal shield (b/a probably about 1.4) with convex posterior margin. Parietal shield with pointed anterolateral corners. Postorbital notch fairly long (l.i.po/a about 0.75). Cranial roof remarkably narrow at the anterior end of the parietal shield (f/a about 0.65), and narrow also at the spiracular notch (g/a about 1.10). Postorbital about 1.60 times longer than high, with short margin meeting the lachrymal and gently convex margin towards the squamosal. Lower jaw about 2.80 times longer than the parietal shield. Submandibular series extending far forwards, the most anterior element of the series meeting the adjacent element in a median suture between the median gular plate and the symphysis of the jaws. Median gular plate almost as long as the parietal shield (l.G.m/a about 0.90) and about 1.27 times longer than broad. Posterior process lacking. Principal gular plate about 2.40 times longer than broad and about 1.75 times longer than the parietal shield. Frontal pitline probably short. Pitline of principal gular situated a little in front of the middle of the bone (p/n about 1.10). Clavicles meet in a median suture. Interclavicle probably absent. Anterior division of dorsal median scale row about 13 times longer than the parietal shield, and includes about 42 scales.
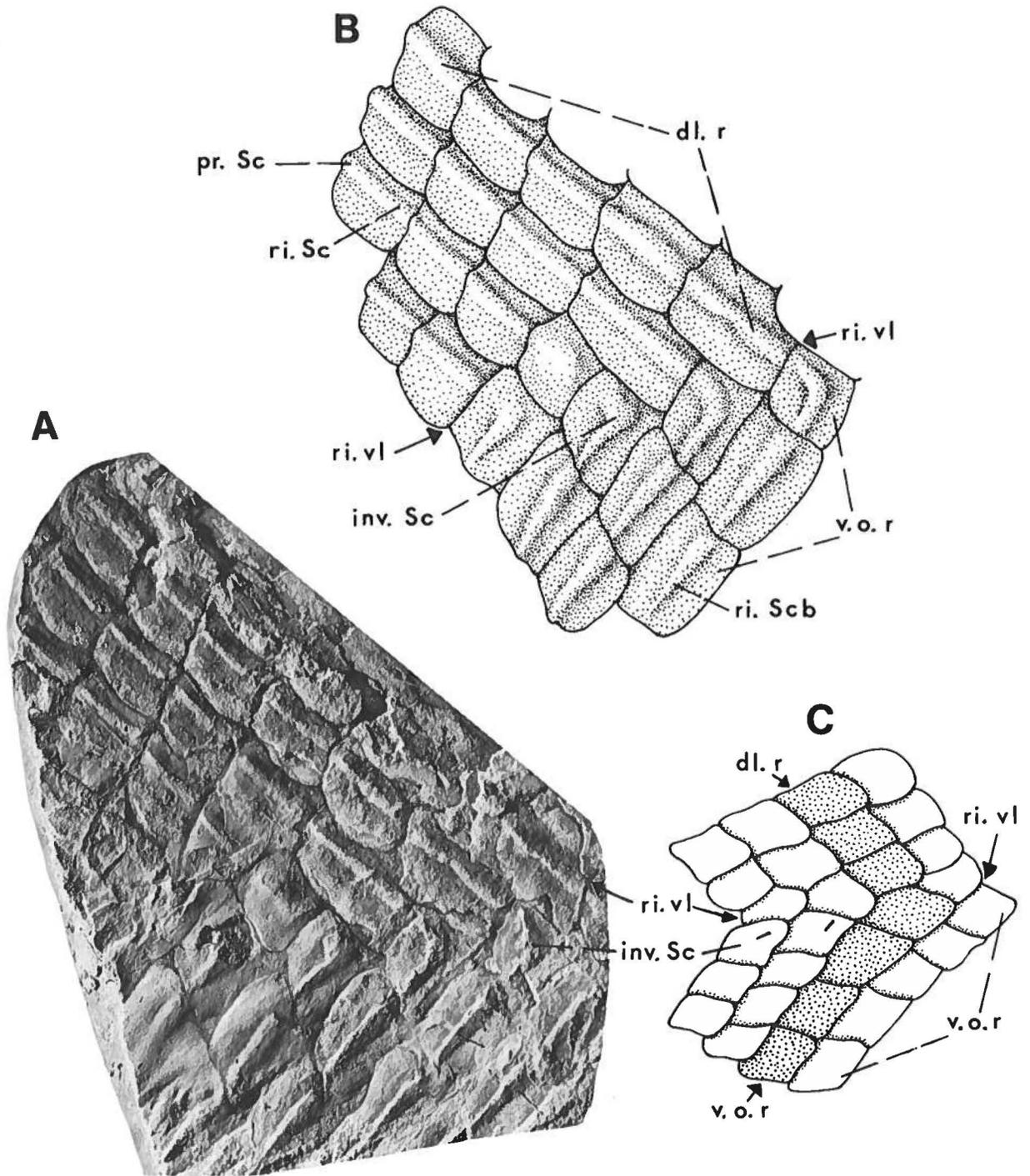
Fig. 10. **A**, **B**: *Gyroptychius groenlandicus*. Part of flattened squamation showing some of the dorsolateral transverse (ante-rodorsally directed) scale rows meeting the ventral oblique scale rows at the ventrolateral ridge (cf. Jarvik 1948, fig. 26). Right side, visceral view. **A**: P. 1704, Wängsjö's loc. E. c, about 12 km W of Kap Franklin. Coll. 1950. × 2. **C**: *Latvius niger* Jessen. Sim-ilar part of squamation as in **A**. Left side, external view. From Jessen 1972, fig. 2 E.

Fig. 11. *Gyroptychius dolichotatus* sp. nov. Almost complete fish in ventral view. P. 1492 (*holotype*), Hesteskoen, Canning Land (division with *Asterolepis saevesoederberghi*). Coll. 1956. Total length 360 mm. Same specimen as in Figs 6 F, 12, 14, 18 B, 21.
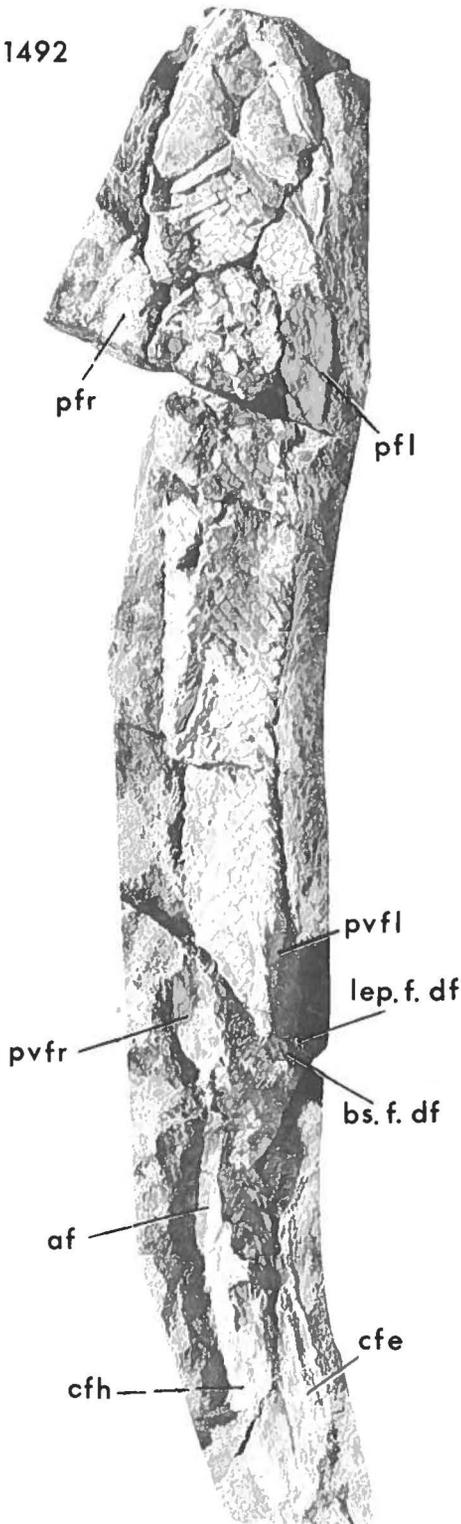
Scale row formula approximately

$$\frac{44\ 54\ 60}{34\ 44\ 53}\ (120).$$

Anteroventrally directed scale rows on tail form an obtuse angle (about 115°) with the anterodorsally running rows. Pectoral fin long, about 3.10 times longer than the parietal shield. Pelvic fin about twice as long as that shield. First dorsal fin probably small and situated a little farther back than the pelvic fins. The diphycercal caudal fin long and low, about 3.10 times longer than high and about 4 times longer than the parietal shield. Hypochordal lobe about 1.6 times higher than the epichordal lobe. Each lobe includes about 90 lepidotrichia.

Material and geological horizon. – The material includes only two specimens, P. 1492, which is the holotype, and P. 1528. The holotype is an almost complete fish (Fig. 11) found in 1956 (Jarvik 1959: 21) together with several more or less complete specimens of the porolepiform *Glyptolepis groenlandica* (Jarvik 1972) in sandstones at about 410 m in the southeastern slope of Hesteskoen in Canning Land (Fig. 1). P. 1528 is an imperfect head preserving the anterior part of the squamation, found on the same slope. The deposits belong to the division with *Asterolepis saevesoederberghi* (Upper Middle Devonian) which is separated from the overlying divison with *Gyroptychius groenlandicus* by plant-bearing beds more than 500m thick (Säve-Söderbergh 1937: 14, Bütler 1948: 52-53, Jarvik 1961, table 1).

Description

The description is based almost entirely on the holotype, which is compressed dorsoventrally but is twisted so that the tail is exposed in lateral view. Because the caudal fin is diphycercal I (1959) found it reasonable to refer the specimen to *Gyroptychius*, and the striking similarities in the ventral aspect of the skull (Fig. 6 D, F) indicated that it is closely allied to or possibly belongs to *G. groenlandicus*. However, negative preparation recently carried out has revealed considerable differences in the skull roof and for these and other reasons I have found it necessary to introduce a new specific name.

P. 1492 is about 360 mm long and thus of moderate size. It is remarkably slender and somewhat more eel-like than *G. agassizi* (Fig. 20 A) and other osteolepids known in this respect (Jarvik 1948, figs 1,27, 47, 57, 61, 64, 70, 76; 1950b, fig. 7; cf. Jessen 1973, fig. 2 A, Thomson 1972, fig. 1). The skull (length about 55 mm) is thus about 6.5 times shorter than the body length and the fish is about 22 times longer than the parietal shield. In *G. agassizi* the corresponding ratios are about 5.0 and 17.

Skull and exoskeletal shoulder girdle. – The dorsoventrally compressed skull in P. 1492 (Figs 6 F, 12, 13 A, B) is somewhat deficient anteriorly, in particular in the
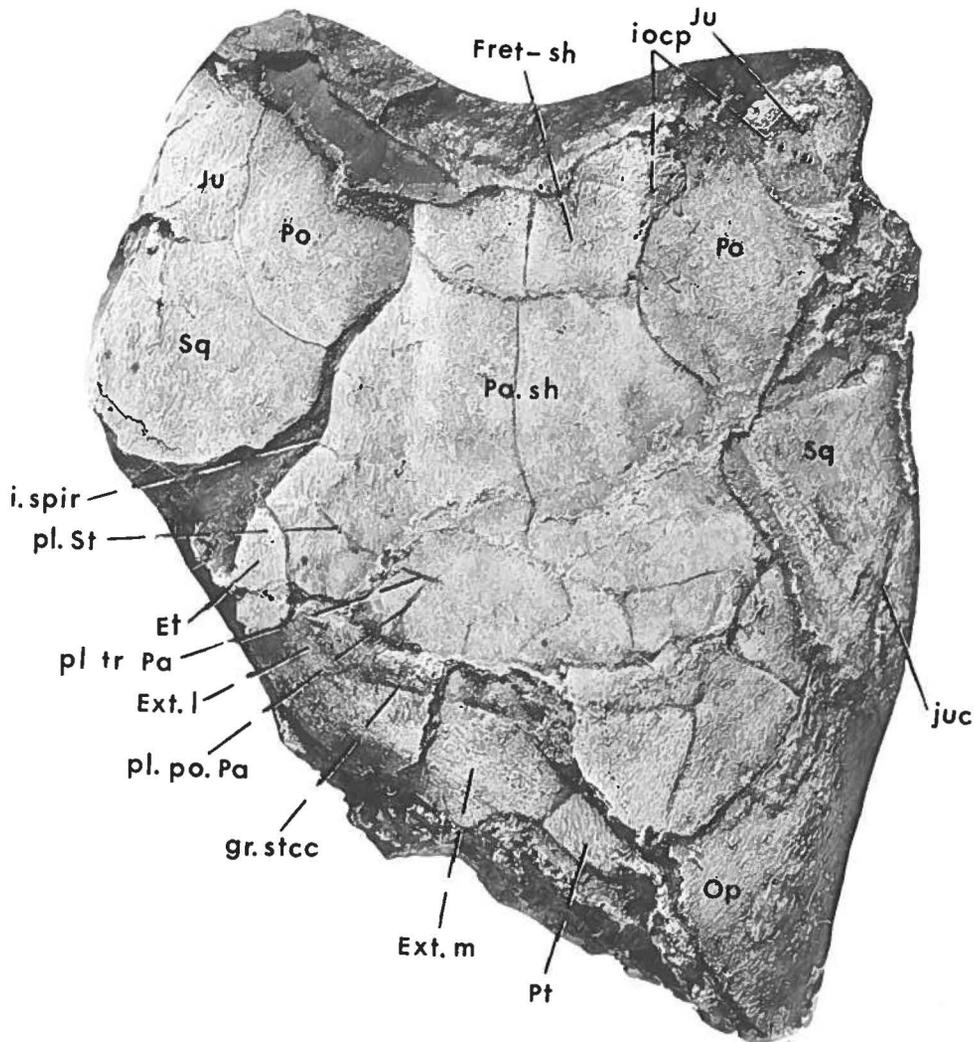
Fig. 12. *Gyroptychius dolichotatus* sp. nov. Latex cast of impression of preserved part of dorsal side of skull. P. 1492 (*holotype*). Same specimen as in Fig. 11. × 3.

skull roof. The main anterior part of the frontoethmoidal shield is lacking and the preserved part shows only the posterior parts of the frontals together with the dermosphenotics. There are no traces of the frontal pit-line, which was probably short and situated as in *G. groenlandicus* (Fig. 13 C) and the Scottish species of the genus. However, in contrast to these species, the posterior margin of the frontoethmoidal shield is convex and the intertemporal portion of the parietal shield projects forwards in a pointed process (somewhat as in *G? kiaeri*, Jarvik 1949, fig. 4, pl. 3). The most remarkable difference from *G. groenlandicus* is in the breadth of the skull roof at the postorbital notch, the ratio f/a being about 0.65 in *G. dolichotatus* but no less than 0.90–1.05 in *G. groenlandicus*. As shown in Fig 13 the cranial roof in *G. dolichotatus* is also narrower than in *G. groenlandicus* at the spiracular notches and the posterolateral

corners. The undulating course of the median suture between the parietals indicates that elements of the central parietal series of bones (Jarvik 1948: 64, 67; 1950: 68; Jessen 1966: 320; see also Vorobyeva 1977, figs 27, 34) are also present in *G. dolichotatus*. As tentatively suggested recently (Jarvik 1980a: 104) these median bones are developed in relation to the underlying endoskeletal median elements of the cranial tecta. As is often the case in osteolepids (Jarvik 1948: 61; 1950: 66), the extratemporals are independent (cf. Jarvik 1980: 205). The extrascapulars are as usual (cf. Jarvik 1980, fig. 185).

The dermal bones of the external cheek plates are preserved only partly in P. 1492 (Figs 12, 13 A) and only the postorbital has been restored (Fig. 13 B). This bone is about 13.2 mm long, about 1.60 times longer than high, and its length is about 0.77 that of the parietal
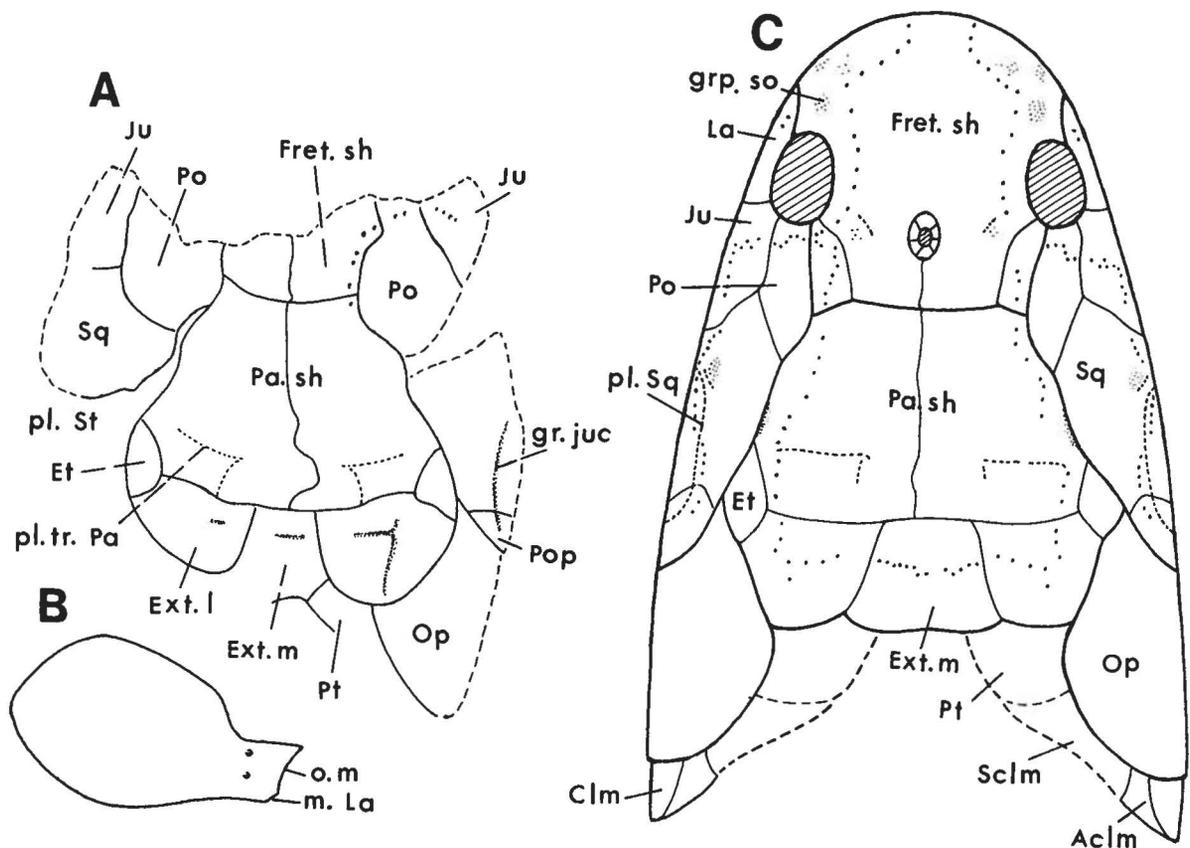
Fig. 13. **A, B**: *Gyroptychius dolichotatus* sp. nov. **A**: sketch of preserved part of dorsal side of skull shown in Fig. 12. **B**: restoration of postorbital. **C**: *Gyroptychius groenlandicus*. Restoration of skull in dorsal view. From Jarvik 1950, fig. 12 B. Length of parietal shield the same as in A.

shield. Its margin meeting the squamosal is gently convex but in other respects it agrees well with the postorbital of *G. groenlandicus* in P. 1651 (Fig. 6 B). Judging from P. 1528 in which the orbital fenestra is fairly well shown the postorbital in *G. dolichotatus* also has a short margin (m.La) meeting the lachrymal (cf. also P. 1686, Fig. 5 A, B).

The ventral side of the skull is preserved in P. 1492, and as a whole it resembles that of *G. groenlandicus* in P. 1651 (Fig. 6 D, F). As in that species the lower jaw is about 2.80 times longer than the parietal shield and the anterior submandibulars overlap the median gular plate. A remarkable difference, however, is that the anterior submandibulars (Sbm.1) in *G. dolichotatus* meet in a median suture between the median gular and the symphysis of the lower jaws (as in *Panderichthys*, Vorobyeva 1975a, fig. 1; cf. also *Megalichthys*, Miall 1885, fig. 2). The principal gular plate (length about 28 mm) is about 2.40 times longer than broad and about 1.75 times longer than the parietal shield. The pitline lies a little in front of the middle of the bone (p/n about 1.10). The bone is more slender than in *G. groenlandicus* (l.G/br.G about 1.93 – 2.18), and the notch for the median gular

plate is less deep. The latter plate (length about 14 mm) is almost as long as the parietal shield (l.G.m/a about 0.90) as in *G. groenlandicus,* but about 1.27 times as long as broad and thus a little more slender than in that species (p. 15). No blunt posterior process is discernible. The pitline is V-shaped.

The cleithrum is incompletely preserved. The ventromedial horizontal lamina of the clavicle (Clav, Figs 6 F, 19 B; shown also in P. 1528) resembles that in P. 1651 (Figs 6 D, 19 A) but is narrower, the exposed part being about 3.50 times longer than wide in *G. dolichotatus* but only about 2.80 times longer in *G. groenlandicus*. The main part of the medial margin in *G. dolichotatus* meets the corresponding margin of the other side in a median (in P. 1528 slightly undulating) suture, and although the medial margins diverge slightly in the most anterior parts there is no trace of the interclavicle. Most probably, this element is lacking, as it probably is also in *G. groenlandicus*.

Squamation and fins. – The tail in P. 1492 is shown in lateral view (Figs 11, 15, 18 B, 20 B, 21) but the main part of the trunk is (like the skull) compressed dorso-
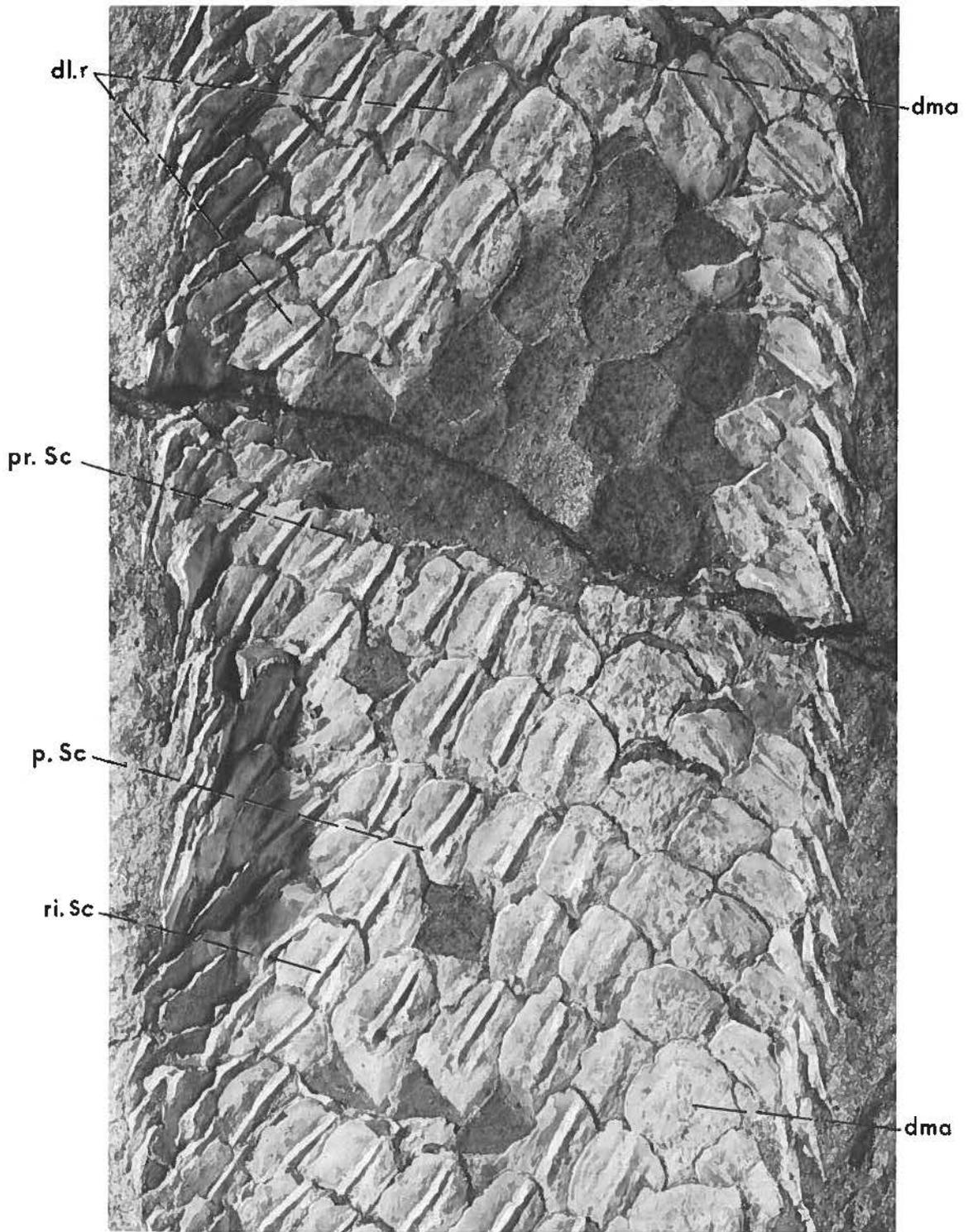
Fig. 14. *Gyroptychius dolichotatus* sp. nov. Squamation of part of dorsal side of fish in visceral view. P. 1492 (*holotype*). × 4.

Fig. 15. *Gyroptychius dolichotatus* sp. nov. Restoration of posterior part of trunk and tail in lateral view. Part of squamation of right side shown in visceral view to illustrate the change in direction of the scale rows in the area between the second dorsal and anal fins. Based on the holotype (cf. Figs 11, 18 B, 21).

ventrally. Because of this the lateral line scales are not shown and since the adjoining scales in the transverse dorsolateral scale rows are imperfectly preserved and in disorder it has not been possible to make a restoration in lateral view of the whole fish with squamation (Fig. 20 B). However, the squamation of the dorsal and ventral sides, the basal scales and scutes, and the lepidotrichia are partly well shown, and P. 1492 exhibits structural details that are indistinct or have not been observed so far in osteolepids.

As described previously (Jarvik 1959: 21, figs 9 B, 10 A, pl. 2; 1980, fig. 138 A2) the gradual transition from scales to dermal fin rays (lepidotrichia) is well shown in this specimen and the structure of the lepidotrichia could be made out. It has also been demonstrated that the intercalation of new lepidotrichia occurs in the same way as the intercalation of new longitudinal scale rows on the trunk (Jarvik 1948: 108–109, fig. 29; 1959: 22–23, fig. 10 A).

Another interesting feature is that the squamation of a large part of the back of the fish is displayed in inner view, allowing observation of the relations between the dorsolateral transverse scale rows (dl.r) and the anterior division (dma) of the dorsal median scale row (Fig. 14). The articular ridges (ri.Sc) of the scales of the dorsolateral scale rows form, in each row, a narrow continuous ridge running in the same direction as the scale row. However, the ridge of the dorsalmost scale in each row is broadened and has a fairly long dorsomedial margin which abuts against the posterolateral margin of a distinct median elevation on the inner side of each of the scales of the dorsal median row.

The squamation of the tail in specimen P. 1492 is exposed to a considerable extent in inner view, showing well the articular ridges of many of the scales (Figs 15, 18 B, 21). Because of this favourable condition it has been possible to establish (Jarvik 1959: 21, pl. 2:1; 1980:214 – 216, figs 148–150) that the change from anterodorsally (sr.ad) to anteroventrally (sr.av; not posterodorsally, see below) running scale rows occurs in osteolepids in the same way as in early (*Moythomasia*, Jessen 1968, fig. 4), advanced fossil (Schultze 1966: 255, fig. 11) and living actinopterygians (*Lepisosteus*, Fig. 16A; *Acipenser*, Jarvik 1980, fig. 150 A) as well as in polypteriforms (Fig. 16 B; cf. Pearson 1981: 98). In *G. dolichotatus* the anteroventrally running rows occur behind the second dorsal fin and (judging from the conditions in other osteolepids, Jarvik 1948, 1980, figs 148, 149, Jessen 1973, fig. 2A, pl. 22) dorsal to the main sen-
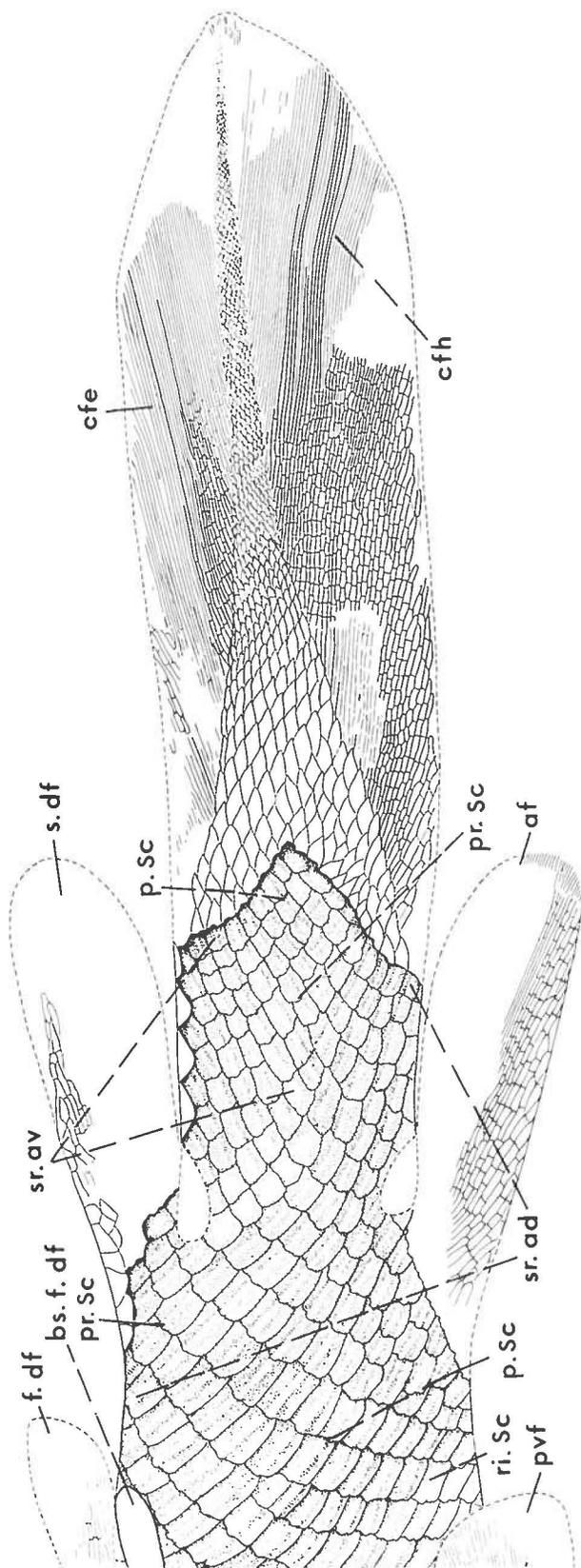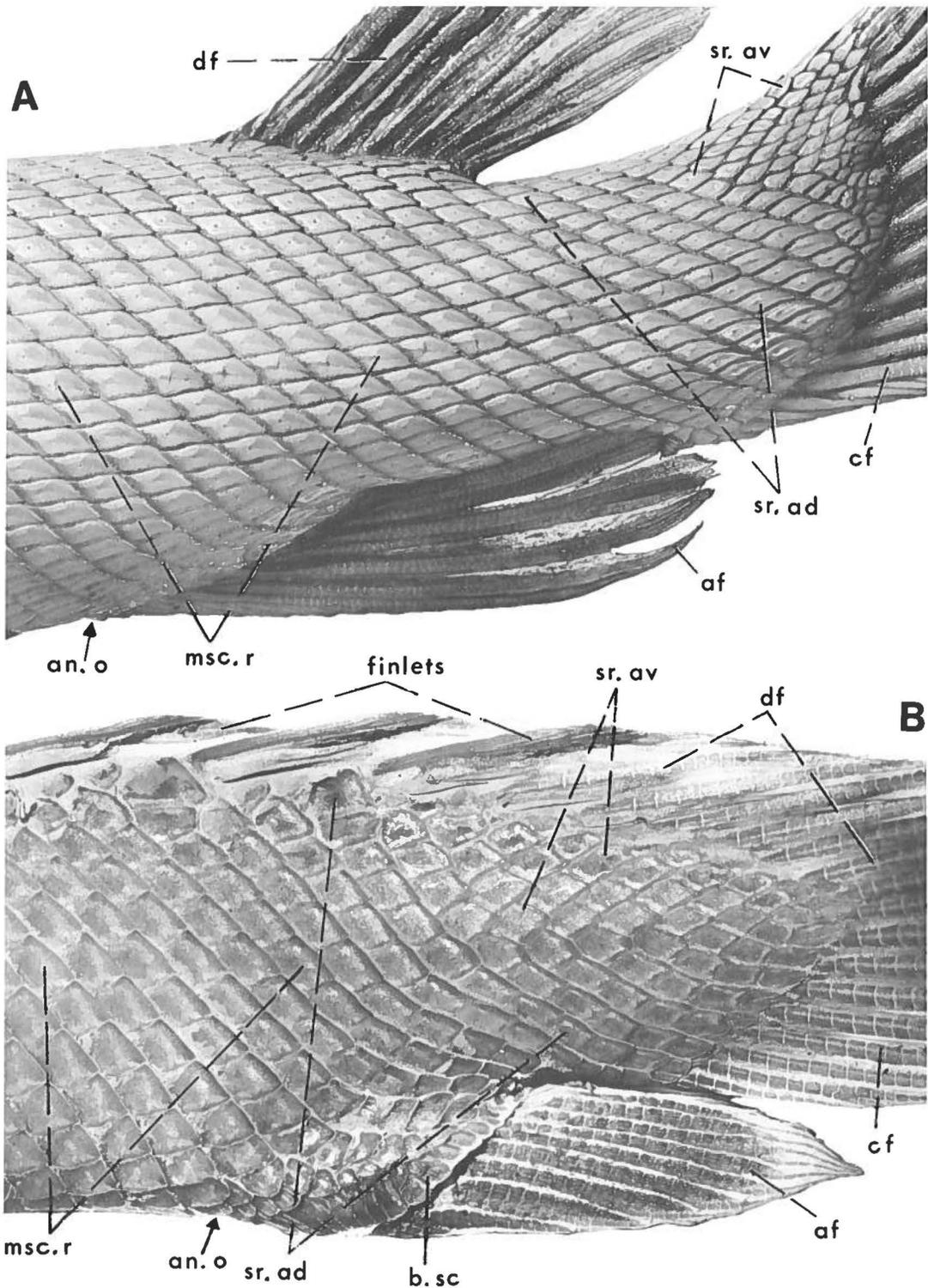
Fig. 16. Part of the tail illustrating the change in direction of the scale rows in A: an actinopterygian (*Lepisosteus tristoechus*), and B: a brachiopterygian (*Polypterus senegalus*). Specimens in the Swedish Museum of Natural History. For the structure of the caudal fin in *Polypterus* see Jarvik 1980: 308, fig. 238.
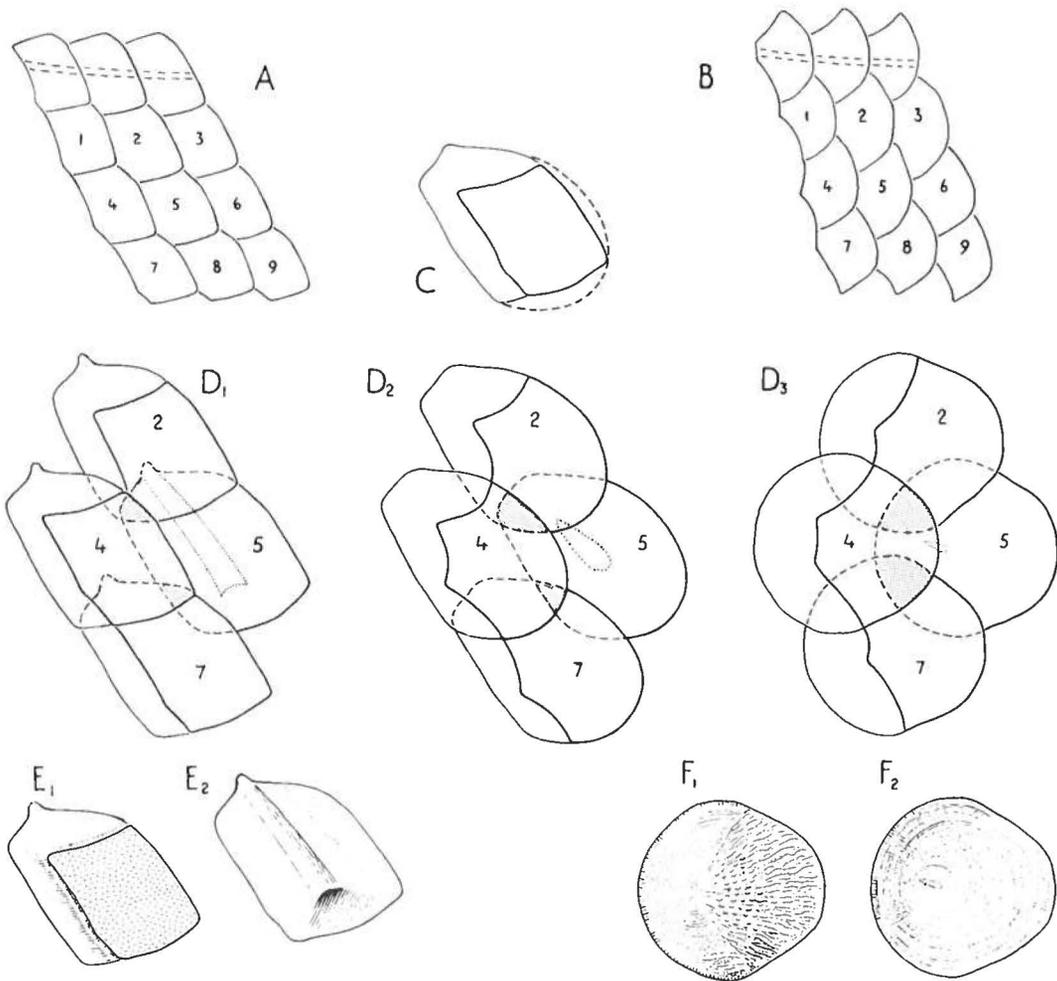
Fig. 17. Diagrammatic representations of the transformation of the rhomboid scales of osteolepids (**E**) into the cycloid scales characteristic of rhizodontids (**F**). As shown in these diagrams each of the flank-scales, for example that denoted **5**, is overlapped in both osteolepids (**A**, **D₁**) and rhizodontids (**B**, **D₃**) by three scales (**2**, **4**, **7**) and overlaps three (**3**, **6**, **8**) of the adjoining six scales. Moreover, scale **5** in two areas (denoted by shading in **D₁–D₃**) is overlapped by two scales, in the dorsal area by **2** and **4** and in the ventral area by **4** and **7**. There are differences in the relative length and configuration of the boundaries between adjoining scales. In osteolepids the boundaries on the external side between **4** and **5** and between **4** and **7** are about equal in length and longer than the boundary between **4** and **2**. In rhizodontids, in contrast, it is the boundaries between **4** and **2** and between **4** and **7** that are of about the same length, and longer than the boundary between **4** and **5** which belong to the same longitudinal scale row. The latter boundary is sometimes very short or absent, the exposed part of some of the scales having no contact at all with the exposed part of the scale following immediately behind in the same longitudinal row. A typical osteolepid scale (**E**) thus undergoes areal growth which is forwards (cf. Jarvik 1980: 13–14), and also in the direction of the overlaps; that is, with regard to the flank-scales the growth is chiefly posteriorly and posteroventrally. Given these conditions, only an inconsiderable growth in these directions – about to the extent marked by an interrupted line in **C** – will change the course and relative length of the boundaries between the scales of an osteolepid (**D₁**) to those characteristic of rhizodontids (**D₂**, **D₃**). By these small changes the scales also become more regular and rounded, and oblique scale rows running from in front and below in the posterodorsal direction (e.g. **7**, **5**, **3**), and similar to those running from below in the anterodorsal direction (e.g. **8**, **5**, **2**), become easily discernible. In connection with these changes the retrogressive phyletic development of the skeleton (Jarvik 1980: 13) obviously brought about a reduction in thickness (including loss of the cosmine layer), and as evidenced by the conditions in *Spodichthys* (p. 45, Fig. 35; see also ri.Scb, Fig. 10 A, B), the articular ridge on the inner side of the osteolepid scale (**E₂**) became partly reduced and transformed into the wedge-shaped boss characteristic of rhizodontids (**F₂**).

sory canal row (msc.r) as in actinopterygians and *Polypterus*. How the transition between the differently directed rows takes place in detail could not be made out in P. 1492. However, as is well shown in this specimen (Figs 15, 18 B, 21) the articular processes (pr. Sc) of the

articular ridges on the inner sides of the anterodorsally running scale rows (sr.ad) are directed anterodorsally. Because the articular processes of the scale rows, which I have referred to previously (Jarvik 1959:21, pl. 2:1; 1980:214 – 215, figs 148–150; for actinopterygians see

also Schultze 1966: 255) as posterodorsally directed, as is also clearly seen in P. 1492, point anteroventrally, I have found it logical to speak of these rows as anteroventrally directed or running scale rows (sr.av).

The significance of this remarkable change in direction of the scale rows on the tail has been discussed by several writers (see Jarvik 1980: 215) but no satisfactory explanation has been presented. This change has been observed previously only in fishes with rhomboid scales, but my assumption (1980: 215–216) "that the unknown anatomical conditions underlying this change were present also in fishes with cycloidal scales" can now be confirmed by a specimen (P. 15 Stockh.) of *Eusthenopteron* (Fig. 18 A).

In external appearance the rhomboid scales of osteolepids and the cycloid scales of rhizodontids are certainly very different (Fig. 17 E, F; Jarvik 1980, fig. 138). However, as is well known, changes from rhomboid to cycloid scales have occurred in several evolutionary lines in actinopterygians (Schultze 1966) and also independently in dipnoans, porolepiforms and osteolepiforms; and both types of scales may be present on the same individual, as in *Dipterus* (Jarvik 1959: 35, fig. 18) and the porolepiform *Heimenia* (Ørvig 1969: 291–293). In view of these facts, and considering the close agreement between osteolepids and rhizodontids in the pattern of the dermal bones and many other respects (Jarvik 1980: 203–212), it is evident that the transformation of the osteolepiform scale from the rhomboid to the cycloid condition cannot have implied any great changes. As already suggested (Jarvik 1980: 203, fig. 139), and explained further in Fig 17, the main changes seem to be due to an areal growth of the scales in the directions of the overlapped areas of adjoining scales. Moreover, the retrogressive development of the skeleton, following a general trend (Jarvik 1980: 13), has brought about a reduction in thickness (e.g. loss of the cosmine layer) and transformation of the articular ridge into the wedge-shaped boss characteristic of rhizodontids. That this boss really is a vestige of the articular ridge is supported by the fact that in rhizodontids it may be large (as e.g. in *Spodichthys*, Fig. 35) and also that the articular ridge in osteolepids may be wedge-shaped (ri.Scb, Fig. 10B).

Turning next to *Eusthenopteron* it is important to note that the pointed end of the wedge-shaped boss is directed as the articular process of the osteolepid scale, and that accordingly its truncate end is directed as the articular pit (Figs 17, 18). In the specimen of *Eusthenopteron* (P. 15 Stockh.) referred to above, the scales of the squamation of large parts of the flank and tail are exposed in internal view. As indicated by this specimen (Fig. 18 A) the pointed ends of the wedge-shaped bosses of the trunk scales are directed forwards and slightly upwards; that is, the bosses are directed anterodorsally, as are the articular ridges of the anterodorsally running scale rows (sr.ad) in *Gyroptychius dolichotatus* (Figs 15, 18 B). In that species the anteroventrally directed scale rows (sr.av) are found in the area

posteroventral to the second dorsal fin (s.df). It is remarkable therefore that in the corresponding area in *Eusthenopteron* (Fig. 18 A) the wedge-shaped bosses (shown on a few scales only) are clearly directed anteroventrally, which implies that they have about the same direction as the articular ridges of the anteroventrally running scale rows in *G. dolichotatus*. This demonstrates that the remarkable change from anterodorsally to anteroventrally running scale rows on the tail in osteolepids and other fishes with rhomboid scales is retained in rhizodontids, but whether it also occurs in other fishes with cycloid scales I would not venture to decide.

The anteroventrally directed scale rows in *G. dolichotatus* form an obtuse angle (about 115°) with the anterodorsally running rows. In this respect *G. dolichotatus* differs distinctly from *G. agassizi* and other osteolepids in which this angle is nearly normal (Jarvik 1948, 1980, figs 148, 149, Jessen 1973, pl. 22). It also differs from *G. agassizi* (and as far as known from *G. groenlandicus*) in other respects of squamation. The anterior division of the dorsal median scale row is thus about 13 times longer than the parietal shield in P. 1492 and includes about 42 scales, whereas it in *G. agassizi* is only about 7.8 times longer than that shield and consists of about 37–38 scales (Jarvik 1948: 254, tables 2, 10). The dorsolateral transverse, or anterodorsally directed, scale rows are partly in disorder and their number could not be established. However, they are clearly more numerous than in the Scottish osteolepids (Jarvik 1948: 104–106 table 2; 1950: 24) and probably about 120 in number. There seem to be about 44 rows in front of the first dorsal and anal fins and the scale row formula is approximately

$$\frac{44\ 54\ 60}{34\ 44\ 53}\ (120).$$

G. dolichotatus differs distinctly in this formula from *G. agassizi,* in which it is about

$$\frac{39\ 47\ 57}{29\ 39\ 47}\ (80).$$

The squamation of the ventral side of the fish is partly well shown in P. 1492 (Figs 6 D, 11; Jarvik 1959, pl. 2:2). The oblique ventral scale rows (v.o.r) are more numerous than in other osteolepids in which they are known (Jarvik 1948: 108; 1950b: 23) and total about 40 in number in front of the pelvic fins (about 37 in *Glyptopomus kinnairdi*). As in other osteolepids they form an angle with the dorsolateral transverse rows at the ventrolateral ridge (ri.vl), and as in *Gyroptychius groenlandicus* (Fig. 10 A, B) the articular processes on the inner sides of the scales point anteromedially. As a whole the ventral median scale row is imperfectly preserved and difficult to distinguish. However, it is fairly well
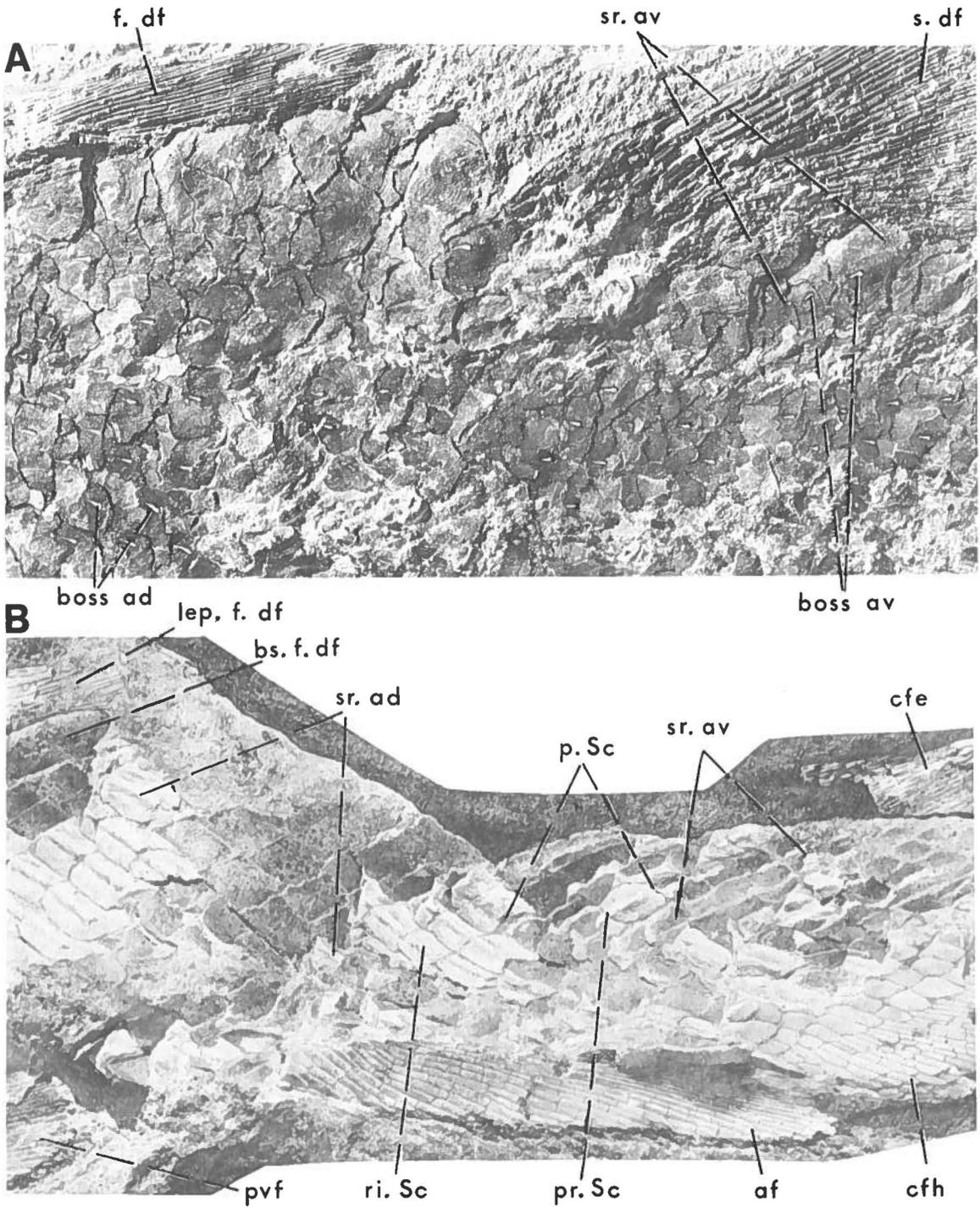
Fig. 18. Part of squamation of right side in visceral view to demonstrate the change in direction of the scale rows in the area between the second dorsal and anal fins in **A**: a rhizodontid with cycloid scales, and **B**: an osteolepid with rhomboid scales. A: *Eusthenopteron foordi*. P. 15. Sw. Mus. Nat. Hist., Escuminac Bay. Coll. E. Stensiö, 1922. × 2.8 approx. **B**: *Gyroptychius dolichotatus* sp. nov. Part of P. 1492 (holotype), Hesteskoen, Canning Land. × 2.6 approx.

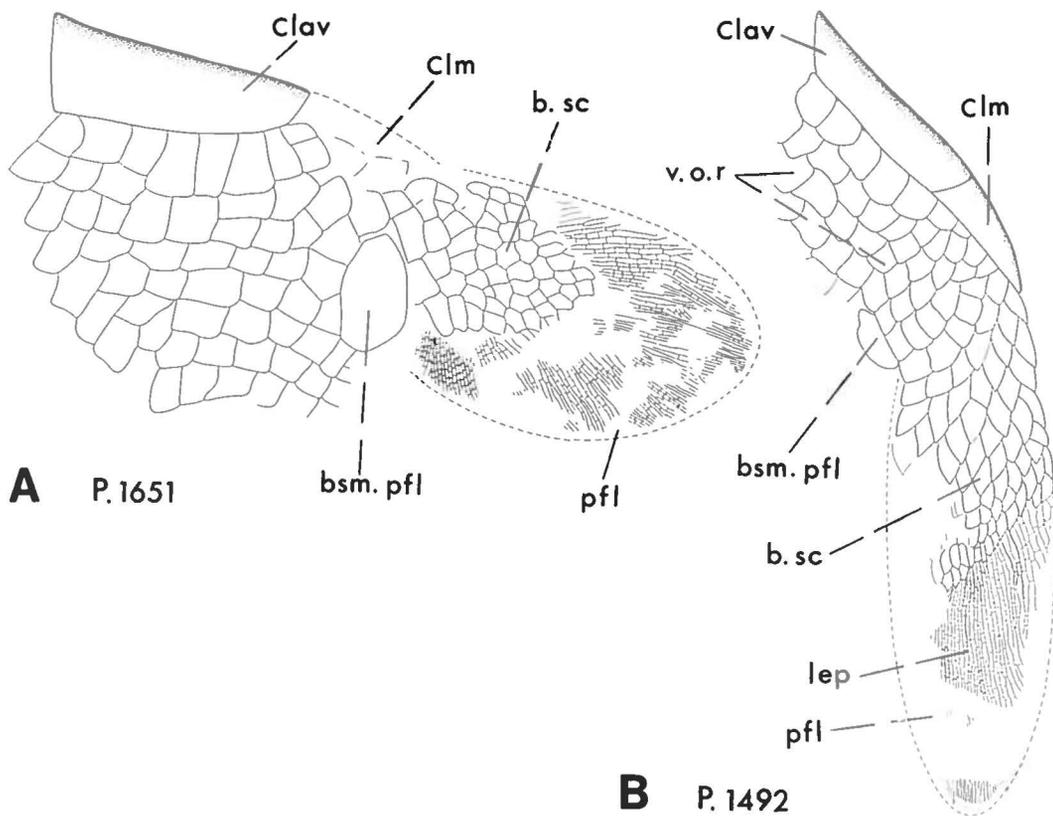Fig. 19. Sketches of left pectoral fin in inner aspect and adjoining parts of the squamation and the exoskeletal shoulder girdle of A: *Gyroptychius groenlandicus* (after specimen shown in Fig. 8), and B: *Gyroptychius dolichotatus* (after specimen shown in Fig. 6 F; see also Jarvik 1959, pl. 2:3).

shown in the area between the pelvic fins (Jarvik 1959, pl. 2:2), and it is remarkable that no traces of modified scales indicating the position of the anal opening can be seen in this area (cf. *Megalichthys* and *Sterropterygion*, Miall 1885, fig. 7, Thomson et al. 1976). Therefore it is most probable that the anal opening was situated farther back, but whether it was situated as far back as it is e.g. in *Polypterus* and *Lepisosteus*, in which it (an.o) lies close in front of the anal fin (Fig. 16), could not be established.

The pectoral fin of the left side and the proximal parts of the right fin are well shown in inner views (Figs 6 F, 11, 19 B, 20 B; Jarvik 1959, pl. 2:3). The fin is remarkably long and slender, about 3.10 times longer than the parietal shield, and much longer proportionally than in other osteolepids (this ratio is only about 1.90 in *G. groenlandicus*). In 1959 (fig. 9 B) I published a photograph of the endoskeleton of the right pectoral fin of *G. dolichotatus* showing the radius, the ulna and some distal parts of the endoskeleton (cf. Andrews & Westoll 1970: 410, Thomson 1972). The endoskeleton of the left fin was also uncovered later. Unfortunately it is preserved too imperfectly to be described, but it is worth

noting that as far as it is exposed the endoskeletal shoulder girdle resembles that in *Eusthenopteron* (Fig. 34 B; Jarvik 1980, figs 100–102, 165 A). The pelvic fins are also shown in inner view (Figs 11, 18 B, 20 B, 21; Jarvik 1959, pl. 2:2). As in other osteolepids they are distinctly smaller than the pectorals, only about twice as long as the parietal shield (cf. Jarvik 1948: 113). The inner basal scute of the left pelvic fin is well shown (Jarvik 1959, pl. 2:2). As with the basal scutes in general (Jarvik 1948: 110, Jessen 1973, pls 19, 22), it is bent along its longitudinal axis, consisting of one lamina incorporated in the body wall and one which covers the basal part of the fin (cf. Thomson et al. 1976: 2).

The first dorsal fin, represented only by an impression of the left basal scute and fragments of some lepidotrichia (Figs 11, 15, 18 B), is situated far back and slightly farther back than the pelvic fin, as in *G. agassizi* (Fig. 20). The second dorsal and the anal fins (Figs 11, 15, 18 B, 21) are also preserved imperfectly. The diphycercal caudal fin is long and low (Figs 15,20), about 3.10 times longer than high and a little more than 4 times longer than the parietal shield. The number of fin rays in each of the lobes is about 90. In all these respects *G.*
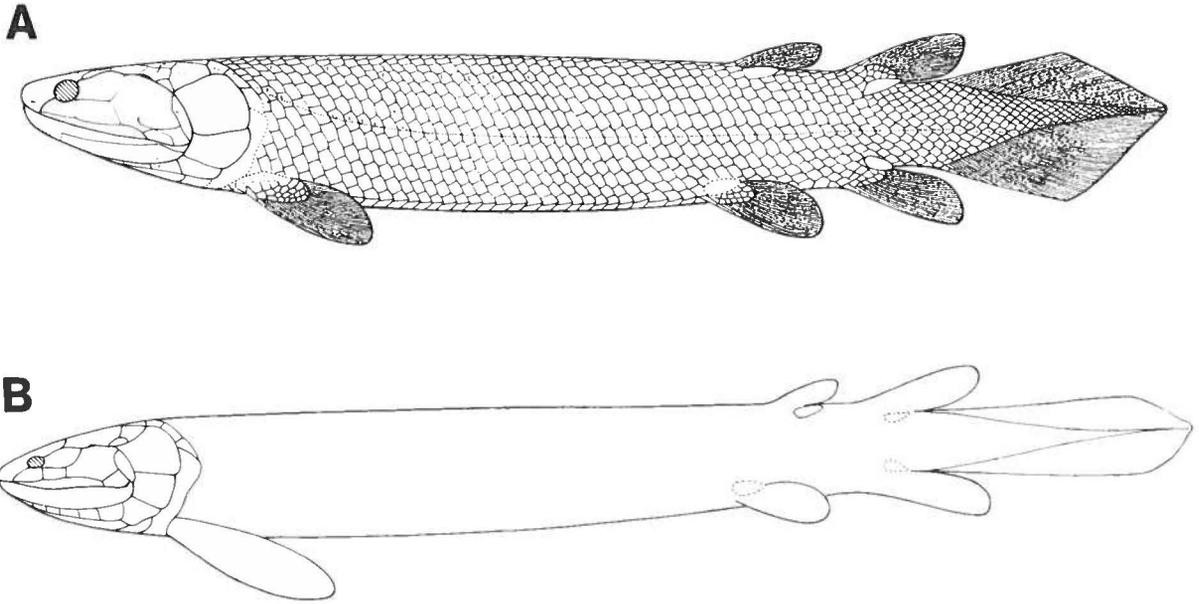
Fig. 20. Restorations of **A**: *Gyroptychius agassizi* (Traill), from Jarvik 1948, fig. 76 A, and **B**: *Gyroptychius dolichotatus* sp. nov., after the holotype (P. 1492). × 0.4 approx. Scales and lepidotrichia omitted in B.

dolichotatus differs considerably from *G. agassizi,* but as in this form the hypochordal lobe is about 1.6 times higher than the epichordal lobe.

Remarks. – *G. dolichotatus* differs clearly from *G. groenlandicus* and *G. milleri* in being much narrower at the postorbital notch (f/a), and the parietal shield as a whole and the principal gular plate are narrower than in these species. Moreover, the pectoral fin is much longer proportionally than in *G. groenlandicus*. In this respect, in the slender shape of the body, and the long and low caudal fin it differs considerably from *G. agassizi*. In
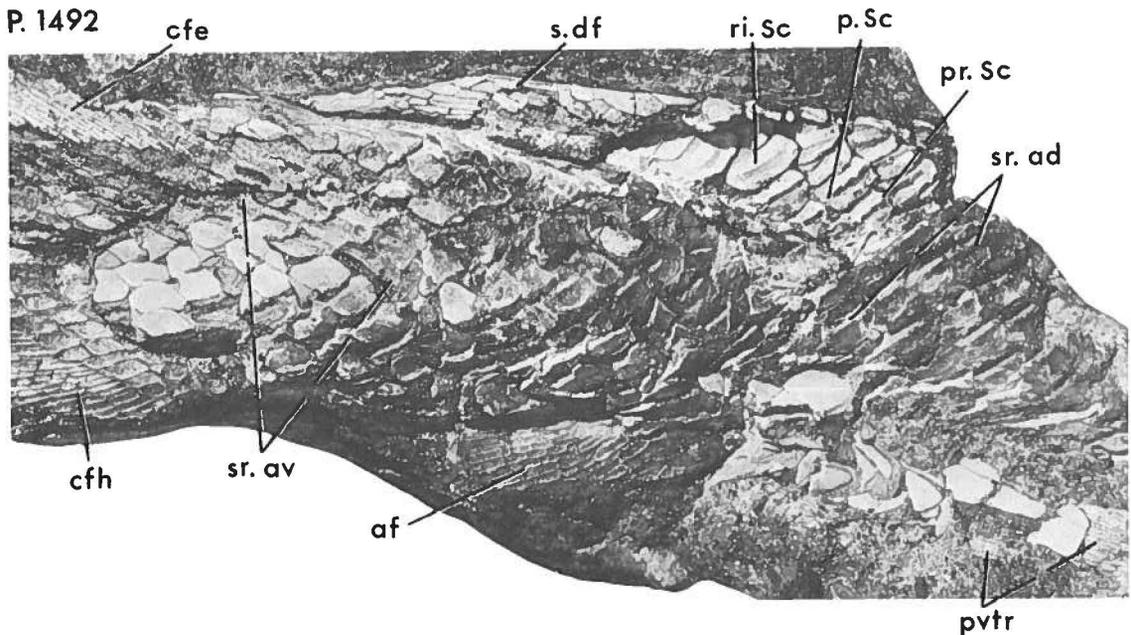

Fig. 21. *Gyroptychius dolichotatus* sp. nov. Posterior part of trunk and anterior part of tail with remains of right pelvic, anal, and second dorsal fins. Lateral aspect. Most scales shown in visceral view. P. 1492 (holotype), same specimen as in Figs 6 F, 11, 12, 14, 18 B. × 1.7 approx.

proportions of the parietal shield (f/a, g/a) it agrees with *G? australis* (Young & Gorter 1981), and *G? kiaeri* (Jarvik 1949). As in the latter, but in contrast to other species assigned to *Gyroptychius,* the posterior margin of the frontoethmoidal shield is convex and the parietal shield has projecting anterolateral corners. The principal gular plate is of a broader type than in *G? kiaeri, G? australis* and *G. elgae* (Vorobyeva 1977). In contrast to conditions in *G? australis, G? kiaeri* and *G? taylori* (Jessen 1968a) the frontal pitline is short.

Genus *Thursius* Traquair, 1888

Thursius (see Jarvik 1948) is characterised firstly by the position of the fins, well shown in the three Scottish species, *T. macrolepidotus* (Sedgwick & Murchison, 1829), *T. moythomasi* Jarvik, 1948 and *T. pholidotus* Traquair, 1888. Other species, *T? sp.* Jessen, 1966, from Germany, *T. talsiensis* Vorobyeva, 1971, *T. fischeri* (Eichwald, 1860), *T. estonicus* Vorobyeva, 1977 from the Soviet Union, and *T? minor* from East Greenland described below have been assigned to the genus on the basis of similarities to the Scottish species in the skull. *T. clappi* Romer, 1942 from Escuminac Bay cannot belong to this genus (Jarvik 1948: 199), and has been placed in the new genus *Callistiopterus* Thomson & Hahn, 1968 (see also Schultze 1973).

Thursius? minor sp. nov.

(Figs 22, 23)

Cf. *Thursius macrolepidotus* (Bütler 1954: 113; 1959: 170; 1961: 191; Jarvik 1961: 202, table 1).

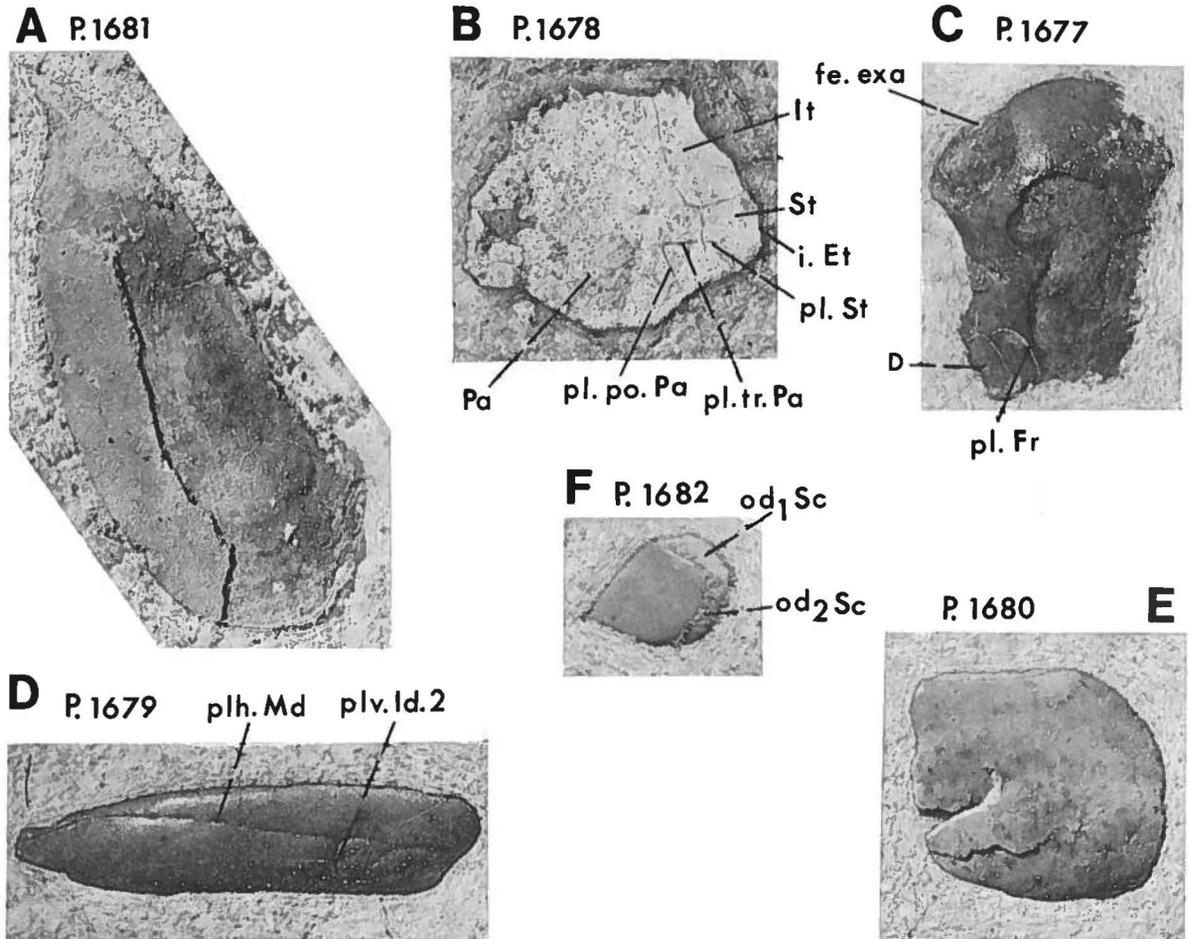Diagnosis. – Imperfectly known osteolepid fishes of small size, probably not exceeding 100 mm in total

Fig. 22. *Thursius? minor* sp. nov. **A**: P. 1681, principal gular plate. **B**: P. 1678, parietal shield. **C**: P. 1677, frontoethmoidal shield (*holotype*). **D**: P. 1679, lower jaw. **E**: P. 1680, opercular. **F**: P. 1682, scale. From Randbøldalen, Huitfeldt Bjerg (Randbøl Group, Upper Middle Devonian). Coll. 1950. × 6.
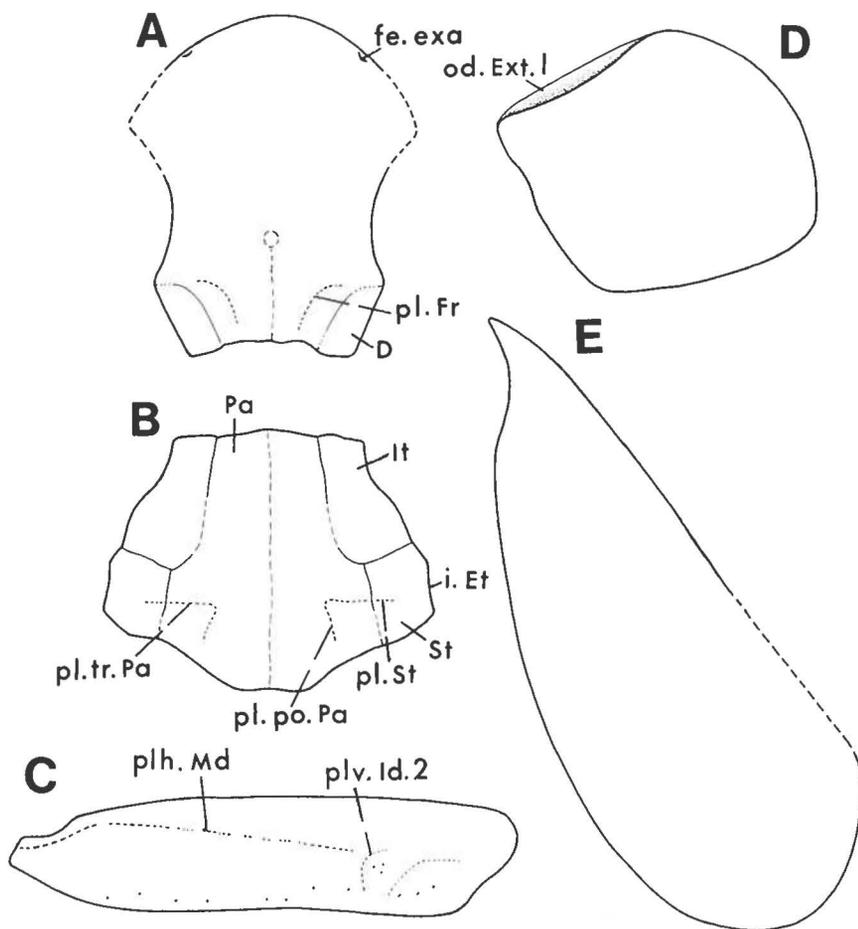
Fig. 23. *Thursius? minor* sp. nov. Restorations after the specimens shown in Fig. 22 of **A**: frontoethmoidal shield, **B**: parietal shield, **C**: lower jaw, **D**: opercular, and **E**: principal gular plate.

length. Frontoethmoidal shield posteriorly about half as broad as long (f/b about 0.54). Orbital and postorbital notches fairly long and shallow. Parietal shield distinctly broader than long at the spiracular notch (g/a about 1.15). Pineal foramen situated between the orbital notches, distinctly in front of the transverse line through the anterior ends of the frontal pitlines (c/b about 0.30). Frontal pitline long, reaching the posterior margin of the frontal about midway between the lateral and medial ends of that margin. Lower jaw short and high, about 4.5 times longer than high. Pitline of infradentary 2 situated comparatively far back (k/m about 2.20). Opercular longer than high. Principal gular plate about 2.8 times longer than broad.

Material and geological horizon. – The holotype is the imperfect frontoethmoidal shield (P. 1677) shown in Fig. 22 C. In addition the material includes only a parietal shield, a lower jaw, an opercular, a principal gular plate, and scales (Figs 22, 23). The specimens, collected by H. Bütler and G. Wängsjö during the Danish expedition to East Greenland in 1950, come from a locality about 300 m above sea-level in the eastern part of Huitfeldt, Bjerg, Randbøldalen, Gauss Halvø (Fig. 1). According to Bütler (1954: 113; 1959: 170) the deposits belong to the lower part of the Randbøl Group. The age is probably upper Middle Devonian (Bütler 1961, table 1, Jarvik 1961, table 1).

Description

The frontoethmoidal shield (Fig. 22 C) is only 7 mm long. It is thus much shorter than in the Scottish species of *Thursius* which I described in 1948 (cf. also Jessen 1966, Vorobyeva 1977) and of about the same length as in the smallest specimens of *Osteolepis panderi*. Its length suggests a total length of the fish of about 80 mm. The parietal shield (5 mm), the lower jaw (10.5 mm), the opercular (length 6 mm) and the scales (length of the non-overlapped portion about 2 mm) obviously come from specimens of about the same size, whereas the principal gular plate (length 14 mm) probably belongs to a somewhat larger individual.

32

The frontoethmoidal shield, which is imperfectly preserved, particularly on the right side, is reminiscent of that in *T. macrolepidotus* (Jarvik 1948, pl. 17), and as in that form, the frontal pitline extends to the posterior margin of the frontal. However, it reaches that margin about midway between its lateral and medial ends, as generally in *T. pholidotus*. Moreover, it also agrees with the latter species in the fact that the pineal foramen is situated comparatively far forwards, between the shallow orbital notches, and distinctly in front of the transverse line through the anterior ends of the frontal pitlines. The ratio c/b is about 0.30, and thus about the same as in *T. pholidotus* and in *Osteolepis* (Jarvik 1948, table 1). The dermosphenotic is about as broad posteriorly as anteriorly, and does not decrease in breadth backwards in the way characteristic of *T. pholidotus*. The breadth of the frontoethmoidal shield most posteriorly amounts to about half its length (f/b about 0.54) as in *T. macrolepidotus*, and judging also from the shape of the parietal shield the postorbital notch is long and shallow as in that form. The parietal shield is flattened but seems to have been comparatively short and broad. In the present state of preservation the ratio f/a is about 0.75 and g/a about 1.15, whereas the corresponding ratios in *T. macrolepidotus* are 0.65–0.68 and 0.92–1.04, and in *T. pholidotus* 0.48–0.56 and 0.92–0.99. The extratemporal is lacking on both sides but there are distinct extratemporal notches (i.Et). The lower jaw is as in osteolepids in general, but is comparatively short and high, only about 4.5 times longer than high (in *T. macrolepidotus* and *T. pholidotus* the corresponding ratio is about 5.5). The pitline of infradentary 2 is situated relatively far back (k/m about 2.20). The opercular is a little longer than high, and the gular plate is about 2.80 times longer than broad. The scales are developed as in osteolepids in general.

Remarks. – *Thursius? minor* is known only imperfectly. It has been provisionally referred to the genus *Thursius* because of general resemblances, and in particular because of its similarities to *T. pholidotus* in the course and extent of the frontal pitline and the position of the pineal foramen in relation to that pitline. In these respects it differs from *T. macrolepidotus*, *T. moythomasi*, and most other Devonian osteolepids (Jarvik 1948, 1949, 1950, 1950a, 1950b, Jessen 1968a, Vorobyeva 1977, Young & Gorter 1981; cf. however, *Latvius*, Jessen 1973, Greiner 1977). *T? minor* differs from *T. pholidotus inter alia* in the development of the dermosphenotic and in the fact that the cranial roof is slightly broader proportionally at the postorbital and spiracular notches.

Family Rhizodontidae Traquair, 1881

When Traquair (1881: 179) introduced the name Rhizodontidae to replace the "Cyclodipteridae" he included the genera *Rhizodus, Rhizodopsis, Strepsodus* and *Tristichopterus,* and the family, which also includes *Eusthenopteron* and some other fishes has been used in that sense by Woodward (1891), Goodrich (1909), Jarvik (1942, 1980), Romer (1966), and others (cf. Andrews & Westoll 1970a: 480, and p. 12 above).

Genus *Spodichthys* nov.

(Figs 24, 25, 26 A, 27 B, 28–33, 35)

The generic name from Gr. *spodos,* ashes, and *ichthys,* fish) refers to the ash-grey colour of the rocks and many of the fossils in the type locality.

Diagnosis. – Rhizodontid fishes of small or moderate size. Dermal bones ornamented with fairly broad ridges forming net-works, or more or less isolated tubercles. Scales ornamented with delicate longitudinal ridges often connected by faint cross-ridges. Occipital region of the neural endocranium long, about half as long as the parietal shield. Frontoethmoidal shield about 1.24 times longer than the parietal shield. Preorbital portion of the frontoethmoidal shield short (r/s+t about 0.40–0.45). Orbital margin of the supraorbitotectal fairly long. Orbital notch far forwards; its midpoint is situated in front of the transverse line through the midpoint of the frontoethmoidal shield (v/w about 0.90). Pineal foramen situated a little in front of the midpoint of the suture between the frontals, medial to the frontal pitline (c/b about 0.30–0.35). The breadth of the cranial roof at the postorbital notch (f) is about 0.70 of the length of the parietal shield, and at the spiracular notch (g) is about equal to the length of that shield. Portion of the postorbital situated behind the postorbital notch small, caudally not reaching the spiracular notch. Maxillary about 6.5 times longer than high. Lower jaw comparatively short, about 2.2 times longer than the parietal shield. Opercular about as long as high. Principal gular plate slightly more than three times longer than broad. Pitline of principal gular plate situated a little in front of the middle of the bone (p/n about 1.05). Vomer not firmly joined to the parasphenoid and the frontoethmoidal shield. Ventral portion of cleithrum fairly long.

Remarks. – As far as is known, *Spodichthys* is a typical rhizodontid. In most respects it agrees well with *Eusthenopteron, Tristichopterus* and other Devonian representatives of the family, differing mainly in proportions. The frontoethmoidal shield is only about 1.24 times longer than the parietal shield and is proportionally shorter than in *Tristichopterus* (b/a about 1.4; see p. 8) and much shorter than in *Eusthenopteron foordi* and other species referred to that genus (Jarvik 1950b: 26–28) and in *Eusthenodon* (Jarvik 1952) and *Jarvikina* (Vorobyeva 1977, fig. 42). The preorbital division of the frontoethmoidal shield is also proportionally shorter
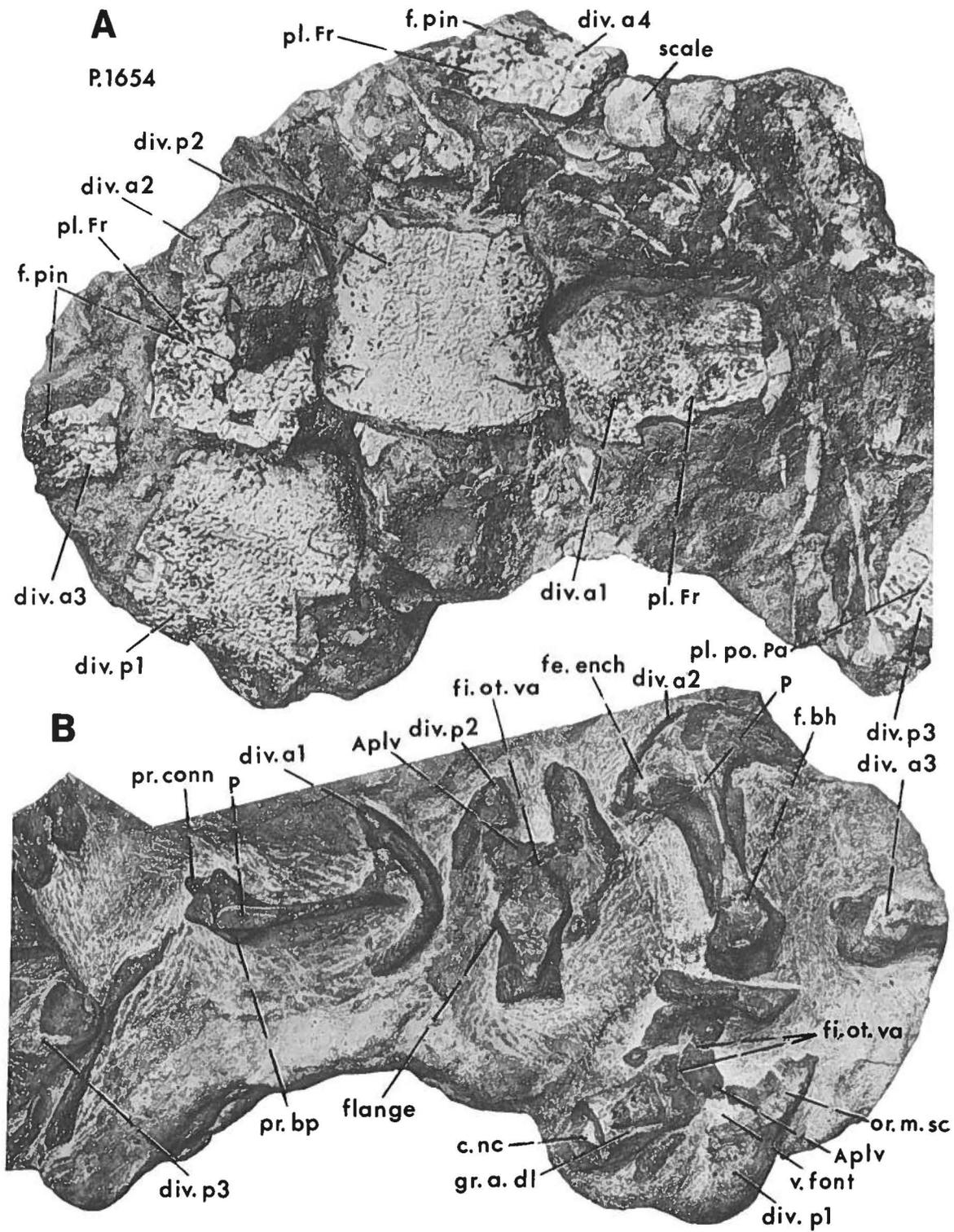
Fig. 24. *Spodichthys buetleri* gen. et sp. nov. Small slab containing four anterior (div.a1-div.a4) and three posterior (div.p1-div.p3) cranial divisions in **A**: dorsal, and **B**: ventral aspect, scales and other skeletal remains. P. 1654, Högbom Bjerg. Coll. 1954. × 2.8 approx.

than in other genera, and the orbital fenestra is fairly large and situated remarkably far forwards. The pitline of the principal gular plate lies farther forwards than in *E. foordi* and in *Eusthenodon*. An interesting feature is that the occipital region of the neural endocranium is almost half as long as the parietal shield and much longer, proportionally, than in *E. foordi* and other Devonian rhizodontids known in this respect.

Spodichthys buetleri gen. et sp. nov.

(Figs 24, 25, 26 A, 27 B, 28 A–E, 29 A, 30–33, 35)

1961 – indet. Rhizodontidae (cf. *Eusthenopteron*), Jarvik, table 1.
1971 – Middle Devonian osteolepiform, Bjerring, fig. 21 B
1980 – Small rhizodontid, Jarvik 1980a, fig. 37 B.

The species is named in honour of Dr. Heinrich Bütler, Schaffhausen, Switzerland.

Diagnosis. – As for the genus.

Material. – The material, collected during the Danish expeditions to East Greenland in 1952 (H. Bütler) and 1954 (E. Jarvik), consists of numerous isolated cranial remains and scales. Holotype is specimen P. 1655 (Fig. 28 A), which is the most complete specimen showing the frontoethmoidal and parietal shields together with the lower jaw. The specimen is damaged by crushing. Disregarding this example the following dermal bones or complex units have been identified with certainty: the frontoethmoidal shield with the ethmosphenoid and parasphenoid (divisio cranialis anterior, Jarvik 1937: 70–71; P. 1654, P. 1657, 1658, P. 1659, Figs 24, 25 A, B, 28 B–D; the vomer is missing and the parasphenoid is imperfectly preserved), the parietal shield with the otoccipital (divisio cranialis posterior; P. 1654, P. 1660,
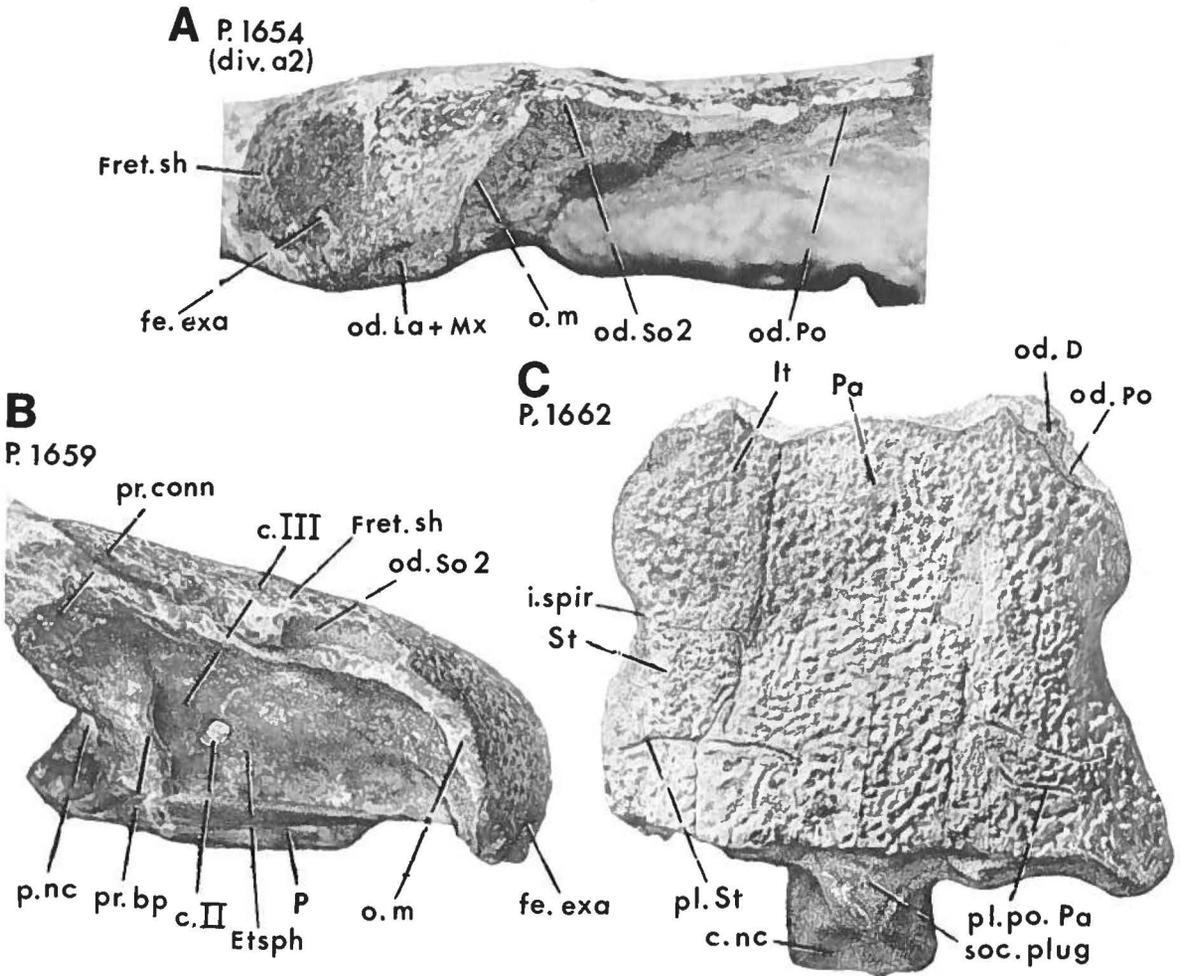

Fig. 25. *Spodichthys buetleri* gen. et sp. nov. **A,, B**: anterior cranial divisions in lateral aspects, and **C**: posterior cranial division in dorsal aspect. **A**: P. 1654 (div. a2, Fig. 24). × 6/1. **B**: P. 1659 (same specimen as in Fig. 28 D). × 6. **C**: P. 1662 (same specimen as in Figs 26 A, 27 B). × 4.
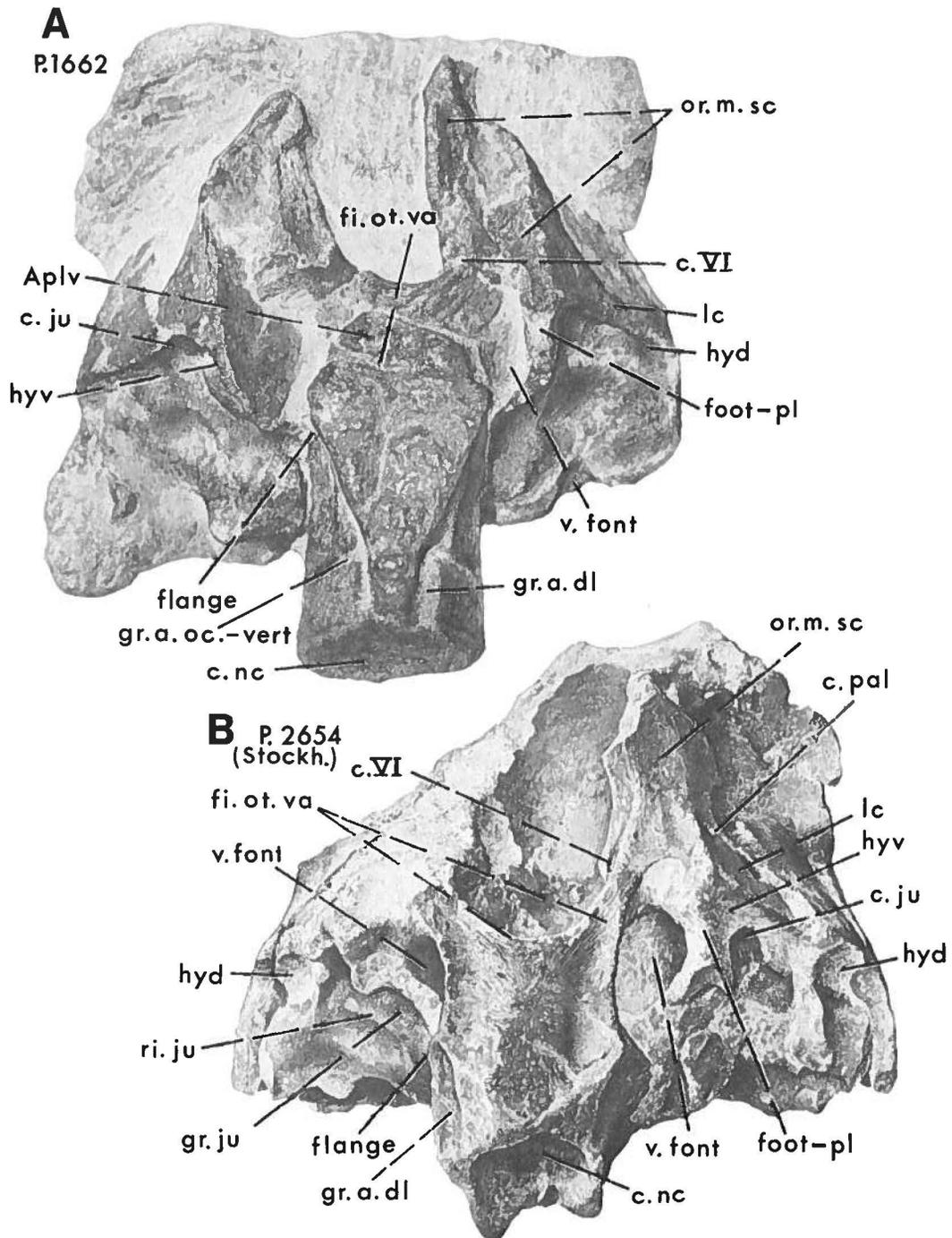
Fig. 26. Posterior cranial division in ventral aspect of **A**: *Spodichthys buetleri,* × 5 approx., and **B**: *Eusthenopteron foordi,* × 2 approx. Parietal shield in both specimens made equal in length. Same specimens as in Fig. 27.

P. 1661, P. 1662, P. 1687, Figs 24, 25 C, 26 A, 27 B, 28 E, 32 A, B), the lower jaw (P. 1659, P. 1668, P. 1676, Figs 28 D, 30 A, B), the postorbital (P. 1663, Fig 30 C), the maxillary (P. 1664, P. 1665, Fig. 30 D, E), the opercular (P. 1666, Fig. 30 F), the subopercular (P. 1667, Fig. 30 G), the principal gular plate (P. 1672, P. 1674, P. 1675, Fig. 30 H–J), the cleithrum with the endoskeletal shoulder girdle (P. 1669, P. 1670, P. 1671, Fig. 32 C–F) and the clavicle (Fig. 33 C).
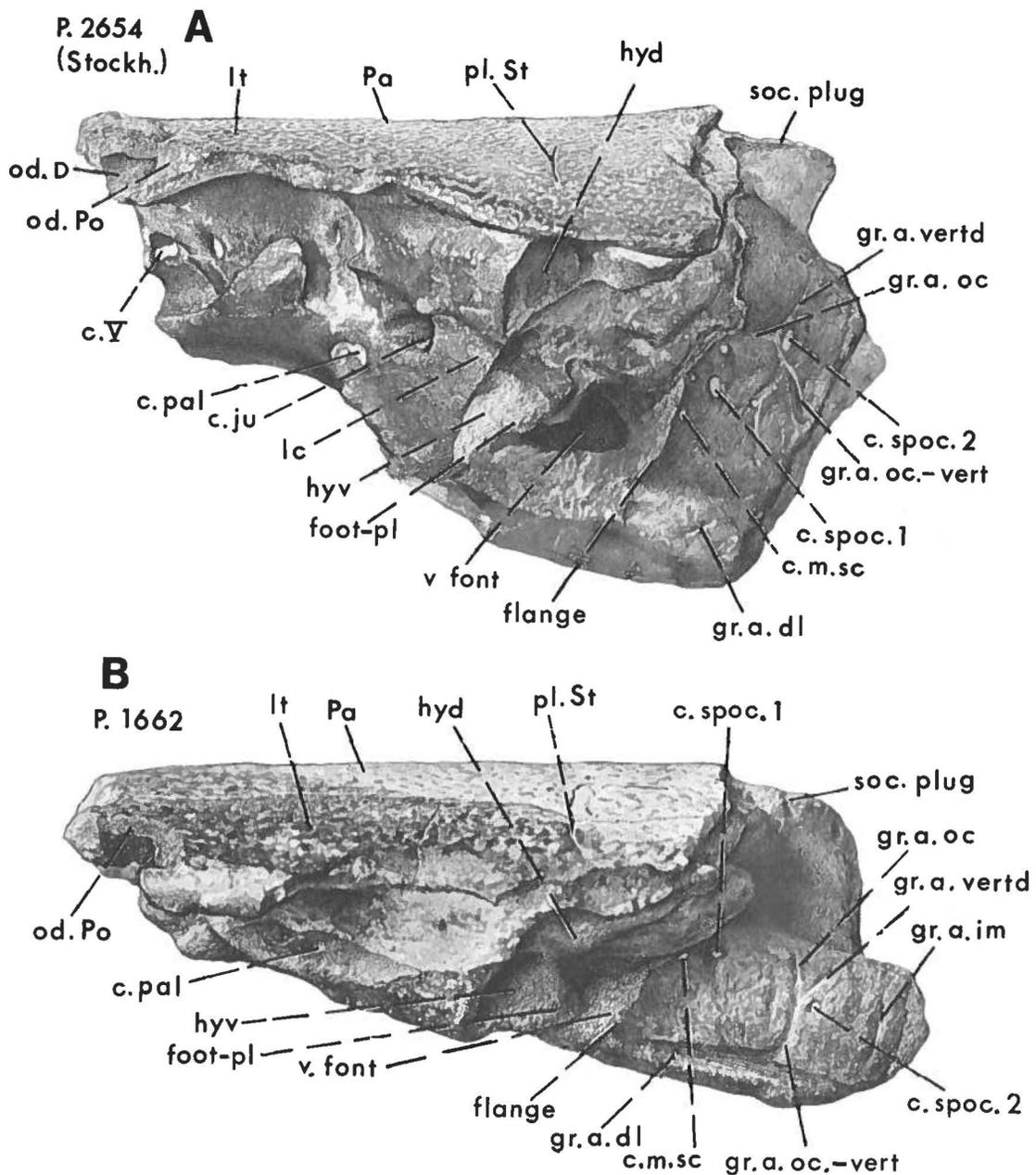
Fig. 27. Posterior cranial division in lateral aspect of A: *Eusthenopteron foordi*, and B: *Spodichthys buetleri*. A: P. 2654, Stockh. Same specimen as in Fig. 26 B; figured by Bjerring 1971, figs 3 B, 18, 21 A, and by Jarvik 1980a, fig. 37 A. × 2.5. B: P. 1662, Copenh. Same specimen as in Figs 25 C, 26 A; figured by Bjerring 1971, fig. 21 B, and by Jarvik 1980a, fig. 37 B. × 6.

Locality and geological horizon. – *Spodichthys buetleri* is known only from one locality in Hudson Land (Högbom Bjerg), East Greenland, about one mile to the north of the northern shore of the Moskusokse Fjord and about opposite the mouth of the Vastidal in Gauss Halvø (Fig. 1). The precise geological age is unknown. According to Bütler (1959: 164–165) the fossiliferous deposits belong to the lowermost part of the Kap Kolt-

hoff Group which means that they are younger than the upper Middle Devonian Gyroptychius groenlandicus Group and older than the upper Upper Devonian Phyllolepis Group which in its lower part probably includes the uppermost parts (the *Bothriolepis jarviki* Beds) of the Kap Kolthoff Group (Jarvik 1950a, table 2; 1961, table 1, Bütler 1959: 164–165; 1961, table 1). Bütler suggests that the boundary between the Middle and

Upper Devonian possibly passes through the lower part of the Kap Kolthoff Group, and if this is true then the *Spodichthys* Beds would be contemporaneous with, or slightly older than the Escuminac Beds with *Eusthenopteron foordi*. However, the *Spodichthys* Beds have also yielded a few plates of an antiarch. As recently established this form is suggestive of, and possibly identical with, *Remigolepis? tuberculata* (Stensiö 1931: 192–193), a species represented by a single imperfect anterior median dorsal plate collected on the northern side of the Moskusokse Fjord, a few miles to the east of the *Spodichthys* locality. Since, *R? tuberculata* differs consider-

ably from the typical *Remigolepis*-species in its ornamentation (Stensiö 1931: 193), and it is not known when the genus *Remigolepis* arose, this discovery gives no safe information as to the age of the deposits. It can only be stated that the presence of *Remigolepis* in the lowermost part of the Kap Kolthoff Group indicates that this division as a whole is Upper Devonian in age.

Description

In the holotype the parietal shield is 10 mm and the frontoethmoidal shield 12 mm long. In the material the
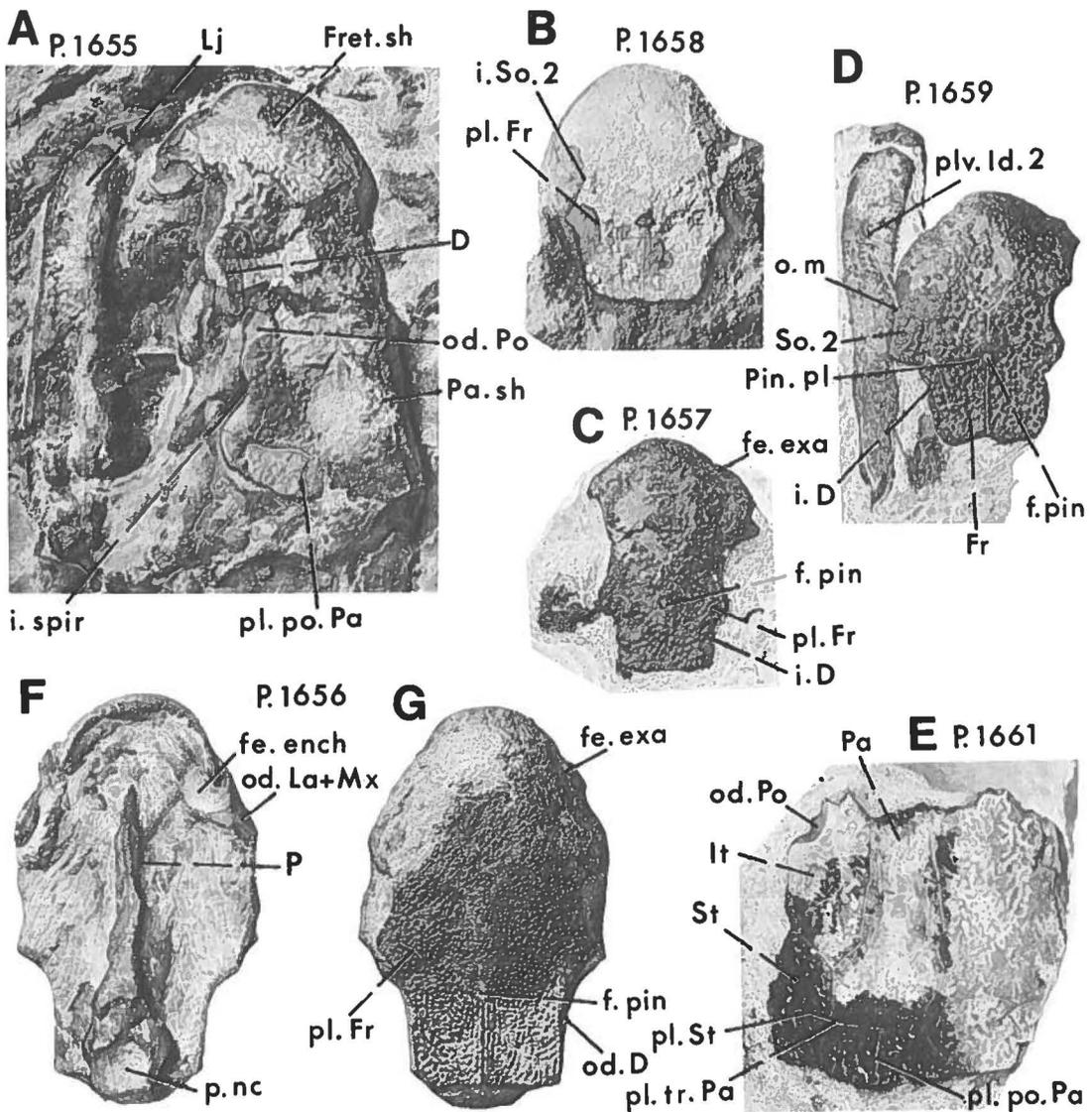
Fig. 28. **A–E**: *Spodichthys buetleri* gen. et sp. nov. Högbom Bjerg. × 2.5. **A**: P. 1655, *holotype*. Coll. 1954. Imperfect skull in dorsal view showing mainly frontoethmoidal and parietal shields, and left lower jaw. **B, C**: P. 1658, P. 1657. Coll. 1954. Fronto-ethmoidal shields. **D**: P. 1659. Coll. 1954. Frontoethmoidal shield with lower jaw. **E**: P. 1661. Coll. 1952. Parietal shield. **F, G**: *Spodichthys* cf. *buetleri*. P. 1656, Högbom Bjerg. Coll. 1954. Anterior cranial division in ventral and dorsal aspects. × 1.3.

Fig. 29. A: *Spodichthys buetleri* gen. et sp. nov. Restoration of exoskeletal skull roof in dorsal view. Mainly after holotype (Fig. 28 A). × 5. B, C: *Spodichthys* cf. *buetleri*. Restorations of frontoethmoidal shield in lateral and dorsal aspects. After specimen in Fig. 28 F, G. × 2.

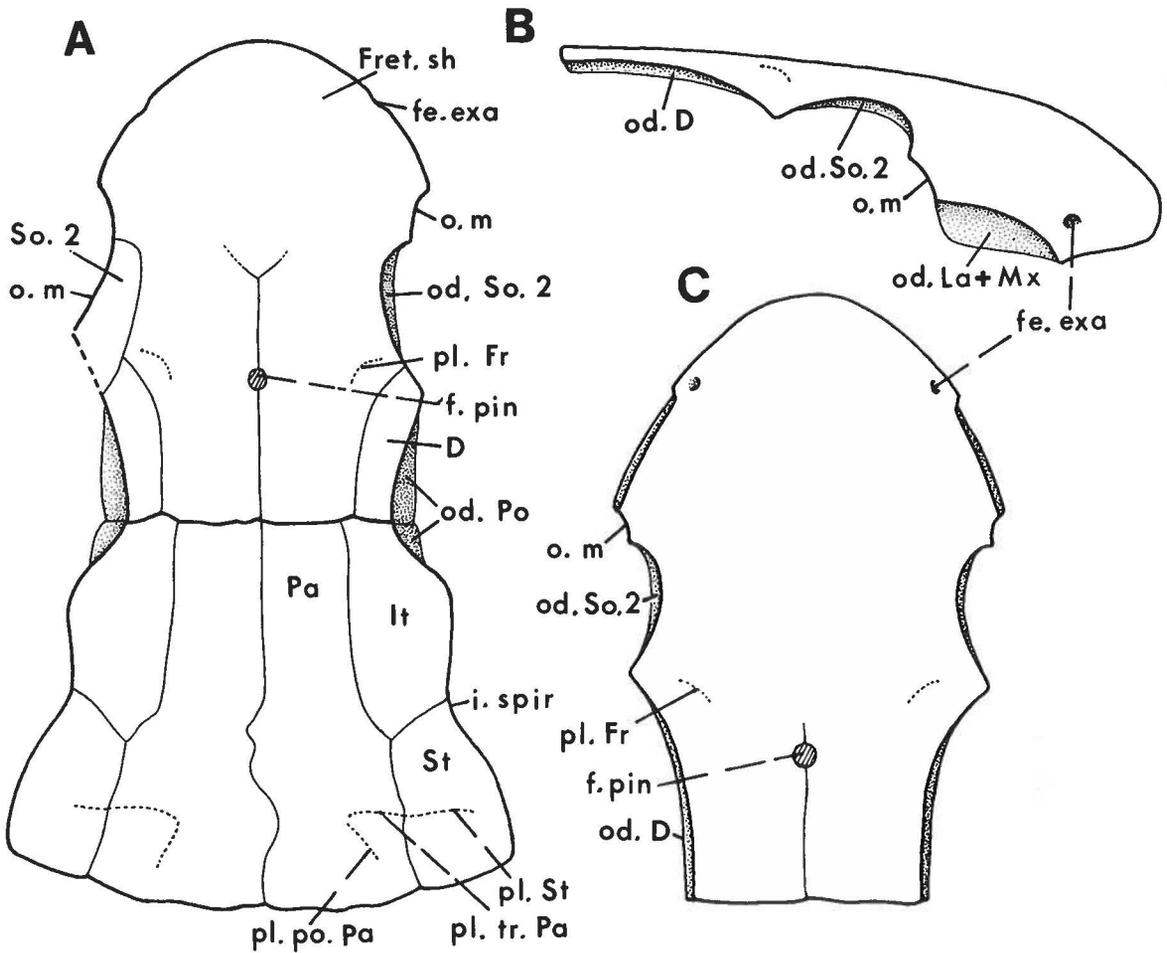length of the former ranges from 10 to 15 mm and the latter from 12 to 15 mm. In *Eusthenopteron foordi* the fish is about 19 times longer than the parietal shield, in *Gyroptychius agassizi* about 18 times longer, and in *Osteolepis macrolepidotus* about 16 times longer. The largest parietal shield (15 mm) thus probably belonged to a fish that attained a total length of 240 to 285 mm. Specimen P. 1654 is of particular interest. It (Fig. 24) shows four more or less complete anterior (div. a 1–4) and three posterior (div.p 1–3) cranial divisions contained in a small slab of rock. This may indicate that a shoal of fish was buried and the possibility cannot be excluded that this shoal included young individuals (cf. *Spodichthys* cf. *buetleri*).

Neural endocranium. – The ethmosphenoid and the otoccipital which are shown in several specimens, generally in association with the frontoethmoidal or parietal shields, are well ossified. In most respects they agree with the corresponding ossifications in *Eusthenopteron foordi* (Jarvik 1980) and only a few remarks concerning the otoccipital are given here (with regard to the ethmosphenoid see Figs 24 B, 25 A, B).

As in *Eusthenopteron* (Fig. 26 B) the ventral side of the otoccipital in *Spodichthys* (Figs 24 B, 26 A) has an elongated depression (or.m.sc) for the origin of the subcranial muscle, and medial to that is the opening of the abducens canal (c.VI). It is interesting that the ventral wall of the notochordal canal extends forwards about to the level of that opening, that is farther forwards than in most specimens of *Eusthenopteron foordi*, but not as far as in the aberrant specimen of *E. foordi* which I figured in 1954 (fig. 7; see also 1980, fig. 93) in which it extends forwards to the level of the opening of the palatine canal (c.pal). This is due to the incorporation of a subchordal arcual plate (Jarvik 1980: 127–129), and it is remarkable that the cranial fissure, the fissura oticalis ventralis anterior (fi.ot.va, Jarvik 1972, fig. 99; 1980, fig. 93; 1980a,
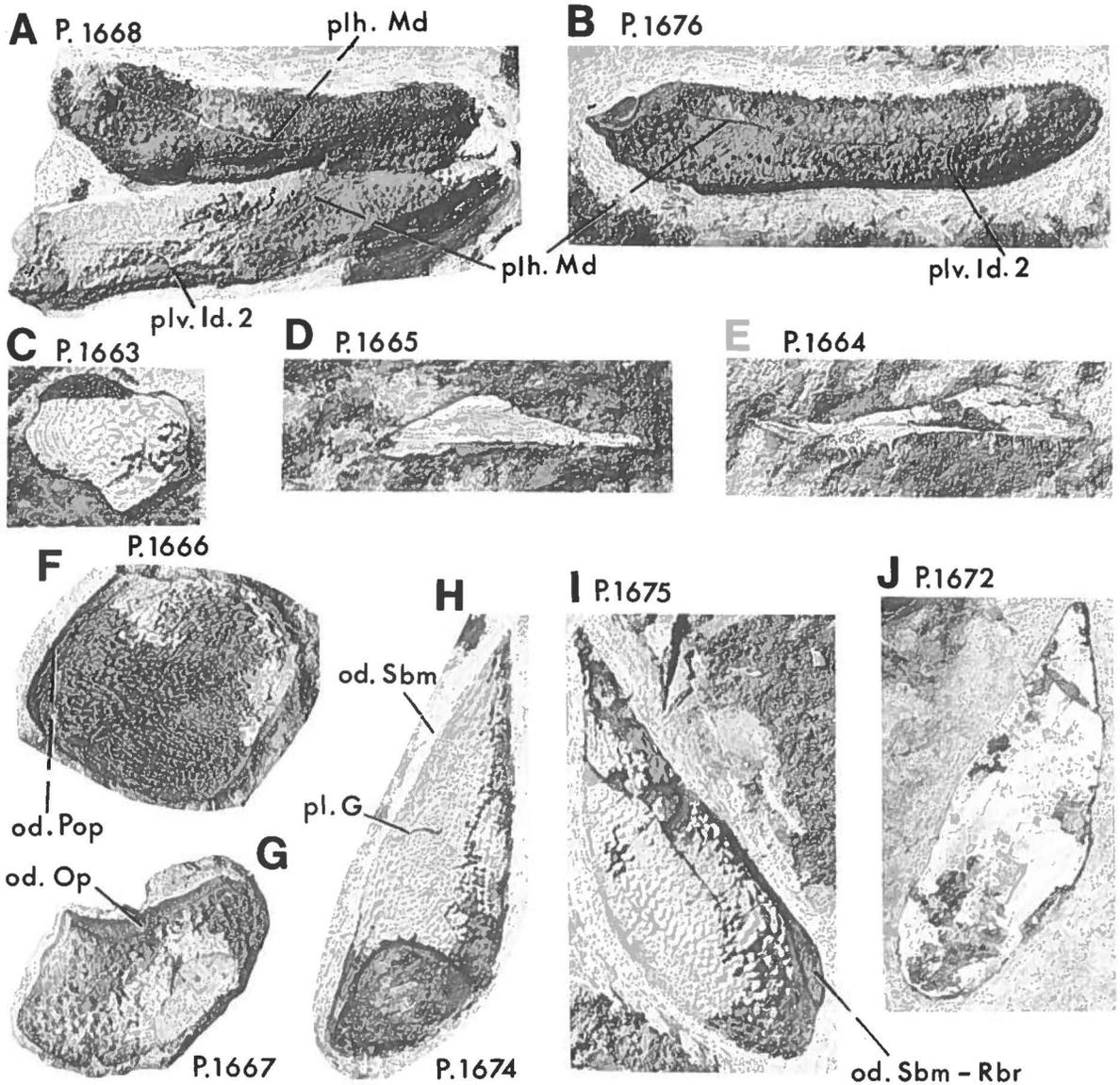
Fig. 30. *Spodichthys buetleri* gen. et sp. nov. **A**, **B**: P. 1668, P. 1676. Coll. 1954. Lower jaws in lateral aspects. **C**: P. 1663. Coll. 1952. Postorbital. **D**, **E**: P. 1665, P. 1664. Coll. 1954. Maxillaries in visceral aspects. **F**: P. 1666. Coll. 1952. Opercular, impression of external side. **G**: P. 1667. Coll. 1954. Subopercular in lateral view. **H**, **I**: P. 1674, P. 1675. Coll. 1954. Principal gular plates in external views. **J**: P. 1672. Coll. 1954. Principal gular plate in visceral view. All specimens from Högbom Bjerg. × 3 approx.

figs 40–42) bounding this plate (Aplv) posteriorly is represented by a distinct suture seen in several specimens (Fig. 24 B, div.p1, div.p2; Fig. 26 A). Because the subchordal plate in *Spodichthys* only extends forwards about to the level of the abducens foramen it is evident that it represents only a posterior part of the anterior subchordal plate incorporated in the aberrant specimen of *Eusthenopteron*. According to my interpretations of the cranial vertebrae (CV; Jarvik 1972: 247–255; 1980a: 68–69, figs 40–42), the anterior subchordal arcual plate

represents the ventral vertebral arch of CV 3+4 (in 1972, when the existence of the terminal metamere was not yet reestablished – see Bjerring 1973, addendum; 1977; Jarvik 1980a: 9–11 – this vertebra was referred to as CV 2+3). It can be suggested therefore that the short subchordal arcual plate in *Spodichthys* represents only the part of CV 3+4 belonging to the fourth metamere, that is interventral 4 (cf. Jarvik 1980a, fig. 39; see also Bjerring 1971, Cz.3a, fig. 10 B).

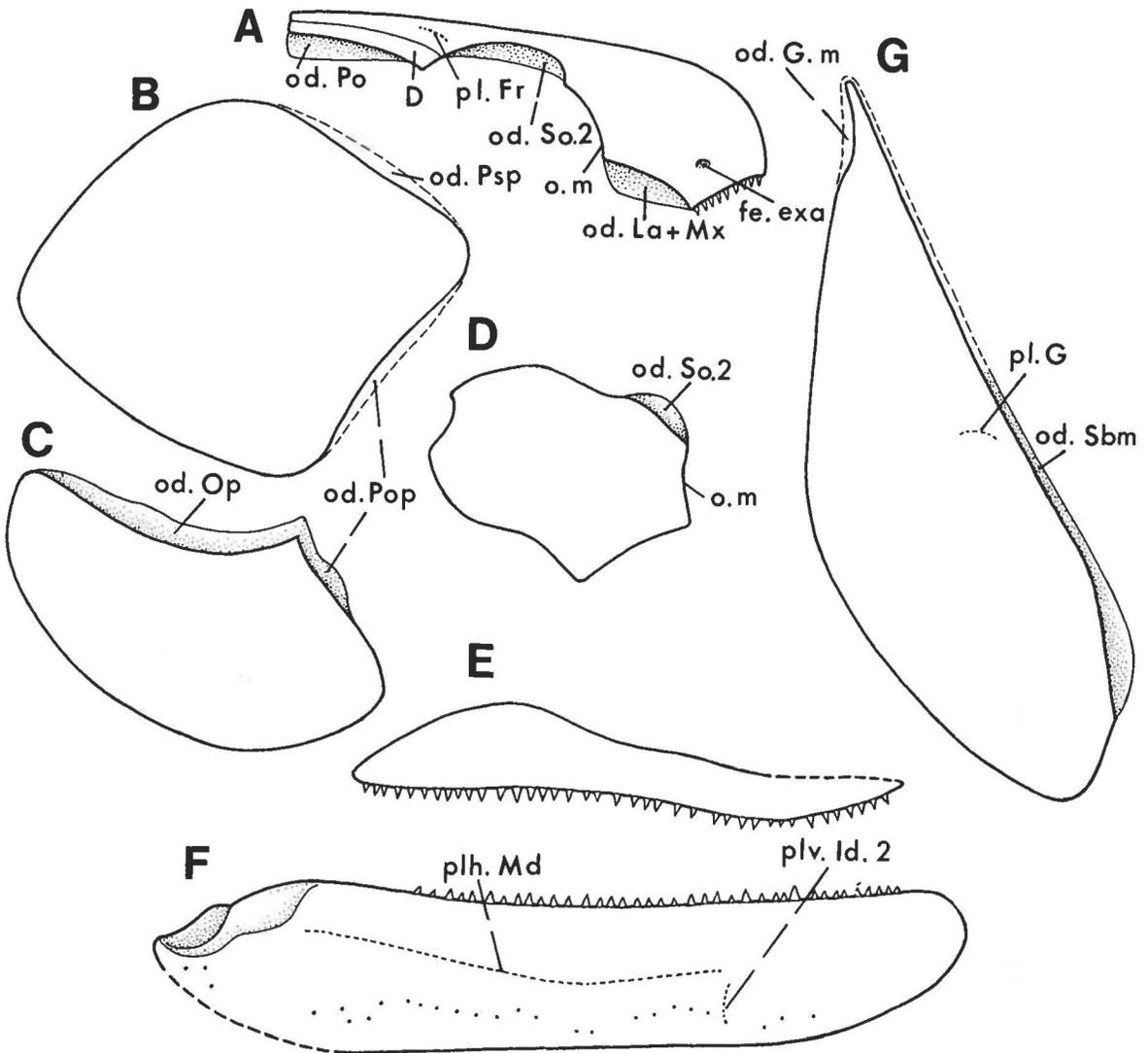In *Spodichthys* (Figs 24 B, 26 A, 27 B), too, there is a

Fig. 31. *Spodichthys buetleri* gen. et sp. nov. Restorations mainly after specimens shown in Figs 25 B, 30 of **A**: frontoethmoidal shield in lateral view, **B**: opercular, **C**: subopercular, **D**: postorbital, **E**: maxillary, **F**: lower jaw, and **G**: principal gular plate.

lateral commissure (lc), dorsal and ventral articular areas (hyd, hyv) for the hyomandibula, jugular canal (c.ju) and grooves (gr.ju), vestibular fontanelle (v.font), and supraoccipital plug (soc.plug). There is also a canal for the occipital artery (Bjerring 1971, fig. 21 B), a groove for that artery (gr.a.oc), distinct grooves for the occipito-vertebral (gr.a.oc.vert) and the dorsal vertebral (gr.a.vertd) arteries, and a canal (c.m.sc) for the nerve (n.rarus, Bjerring) supplying the subcranial muscle. As in *Eusthenopteron* (Fig. 27 A) the latter canal opens on the posterior side of a prominent lateral flange situated behind the vestibular fontanelle (v.font) and the fissura occipitalis lateralis (Jarvik 1980,

figs 86 C, 97 A, B), that is about at the transition between the otic and occipital regions of the neural endocranium. However, whereas the distance from the flange to the posterior end of the neurocranium (that is almost the whole length of the occipital region) in *Eusthenopteron foordi* is only about 0.21 of the length of the parietal shield, the corresponding ratio in *Spodichthys* is about 0.43. This means that at the same length of the parietal shield (Figs 26, 27) the occipital region in *Spodichthys* is about twice as long as in *E. foordi*. The aorta groove (gr.a.dl) is much longer proportionally, and most posteriorly it lies close to or meets the corresponding groove of the other side of the skull (cf. Jarvik

1975: 199; 1980, fig. 131). In *E. foordi* there are canals for two spino-occipital nerves and I have suggested (1972: 251, fig. 99) that the occipital region includes two cranial vertebrae, which according to my revised interpretation (Jarvik 1980a, fig. 49) are CV6+7 and CV7+8. In *Spodichthys,* too, only the canals for spinooccipital nerves 1 and 2 (c.spoc.1, c.spoc.2) have been identified. However, considering the length of the occipital region and the facts that the groove for the occipito-vertebral artery is situated far from the posterior end of the endocranium and that there is one distinct groove (gr.a.im, Fig. 27 B) for an intermetameric artery behind it, it can be concluded that the neural endocranium in *Spodichthys* includes one or possibly two more cranial vertebrae than in *E. foordi.*

Dermal cranial roof. – The frontoethmoidal and parietal shields in *Spodichthys buetleri* (Figs 24, 25, 27 B, 28 A-E, 29 A, 31 A, 32 A, B) agree well with the corresponding shields in *Eusthenopteron foordi* (Jarvik 1944, 1980) and other rhizodontids known in this respect (cf., however, Andrews 1973, fig. 2 D). Only some few remarks are given here, mainly about proportions. The frontoethmoidal shield is about 1.2 times longer than the parietal shield and it is thus proportionally shorter than in *E. foordi* (b/a about 1.80) and other forms referred to that genus, and shorter even than in *Tristichopterus alatus* (b/a about 1.4). The preorbital division is also remarkably short. Its length (r; see Fig. 2) is thus only about 0.45 of the length (s+t) of the orbital and postorbital divisions together, whereas in the Scottish osteolepids the corresponding ratio (Jarvik 1948, table 1) ranges from 0.54 to 1.00, and in *E. foordi* amounts to about 0.9. The lachrymo-maxillary notch is shorter than in *E. foordi* and less distinct. The pineal foramen, as in *E. foordi* and *T. alatus* (Westoll 1937, fig. 5), is situated a little in front of the midpoint of the suture between the

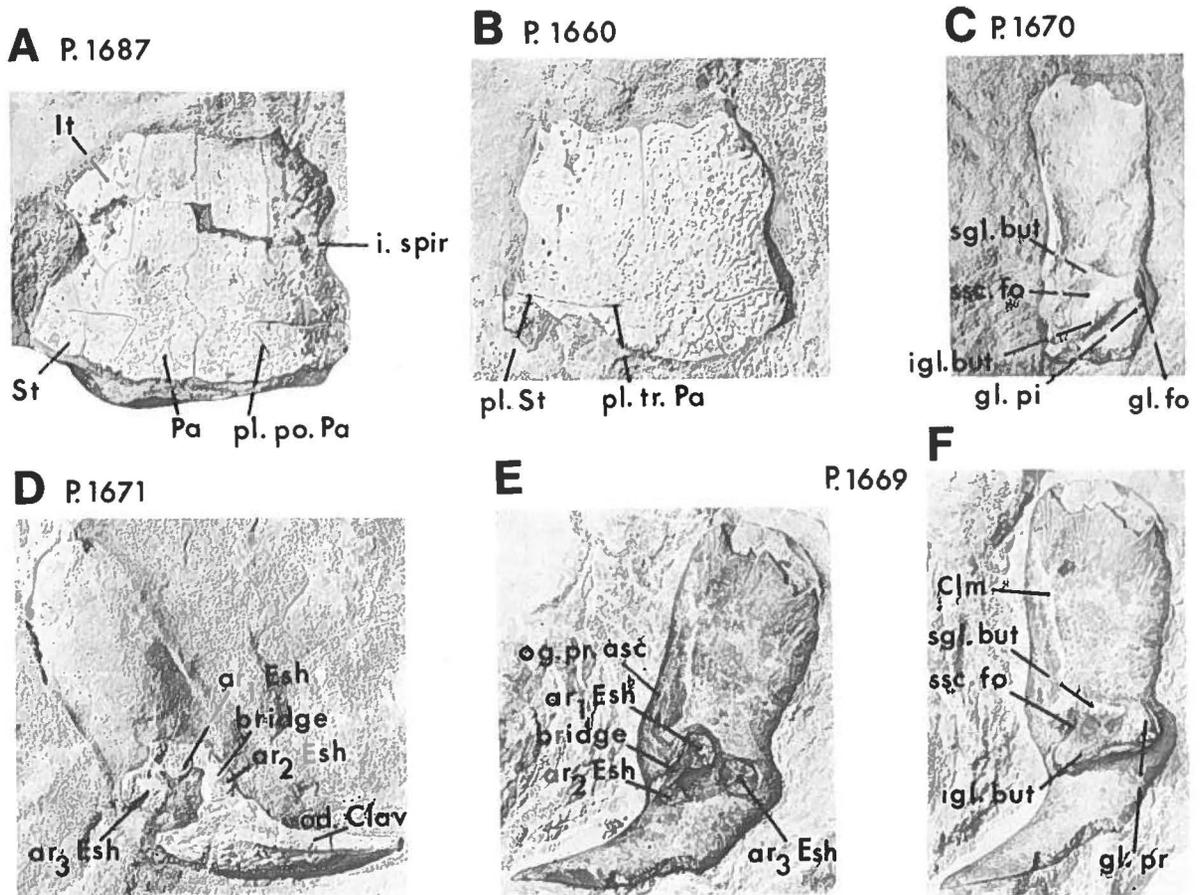Fig. 32. *Spodichthys buetleri* gen. et sp. nov. **A, B**: P. 1687, P. 1660. Coll. 1954. Parietal shields. **C**: P. 1670. Coll. 1954. Imperfect cleithrum with endoskeletal shoulder girdle in visceral view. **D**: P. 1671. Coll. 1952. Imperfect cleithrum in external view. **E, F**: P. 1669. Coll. 1954. Cleithrum with endoskeletal shoulder girdle (removed in E) in visceral view. All specimens from Högbom Bjerg. × 2.7 approx.
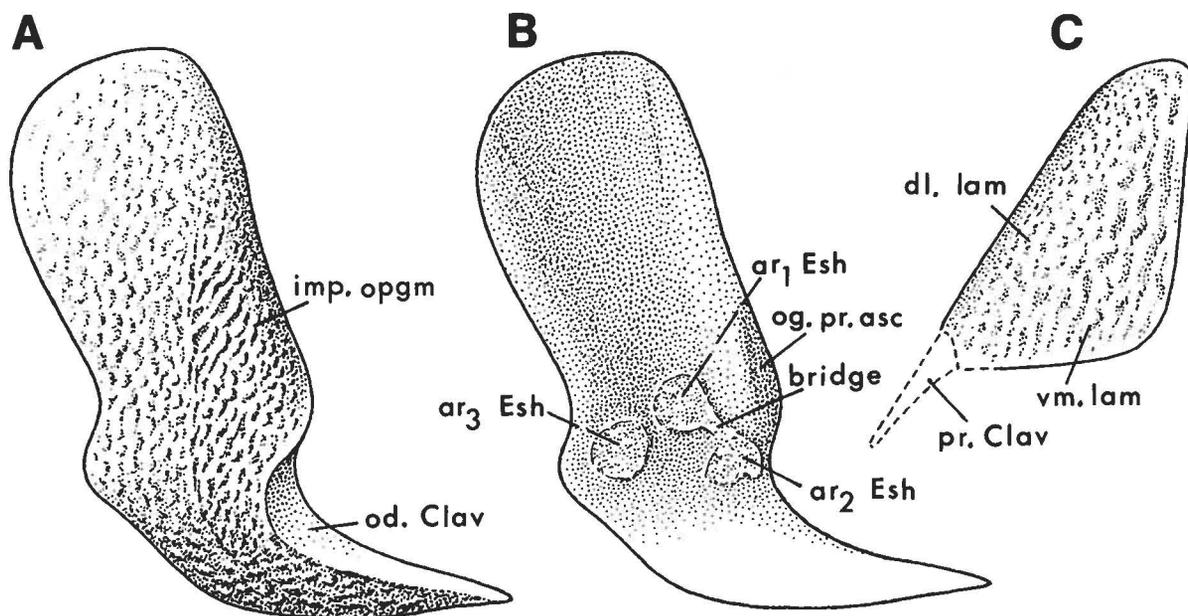
Fig. 33. *Spodichthys buetleri*. Restorations of **A**, **B**: cleithrum in external and visceral views; **C**: clavicle in external view.

frontals (c/b about 0.30–0.35; cf. Jarvik 1948, table 1, col. 18), between the anterior parts of the frontal pitlines. The parietal shield, which as in *Eusthenopteron*, *Tristichopterus* and other rhizodontids is composed of three paired bones (there is no extratemporal), is as broad as it is long at the spiracular notch, whereas the breadth most anteriorly, at the postorbital notch, is only about 0.7 of the length of the shield. In these respects *S. buetleri* differs somewhat from *E. foordi* in which the corresponding ratios (g/a, f/a, Fig. 2; cf. Jarvik 1948, table 1) are about 0.80–0.90 and 1.15–1.20, respectively.

Lower jaw. – The lower jaw (Figs 28 A, D, 30 A, B, 31 F), which is shown in external view only, resembles that in other osteolepiforms. It is comparatively short, only about 2.2 times longer than the parietal shield, whereas in *E. foordi* it is more than three times longer than that shield. The vertical pitline of infradentary 2 is situated about as in that form (k/m in both about 2.25).

Isolated dermal bones. – Only two bones of the external cheek plate, the postorbital and the maxillary, have been identified. The postorbital (Figs 30 C, 31 D) shows

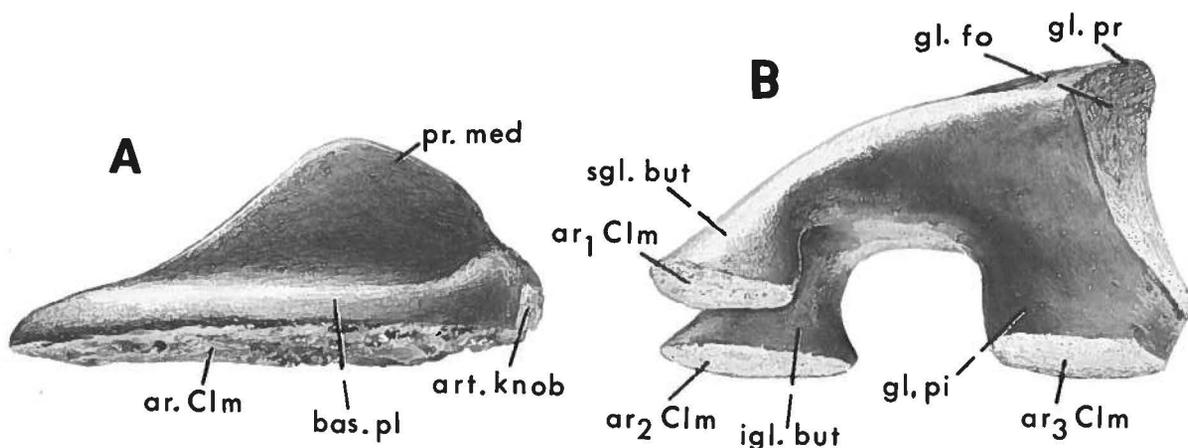Fig. 34. Models of left endoskeletal shoulder girdles in dorsolateral aspects of **A**: *Glyptolepis groenlandica* Jarvik, and **D**: *Eusthenopteron foordi* Whiteaves to illustrate the fundamental differences between porolepiforms and osteolepiforms. **A**: after P. 1490 (Copenh.); Jarvik 1972, fig. 59 C; 1980, fig. 200 A–C. × 6 approx. **B**: after P. 222 (Stockh.); cf. Jarvik 1972, fig. 59 A; 1980, figs 100–102. × 3.

Fig. 35. *Spodichthys buetleri* gen. et sp. nov. P. 1673. Coll. 1954. Slab showing mainly two scales in external and two in internal views. × 8 approx.

the area overlapped by the dermosphenotic and the posterior supraorbital, but no area is discernible corresponding to that in *E. foordi* (Jarvik 1944: 35–36, od₂It, figs 9 A, 15 K) which is overlapped by the intertemporal. However, the shape of the bone indicates that, when in its natural position, it extends behind the postorbital notch as it does in other rhizodontids (*Eusthenopteron, Eusthenodon*) but in contrast to the situation in *E. foordi* it probably does not reach the spiracular fenestra (cf. *Jarvikina,* Vorobyeva 1977, fig. 42). The proportions of the maxillary (Figs 30 D, E, 31 E) seem to be somewhat as in *E. foordi*. The opercular (Figs 30 F, 31 B) is about as long as high, whereas the subopercular (Figs 30 G, 31 C) is about 2.10 times longer than high. The principal gular plate (Figs 30 H-J, 31 G) is moderately long and narrow, a little more than three times longer than broad. It is thus somewhat as in *T. alatus* (Jarvik 1950: 87, fig. 26), but broader than in *E. foordi* in which it is about 4.5 times longer than broad. The pitline is found a little in front of the midpoint of the bone (p/n about 1.10).

Shoulder girdle. – The cleithrum (Figs 32 C-F, 33 A, B) and the clavicle (Fig. 33 C) resemble those in *E. foordi* in most respects (Jarvik 1944a, 1980, figs 100–101, 126, 165, Andrews & Westoll 1970). However, the dorsal rectangular portion of the cleithrum is lower and broader proportionally, and the ventral triangular portion is produced anteriorly into a fairly long and pointed process. Moreover, the anterior process of the bone found in *E. foordi* at the transition between the dorsal and ventral portions is replaced by a rounded corner and the area (od.Clav) overlapped by the clavicle is relatively broad. The endoskeletal shoulder girdle ("scapulocoracoid"; cf. Jarvik 1980: 139), which in two specimens is found in association with the cleithrum is also suggestive of that in *E. foordi* (Fig. 34 B; Jarvik 1944a, figs 4 D, 6 C; 1964, fig. 25 C; 1980: 139–140, figs 100–103, 165 A; Andrews & Westoll 1970). It is thus a three-legged structure produced backwards into a short glenoid process (gl.pr) overhanging the oval-shaped articular area, the glenoid fossa (gl.fo), for the humerus. However, the two anterior legs, the supra- and infragle-

noid buttresses (sgl.but, igl.but), have fused in their basal parts and their areas of attachment (ar$_1$Esh, ar$_2$Esh) on the inner side of the cleithrum are connected by a bridge of bone. Because of this the subscapular fossa (ssc.fo) seems to be closed at its base and the openings (supraglenoid and supracoracoid foramina) between the two anterior legs and the posterior one, the glenoid pillar (gl.pi), are smaller than in *E. foordi.*

As in *Eusthenopteron* (Jarvik 1944a:15, figs 4 D, 6 C; 1980, fig. 126 B) and *Spodichthys* (Figs 32 D, E, 33 B) the inner side of the cleithrum in several other osteolepiforms (*Gyroptychius groenlandicus,* Jarvik 1950, pl. 21: 2, *Tristichopterus,* Andrews & Westoll 1970a: 395, *Viluichthys,* Vorobyeva 1977, fig 38) has three more or less rounded areas of attachment for the endoskeletal shoulder girdle. This fact indicates that this structure is three-legged and similar to that in *Eusthenopteron* (Fig. 34 B) as it is also in "*Ectosteorhachis*" (Thomson & Rachoff 1974). In *Gyroptychius dolichotatus,* too, the endoskeletal shoulder girdle is of the same type (p. 29; see also Janvier 1977, fig. 2). It is therefore of interest that the endoskeletal shoulder girdle in one specimen of the porolepiform *Glyptolepis groenlandica* – found together with the holotype of *Gyroptychius dolichotatus* in beds with *Asterolepis saevesoederberghi* – the endoskeletal shoulder girdle has been completely freed from the matrix and removed from the exoskeletal girdle. It is clear that this endoskeletal girdle (Fig. 34 A; Jarvik 1980: 269, fig. 200 A-C) is quite different from that in *Eusthenopteron* (Fig. 34 B) and other osteolepiforms. It has an oval basal plate (bas.pl) attached to the inner side of the cleithrum and has a medial process (pr.med). Moreover, there is an articular knob (art.knob) articulating with a fossa at the proximal end of the first mesomere of the pectoral fin, and, also in contrast to osteolepiforms, there are no foramina. Since a single attachment area for the endoskeletal girdle is found on the cleithrum in the Lower Devonian *Porolepis* (Jarvik 1972, fig. 51 G, pl. 13: 5) as well as in other species of *Glyptolepis* (1972, fig. 53 F, G) and in *Holoptychius* (fig. 52 B, pl. 34: 4), it is evident that the type of girdle discovered in *Glyptolepis groenlandica* is characteristic of the porolepiforms in general.

This important fact that the endoskeletal shoulder girdle is of a quite different type, and the well known differences in the shape of the pectoral fin as well as in its endoskeleton (Jarvik 1972: 143, fig. 59; 1980, figs 71, 72, 100–102, 176, 200 C), should be borne in mind when discussing interrelationships between the osteolepiforms and porolepiforms and in the assiduous and still futile search for intermediate forms between these two distinct groups of fishes (Jarvik 1980a: 264).

Scales. – Numerous detached scales occur together with the cranial remains. As in other rhizodontids they are cycloid and provided with a sometimes unusually large, wedge-shaped boss on the inner side (Fig. 35). The ornamentation consists mainly of faint, irregular long-itudinal ridges, often connected by delicate, short crossridges. The total length of most of the larger scales is about 6–7 mm. However, one of the scales is considerably larger (total length about 15 mm) and it is possible that it belongs to *Spodichthys* cf. *buetleri.*

Spodichthys cf. *buetleri*

(Figs 28 F, G, 29 B, C)

Among the material from the locality in Hudson Land that has yielded *Spodichthys buetleri* and *Remigolepis* there is a single divisio cranialis anterior which differs so much from the corresponding unit in *S. buetleri* that I have found it reasonable to treat it separately. This specimen (P. 1656, Figs 28 F, G, 29 B, C) shows well the frontoethmoidal shield and the ethmosphenoid, but as in *S. buetleri* the vomer is missing and the parasphenoid is imperfectly preserved. Moreover, the dermosphenotic and the posterior supraorbital are lacking, as they are in most specimens of *S. buetleri.*

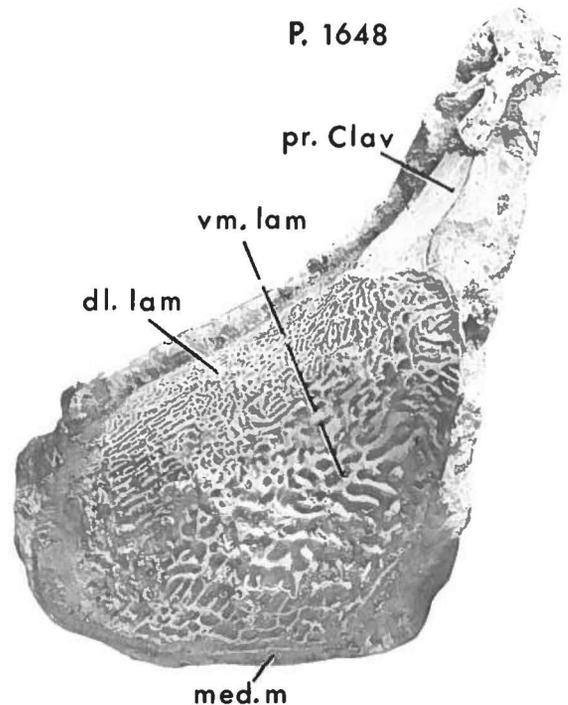*S.* cf. *buetleri* differs from *S. buetleri* mainly in the following respects:

Fig. 36. *Eusthenodon waengsjoei* Jarvik. Right clavicle, latex cast of external side. Ventrolateral view. P. 1648, Sederholm Bjerg. Coll. 1936. × 1.
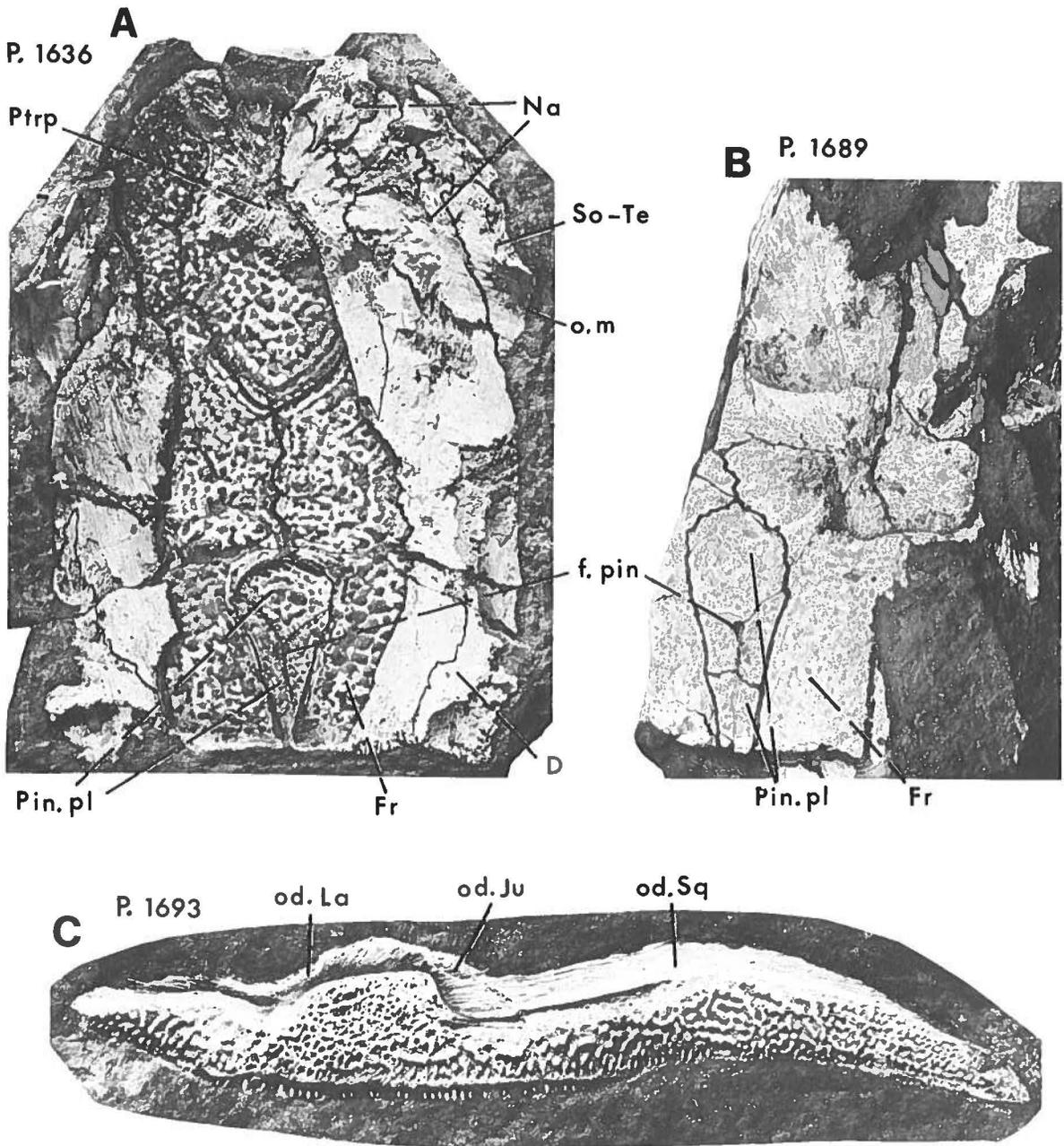
Fig. 37. *Eusthenodon waengsjoei*. Part of frontoethmoidal shield in **A**: internal and **B**: external views showing pineal plates in large pineal fenestra. × 0.8. **A**: P. 1636, Smith Woodward Bjerg. Coll. 1951. **B**: P. 1689, Celsius Bjerg. Coll. 1955. **C**: maxillary, photograph of latex cast of external side. P. 1693, Celsius Bjerg. Coll. 1955. × 1.1.

1. The frontoethmoidal shield is 40 mm long and is thus almost three times longer than the largest shield in *S. buetleri* (15 mm).

2. The preorbital division of the frontoethmoidal shield is proportionally much longer than in *S. buetleri*. The ratio r/s+t is thus about 0.56, whereas in the latter it is only about 0.40–0.45. The lachrymo-maxillary notch is longer, too, whereas the orbital margin (o.m) is comparatively short (cf. Fig. 31 A).

3. The pineal foramen is situated farther back. It lies distinctly behind the anterior ends of the frontal pitlines and the ratio c/b is only about 0.24 but about 0.30–0.35 in *S. buetleri*.

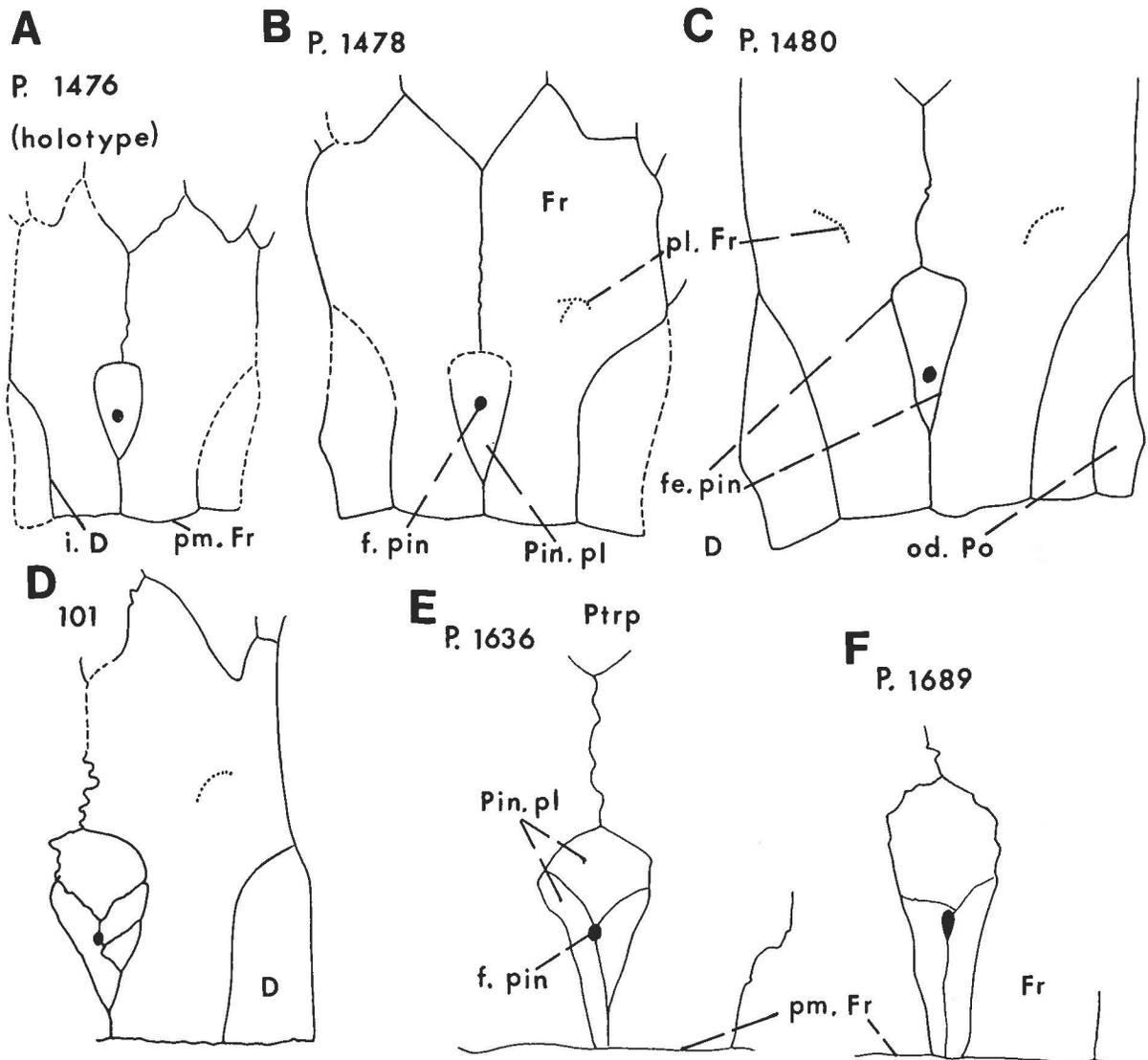Fig. 38. *Eusthenodon waengsjoei*. Restorations showing variations in the shape and position of the pineal fenestra and in the number and shape of the pineal plates. A–D: from Jarvik 1952, fig. 23. E, F: after specimens shown in Fig. 37 A, B.

Remarks on *Eusthenodon* Jarvik, 1952

The genus *Eusthenodon* with the single species *E. waengsjoei* was described in 1952 on the basis of material collected in the upper Upper Devonian ichthyostegid-bearing Remigolepis Group during the Danish expeditions to East Greenland 1929–1949. In two papers (1960, 1962) Vorobyeva claimed that the large rhizodontid, which I described in 1937 from the Baltic Devonian under the name *Eusthenopteron wenjukowi*, belongs to *Eusthenodon*, but she later referred it to a new genus (*Jarvikina*, Vorobyeva 1977). Apart from East Greenland, *Eusthenodon waengsjoei* has been recorded from the Uppermost Devonian in the Catskill of the

Apalachian basin, Pennsylvania, U. S. A. (Thomson 1976) but as far as I know this material and the material of cf. *Eusthenodon* from the Upper Fammenian in the same area are still undescribed.

New material of *E. waengsjoei* was collected during the expeditions to East Greenland in 1951, 1954 and 1955, as earlier in Sederholm and Smith Woodward Bjerg in Gauss Halvø and in Celsius Bjerg on Ymer Ø (Fig. 1). Before proceeding to that material (as to the lower jaw see also Jarvik 1972: 115, fig. 49 A) it is worth mentioning that a well preserved impression of the external side of the clavicle (Fig. 36) has been identified in the material collected by Säve-Söderbergh in 1936 in Sederholm Bjerg. As evidenced by this impression the

clavicle is larger than that in *Eusthenopteron foordi* (the distance from the base of the ascending process to the anterior end of the bone is 70 mm and only 30 mm in P. 222 of *E. foordi,* Jarvik 1944a), but in other respects it is very similar.

Of the new material only three specimens are considered here (Fig. 37), one showing the maxillary (P. 1693, coll. 1951, Celsius Bjerg) and two (P. 1636, coll, 1951, Smith Woodward Bjerg, and P. 1689, coll. 1955, Celsius Bjerg) showing the area of the pineal plates. One of the characteristic features of *E. waengsjoei* recorded in the original description (Jarvik 1952: 64) is that the maxillary attains its greatest height in the anterior part of the bone, close behind the centre of radiation of the bone. This detail is well shown in P. 1693 (Fig. 37 C), which is an impression of the external side of the bone. It is also remarkable that the maxillary is overlapped by the squamosal (od.Sq), again in contrast to conditions in other osteolepiforms (Jarvik 1944, fig. 9 A; Jessen 1966, pl. 10:5, 6; 1973 pl. 20:1)

Other characteristic features of *E. waengsjoei* involve the pineal fenestra and the pineal plates (Figs 37 A, B, 38; Jarvik 1952: 62–63). The pineal foramen is small whereas the pineal plates (Pin.pl) are larger, proportionally, than in other osteolepiforms and occupy a large pear-shaped pineal fenestra (fe.pin). However, there are considerable variations. In the specimens described in 1952 (fig. 23) the pineal fenestra ends distinctly in front of the posterior margin (pm.Fr) of the frontoethmoidal shield, but as mentioned in a foot note (1952: 63), in one specimen collected in 1951, namely in P. 1636 (Figs 37 A, 38 E), this fenestra extends backwards to that margin. A still more remarkable specimen (P. 1689, Figs 37 B, 38 F) was found in 1955. Here the pineal plates have a short posterior margin, which shares the posterior margin (pm.Fr) of the frontoethmoidal shield. Whether these considerable variations mean that more than one species is involved is difficult to say. However, in the absence of other distinctive data, and since there are intermediate forms (Fig. 38 B-E) linking the extreme variants (A, F), I have found it most reasonable to refer all specimens to *Eusthenodon waengsjoei*. Nevertheless, these considerable variations exemplify the difficulties involved in evaluating correctly the morphological variants often encountered in fossil material (cf. p. 7).

Acknowledgements

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List of Abbreviations

Aclm: anocleithrum
Aplv: portion of anterior subchordal arcual plate interpreted as interventral of cranial vertebra CV3+4
a: length of parietal shield
af: anal fin
an.o: anal opening
ar.Clm: single attachment area of endoskeletal shoulder girdle to cleithrum in porolepiform
$ar_1Clm-ar_3Clm$: attachment areas of endoskeletal shoulder girdle to cleithrum in osteolepiform
$ar_1Esh-ar_3Esh$: attachment areas of cleithrum to endoskeletal shoulder girdle in osteolepiform
art. knob: articular knob

b: length of frontoethmoidal shield
bas.pl: basal plate of endoskeletal shoulder girdle
boss ad: boss of anterodorsally directed scale row
boss av: boss of anteroventrally directed scale row
br.G: breadth of principal gular plate •
bs.af: basal scute of anal fin
b.sc: basal scale of fin
bs.f.df: basal scute of first dorsal fin
bsm.pfl: medial basal scute of left pectoral fin

Clav: clavicle
Clm: cleithrum
c: distance from posterior margin of frontal to pineal foramen
cf: caudal fin
cfe, cfh: epichordal and hypochordal lobes of caudal fin
c.ju: jugular canal
c.m.sc: canal for nerve to subcranial muscle
c.nc: canal for notochord
c.pal: palatine canal
c.spoc.1,c.spoc.2: canals for spinooccipital nerves 1 and 2
c.II, c.III,c.V,c.VI: canals for nervus opticus, oculomotorius, trigeminus and abducens

D: dermosphenotic
d: breadth of cranial roof at preorbital corner
df: dorsal fin
div.a1-div.a4: anterior cranial divisions
div.p1-div.p3: posterior cranial divisions
dl.lam: dorsolateral lamina of clavicle
dl.r: dorsolateral transverse scale row
dma: anterior division of dorsal median scale row
dp.io: depth of orbital notch

Et: extratemporal
Etsph: ethmosphenoid
Ext.l,Ext.m: lateral and median extrascapulars
e: breadth of cranial roof at orbital notch

Fr: frontal
Fret.sh: frontoethmoidal shield
f: breadth of cranial roof at postorbital notch
f.bh: foramen for buccohypophysial duct
f.df: first dorsal fin
fe. ench: fenestra endochoanalis
fe.o: orbital fenestra
fe.pin: pineal fenestra
fi.ot.va: fissura oticalis ventralis anterior
foot-pl: lamina probably forming foot-plate of stapes in tetrapods
f.pin: pineal foramen

G: principal gular plate
G.m: median gular plate
g: breadth of cranial roof at spiracular notch
gl.fo: glenoid fossa
gl.pi: glenoid pillar
gl.pr: glenoid process
gr.a.dl: groove for lateral dorsal aorta
gr.a.im: groove for intermetameric artery
gr.a.oc: groove for occipital artery
gr.a.oc.-vert: groove for occipito-vertebral artery
gr.a.vertd: groove for dorsal vertebral artery
gr.ju: groove for jugular vein
gr.juc: groove marking course of jugal sensory canal
grp.so: openings of canals for nerve twigs to group of special sensory organs
gr.stcc: groove marking course of supratemporal commissural canal

h: breadth of cranial roof at posterolateral corner
ht: height of posterior margin of lachrymal
ht.Ch: height of external cheek plate

ht.Sq: height of squamosal
hyd,hyv: dorsal and ventral articular areas for hyomandibula

It: intertemporal
i.D: notch for dermosphenotic
i.Et: notch for extratemporal
igl.but: infraglenoid buttress
i.La+Mx: lachrymo-maxillary notch
imp.opgm: impression of operculogular membrane
inv.Sc: inversion scales at ventrolateral ridge
i.o: orbital notch
ioc: infraorbital sensory canal
iocp: pores of infraorbital sensory canal
i.po: postorbital notch
i.So.2: notch for posterior supraorbital
i.spir: spiracular notch

Ju: jugal
juc: jugal sensory canal

k: distance from vertical pitline of infradentary 2 to posterior
end of lower jaw

La: lachrymal
Lj: lower jaw
lc: lateral commissure
l.Ch: length of external cheek plate
lep: lepidotrichia
lep.f.df: lepidotrichia of first dorsal fin
l.G: length of principal gular plate
l.Po: length of postorbital
l.Sq: length of squamosal

Mx: maxillary
m: distance from vertical pitline of infradentary 2 to anterior
end of lower jaw
med.m: medial margin of clavicle
m.La: margin of postorbital meeting lachrymal
m.Lj: margin of submandibulo-branchiostegal plate meeting
lower jaw
msc: main sensory canal
msc.r: main sensory canal row of scales

Na: nasal
n:distance from pitline of principal gular to anterior end of
non-overlapped part of bone

P: parasphenoid
Pa: parietal
Pa.sh: parietal shield
Pin.pl: pineal plates
Po: postorbital
Pop: preopercular
Pt: posttemporal
Ptrp: posterior postrostral
p: distance from pitline of principal gular to posterior end of
bone
pfl, pfr: left and right pectoral fin
plc: posterolateral corner of cranial roof
pl.Fr,pl.G,pl.G.m: pitlines of frontal, principal and median gu-
lar plates
plh.Md: horizontal mandibular pitline
pl.po.Pa: posterior oblique parietal pitline
pl.Qj: quadratojugal pitline

pl.Sbm.7: pitline of submandibular 7
pl.Sq: squamosal pitline
pl.St: supratemporal pitline
pl.tr.Pa: transverse parietal pitline
plv.Id.2: vertical pitline of infradentary 2
pm.Fr: posterior margin of frontal
p.nc: notochordal pit
pr.bp: basipterygoid process
pr.Clav: ascending process of clavicle
pr.conn: processus connectens
pr.med: medial process of endoskeletal shoulder girdle
proc: preorbital corner of cranial roof
pr.p: posterior process of median gular
pr.Sc: articular process of scale
p.Sc: articular pit of scale
ptoc: postorbital corner of cranial roof
pvf: pelvic fin
pvfl,pvfr: left and right pelvic fin

Qj: quadratojugal

Rad: radial of epichordal lobe of caudal fin
r: median length of preorbital division of frontoethmoidal
shield
ri.ju: jugular ridge
ri.juc: ridge caused by jugal sensory canal
ri.Sc: articular ridge of scale
ri.Scb: boss-like articular ridge
ri.vl: ventrolateral ridge
rod: endoskeletal rod probably formed by fused vertebrae

Sbm-Rbr: submandibulo-branchiostegal plate
Sbm.1: submandibular 1
Sclm: supracleithrum
So-Te: supraorbito-tectal
So.2: posterior supraorbital
Sq: squamosal
St: supratemporal
s: median length of orbital division of frontoethmoidal shield
s.df: second dorsal fin
sgl.but: supraglenoid buttress
snc: subnarial corner of cranial roof
soc: supraorbital sensory canal
soc.plug: supraoccipital plug
sr.ad,sr.av: anterodorsally and anteroventrally directed scale
rows
ss.fo: subscapular fossa
stcc: supratemporal commissural sensory canal

t: median length of postorbital division of frontoethmoidal
shield

v: distance from middle point of orbital notch to anterior end
of frontoethmoidal shield
v.font: vestibular fontanelle
vm.lam: ventromedial lamina of clavicle
v.o.r: ventral oblique scale row

w: distance from middle point of orbital notch to posterior end
of frontoethmoidal shield

x: distance from quadratojugal pitline to anterior end of bone

y: distance from quadratojugal pitline to posterior end of bone

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In the list of references the following usage is adopted:

Journal: Tarling, D. H. 1967. The palaeomagnetic properties of some Tertiary lavas from East Greenland. – Earth planet. Sci. Lett. 3: 81–88.

Book: Boucot, A. J. 1975. Evolution and extinction rate controls. – Elsevier, Amsterdam: 427 pp.

Chapter (part): Wolfe, J. A. & Hopkins, D. M. 1967. Climatic changes recorded by Tertiary landfloras in northwestern North America. – In: Hatai, K. (ed.), Tertiary correlations and climatic changes in the Pacific. – 11th Pacific Sci. Congr. Tokyo 1966, Symp.: 67–76.

Title of journals should be abbreviated according to the last (4th) edition of the World List of Scientific Periodicals (1960) and supplementary lists issued by BUCOP (British Union-Catalogue of Periodicals). If in doubt, give the title in full.

Meddelelser om Grønland, Geoscience should be registered under *Meddelelser om Grønland*. Example (with authorized abbreviations): *Meddr Grønland, Geosci.* 1, 1979.

Illustrations

General. – Submit two copies of each graph, map, photograph, etc., all marked with number and author's name. Normally all illustrations will be placed within the text; this also applies to composite figures.

All figures (incl. line drawings) must be submitted as glossy photographic prints suitable for direct reproduction, i.e. having the format of the final figure. Do not submit original artwork. Where appropriate the scale should be indicated in the caption or in the illustration.

The size of the smallest letters in illustrations should not be less than 1.5 mm. Intricate tables are often more easily reproduced from line drawings than by type-setting.

Colour plates may be included at the author's expense, but the editor should be consulted before such illustrations are submitted.

Size. – The width of figures must be that of a column (77 mm), 1½ column (117 mm) or of a page (157 mm). Remember to allow space for captions below full page figures. Maximum height of figures (incl. captions) is 217 mm. Horizontal figures are preferred.

If at all possible, fold-out figures and tables should be avoided.

Caption. – Captions (two copies) to figures should be typed on separate sheets.