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EVOLUTION AND CLASSIFICATION OF PLACODERM FISHES

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ABSTRACT. The assumption is made that within the Subclass Placodermi a shoulder girdle that is short anteroposteriorly is primitive. Most orders retaining this feature show distinctive specializations: thus the Rhenanida are ray-like, the Ptyctodontida are chimaeroid-like, the Pseudopetalichthyida have large, dorsal eyes, and many Acanthothoraci have dorsal nostrils. The Stensioellida show few specializations and are believed to be the most primitive known Placodermi, yet they possess the three characters that distinguish the subclass: 1) gills anteriorly placed under the neurocranium; 2) a neck joint between the neurocranium and synsacrum; and 3) dermal bones. The primitively short shoulder girdle becomes lengthened to form a thoracic shield in several stages. Some Acanthothoraci add posterior lateral and posterior dorsolateral plates. The Petalichthyida add a long ventral shield. Primitive Arthrodira lengthen the lateral shield and close it behind the pectoral fins which then attach through fenestrae. Finally, the Antiarcha develop a long, boxlike shield and transform the spinal plates into peculiar pectoral appendages. A phyletic classification of Placodermi is attempted.

INTRODUCTION

The Placodermi are a suborder of fishes whose known history is practically restricted to the Devonian period unless, as some think, they were ancestral to the chimaeroids. During that relatively short time span they underwent a considerable radiation and gave rise to 34 families and about 170 genera. In recent years they have been the subject of considerable research by many paleontologists. Yet, in spite of a great advance in our knowledge of the group, there is still little agreement about their evolutionary history and classification. This results from widely different assumptions about what constitutes primitive or derived characters within the group. Gross (1954) argued that an elon-

gated thoracic shield such as occurs in early Arthrodira is primitive, and the well-documented reduction of this shield within Arthrodira may be adduced to support this. Westoll (1945) likewise placed the long-shielded "Arctolepida" at the base of his placoderm phylogeny, and Miles (1969) has concluded that the formation of a firm thoracic shield, together with the development of a neck joint, was the fundamental placoderm adaptation. On the other hand, Stensiö in various works (e.g., 1969–1971) has based his classification primarily on the pectoral fin and endoskeletal shoulder girdle; following the fin-fold theory of paired fin origins, he believes that the primitive state is long-based pectoral fins together with an elongated endoskeletal shoulder girdle for their articulation.

CHARACTERS OF PRIMITIVE PLACODERMI

In my opinion, neither of these theories is correct, and my classification and phylogeny is based on the assumption that within the Placodermi an anteroposteriorly short shoulder girdle is primitive. The justification for this assumption is the fact that a short exoskeletal shoulder girdle occurs in all other groups of fishes with bony exoskeletons, and a short scapulocoracoid is characteristic of Chondrichthyes. It is only in certain groups of Placodermi, the Petalichthyida, Arthrodira, Phyllolepidida and Antiarcha, that the exoskeletal shoulder girdle is elongated to form a thoracic shield, and this can be taken as an indication that it is a derived state within Pisces and within Placodermi as well. On the assumption, then, that a short shoulder girdle is primitive within Placodermi, we may look at the groups that possess this character for other primitive states. The classification used in this discussion is given in the appendix, and is indicated pictorially in the phylogenetic chart (Fig. 6); some parts of it will be discussed later.

The following orders have a short exoskeletal shoulder girdle:

Stensioellida (*Stensioella*)

Rhenanida (*Gemuendina*, *Asterosteus*, *Ohioaspis*, *Jagorina*)

Pseudopetalichthyida (*Pseudopetalichthys*, *Paraplesiobatis*)

Acanthothoraci (*Palaeacanthaspis*, *Kosoraspis*, *Radotina*,
Kolymaspis, *Kimaspis*)

Ptyctodontida (8 genera)

All of these orders appear in the Lower Devonian; they show the following characters which may be primitive:

Thoracic region.

1) The ventral shoulder girdle (Figs. 1–2, sh) consists of a single pair of plates homologous either to the interlaterals or anterior ventrolaterals of *Arthrodira*; between them a median plate has been identified only in *Ptyctodontida*.

2) The lateral shoulder girdle consists only of anterior laterals and anterior dorsolaterals, except in some *Acanthothoraci* (Fig. 1C) where posterior laterals and posterior dorsolaterals are also present.

3) The spinal plates are absent, or small and doubtfully distinct, except in *Acanthothoraci* and some *Ptyctodontida* (Fig. 1C–D, Sp).

4) A median dorsal plate is probably absent in *Stensioellida* and *Pseudopetalichthyida*.

5) Pectoral fins are narrow-based, even in *Rhenanida* where the fins are much expanded distally (Fig. 1B).

6) There is no exoskeletal craniothoracic joint, except in *Ptyctodontida* where it is developed differently than in *Arthrodira* and *Antiarcha*.

7) The anterior vertebrae are fused to form a synarcual (Figs. 1–2, syn) which articulates with the occipital region of the neurocranium (not known in *Acanthothoraci*).

Skull.

8) The neurocranium is long and slender with a long occipital region, except in *Ptyctodontida* where it must have been short.

9) The dermal cranial roof bone pattern may be variable and unstable with relationships between bones and sensory canals not firmly established, except in *Ptyctodontida*.

10) Dermal cranial roof bones may be small and part of the roof may be covered with thin, superficial tesserae in *Acanthothoraci* (Fig. 3, te) and *Rhenanida*; much of the skull in *Stensioellida* (Fig. 2A) is covered with denticles or tesserae; the central part of the cranial roof of *Pseudopetalichthyida* is covered with small dermal bones, but there may have been denticles or tesserae elsewhere. Denticles or tesserae are unknown in *Ptyctodontida*, but may have covered the snout and cheeks where dermal bones are largely absent (Fig. 1D).

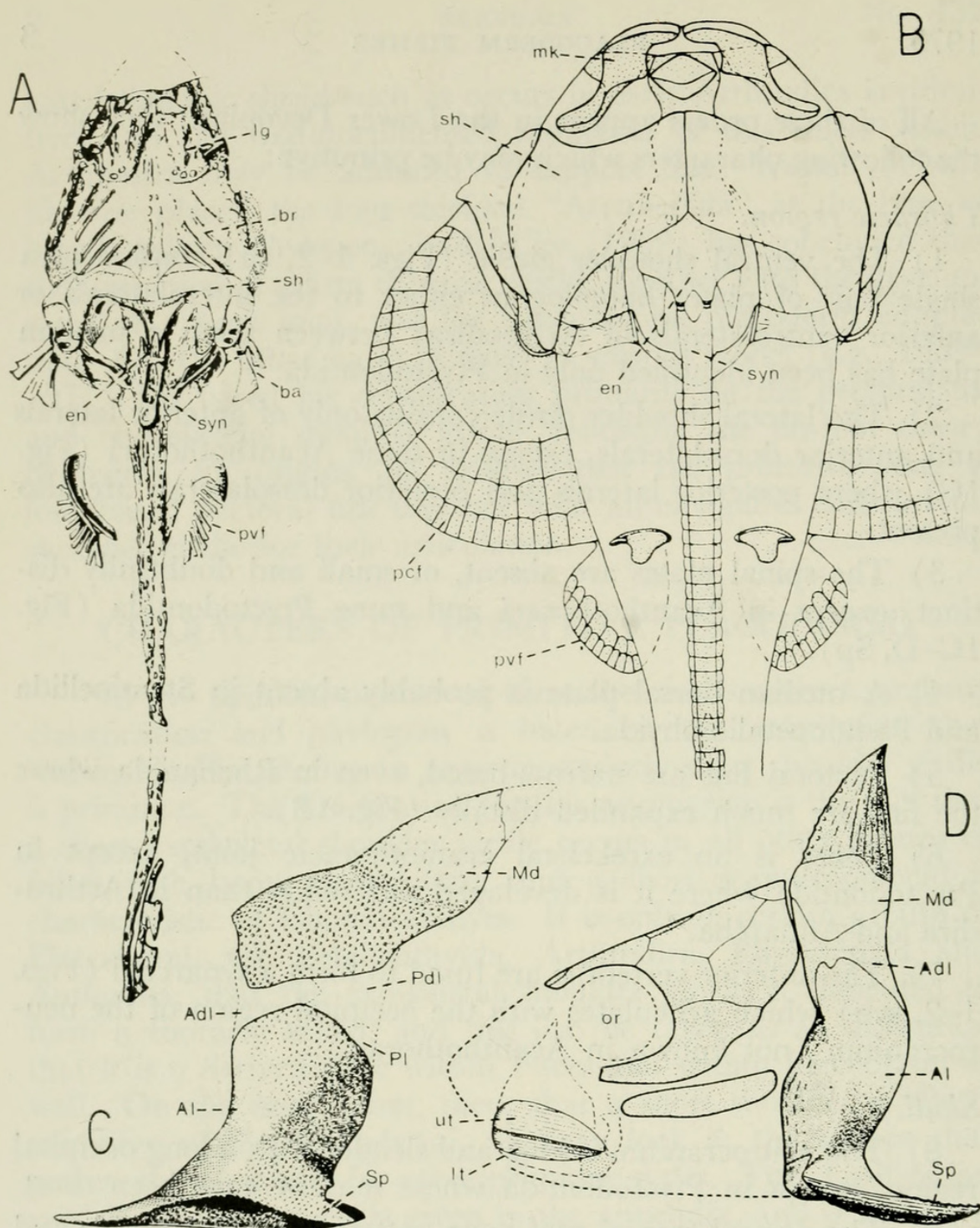


Figure 1. Placodermi with short shoulder girdles: A, Order Pseudopetalichthyida (ventral view of *Pseudopetalichthys problematica*, $\times 0.66$, from Gross, 1962); B, Order Rhenanida (ventral view of *Gemuendina stuarti*, $\times 0.60$, from Gross, 1963); C, Order Acanthothoraci (lateral view of shoulder girdle of *Palaeacanthaspis vasta*, $\times 0.94$, from Stensiö, 1944); D, Order Ptyctodontida (lateral view of head and shoulder girdle of *Rhamphodopsis threiplandi*, $\times 2.5$, from Miles, 1967). Adl, anterior dorsolateral plate; Al, anterior lateral plate; ba, basal elements of pectoral fin; br, branchial arches; en, endocranium; lg, lower jaw; lt, lower dental plate; Md, median dorsal plate; mk, Meckel's cartilage; or, orbit; pcf, pectoral fin; Pdl, posterior dorsolateral plate; Pl, posterior lateral plate; pvf, pelvic fin; sh, shoulder girdle; Sp, spinal plate; syn, synarcual; ut, upper dental plate.

Jaws and Gills.

11) The jaws, where known, are more or less transverse and lack large dermal elements (Fig. 1A-B, 2B), except in Ptyctodontida where they are directed more anteroposteriorly and carry large crushing or sectorial tooth plates (Fig. 1D, ut, lt).

12) Gill covers (submarginals) may be present, though they are not known in Acanthothoraci and their dermal bones are small in Ptyctodontida.

Sensory organs.

13) The orbits are small and lateral in Stensioellida and most Acanthothoraci, large and dorsolateral in Ptyctodontida, and dorsal in Pseudopetalichthyida, Rhenanida and one late genus of Acanthothoraci; the last condition is surely specialized.

14) The nostrils are known only in Rhenanida and Acanthothoraci (Fig. 3, no) where they are usually dorsal, a condition that is surely specialized. In Stensioellida, Pseudopetalichthyida and primitive Acanthothoraci they are presumed to be anterior or anteroventral; there are no clues to their position in Ptyctodontida.

Body and fins.

15) The body is depressed and tapers to a diphyccercal tail (not known in Acanthothoraci).

16) Dorsal fins are little developed except in Ptyctodontida; there are dorsal ridge scales in Pseudopetalichthyida (Fig. 1A) and Stensioellida and the latter has a small dorsal fin (Fig. 2A, df) at the base of the tail; an enlarged ridge scale forms a small dorsal spine in Rhenanida. (This region is not known in Acanthothoraci.)

17) Pelvic fins (Figs. 1-2, pvf) are long-based and semicircular in Rhenanida, Stensioellida and Pseudopetalichthyida; they are specialized by the development of claspers in male Ptyctodontida.

Histology.

18) The histology of the Lower Devonian members of the groups under discussion is practically unknown. There is a possibility that the Stensioellida had denticles composed of dentine, and if so, this would be the only occurrence of this tissue in Placodermi except for the tooth plates of Ptyctodontida. Typically in other Placodermi the superficial layer is reduced and the external part of dermal bones is composed of semidentine or bone.

PRIMITIVENESS OF PLACODERM ORDERS WITH SHORT SHOULDER GIRDLES

In reviewing the list of probable primitive characters, it is clear that the Ptyctodontida (Fig. 1D) do not share many of them. This may be due to the fact that only the shoulder girdle is known in Lower Devonian ptyctodonts while other characters are determined from Middle or Upper Devonian genera which are specialized or advanced in the following ways: the presence in the shoulder girdle of an anterior medioventral, a median dorsal, spinal plates in some, and an exoskeletal craniothoracic joint; in the shortness of the exo- and endocranium, well-established cranial roof pattern without tesserae (except perhaps anteriorly and on the cheeks), large dorsolateral eyes, large dermal jaw elements, firm attachment of palatoquadrate to endocranium, dorsal fins, and pelvic fins with claspers in males.

It is clear that the ray-like Rhenanida (Fig. 1B) are also specialized, even in the earliest known Lower Devonian forms. They have a much flattened body, greatly expanded pectoral fins, dorsal eyes and nostrils, a median dorsal plate, and a dorsal spine on the body.

The Acanthothoraci, with the exception of the Radotinidae, are advanced in having the lateral parts of the shoulder girdle lengthened by the addition of posterior lateral and posterior dorsolateral plates (Fig. 1C); well-developed, projecting spinal plates as well as median dorsal plates are present. The skull in all members of the order is distinguished by its narrow proportions, subparallel sides, and deeply embayed posterior margin with strongly projecting paranuchals. Primitively, (Palaeacanthaspidae) the eyes were lateral and the nostrils probably ventral, but the nostrils, or both the nostrils and eyes have moved to the dorsal side in Radotinidae (Fig. 3) and Kolymaspidae, both of which have a prominent rostrum.

The poorly known Pseudopetalichthyida (Fig. 1A) are surely specialized in their relatively large, dorsal eyes, the long preorbital region, and possibly in the absence of tesserae, at least on the cranial roof. Their jaws (Fig. 1A, lg), though not well understood, appear to be peculiarly specialized.

This leaves only the Stensioellida, which exhibit very few characters that can be interpreted as advanced, and are considered to be the most primitive Placodermi known, even though

they are not the earliest members of the subclass. Based on the two specimens of *Stensioella* (Fig. 2) from the Hunsrückschiefer of Germany, the body appears to be somewhat depressed, broadest in the head and shoulder regions, and tapering backwards towards the tail. Flattening after burial spread apart the two halves of the shoulder girdle (Fig. 2, sh), making it difficult to

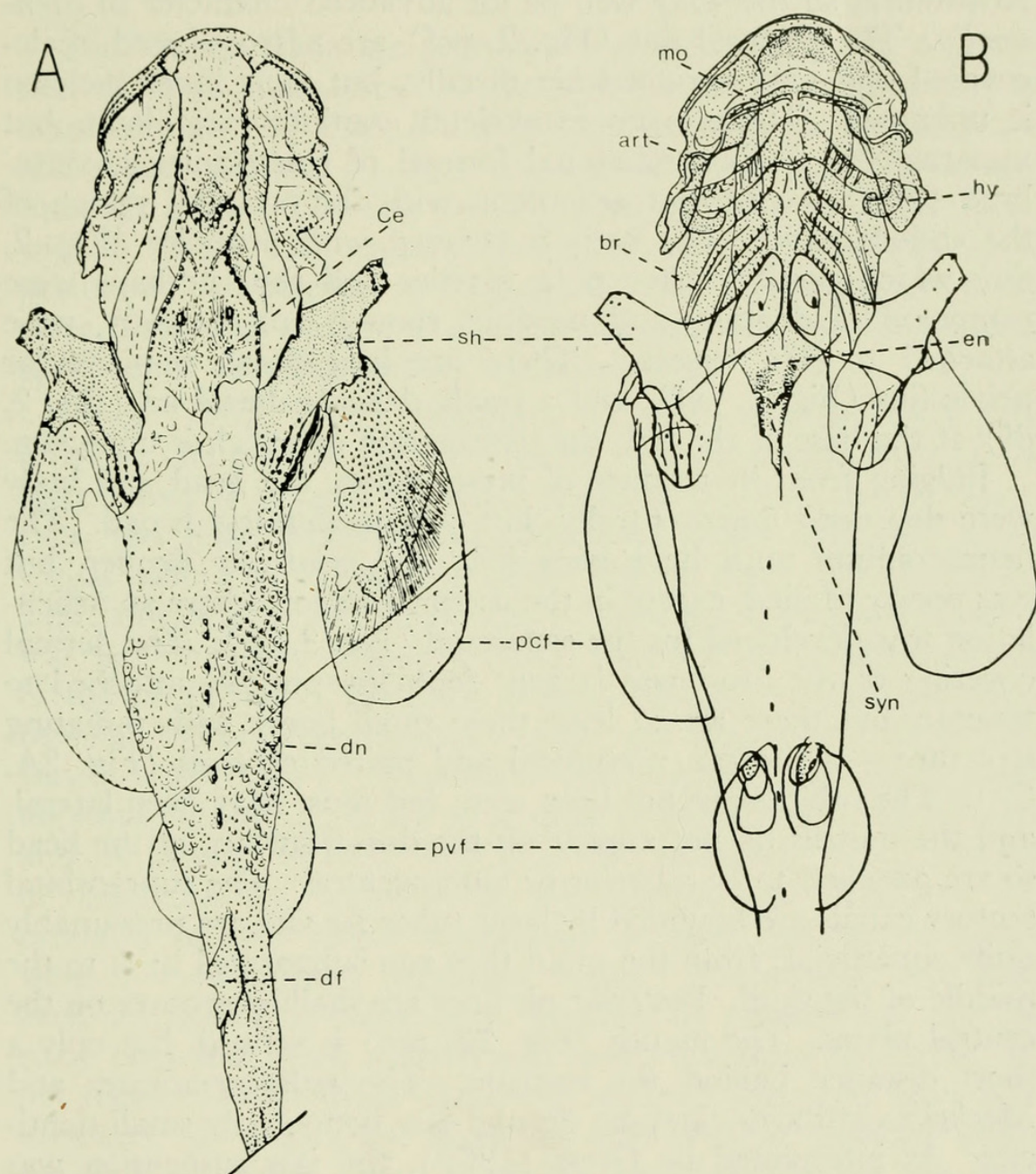


Figure 2. *Stensioella heintzi* (the only known representative of the Order Stensioellida), $\times 0.44$, from Gross, 1962: A, dorsal; B, ventral. art, jaw articulation; br, branchial arches; Ce, central plate; df, dorsal fin; dn, denticles; en, occipital region of endocranium; hy, hyomandibular; mo, mouth; pcf, pectoral fin; pvf, pelvic fin; sh, shoulder girdle; syn, synarcual.

interpret, but the bones are tuberculate and thus largely exoskeletal, even though individual dermal bones cannot be identified. Clearly the shoulder girdle is short anteroposteriorly, lacks a median dorsal and median ventral, and has no large or projecting spinal plates. Each half of the shoulder girdle has an inner or medial lamina which forms a postbranchial wall; such a wall occurs in many placoderms, but is absent in primitive Arthrodira, so this may well be an advanced character in *Stensioella*. The pectoral fins (Fig. 2, pcf) are narrow-based, scale-covered and with ceratotrichia distally, but their inner skeleton is unknown. There is no exoskeletal craniothoracic joint, but apparently there is a synarcual formed of fused anterior vertebrae (Fig. 2, syn) that articulates with the occipital region of the endocranium. The body is covered with denticles (Fig. 2, dn) which possibly have pulp cavities and thus perhaps were composed of dentine, and possibly, though not certainly, were attached to thin tesserae. There are long-based, semicircular pelvic fins (Fig. 2, pvf), and a small, delicate dorsal fin (Fig. 2, df) at the base of the tail, the termination of which is unknown.

Judging from its manner of preservation, the head and body were depressed dorsoventrally, but only moderately broad. The neurocranium must have been long and relatively slender, but was poorly ossified, except in the occipital region where an articulation was developed for the synarcual (Fig. 2, en). The dermal covering of the head was largely denticles, possibly attached to tesserae, but there are at least three small bones with radiating structure — a median postpineal and paired centrals (Fig. 2A, Ce). The orbits have not been seen, but must have been lateral, and the nostrils do not appear on the dorsal surface of the head so are assumed to be anterior or anteroventral. The supraorbital sensory canals are bounded by large tubercles and are presumably quite superficial; from the snout they run subparallel back to the middle of the skull. Posterior pit lines are shallow grooves on the central plates. The mouth (Fig. 2B, mo) is ventral, but only a short distance behind the rostrum. The palatoquadrates and Meckel's cartilages carry no dermal jaw bones, only small denticles. As interpreted by Gross (1962), the jaw suspension was hyostylic, but this is not certain. There appear to be five branchial arches (Fig. 2B, br) and these extend far anterior under the endocranium.

The single species that constitutes the Order Stensioellida has many characters that are considered primitive within the placo-

derms, but shows no easily identifiable specializations or unique derived characters that can be used to distinguish it from other placoderm orders. Nonetheless, it seems to be a distinct order occupying an isolated position as an offshoot from the base of the placoderm stem.

DIAGNOSTIC CHARACTERS OF PLACODERMS

That Stensioellida are placoderms is indicated by their possession of three characters: 1) the gills lie far forward under the neurocranium; 2) there is a neck joint between the endocranium and synarcual; and 3) there are dermal bones on the head and shoulder girdle. The first two characters are shared by the Holocephali which may support, though it does not establish, their postulated relationship to Placodermi. But the possession of all three features is unique to Placodermi, and for that reason their significance requires further consideration.

Miles (1967, 1969) attempted to show that the neck joint arose to compensate for the rigidity of the anterior part of the body when it became enclosed within a thoracic shield. However, this joint occurs in the placoderm orders discussed above which have a short shoulder girdle and no rigid thoracic armor. The same is true in chimaeroids so one may question whether it was the evolution of a stiff armor that led to the development of the neck joint. The joint permits largely vertical movement between the head and shoulder girdle and functions in three main ways (Miles, 1967): 1) to aid in locomotion by control of pitching equilibrium; 2) to aid in feeding by permitting a wider gape and by helping to force food into the esophagus; and 3) to aid in respiration by forcing water through the gills. The first was probably of only minor importance to early placoderms which were slow-swimming, benthonic forms. The second may have been important to some later, predaceous placoderms, but the early ones had small mouths and surely ate small food that did not require a wide gape. However, the neck joint may have been necessary for respiration when the gills became crowded under the neurocranium; then, a raising and lowering of the head would help to force a stream of water through the gills. Thus the neck joint may have been related to the anterior position of the gills under the head; instead of being a response to the rigidity of the thoracic region, it may have permitted the later development in some groups of a stiff trunk armor.

Dermal bones are characteristic of Placodermi, and typically a superficial layer of dentine is absent and their surface is formed of semidentine or bone. In the Lower Devonian groups with a short shoulder girdle, specimens are either unavailable or unsuitable for histologic study so superficial tissues have not been identified. Primitive or ancestral Placodermi might be expected to retain dentine in teeth, denticles or tubercles, and Gross (1962) has recognized what may be pulp cavities in the denticles of *Stensioella*, suggesting that they were made of dentine. Lower Devonian Rhenanida have not been studied histologically, but the Middle Devonian members have semidentine superficially. Ptyctodontida have dentine in their tooth plates (Ørvig, 1957), the only occurrence of this tissue in later Placodermi.

The problem of dermal bone origins in placoderms is complicated by the presence of tesserae in certain groups—the Rhenanida, Acanthothoraci, Lower Devonian Petalichthyida, and possibly Stensioellida. Since tesserae occur mostly in early

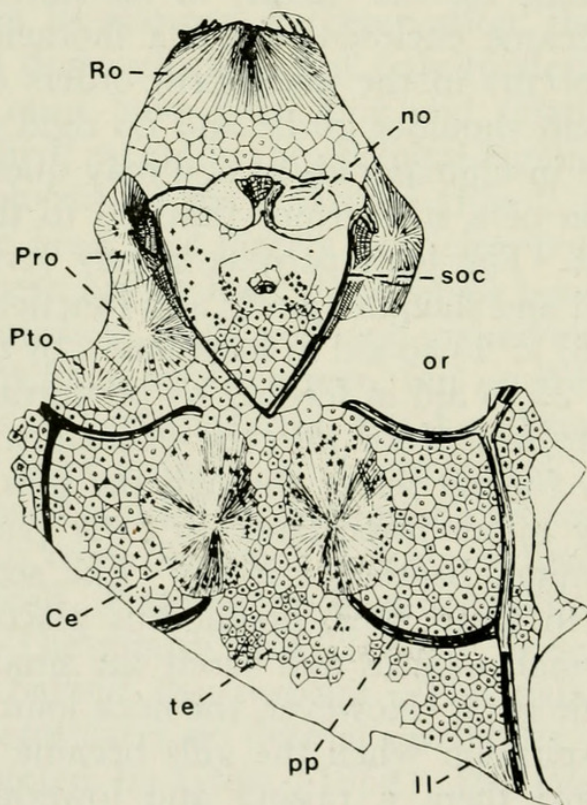


Figure 3. *Radotina kosorensis*, dorsal view of incomplete cranial roof, $\times 0.9$, from Gross, 1958. Ce, central plate; ll, main lateral line; no, nasal opening; or, orbit; pp, posterior pit line; Pro, preorbital plates; Pto, post-orbital plate; Ro, anterior plate perhaps homologous to rostral or pre-median; soc, supraorbital sensory canal; te, tesserae.

forms, they are probably a primitive character, as has been maintained by Gross (1959). He has shown in *Radotina* (Fig. 3, te) that tesserae are thin, superficial structures that occur for the most part between bones, and that do not fuse together to form bones or even their superficial parts. In Rhenanida they are homologous to the scales that cover the body (Gross, 1963). They may be considered remnants of the dermal scales that were the only exoskeleton of ancestral placoderms, and as such are comparable in general to chondrichthyan scales. When bones first appeared in placoderms, they apparently arose deeper in the dermis quite independently of the tesserae and also of the lateral line system. The depth of their formation may account for the absence of any true dentine on the bones of typical Placodermi, and also for the fact that the course of the lateral line canals in Rhenanida and Acanthothoraci is not dependent on the dermal bones. Presumably the close relationship between the dermal bones and lateral line canals was secondary and, as suggested by Parrington (1949), the precursors of dermal bones may later have come to influence the direction of growth of lateral line primordia.

The pattern of dermal bones on the skull differs in the various groups of Placodermi yet shows enough similarities to suggest that, in most cases at least, it was derived from a common ancestral pattern. In Stensioellida the pattern is hardly developed for in the cranial roof there is only a median bone identified as a postpineal and paired bones that resemble centrals (Fig. 2A, Ce). Likewise in the Lower Devonian Rhenanida the cranial roof largely lacks dermal bones, though laterally there are suborbitals, submarginals and possibly paranuchals. In all other groups, except perhaps the poorly known Pseudopetalichthyida, the skull bones are developed according to a similar pattern. This pattern includes some or all of the following: 1) median nuchal, postpineal, pineal and rostral; 2) paired centrals over the otic region; 3) paired paranuchals and marginals carrying the main lateral line forward; 4) paired pre- and postorbitals over the orbits; 5) paired postnasals beside the nostrils; and 6) paired suborbitals, postsuborbitals, postmarginals and submarginals in the cheek and opercular region. Much of this pattern is becoming established in the Acanthothoraci (Fig. 3), while in Ptyctodontida, Arthrodira, Phyllolepidi and Antiarcha there are relatively stable cranial bone patterns, though with characteristic modifications in the various subgroups (Figs. 4-5).

PHYLETIC HISTORY OF PLACODERMI

In my theory of placoderm evolution, as presented pictorially in the phylogenetic chart (Fig. 6), particular emphasis is given to the dermal shoulder girdle. This remains short in Stensioellida, Pseudopetalichthyida, Rhenanida and Ptyctodontida, while the first steps towards lengthening it to form a thoracic shield are seen in some Acanthothoraci (Palaeacanthaspidae and Koly-maspidae), where posterior laterals and posterior dorsolaterals are added (Fig. 1C, Pl, Pdl). The second stage is the development of a ventral shield composed, in addition to interolaterals, of anterior and posterior ventrolaterals and anterior and posterior medioventrals; this is seen in Petalichthyida and Arthrodira. Early members of the latter group go one step further in uniting the posterior parts of the ventral and lateral shields behind the pectoral fins to enclose pectoral fenestrae (Fig. 5B-F, pf). The Antiarcha have the longest thoracic shield and have a posterior median dorsal incorporated in it (Fig. 5K, Pmd).

There are three major phylogenetic problems that require special mention, the first involving the Petalichthyida (Fig. 5A). Their thoracic shield might have evolved quite independently from that of Arthrodira, in which case a relationship to Pseudopetalichthyida should be considered. However, since the latter group is so poorly known and the petalichthyid thoracic shield is so similar to that of Arthrodira, this theory has little to recommend it. Secondly, the petalichthyid thoracic shield may have arisen as a result of a posterior reduction of the lateral parts of the arthrodire shield. There is no evidence to support this, and in fact it is quite unlikely that the petalichthyid cranial roof was derived from the arthrodire type, so this theory is rejected. The third theory is that the petalichthyid thoracic shield represents an intermediate evolutionary stage, more advanced than in Acanthothoraci in the possession of a ventral shield, but less advanced than early Arthrodira as the pectoral fins are completely behind the shield. This theory seems most probable and is supported by the retention of certain primitive characters in Petalichthyida, such as the two pairs of paranuchals and tesserae on the cheeks.

The evolutionary position of *Phyllolepis* (Fig. 4) is also controversial because, though it has a moderately long thoracic shield, it lacks posterior laterals and posterior dorsolaterals. Is the absence of these plates the result of a phyletic reduction, or did *Phyllolepis* branch off the arthrodiran ancestral line before

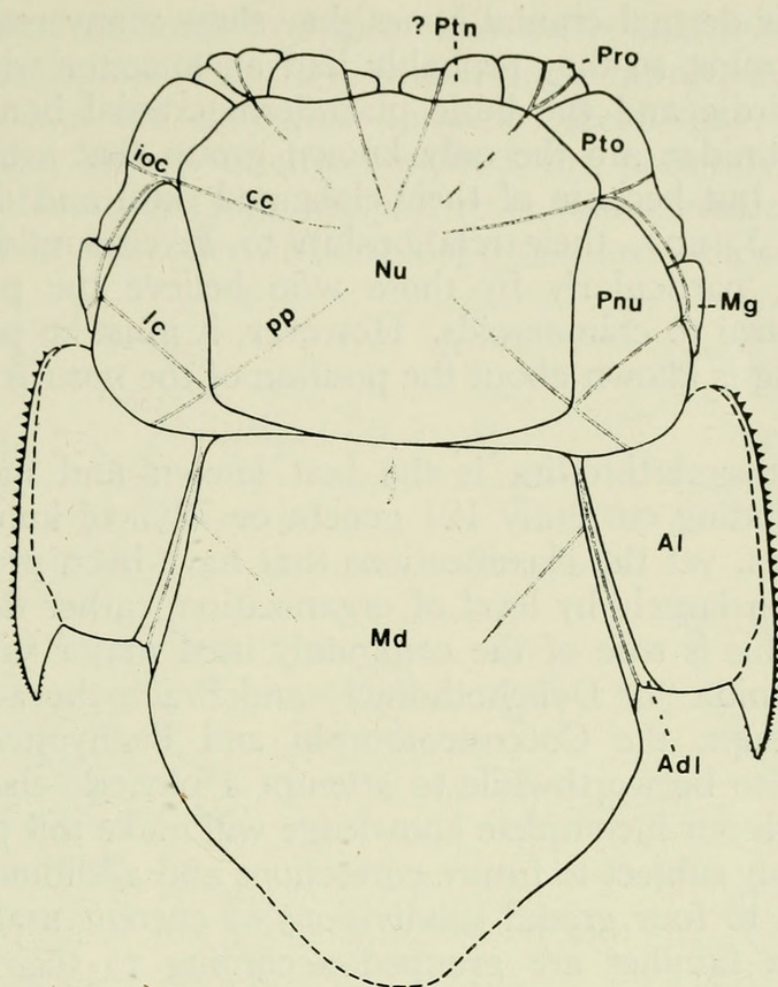


Figure 4. *Phyllolepis orvini*, dorsal view of cranial and thoracic shields, $\times 0.2$, modified from Stensiö, 1936. Adl, anterior dorsolateral plate; Al, anterior lateral plate; cc, central sensory canal; ioc, infraorbital sensory canal; lc, main lateral line; Md, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; Pnu, paranuchal plate; pp, posterior pit line; Pro, pre-orbital plate; ? Ptn, possible postnasal plate; Pto, postorbital plate.

these plates were acquired? Since this genus is known only from the late Famennian there is little evidence to decide this question. However, the genus *Antarctaspis*, known only from an imperfect cranial roof, seems in some ways to bridge the gap between *Phyllolepis* and primitive Actinolepina, which suggests that Phyllolepina were derived from the latter by a reduction of the thoracic shield, and, of course, by considerable modification of the cranial roof.

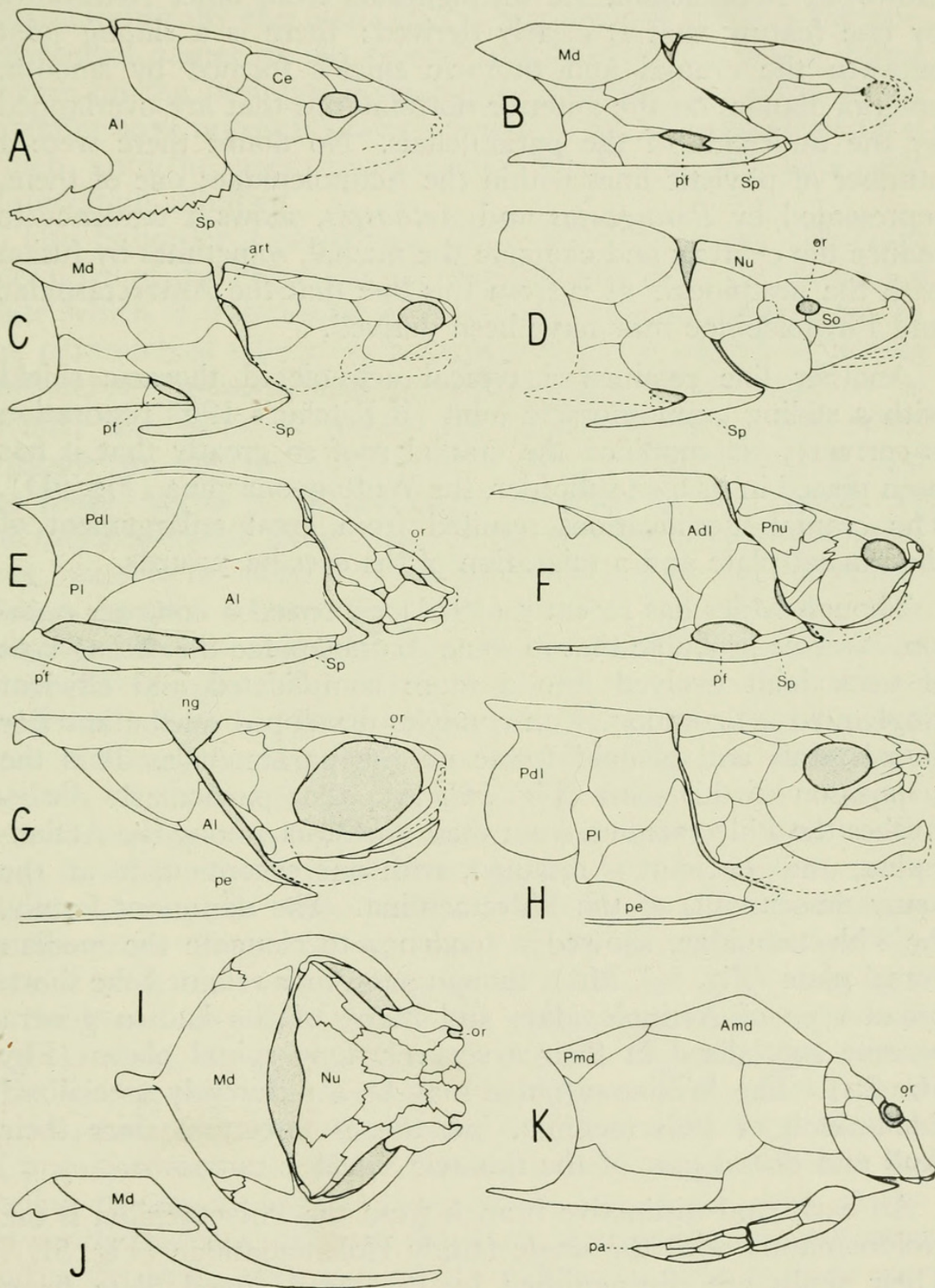
The Ptyctodontida (Fig. 1D) are a third phyletic problem. If it is accepted that their short dermal shoulder girdle is a primitive character and not the result of reduction, they cannot be derived from Arthrodira, Petalichthyida or some Acanthothoraci.

Yet in their dermal cranial bones they show many resemblances to these groups, so they probably had an ancestor with a short shoulder girdle and the basic placoderm cranial bone pattern. The Radotinidae are the only known group that satisfies these conditions, but because of their elongated skull and dorsal nostrils (Fig. 3, no), their relationship to Ptyctodontida will be questioned, particularly by those who believe the ptyctodonts were ancestral to chimaeroids. However, it must be pointed out that nothing is known about the position of the nostrils in ptyctodonts.

The Order Arthrodira is the best known and most varied group, including currently 121 genera or 72% of known placoderm genera, yet the classifications that have been proposed for it have been largely by level of organization, rather than phylogenetic. This is true of the commonly used major subdivisions, the Arctolepida (or Dolichothoraci) and Brachythoraci (and its two subgroups, the Coccosteomorphi and Pachyosteomorphi). It appears to be worthwhile to attempt a phyletic classification, even though our incomplete knowledge will make this provisional and certainly subject to future corrections and additions. Instead of the two to four gradal subdivisions of current usage, the 21 arthrodiran families are grouped according to their probable common ancestry in 8 suborders.

Figure 5. Cranial and thoracic shields of Placodermi with elongated shoulder girdles, lateral views except I. A, Order Petalichthyida (*Lunaspis heroldi*, after Stensiö, 1963); B, Suborder Actinolepina (*Sigaspis lepidophora*, after Miles, 1973); C, Suborder Phlyctaeniina (*Phlyctaenius acadica*, after Heintz, 1934 and Westoll and Miles, 1963); D, Suborder Wuttagoonaspina (*Wuttagoonaspis fletcheri*, attempted restoration based on figures of Ritchie, 1969 and 1973); E, Suborder Holonematina (*Holonema westolli*, after Miles, 1971); F, Suborder Coccosteina (*Coccosteus cuspidatus*, after Miles and Westoll, 1968); G, Suborder Pachyosteina (*Rhinosteus parvulus*, after Stensiö, 1963); H, Suborder Brachydeirina (*Leptosteus bickensis*, after Stensiö, 1963); I-J, Suborder Heterostiina (*Heterostius ingens*); I, dorsal view of cranial and thoracic shields, after Heintz, 1929; J, lateral view of thoracic shield, after Heintz, 1929; K, Order Antiarcha (*Pterichthyodes milleri*, after Traquair, 1914). Adl, anterior dorsolateral plate; Al, anterior lateral plate; Amd, anterior median dorsal plate; art, cranio-thoracic joint; Ce, central plate; Md, median dorsal plate; ng, nuchal gap; Nu, nuchal plate; or, orbit; pa, pectoral appendage; Pdl, posterior dorsolateral plate; pe, pectoral emargination; pf, pectoral fenestra; Pl, posterior lateral plate; Pmd, posterior median dorsal plate; Pnu, paranuchal plate; So, suborbital plate; Sp, spinal plate.

The first suborder to appear and surely the most primitive is the Actinolepina (Fig. 5B), with a single family, the Actinolepidae. It has the elongated thoracic shield that typifies early Arthrodira, and it is closed behind the pectoral fins to form pectoral fenestrae (Fig. 5B, pf), as is characteristic of primitive members of the order. The spinal plates are well developed and



projecting but not greatly elongated (Fig. 5B, Sp), the pectoral fins are narrow-based, the median dorsal short and broad (Fig. 5B, Md), the endocranium platybasic, the orbits small and anterior, and the rostral region containing the nasal capsules sometimes separately ossified. All of these characters are primitive within Arthrodira, though some are advanced for Placodermi. However, Actinolepina are distinguished from other Arthrodira by one feature that is clearly derived: there is a sliding joint between the cranial and thoracic shields formed by smooth, anterior flanges on the anterior dorsolaterals that are overlapped by the underside of the paranuchals. No doubt there were a number of phyletic lines within the Actinolepidae; one of them, represented by *Baringaspis* and *Aethaspis*, shows a tendency to reduce the centrals and elongate the nuchal, sometimes by fusion with the postpineal. It is from this line that the Antarctaspidae and Phyllolepidae may have been derived.

Another line retained a typical actinolepid thoracic shield with a sliding craniothoracic joint (if Ritchie's 1969 restoration is correct), yet modified the cranial roof so greatly that it has been placed in its own suborder, the Wuttagoonaspina (Fig. 5D). The cranial modifications resulted from great enlargement of the nuchal plate and a migration of the eyes backwards.

Though Miles has recently (1973) expressed a contrary opinion, it seems probable that in some Actinolepidae the sliding type of neck joint evolved into a more complicated and efficient ginglymoid articulation, with condyles developed on the anterior dorsolaterals and glenoid fossae on the paranuchals. It is the acquisition of this joint (Fig. 5C, art) that particularly distinguishes the Phlyctaeniina from their ancestors among the Actinolepina, and the joint is retained, with one exception, in all the many descendants of the Phlyctaeniina. The dominant family, the Phlyctaeniidae, showed a tendency to elongate the median dorsal plate (Fig. 5C, Md), though one genus retained the short, broad type of Actinolepidae, and many of the known genera became specialized in their excessively long spinal plates (Fig. 5C, Sp). The Williamsaspidae may be a differently specialized side-branch of Phlyctaeniina, but this is uncertain since their skull and dorsal part of the thoracic shield is unknown.

An early and distinctive branch from the Phlyctaeniina is the Holonematina with the single family Holonematidae (Fig. 5E). Their skulls are distinguished by the large pineal plate lying

between the preorbitals, the orbits that deeply notch the cranial roof, and the moderately small, subtriangular nuchal. The thoracic shield remains long or is even lengthened, and retains the contacts between the lateral and ventral shields behind the pectoral fins. The anterior laterals (Fig. 5E Al) tend to lengthen, crowding the pectoral fins backwards. The posterior laterals are large (Fig. 5E, Pl), and there is a large anterior medioventral. Characteristically the main lateral line extends towards the posteroventral corner of the anterior dorsolateral and has a strong flexure on the posterior dorsolateral. Primitive members of the suborder have previously been referred to the *Groenlandaspidae* which, until the recent discoveries of Ritchie (1974), have been of uncertain affinities.

The Suborder *Coccosteina* (Fig. 5F), the most important derivative of the *Phlyctaeniina*, may be recognized by the nuchal plate which is trapezoidal in shape and widened posteriorly, by the paranuchals which are narrow posteriorly except for strong postnuchal processes, and by the centrals which tend to be divided into anterior, lateral and posterior lobes. The orbits typically are directed more laterally than in *Phlyctaeniidae*, and the pineal comes to lie posteriorly between the preorbitals. In the thoracic shield, the median dorsal, which is primitively rather long, tends to be shortened; the pectoral fenestrae are lengthened though usually remain closed posteriorly (Fig. 5F, pf). The spinals tend to be reduced (Fig. 5F, Sp), and the ventral shield is typically lengthened. These characters are well displayed by the Family *Coccosteidae*, which is also distinguished by the post-branchial laminae projecting from the mesial faces of the anterior laterals, by the course of the main lateral lines parallel to the ventral exposed edges of the anterior dorsolaterals, and by the long, slender suborbital processes of the suborbital plates. The *Gemuendenaspidae* show their relationship to the *Coccosteina* in the shape of the dermal bones of the posterior part of the cranial roof, but retain a number of primitive characters, such as the broad, depressed shield, the long, narrow median dorsal, and the short, deep suborbital processes on the suborbital plates. The *Buchanosteidae* also have the characteristic nuchal and paranuchal plates of *Coccosteina*, but show a peculiar mixture of primitive and specialized characters: they are primitive in not having the rostral capsule fused to the rest of the skull, in the forwardly directed orbits, in the short, deep suborbital processes, and in the short, wide preorbitals; but they are distinctively spe-

cialized in the long postmarginals, the unusually shaped anterior laterals which bend inwards to form postbranchial laminae, and in the short, nonprojecting spinals. A specialized family known only in the Frasnian, the Pholidosteidae, is distinguished by its enlarged eyes and elongated orbitotemporal region, by having the cheek bones rigidly sutured to the cranial roof, and by their long, laterally projecting spinal plates carried by protruding wings of the anterior laterals and anterior ventrolaterals. This family must have diverged early from the Coccosteidae before the reduction of the spinals. The Homostiidae (including both typical Homostiidae and Euleptaspidae) show a relationship to the Coccosteina in the characteristically shaped nuchal, paranuchals, and centrals, and their appearance in the Siegenian suggests an origin from early members of the suborder. The family includes large forms with a broad, depressed head and body, and is characterized particularly by the great elongation of the bones of the posterior half of the cranial roof. The advanced Homostiidae are highly specialized in the dorsal position of the eyes and in the great shortening of the thoracic shield, but retain some primitive characters such as a narrow nuchal gap and tuberculated dermal bones. Finally, the Rachioosteidae are shown to be Coccosteina by the shape and proportions of the nuchal, paranuchals and centrals, but have reduced the lateral and ventral thoracic shields even more than in some advanced Pachyosteina, and have also lost the ornamentation on their dermal bones.

The Pachyosteina (Fig. 5G), the dominant placoderms of the Upper Devonian, are probably, though not certainly, a monophyletic group derived from the Coccosteidae. They are characterized particularly by a thoracic shield shortened dorsally and laterally, anterior laterals reduced ventrally to slender bones (Fig. 5G, A1), reduced or lost spinals, and pectoral fenestrae opened behind so that the bases of the pectoral fins could be lengthened. These trends were initiated in their coccosteid ancestors and are paralleled in some specialized families of Coccosteina. They differ from Coccosteina in having the posterior margin of the skull roof embayed, in the wider nuchal gap between the cranial and thoracic shields (Fig. 5G, ng), in the shorter nuchal plate with a pointed or rounded anterior margin and a concave posterior margin, and generally in the absence of prominent lobes on the central plates. They also show a tendency to lose tuberculation on the dermal bones.

Many Pachyosteina retain primitive, coccosteid-like characters among which are small orbits, long, loosely attached cheeks, a small nuchal gap, a relatively long median dorsal, rudimentary spinal plates, and tuberculated dermal bones. Another primitive character is an anteroventrally sloping neck-slit between the head and thoracic shield. This sloping neck-slit is retained by the Selenosteidae (Fig. 5G) which indicates that they were an early side-branch of the suborder, even though they do not appear until the Upper Frasnian. In many other respects the family was highly specialized, especially in the weak jaws, and in the orbits which had enlarged so much that the marginal plates formed their posterior boundaries and the cheeks were greatly shortened.

The Bungartiidae (new family), known only from a single Upper Famennian genus, *Bungartius*, is another family that retains the sloping neck-slit, but is peculiarly specialized in other ways. The preorbital part of the skull is greatly elongate, the nuchal gap is much enlarged due to the posterior projection of the paranuchal plates, and the jaws are shearing.

The Mylostomatidae are among the most specialized of Arthrodira with their durophagous jaws and their short, broad, flat shield. Their origin is obscure; they show some resemblances to Selenosteidae, but if *Tafilalichthys* is correctly referred here, it is possible that they were independently derived from primitive Pachyosteina.

Three families of Pachyosteina are distinguished by having the cheeks and gill covers extended posteriorly, resulting in a nearly vertical neck-slit. This may also give rise to a sharp angulation in the anterior lateral plates where they bend around and under the posterior edges of the gill covers. The first to appear, and in fact the earliest Pachyosteina, are the Dinichthyidae, which are mostly very large, broad-skulled forms with powerful, trenchant jaws bearing strong anterior cusps on the anterior supragnathals and infragnathals. The Leiosteidae are smaller forms with narrower skulls that are deeply embayed behind, and with crushing jaws. The third family, the Trematosteidae, has rather large orbits, long preorbital and short central plates, a postpineal fenestra, strong shearing jaws, and a tendency to deepen the cheeks and lower the jaw articulations. They are possibly related to Leiosteidae, but could not have been derived from known genera.

The last family referred to the Pachyosteina is the Titanichthyidae, which were highly specialized giants known only from the Famennian. Their shield is broad and depressed, and their

jaws are long and slender, without teeth, cusps or shearing edges. Their origin is obscure but possibly lies in the primitive *Dinichthyidae*.

The two remaining suborders of *Arthrodira* include forms that have generally been referred to *Brachythoraci* or *Pachyosteomorphi*. The *Heterostiina*, including the single family *Heterostiidae* (Fig. 5I-J), would at first sight appear to belong to *Pachyosteina*. Like the *Homostiidae* and *Titanichthyidae*, it includes large forms with a broad, depressed head and body, but is distinguished by a characteristic posterior widening of the cranial roof. The latest forms have a very short thoracic shield (Fig. 5J) in which the anterior laterals send a long, tusklike process to meet the ventral shield, the latter a single plate lying far anterior under the head. Since the *Heterostiidae* occur in the Middle Devonian, it is not surprising to find that they retain a number of primitive characters. Among these are a relatively unspecialized cranial roof, a small nuchal gap, small anteriorly placed orbits that face anterolaterally (Fig. 5I, or), suborbital plates with short suborbital processes and long blades, and tuberculated dermal bones. However, in spite of their early appearance, they show no coccosteid characters and this, together with their phlyctaeniid orbits and suborbital plates, suggests for them a precoccosteid origin. If this is true, they are parallel to *Pachyosteina*, and thus referable to their own suborder.

The last suborder, the *Brachydeirina* (Fig. 5H), includes four genera grouped in two families, the *Leptosteidae* and *Brachydeiridae*, though the three genera of the second family are so distinctively specialized that each is commonly placed in a family of its own. In contrast to all other *Arthrodira*, the head and body are laterally compressed, high and elongate. In contrast to *Pachyosteina*, the lateral walls of the thoracic shield are not greatly reduced and large posterior laterals and posterior dorso-laterals are retained (Fig. 5H, Pl, Pdl). In spite of the long thoracic shield, deep pectoral emarginations (Fig. 5H, pe) separate the lateral and ventral shields except anteriorly, indicating probably that the pectoral fins were long-based. The nuchal gap is never enlarged and in one genus, *Synauchenia*, the cranial and thoracic shields have become sutured together, eliminating the neck joint completely. The *Leptosteidae* (Fig. 5H) have smaller orbits bounded posteriorly by postorbitals and suborbitals, and a very long, slender thoracic shield. The *Brachydeiridae* have larger orbits bounded posteriorly by marginals, and a

shorter thoracic shield in which the ventral part may be reduced. The long thoracic shield of *Brachydeirina* indicates a derivation from a very primitive *Coccosteina* or perhaps even from one of the *Phlyctaeniidae*.

The last order, the *Antiarcha* (Fig. 5K), includes probably the most highly specialized of Placodermi. The thoracic shield is greatly elongated and has incorporated a second median dorsal plate (Fig. 5K, Pmd) behind the anterior one. Instead of pectoral fins, they have peculiar, usually jointed appendages, covered with small dermal plates (Fig. 5K, pa). Though often considered to be modified fins, these appendages were more probably derived from arthrodiran spinal plates. Their skulls, with their dorsal eyes and nostrils and large anterior premedian plate, are so modified that it is difficult to compare them with those of *Arthrodira*. Although antiarchs have been reported in China from beds that are supposed to be Lower Devonian, their first certain record is Eifelian. The first to appear are typical members of the order and so there are no intermediate forms to relate them to more typical placoderms. The elongate thoracic shield suggests an origin from primitive *Arthrodira*, and since their exoskeletal craniothoracic joint was certainly independently acquired, their ancestors probably are to be sought among *Actinolepidae*.

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APPENDIX — CLASSIFICATION OF PLACODERMI

Class Pisces

Subclass Placodermi

- | | |
|----------------------------------|--------------------------------|
| Order Stensioellida | Family Stensioellidae |
| Order Rhenanida | Family Asterosteidae |
| Order Pseudopetalichthyida | Family Paraplesiobatidae |
| Order Ptyctodontida | Family Ptyctodontidae |
| Order Acanthothoraci | Family Palaeacanthaspididae |
| | Family Radotinidae |
| | Family Kolymaspididae |
| Order Petalichthyida | Family Macropetalichthyidae |
| Order Arthrodira | |
| Suborder Actinolepina nov | Family Actinolepidae |
| Suborder Wuttagoonaspina | Family Wuttagoonaspididae |
| Suborder Phlyctaeniina | Family Phlyctaeniidae |
| | Family Williamsaspididae |
| Suborder Holonematina | Family Holonematidae |
| | (including Groenlandaspididae) |
| Suborder Coccosteina | Family Gemuendenaspididae |
| | Family Buchanosteidae |
| | Family Coccosteidae |
| | Family Pholidosteidae |
| | Family Homostiidae |
| | (including Euleptaspididae) |
| | Family Rachiosteidae |
| Suborder Pachyosteina | Family Dinichthyidae |
| | Family Titanichthyidae |
| | Family Leiosteidae |
| | Family Trematosteidae |
| | Family Mylostomatidae |
| | Family Selenosteidae |
| | Family Bungartiidae nov. |
| Suborder Heterostiina | Family Heterostiidae |
| Suborder Brachydeirina nov. | Family Brachydeiridae |
| | Family Leptosteidae |
| Order Phyllolepidida | |
| Suborder Antarctaspina | Family Antarctaspididae |
| Suborder Phyllolepina | Family Phyllolepididae |
| Order Antiarcha | Family Bothriolepididae |
| | Family Asterolepididae |
| | Family Sinolepididae |

Figure 6. Phylogenetic chart of Placodermi. Each branch represents a family except in Acanthothoraci which includes three families. The width of the branches is determined by the number of genera. →



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