THE HAPLOLEPIDAE, A NEW FAMILY OF LATE CARBONIFEROUS BONY FISHES

A STUDY IN TAXONOMY AND EVOLUTION

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INTRODUCTION

THERE HAS BEEN MUCH RESEARCH during the past two decades on the fossil fishes of the old "family" Palaeoniscidae. These fishes were once thought to be a fairly homogeneous group, with many points in common, e.g., the heterocercal tail, a particular microscopic structure of the scales, a common ground plan of cranial anatomy, and certain features of fin structure, and they undoubtedly represent the most generalized among the actinopterygian fishes. It has now for some time been realized that many different groups are present in this assemblage, and the recent brilliant series of works on Triassic Actinopterygii by Stensiö (1921, 1925, 1932), Brough (1931, 1933, 1934, 1936, 1939), White (1932, 1933), Piveteau (1934), Wade (1935, etc.), Nielsen (1936), and Berg (1941), among others, has shown the great diversity of forms apparently modified from the more generalized structure of the earlier fishes. Brough (1931, 1936, etc.) has emphasized the important radiation of these modified forms in the Triassic period. Certain peculiar pre-Triassic forms have, however, been described already, and these indicate a considerable variability in structure—e.g., *Tarrasius*, Lower Carboniferous (Moy-Thomas, 1934; Moy-Thomas and Dyne, 1938, p. 487); *Phanerorhynchus*, Upper Carboniferous (Gill, 1923a); *Aeduella*, Lower Permian (Westoll, 1937b); the remarkable deep-bodied *Dorypterus* (Gill, 1925; Westoll, 1941) and a few other forms—and the most primitive "holostean," the semionotid *Acentrophorus* (Gill, 1923b), is already present in the Upper Permian. There is an indication, therefore, that the "Palaeoniscidae" (*sensu lato*) include many independently evolving groups.

Aldinger (1937) has attempted the classification of the various groups within the old "family"; he recognized seven families (but also included Catopteridae[1]), though he realized that many genera remained to be studied (see especially *op. cit.*, p. 376). Many of these families certainly represent very natural assemblages (e.g., the Palaeoniscidae, *sensu stricto*), but Aldinger's arrangement of the Actinopterygii in orders and suborders (*op. cit.*, pp. 377–378) is extremely questionable. Nevertheless he has succeeded in demonstrating the polyphyletic nature of these early Actinopterygii.

In recent years the problem of the ancestry of the "Holostei" has attracted considerable attention. Although *Acentrophorus*, a true semionotid, occurs in the Upper Permian, most attention has been paid recently to some Triassic forms—e.g., the Parasemionotidae (=Ospiidae) (Stensiö, 1932; Piveteau, 1934; Nielsen, 1936)—in which certain changes in, for example, the disposition of the jaws and opercular bones give some idea of the mode of origin of the "holostean" types. Brough (1936) has dealt particularly with these Triassic "Sub-Holostei" and recently (1939) has demonstrated the descent of amioid Holostei from the Parasemionotidae.

The writer has endeavored for some time to discover, among the smaller Palaeozoic Actinopterygii, possible ancestral types of the holostean structures. One interesting form (*Aeduella*) has already been described (Westoll, 1937b). The structure of *Canobius* (and other forms from the Lower Carboniferous) has been described by Moy-Thomas and Dyne (1938), and the importance of this fish has been emphasized by them and by Westoll (1937b). The present study deals with a well-defined family of small fishes from the Upper Carboniferous, comprising the genera *Haplolepis* Miller (syn. *Mecolepis* Newberry, *Eurylepis* Newberry) and *Pyritocephalus* Fritsch (syn. *Teleopterina* Berg). The various species allow important contributions to be made to the probable origin of certain holostean features, but there can be no doubt that this family represents a separate, probably sterile, stock, in which certain very peculiar morphological characters are developed.

ACKNOWLEDGMENTS

The writer is greatly indebted, for the privilege of examining and borrowing material of these genera, to Dr. William K.

[1] Catopteridae is not a valid name. *Catopterus* Redfield, 1837 (*non Catopterus* Agassiz, 1833) = *Redfieldius* Hay, 1902. See Berg, 1940, pp. 181, 404.

Gregory (American Museum of Natural History); Dr. E. I. White (British Museum of Natural History); Dr. E. C. Olson (Walker Museum, Chicago); Mr. T. Russell Goddard (Hancock Museum, Newcastle-on-Tyne); Prof. A. S. Romer (Museum of Comparative Zoölogy, Harvard); Dr. J. W. Jackson (Manchester Museum); Prof. M. R. Thorpe (Peabody Museum, Yale); Dr. A. C. Stephen (Royal Scottish Museum), and Dr. C. W. Gilmore (United States National Museum). He wishes also to thank Dr. E. I. White for many kindnesses. Dr. M. Steen (Edinburgh), Dr. T. Hallissey (Dublin), Prof. L. B. Smyth (Dublin), Prof. L. S. Berg (Leningrad), Dr. F. Němejc (Prague), and Prof. W. C. Darrah (Harvard) have been most kind in answering queries.

The author is indebted to the Department of Scientific and Industrial Research for a Senior Research Award (1934–1937), and to the Geological Society of London and the Royal Society of London for grants which enabled him to visit North America in 1937.

Finally, the author wishes to acknowledge gratefully the kindly help, advice, and criticism which he received during three years in the laboratories of Prof. D. M. S. Watson, F.R.S., where he enjoyed the use of magnificent comparative material.

PROVENANCE OF MATERIAL

The fishes described in this paper are derived from six well-known, vertebrate-yielding localities, three in the United States, two in England, and one in Czechoslovakia (Bohemia); an additional species is said to have been found at Loanhead, Scotland. Five of these occurrences are in cannel or impure cannel coals; one (Loanhead) is in a cannel interbedded with ironstone; and the last (Mazon Creek), in ironstone nodules. It is important to discover the stratigraphical relations of these deposits, and in this study the application of recent work on fossil floras has been valuable. The writer has used, as a standard of reference, the work of E. Dix (1934) on the floras of the Coal-Measures of the South Wales Coalfield. Criticism of this work has been expressed by certain other writers, but in the part of the Upper Carboniferous mostly involved in this study it seems to offer a clear and useful scale of reference, against which stratigraphical horizons of other localities can be checked. The non-marine lamellibranch succession is also useful in Britain.

Newsham, Northumberland

The "cannel" associated with the Low Main Coal of Newsham has yielded an extremely rich and varied vertebrate fauna. The seam occurs about midway in the Middle or Main Productive Coal-Measures of Northumberland, and is placed by Hopkins (1928, 1929, 1930) and Trueman (1933) very near the top of the *modiolaris* zone of the non-marine lamellibranch succession. A similar position in South Wales would indicate a horizon near the base of Dix's floral zone E.

Longton, Staffordshire

The roof of the Ash Coal at Longton has yielded a large vertebrate fauna; the John Ward collection is very extensive. The coal, about 150 feet above the Gin Mine marine band, is in the *similis-pulchra* zone of the non-marine lamellibranch succession (Gibson, 1925, fig. 5, p. 23; and Trueman, 1933, folding table). It is thus some 800 feet higher than the horizon in this coalfield corresponding to the Low Main at Newsham. According to Dix (1934, fig. 1), the beds in the corresponding lamellibranch zone of South Wales include the Cefn Coed marine band, regarded as the equivalent of the Gin Mine, and are in the floral zone F.

Mazon Creek, Grundy County, Illinois

The famous ironstone-nodule horizon.

Cannelton, Beaver County, Pennsylvania

An impure shaly cannel.

Linton, Jefferson County, Ohio

A shaly cannel.

These three American localities may be discussed together. The Pennsylvanian in the Appalachian region concerned is divided as follows:

Pennsylvanian	Dunkard (Permian in part)	
	Monongahela	
	Conemaugh	
	Alleghany	Freeport group (Linton)
		Kittanning group (Cannelton, Mazon Creek)
		Brookville or Clarion group
Mississippian	Pottsville	

Prof. William C. Darrah of the Botanical Museum, Harvard, has very kindly given me palaeobotanical details concerning the stratigraphical position of these beds. According to his information the Mazon Creek nodules include the following plants:

Neuropteris decipiens Lesquereux (group *scheuchzeri-macrophylla*)
Neuropteris rarinervis Bunbury
Neuropteris vermicularis Lesquereux
Pecopteris lamuriana Heer
Pecopteris unita Brongniart
Pecopteris arborescens Schleiden
Alethopteris sullivanti Lesquereux
Alethopteris serlii

In a letter of March 28, 1938, Professor Darrah writes: "This floral association is clearly Westphalian C-D, being a '*Neuropteris-Pecopteris*' association. It is not quite as 'high' as Radstockian because of the abundant 'earlier' species: *N. rarinervis*, *A. sullivanti* and persistent Lepidodendrids. At Linton, however, the association is a more typically Radstockian with numerous pecopterids: *P. cisti*, *oreopteridea*, *unita*, *hemitelioides*, also *Neuropteris scheuchzeri* and *N. ovata*, and *Alethopteris serlii-grandini* (of Crookall) = *A. pennsylvanica* in part.

"If we convert all of this into the terminology of Doctor Dix: the Linton flora is 'H' and the Mazon Creek 'G-H.' In America, only 150 meters of conformable beds separate the two floras."

After a careful consideration of these authoritative lists the writer ventures to suggest a very slightly higher correlation on Dix's scheme. In the Mazon Creek flora, forms such as *Asterotheca* (*Pecopteris*) *lamuriana* Heer (dominant in I), *A. arborescens* Schleiden (max. in H-I) and *A. serli* (max. H) may outweigh the persistent "lower" elements such as *A. rarinervis* (E-H, max. in G); a horizon in floral zone H is perhaps indicated. Similarly the Linton flora contains such "high" elements as *Pecopteris* (*Ptychocarpus*) *unita* (H-I), *Asterotheca hemitelioides* (I), and *N. ovata* (H-I), which would seem to be consonant with a horizon high in floral zone H, or perhaps better, H-I.

Cannelton lies about 15 miles northeast of Linton, and the vertebrates occur in the roof of the Middle Kittanning coal. This horizon is a little higher than that of Mazon Creek; it may confidently be ascribed to floral zone H.

Nýřany (=Nürschan), Czechoslovakia

The famous "cannel" from this locality has yielded a large fauna of aquatic vertebrates described by Fritsch (1879 on); the amphibians have recently been redescribed by Steen (1938). The authority on the palaeobotanical dating of these beds is F. Němejc. He shows (1932) the Nýřany coal group to be separated by marked stratigraphical break from the underlying Radnice group (of Westphalian C age, corresponding in position to Dix's zone G), and to be mainly of uppermost Westphalian age, extending into the lowermost Stephanian. In the text Němejc shows the Nýřany group to be equivalent to the upper part of the Assize de la Houvre and the very base of the French Stephanian (=floral zone H-I of Dix's table, 1934, p. 829). Němejc's correlation of the Nýřany beds with high Radstockian measures was made before Dix's work on the floral assemblages of those strata (1934). It seems probable that the Nýřany coal group can best be placed in floral zone H or H-I.

Loanhead, Midlothian

The "Loanhead No. 2 Ironstone" or "Borough Lee Ironstone" has yielded almost 40 species of vertebrates; most of the fishes were described by Traquair. Among the species listed by Traquair in a summary paper (1903, pp. 695, 700) is "*Eurylepis scoticus* Traq." The writer has been unable to trace either description or material of this species, which must be treated as a *nomen nudum*. Most of the fishes from this locality occur in an impure "cannel" of Lower Car-

boniferous age; the exact horizon is in the Edge Coals in the Scottish Carboniferous Limestone Series. These strata are below the Roslin Sandstone, but are not improbably equivalent to a high portion of the Bowland Shales and the lower part of the Assize de Chokier. Other references to "*Eurylepis*" and *Pyritocephalus* are erroneous (p. 14). To sum up, the material to be described in this paper comes from various horizons in the Westphalian (and possibly also the very lowest Stephanian), as shown in table 1.

TABLE 1

STRATIGRAPHICAL RELATIONS

STEPHANIAN	Floral zone I	
		Linton, Nýřany
	Floral zone H	Cannelton
		Mazon Creek
	Floral zone G	
WESTPHALIAN	Floral zone F	Longton
	Floral zone E	Newsham
	Floral zone D	
	Floral zone C	
NAMURIAN	Floral zone B	

GENERAL HISTORY OF INVESTIGATION

It is convenient to set out briefly the history of the literature on the relevant parts of the fish faunas from each locality.

LINTON, OHIO

Newberry (1856) published the first account of the vertebrate fauna from this locality. He set up the genus *Mecolepis* for a group of eight species of "Palaeonisci," of which short diagnoses were given. The subsequent taxonomic history of these Linton fishes is given on page 13.

The following fishes from Linton will be described below:

Haplolepis corrugata (Newberry)
(? Syn. *Eurylepis striolatus* Newberry)
Haplolepis tuberculata (Newberry)
(Syn. *Mecolepis granulatus* Newberry
Mecolepis insculptus Newberry)
Haplolepis ovoidea (Newberry)
(Syn. *Mecolepis ornatissimus* Newberry
Eurylepis minimus Newberry
Eurylepis macrops Newberry, MS
?*Mecolepis serratus* Newberry)
Pyritocephalus lineatus (Newberry)

NEWSHAM, NORTHUMBERLAND

Hancock and Atthey correctly recognized (1868a, p. 96; 1868b, p. 358) "a specimen or two of what we take to be a species of *Eurylepis*, Newberry," in their collections from Newsham. This acute observation, before the publication of figures of "*Eurylepis*," was confirmed later by Traquair (1903, pp. 703–704) who referred the material to his species *Eurylepis anglica*, but the material has never been described. Recently the writer has discovered other material, including remains of *Pyritocephalus;* these were mentioned in Westoll (1938b).

The following species will be described below:

Haplolepis attheyi, new species
Haplolepis sp. (aff. *H. anglica* Traquair)
Pyritocephalus rudis, new species

NÝŘANY, CZECHOSLOVAKIA

Fritsch described *Pyritocephalus sculptus* Fritsch in his great work on the Bohemian "Gaskohle" faunas (1893, pp. 86–87, fig. 280, pl. 115). The species was briefly noted by Westoll (1937a, pp. 575–576; 1938b) and by Moy-Thomas (1939, pp. 112–113, 126). This species will be described below.

MAZON CREEK, ILLINOIS

Newberry and Worthen (1870, p. 347, pl. 3, fig. 4) described a small fish from this locality as *Palaeoniscus gracilis* Newberry and Worthen. Later, Newberry (1889, pp. 212, 214–215) noted the presence of a specimen of *Eurylepis*, "probably not distinct from those found at Linton." Hay (1902) and Eastman (1902a, 1902b, 1903) referred *Palaeoniscus gracilis* Newberry and Worthen to the genus *Rhadinichthys*. Later, Eastman (1917, p. 274, pl. 9, fig. 4) described and figured a specimen of *Rh. gracilis* which was later discussed by Berg (1936), who referred it to a new genus and species, *Teleopterina improvisa* Berg, the type of a new family. Westoll (1938b) stated that *Teleopterina* is a synonym of *Pyritocephalus* Fritsch.

The following fishes from Mazon Creek will be described below:

Haplolepis cf. *tuberculata* (Newberry)
Haplolepis cf. *ovoidea* (Newberry)

Pyritocephalus gracilis (Newberry and Worthen)
(Syn. *Teleopterina improvisa* Berg)
Pyritocephalus comptus, new species

Cannelton, Pennsylvania

So far as the writer is aware no account of the fish material from Cannelton has been published. Moodie (1916) and Romer (1930, 1934) mention the locality and note the occurrence of fishes and of Amphibia resembling Linton forms.

A small fish from Cannelton is described below as *Haplolepis* aff. *ovoidea* (Newberry).

Longton, Staffordshire

A very large collection from the Ash Coal horizon of Longton and neighboring collieries was made by John Ward. Traquair (1894, p. 373, pl. 9, fig. 9) described and figured from his collections the type of *Eurylepis anglica* Traquair, an isolated skull roof. This was briefly mentioned later (Traquair, 1914, p. 182).

A single species, *Haplolepis anglica* (Traquair), will be described below.

COLLECTIONS USED

The material from Newsham is almost all preserved in the Hancock Museum, Newcastle-on-Tyne (Atthey and Dinning collections). The only member of the group from Longton is in the John Ward collection in the British Museum (Natural History).

Material from Linton was collected by Newberry and others, and the writer has examined the large collections in the American Museum of Natural History. Small parts of the Newberry collections in the British Museum (Natural History), Manchester Museum, Royal Scottish Museum, and the Museum of Comparative Zoölogy (Harvard), and the Lacoe collection in the United States National Museum have also been studied.

The most important collections from Mazon Creek are in Yale (Peabody Museum) and the United States National Museum; a single important specimen in the Walker Museum (Chicago) is described below.

The important collections from Nýřany in Prague have not been seen by the writer; a few specimens of *Pyritocephalus* have been studied in the British Museum (Natural History), Royal Scottish Museum, and United States National Museum; other specimens, purchased from Krantz of Bonn, are in the collections of Prof. D. M. S. Watson and the writer.

METHODS OF STUDY

The specimens from Mazon Creek are preserved in ironstone nodules, and frequently show something of the form of the uncrushed bones. The material from other localities is preserved in a flattened, crushed form in "cannel" coals, which would more properly be described as canneloid shales.

The Mazon Creek individuals are sometimes preserved only as external molds, but sometimes bone is preserved. The hollows left after removal of the bone during processes of fossilization are often filled with a coherent, rather dense white felt, which seems to be kaolin. Grains of pyrites and other minerals may occur in this white substance and may make preparation difficult.

The specimens preserved in the "cannels" are sometimes very well preserved, but often the heads are very much crushed. The bone is often quite opaque, even when immersed in xylol and examined in a strong light. In such circumstances the bone has usually been removed with dilute acid, and the sharp molds used for study.

The drawings of individuals have been prepared with the aid of a Leitz binocular magnifier and large Abbe-type camera lucida. The examination of such small specimens has been carried out entirely under binocular magnifiers.

The reconstruction of the dermal skulls has been done by two methods. The first is the well-known one of fitting together outline drawings of the bones, made to the same scale, and backed with beeswax, the "bones" being bent until optimum fit is obtained. The models so obtained were compared with carefully constructed drawings in side, top, and bottom elevation made on the ordinary principles of engineering drawing. The results were closely in agreement, and for species of which little material was available the latter method alone was used because of its greater ease.

The reconstructions of the whole fishes show important points of difference from

those of nearly all earlier writers, particularly in the attitude of the paired fins, discussed fully in a later section, and in the depth of the body. The former point necessitates three elevations to show the details. It is the writer's experience that almost all earlier reconstructions of palaeoniscoid fishes err in suggesting too great a depth. By selecting specimens in which the entire squamation of one flank, from mid-dorsal to mid-ventral line, has been preserved relatively undisturbed but flattened, it is possible to determine the girth of the fish at any point along the axis. The measurements obtained in this way for Haplolepidae agreed very closely with the reconstructed shape of the head.

For a list of abbreviations used in the text figures, see page 121 below.

SYSTEMATIC DESCRIPTION

IN THE FOLLOWING ACCOUNT the different species will be described in the order which seems most convenient, from the point of view of making clear their structural peculiarities, rather than in strict order of priority or stratigraphical occurrence.

GENUS HAPLOLEPIS MILLER

Haplolepis MILLER, 1892, p. 715.

Mecolepis NEWBERRY, 1856, *non* Duméril, 1851, p. 87.

Mekolepis NEWBERRY, 1857, *non* Duméril, 1851, p. 87.

Eurylepis NEWBERRY, 1857, *non* Blyth, 1854, p. 739.

GENOTYPE: *Mecolepis corrugata* Newberry, 1856.

The genus *Mecolepis* was set up by Newberry (1856) for a group of small "Palaeonisci" occurring at Linton, Ohio. The following species were named and provided with short diagnoses: *M. corrugatus*, *M. tuberculatus*, *M. granulatus*, *M. lineatus*, *M. ovoideus*, *M. ornatissimus*, *M. insculptus*, and *M. serratus*. In 1857 Newberry announced that "*Mekolepis*" was preoccupied and proposed the new title *Eurylepis* to cover the same group of species.

In 1873 Newberry gave the first illustrated account of the fauna and described the species in the following order: *Eurylepis tuberculatus*, *E. corrugatus*, *E. ovoideus*, *E. insculptus*, *E. ornatissimus*, *E. granulatus*, *E. lineatus*, *E. minimus*, *E. striolatus*. The two last mentioned were described for the first time. *Mecolepis serratus* was never mentioned or listed by Newberry after 1857, and the reasonable conclusion is that he had abandoned the species; the original diagnosis does not correspond to that of either of the two new species of 1873, *E. minimus* and *E. striolatus*.

In 1889 Newberry listed (p. 212) the species of *Eurylepis* found at Linton and added *E. macrops* to the 1873 list. No description of this species seems to have been published, but the intended type specimen has been studied by the writer. Later in the 1889 paper Newberry discussed the status of *Eurylepis lineatus* and proposed that it should be removed and probably referred to *Rhadinichthys* Traquair. The same course was followed by other workers; in this paper the species is placed in *Pyritocephalus* Fritsch. But Newberry further suggested that *Eurylepis corrugatus* should perhaps also be transferred to *Rhadinichthys*, because the two species concerned differed from other *Eurylepis* in having a linear ornament on the head bones and in having less specialized squamation. *Mecolepis corrugatus* was the first species to be described, and the diagnosis is recognizable; it must, therefore, be the genotype of *Mecolepis* Newberry, *non* Duméril, and consequently of *Eurylepis* Newberry.

In 1892 Miller pointed out that *Eurylepis* also was preoccupied and proposed the new genus *Haplolepis*, with *Mecolepis corrugata* Newberry as the genotype. This generic name has been used consistently by Hay, but the better-known *Eurylepis* is still used in some text books.

Newberry (1873, p. 348) recognized the difficulties of separating the Linton species of *Eurylepis*. "These differences have led to the creation of several species, but their distinctive characters can only be clearly seen where there is much good material in hand for comparison, and where the material is carefully scrutinized. . . . Whether some of these distinctions are not dependent upon age or sex we have not yet ascertained; but, since the characters that have served to distinguish the species are such as are usually regarded as having specific value, there has seemed no other way than to give them this value until such time as they may be found to shade into each other, and thus obliterate specific lines."

Smith Woodward (1891, pp. 448–449) discussed the material in the British Museum (Natural History); he mentioned most of Newberry's species and referred *Mecolepis insculpta* Newberry to the synonymy of *Eurylepis granulata* (Newberry), and followed Newberry in placing *M. lineatus* Newberry doubtfully in *Rhadinichthys*. The same course was followed by Hay (1902, p. 366, and 1929, p. 688), except that Miller's generic term *Haplolepis* was used in place of *Eurylepis*.

Hussakof (1908, pp. 74–75) mentioned the

type specimens of *Haplolepis corrugata* and *H. ornatissima*. Hussakof and Bryant (1919, p. 191) mentioned material of *Haplolepis* (*Eurylepis*) *tuberculata* and *H.* (*E.*) *granulata* and questioned the distinction of these species, remarking that "all the species of *Haplolepis* are in need of revision."

Westoll (1937b, 1938b) pointed out certain peculiarities of *Haplolepis*, basing his remarks principally on Linton material. He referred *Mecolepis lineatus* Newberry to the genus *Pyritocephalus*.

It should also be mentioned that Newberry's figure (1873, pl. 38, fig. 2) of "*Eurylepis tuberculatus*" has been reproduced in several editions of Zittel's text book and its translations.

Turning to other localities, Hancock and Atthey (1868a, p. 96; 1868b, p. 358) discussed some of their collections from Newsham and recorded "a specimen or two of what we take to be a species of *Eurylepis*, Newberry." This remarkably acute determination has proved to be correct. Traquair (1903, pp. 703–704) listed *Eurylepis anglica* Traquair from Newsham, but at least two species are recognized in this work.

Traquair (1894, p. 373, pl. 9, fig. 9; 1914, p. 182) described a small skull roof from Longton, Staffordshire, as *Eurylepis anglica* Traquair.

A species from the Loanhead No. 2 ironstone of Borough Lee, near Edinburgh, was mentioned by Traquair (1903, pp. 695, 700) as *Eurylepis scoticus* Traquair in a list of fishes from this locality. No description was ever published, and the specimen has not been traced; it is from a horizon very much lower than any other that has yielded *Haplolepis* and is best disregarded for the present.

Eastman (1908, p. 260), in his description of *Rhadinichthys devonicus*, mentions that "patches showing a considerable portion of the squamation of *Eurylepis* have been obtained from the Waverley black shale at Vanceburgh, Kentucky. Several specimens of this nature are to be seen in the State College collection at Lexington." In view of the early Mississippian age of these shales, this record is extremely doubtful.

The genus *Haplolepis* Miller is here regarded as including the following species:

Haplolepis corrugata (Newberry). Linton, Ohio
(Syn.? *Eurylepis striolatus* Newberry)
Haplolepis ovoidea (Newberry). . Linton, Ohio
(Syn. *Mecolepis ornatissimus* Newberry
Eurylepis minimus Newberry
Eurylepis macrops Newberry, MS
?*Mecolepis serratus* Newberry)
Haplolepis cf. *ovoidea* (Newberry) . . . . . Mazon Creek
Haplolepis aff. *ovoidea* (Newberry) . . . . . Cannelton
Haplolepis attheyi, new species. . Newsham
(Syn. *Palaeodopsis newshami*, Atthey, MS)
Haplolepis tuberculata (Newberry)
(Syn. *Mecolepis granulatus* Newberry . . . . . Linton, Ohio
Mecolepis insculptus Newberry)
Haplolepis cf. *tuberculata* (Newberry) . . . . . Mazon Creek
Haplolepis anglica (Traquair) . . Longton
Haplolepis aff. *anglica* . . . . . Newsham

Though all these species share many peculiar characters and are here retained within the genus *Haplolepis* (*sensu lato*), they show considerable variability in the structure of the cheek and skull roof and fall into two groups, each with a range of common characters, which may be regarded as subgenera. It is possible that these should be elevated to generic status, but they are here united in order to emphasize their remarkable resemblance. The subgenera are:

1. *Haplolepis* (*sensu stricto*), new subgenus, including *H. ovoidea* (Newberry), *H.* cf. *ovoidea* (Newberry), *H.* aff. *ovoidea* (Newberry), *H. corrugata* (Newberry), *H. attheyi*, new species.

2. *Parahaplolepis*, new subgenus, including *H. tuberculata* (Newberry), *H.* cf. *tuberculata* (Newberry), *H. anglica* (Traquair), and *H.* aff. *anglica* (Traquair).

Eurylepidoides socialis Case was described in 1935 from the Wichita formation and named because of the resemblance of the squamation to that of *Eurylepis* Newberry (=*Haplolepis* Miller). The fins and skull structure are quite different from those of *Haplolepis*, and the two genera are not at all closely related. (See also Westoll, 1937b, p. 575, footnote.) The writer has examined the type material of *Eurylepidoides socialis* at Ann Arbor, Michigan, and desires to thank Prof. E. C. Case for the privilege of access to his interesting collections.

The following generic diagnosis of *Haplolepis* (*sensu lato*) may be attempted: actinopterygian fishes of small size, rarely exceeding, and usually less than, 70 mm. in length. Head broad and short, with large orbit, no overhanging rostrum. Suspensorium almost vertical. Skull roof in certain species of normal "palaeoniscid" pattern; in others the "parietals" are not present, and the dermopterotics (=supratemporals or supratemporo-intertemporals) meet in the midline. Extrascapular series small. Premaxillaries are apparently dentigerous rostrals; nasal openings unlike those of typical "palaeoniscoids" but with anteromesial paired openings between nasal and premaxillary on each side. Maxillary with greatly modified cheek expansion, preopercular without well-developed anterodorsal shank. Quadratojugal may be present. Dentition strong in a few species, usually feeble. Opercular system curiously reduced, gulars few and enlarged; some tendency for division into separate dorsal and ventral flaps. Ornament of head bones somewhat variable. Cheeks and gulars with fairly strong, terraced rugae, skull roof with rugae or more rounded tubercles. Caudal pedicle deep and very short. Body shape stoutly fusiform, with broad head. Flattened venter between paired fins. Whole body covered by comparatively few rows of almost smooth, lustrous scales; anterior lateral-line scales characteristically very deep. Enlarged median scales only in front of each median fin. Hinder margins of scales usually entire, may be denticulated on anterior flank. Probably no peg-and-socket articulation. Anterior scale rows show abrupt change of direction at the ridge marking the junction of flank and flattened venter. Scales thin; cosmine layer well developed, ganoine layer thin, bony layer (isopedin) remarkably thin; details not known in most species.

Fins composed of few, well-separated rays in characteristic fan-like arrangement. Each ray is broad, segmented but not bifurcated. Anterior margins of each fin with well-developed fulcra which may not reach tip of fin. Tail completely heterocercal; caudal fin more or less triangular, with slightly concave free margin and poorly developed lower lobe only about half the length of the body lobe. Dorsal fin arising immediately above, or very slightly in front of, the anal. Pelvics nearer to pectorals than to anal; anal nearer to caudal than to pelvics (all distances measured from anterior insertions).

Three paired lateral lines with accessory lateral line on body in at least some forms. Ventral lateral line indicated by series of grooves in the scales of the flattened venter in front of the anal fin, and on the cleithrum. Main lateral-line group represented both by grooves (the accessory lateral line), on the scales of the "lateral-line series," also by lunate pores opening irregularly. Dorsal lateral line rising from anterior flank to region of dorsal fin represented by lunate pores in anterior parts, in some forms replaced by pit-line grooves near the dorsal fin. Latero-sensory canals of head of the normal palaeoniscoid arrangement for the most part. Pit-line grooves very fully developed on skull roof, cheek, mandible, and gulars.

HAPLOLEPIS (SENSU STRICTO), NEW SUBGENUS

Haplolepis with very broad head and bluntly fusiform body. Posterior margin of skull roof not embayed, extrascapulars and posttemporals greatly modified and not meeting in the midline. Quadratojugal not developed, so far as is known. Anterior median dorsal scales usually broadly arcuate. Lateral-line scales very deep anteriorly, gradually becoming shallow farther back. No definite trace of ventral lateral line has been seen. Dorsal fin slightly in advance of anal.

Scale counts of adequately known species (see p. 20):

H. ovoidea $\frac{18}{6\ \ 13\ \ 21}$ 23

H. cf. *ovoidea* $\frac{18}{6\ \ 13\ \ 22}$ 24

H. corrugata $\frac{20}{6\text{–}7\ \ 15\ \ 22\text{–}23}$ 25

PARAHAPLOLEPIS, NEW SUBGENUS

Haplolepis with slightly more slender form. Posterior margin of skull roof deeply embayed for greatly reduced extrascapulars and the posttemporals, which normally meet in the midline. Quadratojugal present. Usually no median dorsal row of scales except in front of fins. Anterior lateral-line scales very deep

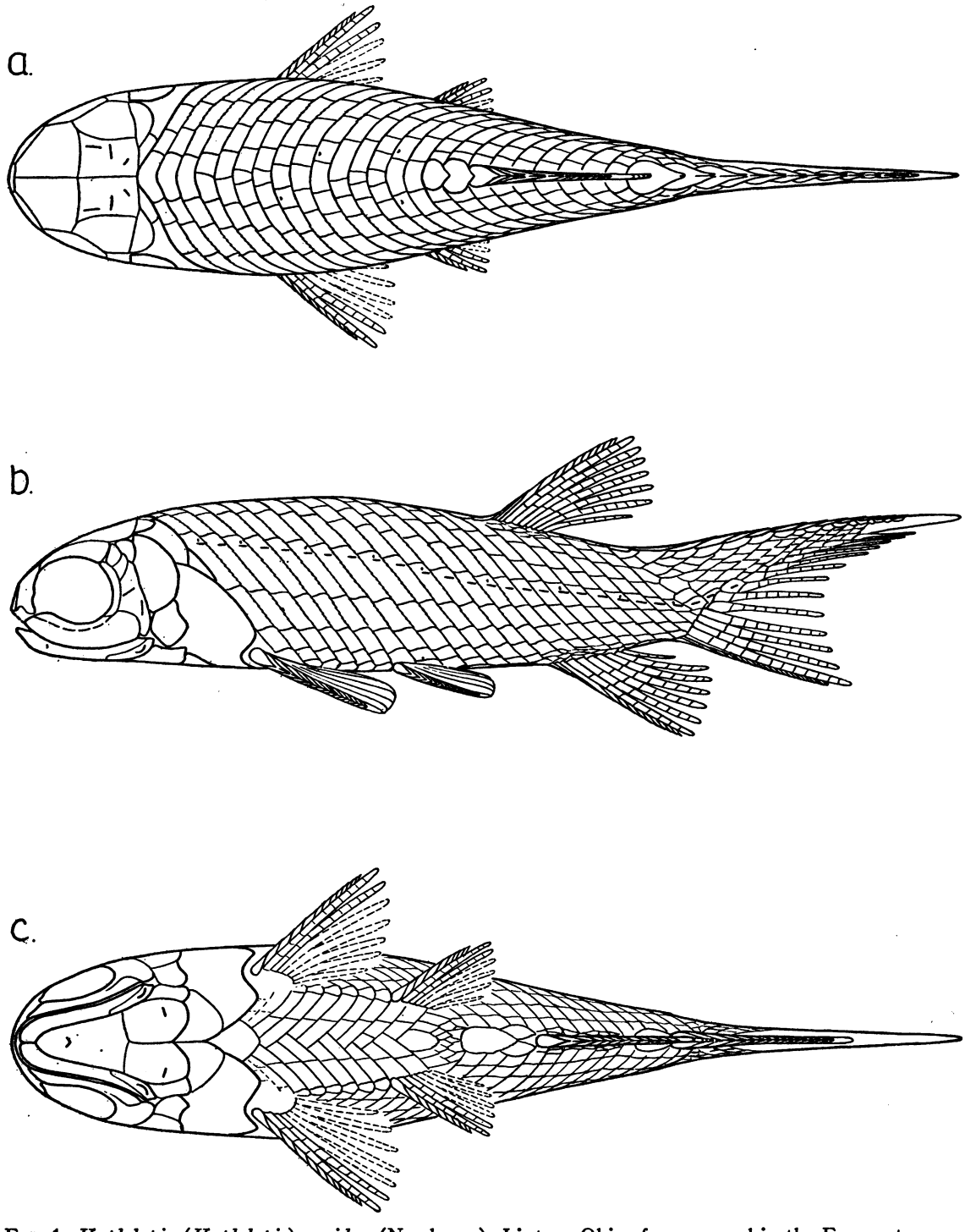


FIG. 1. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry), Linton, Ohio; from cannel in the Freeport group, Alleghany series, Pennsylvanian. Reconstruction of whole fish in a, dorsal, b, lateral, c, ventral views.

for *ca.* 16 rows, succeeded abruptly by two scales in corresponding region. Ventral lateral line present. Dorsal fin almost exactly opposed to the anal.

Scale count of *H. tuberculata:*

$$\frac{23\text{–}24}{7\quad 17\quad 26\text{–}27}\ 29.$$

Haplolepis (Haplolepis) ovoidea (Newberry)

Plate 1, figures 1, 2; text figures 1–5, 44

Mecolepis ovoideus NEWBERRY, 1856, p. 96.
Eurylepis ovoideus NEWBERRY, 1857, p. 150.
Eurylepis ovoideus NEWBERRY, 1873, p. 351, pl. 39, fig. 1.
Eurylepis ovoideus NEWBERRY, 1889, p. 212.
Eurylepis ovoidea WOODWARD, 1891, p. 450.
Haplolepis ovoidea HAY, 1902, p. 366.
Haplolepis ovoidea HAY, 1929, p. 687.
Mecolepis ornatissimus NEWBERRY, 1856, p. 96.
Eurylepis ornatissimus NEWBERRY, 1857, p. 150.
Eurylepis ornatissimus NEWBERRY, 1873, p. 352, pl. 39, figs. 4, 4a.
Eurylepis ornatissimus NEWBERRY, 1889, p. 212.
Eurylepis ornatissima WOODWARD, 1891, p. 450.
Haplolepis ornatissima HAY, 1902, p. 366.
Haplolepis ornatissima HUSSAKOF, 1908, p. 75.
Haplolepis ornatissima HAY, 1929, p. 687.
Eurylepis minimus NEWBERRY, 1873, pp. 353–354, pl. 39, fig. 3.
Eurylepis minimus NEWBERRY, 1889, p. 212.
Eurylepis minima WOODWARD, 1891, p. 450.
Haplolepis minima HAY, 1902, p. 366.
Haplolepis minima HAY, 1929, p. 687.
Eurylepis macrops NEWBERRY, 1889, p. 212 (*nomen nudum*).
Mecolepis serratus NEWBERRY, 1856, p. 96.
Eurylepis serratus NEWBERRY, 1857, p. 150.
Mecolepis serratus WOODWARD, 1891, p. 450.
Haplolepis serrata HAY, 1902, p. 366.
Haplolepis serrata HAY, 1929, p. 687.

The original figured specimens of most of these, including the intended type specimen of *E. macrops*, are in the American Museum of Natural History. The type of "*Mecolepis serratus*" has not been seen; it is probable that Newberry discarded the species. The original figured specimens are numbered as follows: *H. ovoidea*, A.M.N.H. No. 1960 (labeled "*E. striolatus*"); *H. ornatissima*, Newberry No. 445G (counterpart of figured specimen); *H. minima*, A.M.N.H. No. 1979 (Newberry No. 1024G, pl. 1, fig. 1); intended type of *E. macrops*, Newberry No. 449G (labeled by Newberry, pl. 1, fig. 2), with its counterpart No. 2493.

The hypodigm (Simpson, 1940) of this description of *H. ovoidea* comprises the following specimens, all in the American Museum of Natural History, in addition to the specimens just mentioned: A.M.N.H. Nos 983b, 1959 (=1016G), 1962 (with its counterpart), 1980, 1983, 2228, and Newberry collection Nos. 450G and 943G.

Several specimens of this species are well preserved and allow most of the anatomy to

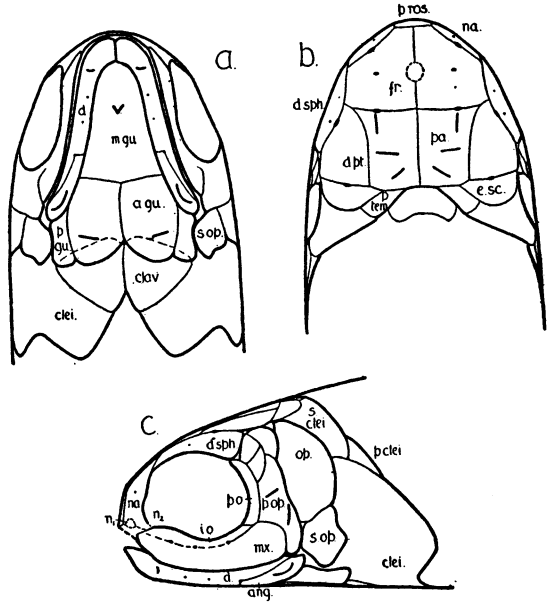


FIG. 2. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry). Reconstruction of dermal skull and shoulder girdle in a, ventral, b, dorsal, c, lateral views. Ornament omitted. For explanation of lettering of text figures, see page 121.

be described. The species is a small one, ranging from *ca.* 27 mm. to 45 mm. total length in the material studied. It is of stoutly fusiform shape (fig. 1) with a broad head and a flattened ventral region between the mandibles and the paired fins. A short diagnosis follows the description.

SKULL (FIGS. 2–4): It is unusual to find the head bones at all scattered in this species, and in most cases a mass of crushed bone had to be removed by solution in acid before the structure could be studied. In several cases the skull roof has parted along the sagittal

suture after death. This is rarely the case with *H. tuberculata* and suggests that the shape of the head was somewhat different in the two species.

The frontals often enclose, slightly in front of the middle of their length, a thinly ossified region or even an actual vacuity which marks the position of the pineal organ (fig. 3a, b). The posterior part of the skull roof is covered by the normal palaeoniscoid set of bones—paired parietals and dermopterotics (=supratemporo-intertemporals of Stensiö). The parietals narrow somewhat posteriorly and are marked by deep grooves for the anterior, middle, and posterior pit lines. The frontals have a rather variable ornament, very slight

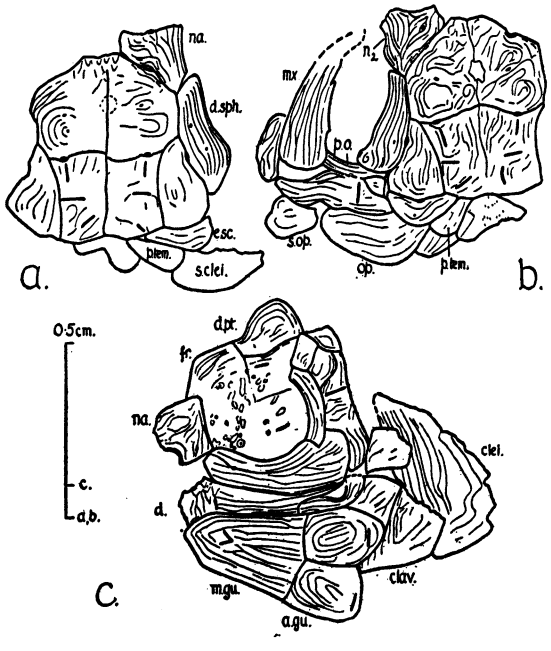


FIG. 3. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry). Details of skull structure. a, A.M.N.H. No. 2228; b, A.M.N.H. No. 1980; c, A.M.N.H. No. 1960 (holotype of *H. ovoidea*).

mesially, and consisting of low rugae separated by sharper grooves. These show a marked "swirling" around two areas. The parietals have a very much slighter ornament directed generally anteroposteriorly, and the dermopterotic has strong ridges parallel to the posterior and lateral margins.

The dermosphenotic is a long and rather slender element roofing the orbit, extending anteriorly to a little in front of the level of the pineal scar; it is ornamented with strong rugae running parallel to the orbital margin. The nasals are never very well shown. Each has a long posterior point which separates the frontal and dermosphenotic, and a broad notch in the anterior margin probably marking the site of the anterior nostril. The nasals are very broad, with an ornament of rugae parallel to the orbital margin in the lateral parts and a more irregular rugose ornament mesially. The postrostral is a narrow element with a strong ornament of somewhat interrupted rugae which are mostly transversely directed. No well-preserved premaxillaries have been seen.

The extrascapular and posttemporal region is not often preserved, but the conditions rather resemble those found in *H. corrugata;* a median dorsal body scale meets the parietals and separates the paired elements on each side.

The cheek is well preserved in most specimens (figs. 3c, 4a, b); the component bones seem to have been strongly bound together during life as they are never very scattered. The preopercular is a very curiously shaped element, not reaching the skull roof dorsally; it bears grooves for the horizontal and vertical cheek lines of pit organs. The postorbital is a long curved bone, often very firmly attached to the preopercular. Between the dorsal projection of the preopercular and the postorbital are two small suborbitals, and between these and the opercular is a small bone which may be regarded as an antopercular. The maxillary appears to be firmly ankylosed with the infraorbitals, as pores of the infraorbital canal emerge from the very deep compound element. The writer regards this as a late ankylosis, perhaps of the surface ganoine only, rather than as a true fusion; the postorbital-preopercular suture suggests that a similar process is less well developed in that case. There is usually no difficulty in following the course of the suture between maxillary and infraorbitals. The maxillary is curiously curved, very deep beneath the orbit, and truncated anteroventrally; teeth have not been observed with certainty and may be absent.

The ornament of the maxillary and infraorbitals consists of strong but sharp grooves

separating slightly sloping terraced areas of ganoine, and generally directed parallel to the orbital margin and to the ventral margin of the maxillary. The postorbital has similar ornament which may be termed "groove-and-terrace" ornament. The grooves on the preopercular are more or less vertical on the ventral limb, and irregular, more or less horizontal or anteroventrally directed on the "expansion." The slight ornament of the suborbitals is often more or less concentrically arranged.

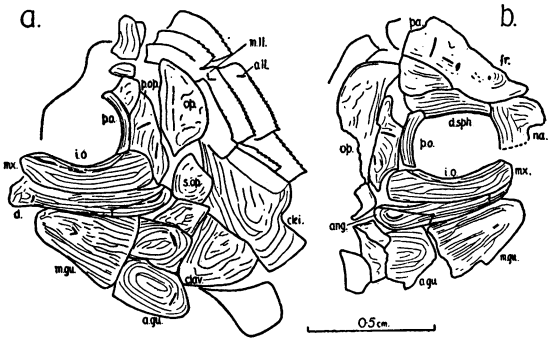


FIG. 4. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry). Details of skull structure. a, A.M.N.H. No. 1959 (=Newberry No. 1016G); b, A.M.N.H. No. 1963.

The mandible is apparently deep in front, shallow posteriorly; there is a well-marked overlap area for the truncated anterior end of the maxillary. The suture between "dentary" and angular is strongly sigmoidally curved. The bones have a strong ornament, consisting of "groove-and-terrace" type posteriorly; the anterior expansion has vertically elongated tubercules and rounded ridges. There is a short vertical groove on the dentary, probably for a pit line. In a few specimens there is a large number of very tiny teeth on the anterior part of the mandible.

The opercular apparatus is very remarkable. The opercular is shown separately in A.M.N.H. No. 1959, and its shape will be clear from the figure (fig. 4a). In A.M.N.H. No. 1963, however, the opercular seems to incorporate the usually separate antopercular (fig. 4b). In A.M.N.H. No. 1959 the remainder of the opercular series is shown. The most dorsal bone may be regarded as the subopercular, and is followed ventrally by the posterolateral paired gular, which is a small bone at the angle of the mandible. There are only two sets of paired gulars, the other pair being larger bones bearing a transverse pit-line groove. The whole series is completed by a very large median gular which extends so far posteriorly that it touches the anterior part of the angular, and which has a V-shaped groove for a pit line. The median bone has a strong ornament of rugae running parallel with the lateral margins. The anterior paired branchiostegals or gulars have a groove-and-terrace ornament which is distinctly concentric in arrangement. The remainder of the opercular series has a much less well-marked ornament.

PAIRED FINS: The shoulder girdle is never shown very clearly; the supracleithrum and postcleithrum are very incompletely known. The cleithrum is a stout element, bearing an ornament of "groove-and-terrace" type parallel to the margins; this ornament is very slight posteriorly and extremely strong along the anterior margin of the bone. The clavicle is of rounded triangular shape, and its ornament is similar to that of the cleithrum. The two halves of the shoulder girdle are separated posteroventrally by an enlarged median ventral body scale (fig. 4a). The pectoral fins are always badly preserved. The leading margin, which arises as usual from the cleithral notch, is provided with about 10 long and stout fulcral scales, of which the first is highly curved; the more distal members of the series show signs of being paired and may have free tips. There is some indication of a small scale-covered lobe, from the distal margin of which the fin rays spring. No useful account of the fin rays can be given.

The pelvic fins arise from the ventrolateral ridge, and their leading margins are provided with about eight stout fulcra which follow an enlarged scale on the ridge. The fin rays are badly preserved.

MEDIAN FINS: The dorsal is a fairly large fin, extending behind the origin of the caudal fin when collapsed. The median dorsal scales just in front of the fin become elongated and transversely convex, and pass into a series of about 10 stout fulcra, of which the distal members show obvious signs of a paired origin. The fin consists of about six or seven

rays; each ray is segmented and undivided and partly overlaps the next posterior ray when the fin is collapsed.

The anal fin is not quite so long as the dorsal and is composed of six or seven well-separated fin rays of the same type as those of the dorsal fin. An enlarged median scale in front of the fin is followed by about 10 stout fulcra of the kind described above.

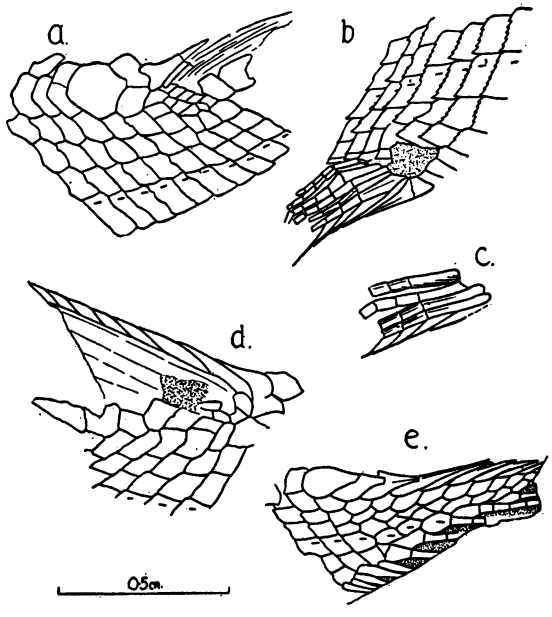


FIG. 5. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry). Details of scales and fins. a, Region in front of dorsal fin, A.M.N.H. No. 1975; b, region of anal fin, A.M.N.H. No. 2228; c, caudal fin rays and fulcra, A.M.N.H. No. 2228; d, dorsal fin of A.M.N.H. No. 449G (intended holotype of *Eurylepis macrops*, Newberry MS); e, caudal region of A.M.N.H. No. 1962.

The caudal fin is usually badly preserved. The web consists of about 12 rays, of which about four form the "lower lobe." The fin rays closely resemble in character those of the other median fins (fig. 5e); the proximal segments are much longer than the distal ones. The fulcra are also similar to those of the dorsal and anal and number *ca.* 13. They follow a much enlarged median ventral scale.

The anterior insertion of the dorsal fin is usually very slightly in advance of that of the anal. The pelvic fins are distinctly closer to the pectorals than to the anal (measured from the anterior insertions).

SQUAMATION: A useful convention for indicating important characters of the squamation and the arrangement of the fins is used throughout this paper. The number of scale rows, counted along the lateral-line series, in front of the origins of the median and pelvic fins, and in front of the caudal inversion are recorded. Above a horizontal line is written the figure for the dorsal fin; below it, in order, the figures for pelvic, anal, and caudal fins; at the end of the line, the figure for the caudal inversion. With reasonably preserved material this count provides material for a delicate statistical test of homogeneity of a group of fishes.

It is not always easy to count the scale rows in these small fishes. The formula is usually

$$\frac{18}{6 \quad 13 \quad 21}\ 23$$

though the origins of the fins show a certain variation in position; thus out of 10 specimens the pelvics always originate at scale row 6; the anal originates at row 13 (6 specimens) or 14 (4 specimens), the dorsal at 18 (7 specimens) or 19 (3 specimens), the caudal at 20 (2 specimens), 21 (6 specimens) or 22 (2 specimens); while the inversion is always two rows behind the origin of the caudal.

In the anterior part of the body each scale row can be traced from a very broad, curved, median dorsal scale. The anterior lateral-line scales are quite deep; although the specimens measured range from 27 mm. to 40 mm. total length, the variation in the depth of scale is only 2.8 to 3.1 mm. The lateral-line scales become about equilateral just behind the dorsal fin and are slightly shallower on the caudal pedicle. The anterior end of the lateral-line series bends dorsally so that the lateral line is carried up towards the back of the skull roof; in this region there are only two scales in each row between the median dorsal and lateral-line scales, but farther back there are three such scales in each row. Between the lateral-line scales and the ventrolateral ridge there are four scales in each row, then a curiously shaped scale on the ridge, and two scales directed anteromesially on the venter. The arrangement of these ventral scales near the anal fins is more irregular. Just behind the anal fin the number

of scales in each row below the lateral line is reduced to three, and more posteriorly to two. The regular pattern of the scales is disturbed in some specimens by areas of smaller scales, at the base of the dorsal and anal fins.

The caudal lobe is covered by more or less rhomboid scales of which there are about four rows across the tail near the pedicle; farther back these dwindle to two and possibly to one at the tip (fig. 5e). In addition there is a modified ventral set of scales bearing the lepidotrichia. The ridge scales begin with somewhat elongated median scales just behind the dorsal fin, and these quickly become pointed and deeply overlapping, and the more posterior ones are split at the tips.

Between the mesial margins of the dermal bones of the shoulder girdle is a large unpaired scale, with a slight ornament of faint grooves (fig. 4a). The enlarged scales in front of the fins have already been mentioned. The vent scales are not well shown; at the posterior ends of the ventrolateral ridges there is a pair of large scales, with pectinated posterior borders, which are followed by the enlarged median scale that marks the beginning of the series of anal fin fulcra, and these scales probably indicate the position of the vent.

The scales near the mid-dorsal line as far back as the dorsal fin have a well-marked ornament of elongated pits arranged more or less longitudinally. Some of the anteroventral scales and the small scales at the base of the dorsal and anal fins have in some specimens an ornament of similarly arranged grooves. The body scales are otherwise quite smoothly covered with lustrous ganoine, in which the only breaks are sparse and very minute pores. In a few specimens an irregular longitudinal rumpling of the smooth surface is found, but is probably not significant, and perhaps a post-mortem change. The anterior flank scales are pectinated on their hinder free margins; this character persists as far back as the dorsal fin, and in one specimen for a few rows behind this. This individual may represent the "species" *M. serratus*, of which only a short diagnosis was published; it is otherwise inseparable from *Haplolepis ovoidea* Newberry.

LATERAL LINE: The main lateral line is represented by a short pit-line groove (the accessory lateral line, see p. 81) near the dorsal margin of each lateral-line scale, and by an enclosed canal which opens by a slit-like pore above the grooves in certain scales. The placing of these pores is very irregular, but in general there is a pore in almost every anterior lateral-line scale, the more posterior scales bearing pores with gradually lower frequency. There are about 27 scales from the shoulder girdle to the lateral-line scale which first touches the fin web, and as a rule this is the posterior end of the series; in A.M.N.H. No. 449G, however, there is a short posterior extension as grooves on the series of scales along the ventral border of the caudal lobe.

There is no sign of a ventral lateral line in the material studied, and no pit-line groove occurs on the cleithrum, which is often favorably preserved. In A.M.N.H. No. 449G (the designated holotype of Newberry's *Eurylepis macrops*, a *nomen nudum*) there is evidence of an enclosed dorsal lateral line; small lunate pores open on certain members of the row immediately lateral to the broad median dorsal scales.

The main lateral line is continued forward in the supracleithrum, but its course before entering the dermopterotic is uncertain. Between the dermopterotic and dermosphenotic there is an obvious pore, and it is certain that the infraorbital canal then traversed the postorbital; it then seems to have perforated the infraorbitals which are ankylosed to the top of the maxillary, and two pores occur in the anterior part of the almost obliterated suture.

The supraorbital canal has a large pore in the frontoparietal suture, and immediately behind this the anterior pit line forms a deep groove. There is a pore in the middle of the frontal and another in the frontonasal suture but no evidence of the more anterior course of the canal.

The preopercular and mandibular canals do not have obvious pores, and their course is a little uncertain.

The parietal bears well-marked grooves for the anterior, middle, and posterior pit lines; the preopercular bears similar grooves for the horizontal and vertical pit lines of the cheek, and there is a short pit-line groove on the anterior part of the "dentary." The anterior

paired gulars and the median gular have grooves for pit lines, as shown in figures 3c, 4a.

DIAGNOSIS OF *H. ovoidea: Haplolepis (sensu stricto)* of small size. Separate parietals and dermopterotics present; pineal macula frequently shown. Skull roof ornamented with rugae, often almost smooth. Suspensorium almost vertical, preopercular of highly modified shape, maxillary without posterior expansion. No quadratojugal. Bones of cheek with sharp, terraced rugae. Dentition very feeble. Opercular apparatus with enormous median gular, two paired gulars, these possibly separated from the small subopercular. Normally a small antopercular. Dorsal fin very slightly in advance of anal. Distance between origins of pelvics and anal greater than that between pectorals and pelvics, and between anal and caudal. Scale formula usually

$$\frac{18}{6\ \ 13\ \ 21}\ 23$$

Lateral-line scales very deep on anterior flank, becoming gradually shallower posteriorly. Anterodorsal and some other scales with comparatively well-marked ornament of longitudinally elongated pits. Main lateral-line opening by occasional lunate pores, accessory lateral line indicated by groove on every scale of the "lateral-line" series. Enclosed dorsal lateral-line opening by lunate pores. No signs of ventral lateral line.

Haplolepis (Haplolepis) cf. ovoidea (Newberry)

Plate 1, figure 3; text figure 6a–c

A nodule collected by R. D. Lacoe from Mazon Creek, near Morris, Grundy County, Illinois, now in the United States National Museum (No. 4303) includes a small fish (in counterpart) which is very close to *H. ovoidea* (Newberry) from Linton. The resemblance extends to structure and ornament of head, position and nature of fins, and character of squamation, but as only one incompletely preserved specimen has been seen it would be misleading to identify it with complete certainty with the Linton species. The specimen is almost exactly 30 mm. long, which is well within the size range of *H. ovoidea.*

SKULL: The specimen is preserved more or less "in the round," and it is impracticable to give a reconstruction of the skull roof, which has been divided when the nodule was broken. The shape of the snout reconstructed from Linton material of *H. ovoidea* is confirmed (fig. 6a). The practically smooth nature of the visible skull roofing bones, the distribution of the pit lines and the large pores at the frontoparietal suture, the presence of separate parietals and dermopterotics, and the enlarged pores at the anterolateral margins of the dermopterotics are all characters common to this specimen and small individuals of *H. ovoidea.* The right nasal and premaxillary are partly shown; the former resembles in shape and ornament the corresponding bone in *H. ovoidea.* The premaxillary has a strong transverse ornament of rugae and with the nasal encloses the anteromesial nostril opening. The cheek is partly shown and is very closely similar to that of *H. ovoidea* in the following points: nature and shape of postorbital, suborbital (lower one shown), preopercular and infraorbito-maxillary; ornament of bones; distribution of pit-line grooves and lateral-line pores. The faint impression of a few tiny marginal teeth on the anterior part of the maxillary may be noted; the anterior tip of that bone is somewhat different in shape from that of *H. ovoidea.*

No details of the structure of the mandible can be given, but the ornament and the small vertical pit-line groove are like those of *H. ovoidea.* The opercular apparatus and shoulder girdle are very badly preserved.

FINS: A notable feature about this specimen is the fine preservation of the fulcra, which are long, rather slender, and with long distal free portions (fig. 6b, c). This feature is apparently a minor difference from *H. ovoidea,* in which the fulcra are a little stouter and do not usually show such long free points, but the difference may be partly or largely due to conditions of preservation; in U.S.N.M. No. 4303 the fulcra are split longitudinally in the breaking of the nodule. There are probably 10 such fulcra on the pectorals, dorsal and anal. None of the fins are well enough preserved for accurate counts of the rays to be made; there are about seven to eight rays in the anal, and eight are preserved in the caudal, which is incomplete at the tip. The fin rays very closely resemble

those of *H. ovoidea*. The relative placing of the fins seems to be slightly different from that in *H. ovoidea;* the pelvics seem to originate midway between the pectorals and anal, while in *H. ovoidea* they are nearer to the pectorals. This difference may possibly be due to slight post-mortem changes, and must be regarded as doubtful until confirmed on other material.

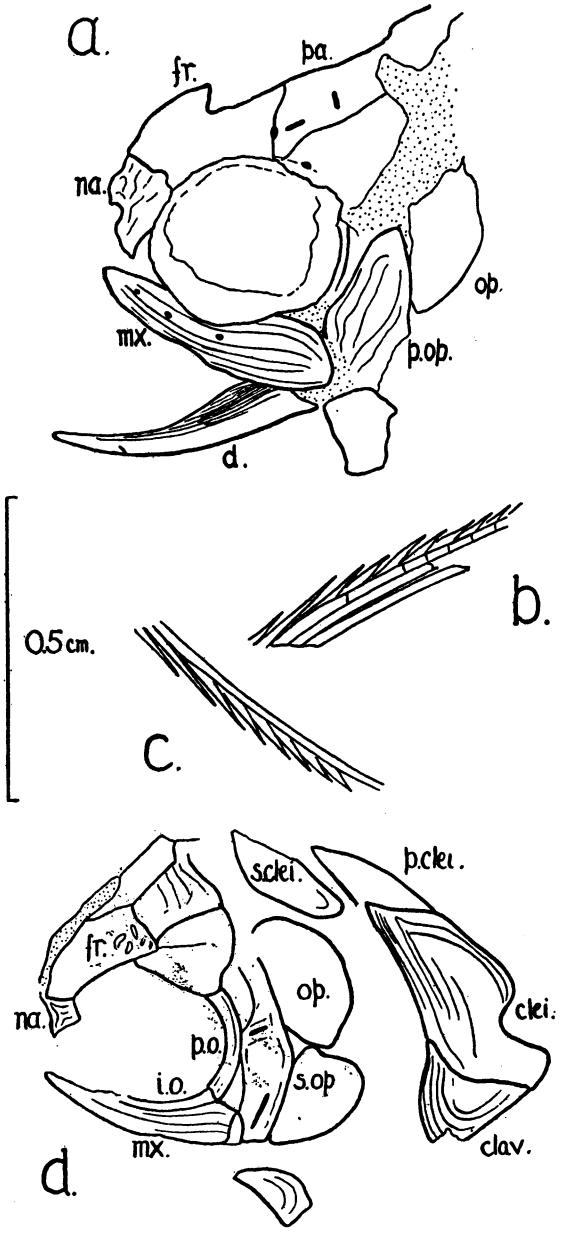


FIG. 6. a–c, *Haplolepis* (*Haplolepis*) cf. *ovoidea* (Newberry), Mazon Creek, Illinois; from ironstone nodule horizon in Kittanning group, Alleghany series, Pennsylvanian. U.S.N.M. No. 4303: a, skull, b, front of dorsal fin, c, front of anal fin. d, *Haplolepis* (*Haplolepis*) aff. *ovoidea* (Newberry), Cannelton, Pennsylvania; from "cannel" in the Freeport group, Alleghany series, Pennsylvanian. U.S.N.M. No. 4560. Skull details.

SQUAMATION: The scale count on this specimen is almost certainly

$$\frac{18}{6\ \ 13\ \ 22}\ 24$$

This may be compared with the

$$\frac{18}{6\ \ 13\ \ 21}\ 23$$

noted as the average for *H. ovoidea*, but some specimens of *H. ovoidea* have the same count.

The squamation is very closely similar to that of *H. ovoidea*, as far as it can be seen; the shape of the lateral-line scales along the body is a most decisive resemblance.

CONCLUSIONS: U.S.N.M. No. 4303 cannot be separated from *H. ovoidea* on any sharply marked characters. It seems to differ slightly in the details of the shape of the front of the maxilla, in the relative position of the pelvic fins, in the nature of the fin fulcra, and possibly in the scale count. None of these differences are sufficiently marked or sufficiently certain to warrant the erection of even a new variety, and until more material is found it will be called *H.* cf. *ovoidea.*

Haplolepis (Haplolepis) aff. ovoidea (Newberry)
Text figure 6d

A single specimen of *Haplolepis* from Cannelton, Pennsylvania, has been studied by the writer. It is from the Lacoe collection in the United States National Museum (No. 4560). It is a very small fish, less than 25 mm. long, and the posterior parts are badly preserved.

The head is partly preserved (fig. 6d), but the skull roof is poor. The cheek shows considerable resemblance to that of *H. ovoidea*, especially in the shape of the following bones: preopercular, postorbital, suborbitals, and infraorbito-maxilla. The mandible is badly preserved. The opercular apparatus is poorly shown, but the subopercular is larger than in *H. ovoidea*. There is, however, a somewhat similar hollow in the posterodorsal outline of

the subopercular. The shoulder girdle is partly preserved and resembles that of *H. ovoidea*.

The squamation is incompletely preserved; the anterior flank scales are very deep, particularly those enclosing the lateral line. The depth of the lateral-line scales decreases slowly posteriorly. There is a rather doubtful appearance of denticulations on the posterior margins of the anterior flank scales.

Eurylepis corrugatus NEWBERRY, 1857, p. 150.
Eurylepis corrugatus NEWBERRY, 1873, p. 350, pl. 38, figs. 4, 4a.
Eurylepis corrugatus NEWBERRY, 1889, pp. 212, 228.
Eurylepis corrugata WOODWARD, 1891, p. 450.
Haplolepis corrugata MILLER, 1892, p. 715.
Haplolepis corrugata HAY, 1902, p. 366.
Haplolepis corrugata HUSSAKOF, 1908, pp. 74–75.

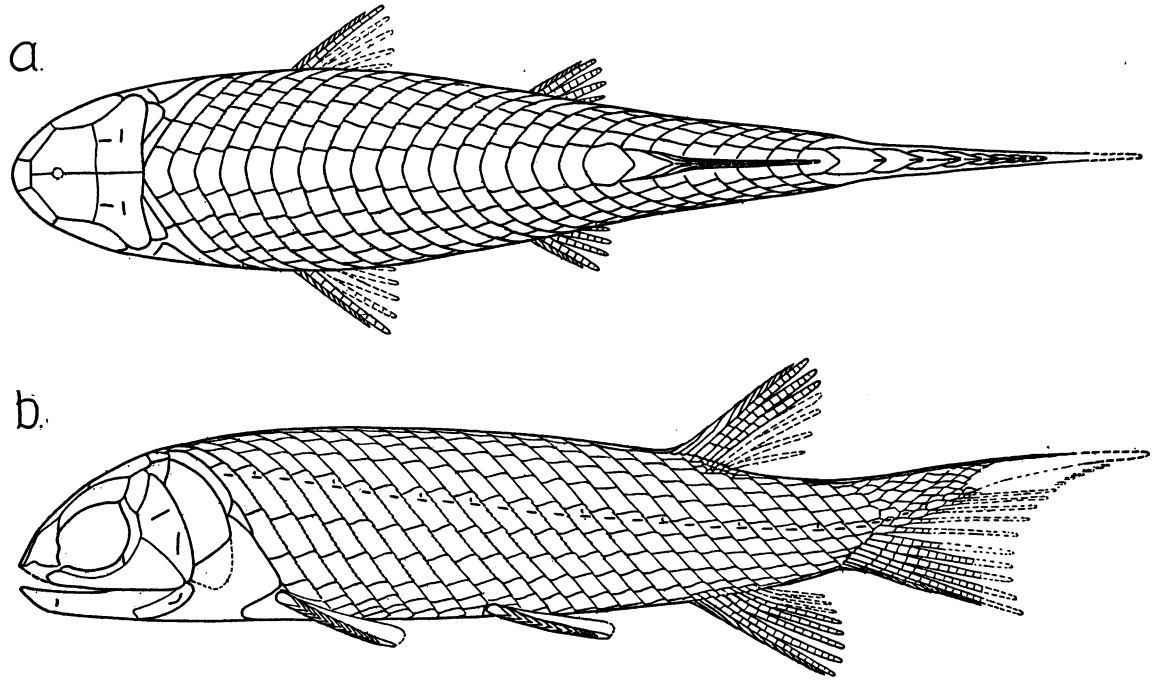


FIG. 7. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry), Linton, Ohio; from cannel in the Freeport group, Alleghany series, Pennsylvanian. Reconstruction of whole fish in a, dorsal, b, lateral views.

The fins are not preserved, but the origins of one of the pelvics and the dorsal can be seen. They occur at scale rows 5 and 15, respectively (cf. 6 and 18 in *H. ovoidea*).

The very close structural resemblance of this fish to *H. ovoidea* is good evidence of close relationship; in view of the differences noted in the scale count and perhaps in the size of the subopercular, the fish cannot be referred to the same species as the Linton material and is here named *H.* aff. *ovoidea* (Newberry).

Haplolepis (Haplolepis) corrugata (Newberry)
Plate 2, figures 1–3; text figures 7–11, 44

Mecolepis corrugatus NEWBERRY, 1856, p. 96.
Haplolepis corrugata HAY, 1929, p. 687.
Eurylepis striolatus NEWBERRY, 1873, p. 355.
Eurylepis striolatus NEWBERRY, 1889, p. 212.
Eurylepis striolata WOODWARD, 1891, p. 450.
Haplolepis striolata HAY, 1902, p. 366.
Haplolepis striolata HAY, 1929, p. 687.

This species is very scarce among the material seen by the writer and only four individuals have been studied. The holotype (A.M.N.H. No. 452G) and the specimen U.S.N.M. No. 4496 have very well-preserved heads, however, while A.M.N.H. No. 1012G shows parts of the head very well. It is probable that A.M.N.H. No. 1975 and its counterpart, No. 1020G, represent the young of this species. The specimens range in length from

31.5 mm. (A.M.N.H. No. 1975) to 73 mm. (the holotype).

SKULL: Most of the skull roof is visible in A.M.N.H. No. 452G (fig. 9a) and in U.S. N.M. No. 4496 (fig. 9b). There are no separate parietals, and reasons for believing that they have been replaced by mesial extensions from the dermopterotics will be advanced later. The enlarged dermopterotics are almost square bones with their posterolateral corners drawn out into rounded projections. The

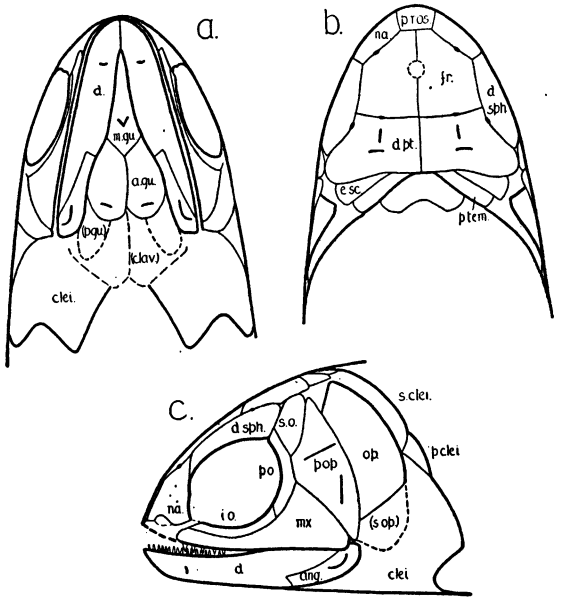


FIG. 8. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Reconstruction of dermal skull and shoulder girdle in a, ventral, b, dorsal, c, lateral views. Ornament omitted. Suboperculars, posterior paired gulars, and clavicles are "restored" and may be subject to considerable inaccuracy.

frontals narrow very slightly for some distance, then much more rapidly. Just in front of the middle of the frontals is a median weakly ossified area which almost certainly indicates the position of an original pineal foramen. The nasals are very broad, though they are not very well preserved; flattened out in the cannel they show a very broad concavity in the orbital margin, and a triangular notch in the anterior margin, which is certainly for the anterior nostril. The postrostral is not adequately preserved but seems to be a narrow bone. The skull roof is completed by a pair of large bones lying over the orbits; these are here called dermosphenotics.

The ornament of the skull roof consists of sharp grooves separating terraced areas of

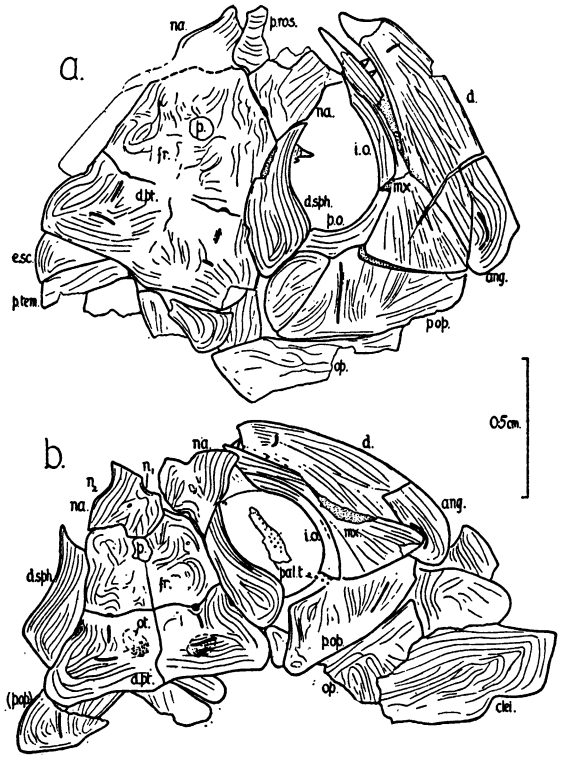


FIG. 9. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Details of skull structure. a, A.M.N.H. No. 452G (holotype); b, U.S.N.M. No. 4496. Cf. plate 2, figs. 2, 3.

smooth ganoine; near the orbital margin the ornament is made up of more rounded ridges between the grooves. On the frontals the ornament swirls in a rather complex fashion, while on the dermopterotics it is generally parallel to the lateral and posterior margins. Near the mid-line both frontals and dermopterotics are comparatively smooth. On the dermosphenotics the ridges of the ornament run almost parallel to the margins of the bone. The nasal has ridges running parallel to the orbital margin, and more irregular rugae mesially. The postrostral has more or less transverse, very coarse ridges.

The cheek is fairly well preserved in A.M.N.H. No. 452G and U.S.N.M. No. 4496. The preopercular is a very broad element,

particularly ventrally, and the suspensorium is almost vertical. The maxillary has a tri-

"suborbital," lying between the preopercular, postorbital, and skull roof, is present in

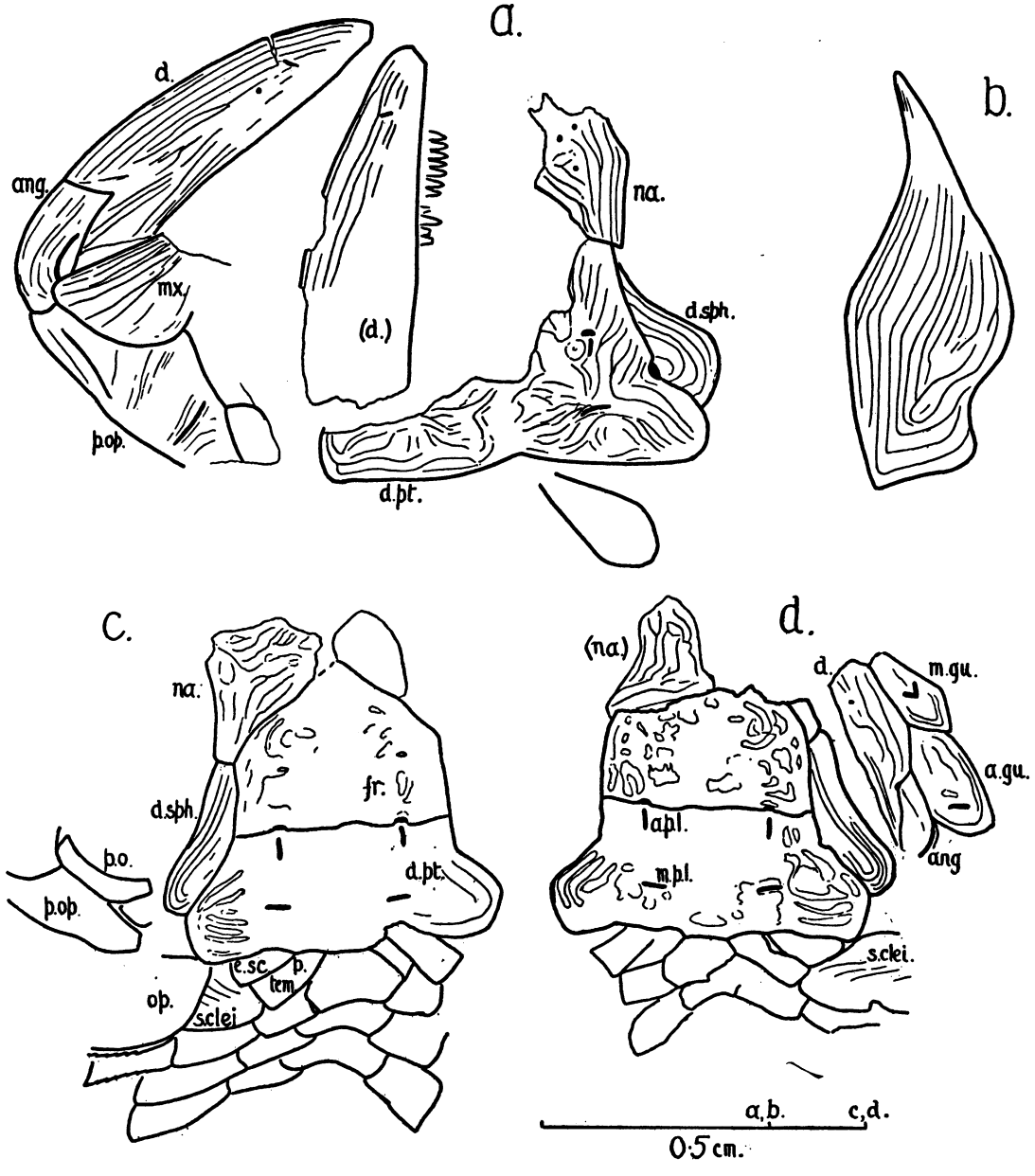


FIG. 10. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Details of skull structure. a, A.M.N.H. No. 1012G: b, cleithrum of same; c, A.M.N.H. No. 1975, and d, its counterpart, A.M.N.H. No. 1020G (questionably referred to this species).

angular posterior expansion and is remarkably deep below the orbit. There are two bones related to the infraorbital canal; they are not very well preserved. A single large

A.M.N.H. No. 452G, but there may be additional elements in this region.

The preopercular has a rather complex ornament, more or less parallel to the poste-

rior and anterodorsal margins; the grooves on the maxillary diverge posteriorly on the expansion. The orbital bones have a marked "groove-and-terrace" ornament parallel to their orbital margin.

There is a much damaged bone in A.M.N.H. No. 452G, which may be a premaxillary, but no details can be given.

The mandible is very deep and is ornamented with numerous rugae which run mainly anteroposteriorly. Near the anterior end of the dentary is a prominent, small, vertical groove, which is probably for a pit line. A break in ornament on the angular indicates the presence of an oralomandibular pit line (fig. 9a, b).

The dentition is partly shown in several specimens. On the dentary and maxillary the teeth are strong, pointed cones with a thick base and are quite closely set. There are several sizes of teeth in both upper and lower jaws. U.S.N.M. No. 4496 shows the points of two rows of teeth perforating the preopercular and maxillary; these presumably belong to the palatal dentition.

The opercular system is very poorly known, but the opercular itself is partly seen in A.M.N.H. No. 452G and U.S.N.M. No. 4496. It has a somewhat irregular groove-and-terrace ornament. If A.M.N.H. No. 1975 really belongs to this species (which is very probable) the median gular is relatively small and diamond-shaped, bearing a V-shaped pit-line groove, and the anterior branchiostegals or paired gulars are large elements bearing a transverse pit-line groove (fig. 10d). There is probably a separate antopercular.

U.S.N.M. No. 4496 shows two small objects, causing elevations of the dermal bones of the posterior part of the skull roof, which probably represent saccular otoliths.

SHOULDER GIRDLE AND PAIRED FINS: The cleithrum is a remarkably narrow bone ventrally, and broad above the insertion of the fin (figs. 10b, 11a). The ornament is of the groove-and-terrace type. There is never any groove for the ventral lateral line. Supracleithrum, postcleithrum, and clavicle are badly shown in the available material.

The pectoral fins (fig. 11a) bear large fulcra, which seem to have been double, at least distally. The pelvic fin is partly shown in A.M.N.H. No. 452G (fig. 11c); it has large fulcra, and the large scales at the origin of the fin are clear, but no exact details of the number and ornament of fin rays can be given.

MEDIAN FINS: These are collapsed and poorly preserved in all the available material.

The anal (fig. 11e) is composed of about seven stout and well-separated rays, which are rather closely jointed and are undivided

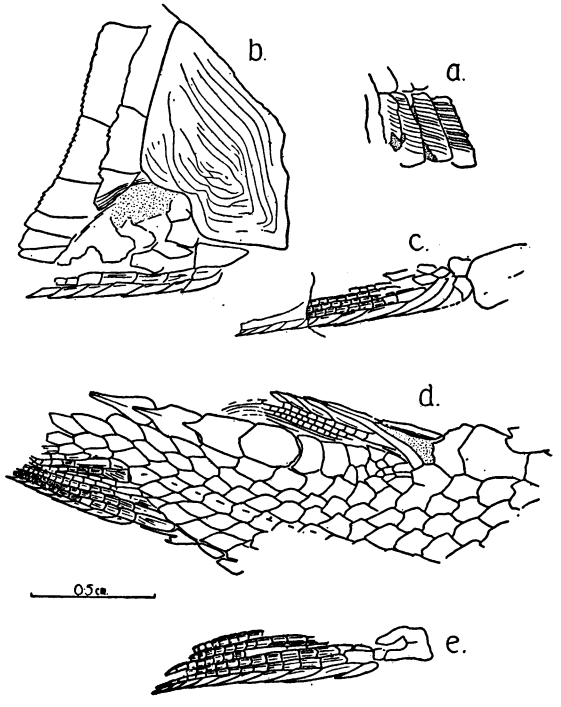


FIG. 11. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Details of scales and fins. a, A.M.N.H. No. 1012G, worn scales showing "ornament" below ganoine. b–e, A.M.N.H. No. 452G (holotype): b, cleithrum and pectoral fulcra; c, pelvic fin; d, dorsal and caudal fins; e, anal fin.

distally. The rays have an anterior area, overlapped when the fin is collapsed by the next fin ray, and the uncovered posterior part bears a longitudinal ornament of grooves. The fulcra are extremely stout.

The dorsal is of the same type, but both dorsal and caudal fins are much too badly preserved for description. The fulcra on both fins, however, are large, and all but the most proximal members seem to be divided (fig. 11d).

The dorsal fin arises very slightly in ad-

vance of the anal; the pelvics are slightly nearer to the pectorals than is the anal, and the anal is distinctly closer to the caudal than to the pelvics.

SQUAMATION: Only two specimens allow the usual scale counts to be made; they give the following figures:

A.M.N.H. No. 452G (holotype) $\frac{20}{6 \quad 15 \quad 22\text{–}23}$ 25

A.M.N.H. No. 1012G $\frac{20}{6 \text{ or } 7 \quad 15 \quad 22\text{–}23}$ 25

In the anterior part of the body each scale row can be traced from a broad, arcuate, but not specially enlarged dorsal median scale in a slightly posterior direction over the flank, to a ridge running through the origin of the pectoral and pelvic fin, which seems to meet its fellow just in front of the anal fin. At this ridge the scale rows are abruptly reflected forward to form on the ventral surface broad V's with the point directed forward.

In the anterior part of the trunk there are four scales in each row between the median dorsal scale and the lateral-line series; the fifth scale below the lateral-line scale marks the change of direction, but the number of ventral scales cannot be estimated. At the dorsal fin there are four paired scales above and below the lateral-line scale, and at the caudal pedicle three and two, respectively.

The anterior lateral-line scales are quite deep, but not so deep as in *H. tuberculata*. The lateral-line scales decline quite gradually in height posteriorly until, under the dorsal fin, they are about equilateral. More posteriorly they become still shallower.

Anterior dorsal scales are ornamented with small elongated pits, more or less parallel to the long axis of the fish. This type of ornament extends backwards almost to the dorsal fin, but is almost restricted to the mid-dorsal scale.

Immediately behind the shoulder girdle a few anteroventral scales have a slight ornament of curved sharp grooves at the anteroventral margins (fig. 11a).

The rest of the scales are smoothly polished, with, on the anterior flank, denticulated posterior margins. This pectination does not extend so far as the region of the dorsal fin. Some of the anterior flank scales show a trace of anteroposterior striations, which are explained by the conditions in A.M.N.H. No. 1012G. Here some flank scales have the ganoine rubbed off and show the underlying cosmine layer of the scale to be quite sharply grooved (fig. 11a); in partly damaged scales there are minute pits arranged parallel to these grooves. In the rather deep row of scales immediately above the lateral lines an anterior member shows about 12 such grooves. In a number of specimens there is a vague appearance of longitudinal striation on the flank scales, and this seems to be due to the "loom" of these grooves through the thin ganoine.

In front of the anal fin there were probably enlarged vent scales, which cannot now be made out. There was also probably a large median scale immediately in front of the fin, and the rest of the scales and fulcra are much like those to be described on the dorsal fin. In front of the dorsal fin a very large scale with a denticulated posterior border is followed by two or three deeply overlapping scales with broad bases and posterior points, and these are followed by the large fulcra. The third and subsequent scales of the whole series are split, at least distally. The caudal fulcra similarly follow one or two enlarged scales and are of the same character as dorsal fulcra. The caudal lobe is covered dorsally by similar scales; the mid-dorsal scale of row 23 is somewhat enlarged, while Nos. 24–26 are larger and posteriorly pointed; more posterior scales are longitudinally split.

In front of the pelvic fin in A.M.N.H. No. 452G is a rather large scale which lies on the ventrolateral ridge and is the base of the fulcral series. There is a well-rounded scale surrounding the origin of the pectoral fin, and this scale is followed distally by the fulcra.

LATERO-SENSORY SYSTEM: It has proved impossible to prepare latero-sensory canals in the material of *H. corrugata*, and even examination with the aid of brilliant illumination under immersion fluids does not give any information about the course of the actual canals. The "main lateral line" (see p. 81) of the body is indicated by a series of short grooves high up on the deepest row of flank scales, and also by a minute lunate pore opening apparently on every second or third scale immediately above the groove. There are 27 lateral-line scales, and the line reaches the

caudal margin at the base of the sixth fin ray. There is no certain trace of either dorsal or ventral lateral lines in the few specimens available.

The main lateral line was probably continued anteriorly through the posttemporal and extrascapular; in the latter there is sometimes a minute pore. There is no certain sign of a pore in the dermopterotic, but one is clearly marked between the dermopterotic and the posterior part of the dermosphenotic. In the rest of the probable course of the infraorbital canal no pores can be seen.

The supraorbital canal is equally badly known, but clear pores between the frontal and nasal, in the middle of the frontal, and between frontal and dermopterotic indicate that it has a normal course through nasal and frontal. Immediately behind the last-mentioned pore there is a short groove for the anterior pit line. The middle pit line of the head is represented by a transverse groove on the dermopterotic, but the posterior pit line has left no trace.

In the preopercular and mandible no pores have been observed, but the preopercular bears grooves for the vertical and horizontal pit lines of the cheek, and grooves probably referable to the oralo-mandibular line occur on the mandible.

DIAGNOSIS OF *H. corrugata:* Fairly large *Haplolepis* without parietals, dermopterotics meeting in mid-line and bearing the pit lines of the skull roof. Skull bones with strong ornament of close-set rugae, often terraced. Cheek with large triangular preopercular and maxillary expansion. No quadratojugal. Dentition comparatively robust, of conical teeth. Opercular apparatus poorly known. Dorsal fin very slightly in advance of anal. Scale formula:

$$\frac{20}{6\text{–}7 \quad 15 \quad 22\text{–}23}\ 25$$

Series of arcuate median dorsal scales, not greatly enlarged. Very slight ornament of elongated pits, almost restricted to anterior dorsal scales; squamation otherwise smooth. Anterior lateral-line scales very deep, declining gradually posteriorly. Main lateral-line opening by occasional lunate pores; accessory main lateral line indicated by a groove on every lateral-line scale. No certain trace of dorsal or ventral lateral line.

Haplolepis (Haplolepis) attheyi, new species
Plate 2, figures 4, 5; text figure 12

In the Hancock Museum (Newcastle-on-Tyne) is a small fish in counterpart labeled "*Palaeodopsis newshami*" in Atthey's handwriting; it is from the Low Main Seam at Newsham and is probably one of the specimens of "*Eurylepis*" mentioned by Hancock and Atthey (1868a, p. 96). It proves to be a new species of *Haplolepis*, and since the name

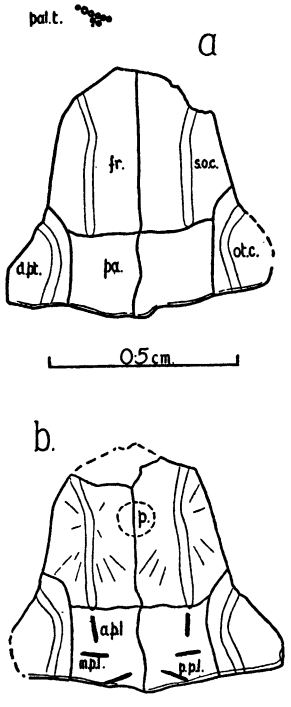


FIG. 12. *Haplolepis* (*Haplolepis*) *attheyi*, new species, Newsham, Northumberland; from the cannel above the Low Main seam, Middle Coal Measures, Westphalian. Holotype, specimen in Hancock Museum, in counterpart.

on the label is a *nomen nudum*, with an error in the construction of the trivial name, it will be designated *H. attheyi*, new species, in honor of the industrious collector and preparator who helped in the description of so much of the Newsham material.

The fish is greatly disturbed and was macerated and scattered before burial. The caudal fin proves its reference to *Haplolepis*, and the skull roof differs from that of other spe-

cies while showing the same basic plan as in *Haplolepis* (*sensu stricto*).

SKULL: Only the dermal skull roof can be distinguished with certainty (fig. 12). It is of almost normal palaeoniscoid pattern, consisting of paired frontals, parietals, and dermopterotics, of which the shape and mutual relations will be clear from the figures. The latero-sensory canals are shown with great clarity; they seem to have been surrounded ventrally by very thin bony cylinders standing out below the cranial surfaces of the bones. The anterior, middle, and posterior pit-line grooves show through the very thin bones. Little can be seen of the external ornament, which probably consists partly of "terraced" areas of smooth ganoine separated by sharp grooves, and partly of more rounded tubercles and tuberculate ridges.

Remarkable features of the skull roof are the shape of the posterior margin, the anterior pit line extending back from the frontoparietal suture, the great curvature of the cranial continuation of the main lateral line in the dermopterotic, and the presence of a depression on the inner face of the frontals in the

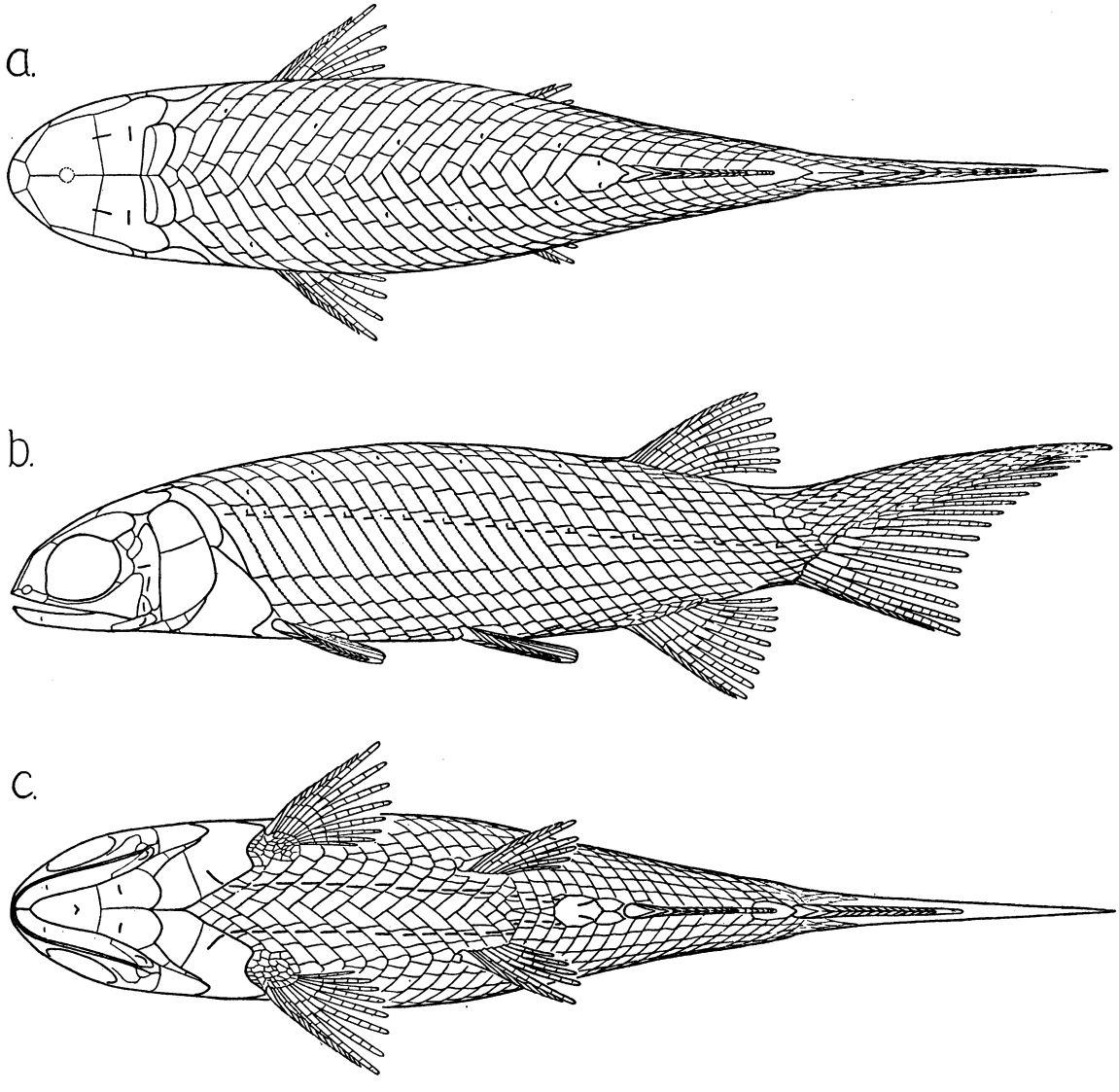


FIG. 13. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry), Linton, Ohio; from cannel in the Freeport group, Alleghany series, Pennsylvanian. Reconstruction of whole fish in a, dorsal, b, lateral, c, ventral views.

position of the "pineal" macula of other species.

The left mandible is preserved; it is a comparatively deep bone with a strong longitudinal ornament of rugae.

On one of the parts of the specimen is the impression of a small bone bearing about eight tiny hemispherical teeth; the provenance of this element is uncertain (fig. 12a; pl. 2, fig. 4).

BODY: The right cleithrum is partly shown and bears a very striking terraced ornament parallel to the anterior and lower margins.

The squamation is very badly preserved, and no detailed account is possible. The scales seem to be entirely smooth, and anterior scales are denticulated on the hinder margins. At least some of the scales are very deep. Part of the caudal fin and lobe are well shown, and disturbed fin rays are of the familiar widely separated segmented kind, with expanded basal segments passing smoothly into the squamation of the caudal lobe.

COMMENTS: The general features of the squamation and fin structure are sufficient to warrant placing the fish in the genus *Haplolepis* (*sensu lato*). The skull-roof structure is that of an unspecialized *Haplolepis* (*sensu stricto*), such as *H. ovoidea*, which it also resembles in shape. The absence of marked concavity in the posterior margin of the skull forms a distinction from *Parahaplolepis* (*H. tuberculata*, *H. anglica*, and allied species) and a resemblance to *H. ovoidea* and *H. corrugata*. The deep mandible is a character linking *H. attheyi* to *H. corrugata*. The large size of the teeth on the small bony plate is compatible with a comparatively strong dentition, such as is possessed by *H. corrugata* alone of the other species. *H. attheyi* may thus be regarded as a primitive form of *Haplolepis* (*sensu stricto*), from which (at least as regards the skull roof) *H. corrugata* could have been derived.

Haplolepis (Parahaplolepis) tuberculata (Newberry)

Plate 3, figures 1–3, plate 4, figures 1–9, plate 5, figures 1–3, plate 6, figures 1, 2; text figures 13–21, 44–46

Mecolepis tuberculatus NEWBERRY, 1856, p. 96.
Eurylepis tuberculatus NEWBERRY, 1857, p. 150.
Eurylepis tuberculatus NEWBERRY, 1873, p. 350, pl. 38, figs. 2–2c, 3, 3a.
Eurylepis tuberculatus NEWBERRY, 1889, p. 212.
Eurylepis tuberculata MILLER, 1889, p. 597, fig. 1130.
Eurylepis tuberculata WOODWARD, 1891, p. 449.
Haplolepis tuberculata MILLER, 1892, p. 715.
Haplolepis tuberculata HAY, 1902, p. 366.
Haplolepis (*Eurylepis*) *tuberculata* HUSSAKOF AND BRYANT, 1919, p. 191.
Haplolepis tuberculata HAY, 1928, p. 687.
Mecolepis granulatus NEWBERRY, 1856, p. 97.
Eurylepis granulatus NEWBERRY, 1857, p. 150.

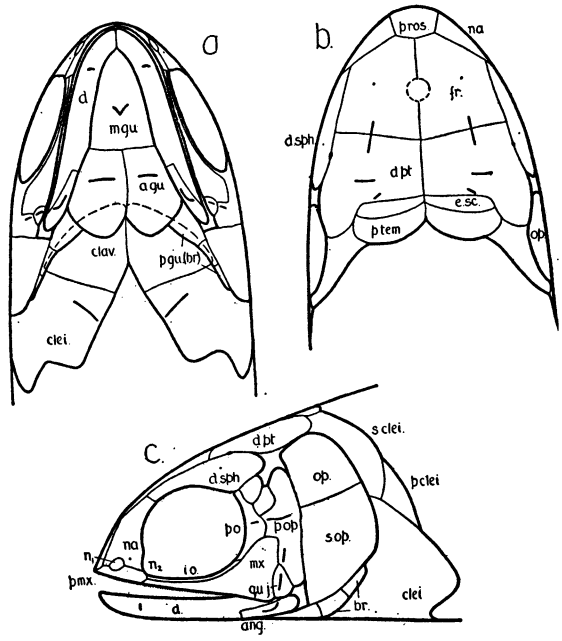


FIG. 14. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Reconstruction of dermal skull and shoulder girdle in a, ventral, b, dorsal, c, lateral views. Ornament omitted.

Eurylepis granulatus NEWBERRY, 1873, p. 352, pl. 39, figs. 5, 5a.
Eurylepis granulatus NEWBERRY, 1889, p. 212.
Eurylepis granulata WOODWARD, 1891, p. 449.
Haplolepis granulata MILLER, 1892, p. 715.
Haplolepis granulata HAY, 1902, p. 366.
Haplolepis (*Eurylepis*) *granulata* HUSSAKOF AND BRYANT, 1919, p. 191.
Haplolepis granulata HAY, 1929, p. 687.
Mecolepis insculptus NEWBERRY, 1856, p. 97.
Eurylepis insculptus NEWBERRY, 1857, p. 150.
Eurylepis insculptus NEWBERRY, 1873, p. 351, pl. 39, figs. 2, 2a.
Eurylepis insculptus NEWBERRY, 1889, p. 212.

The originals of some of Newberry's figures are in the American Museum of Natural History. The figured specimen of *E. granu-*

latus Newberry is the counterpart of No. 448G (labeled "type of *E. insculptus*"), and the original of one of the figures of *E. tuberculatus* (Newberry, 1873, pl. 38, fig. 2) is apparently an unregistered specimen labeled "type of *E. granulatus*." None of the other figured specimens were discovered by the writer.

The hypodigm (Simpson, 1940) of this description of *H. tuberculata* comprises the following specimens in addition to those just mentioned:

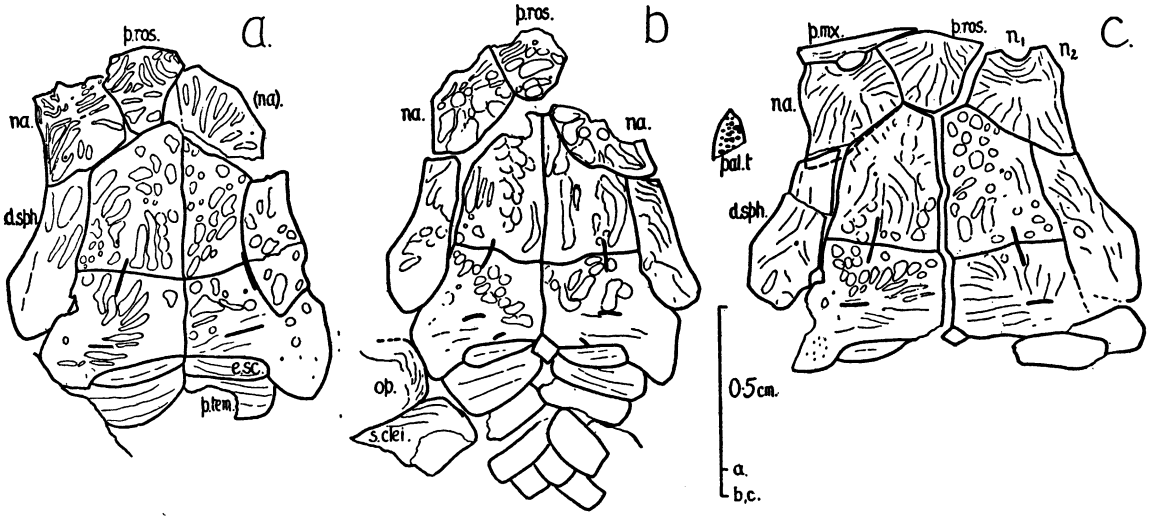


FIG. 15. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of skull roof. a, A.M.N.H. No. 982G; b, B.M.N.H. No. P.1005β; c, A.M.N.H. No. 1136G.

AMERICAN MUSEUM OF NATURAL HISTORY: Nos. 980a, 1895 (=958G), 1920, 2044, 2045, 2150, 441G, 447G, 451G, 973G, 979G, 982G, 985G, 987G, 989G, 990G, 992G, 996G, 1001G, 1136G, 1144G, as well as three unregistered skull roofs.

BRITISH MUSEUM (NATURAL HISTORY): Nos. P.1005α, P.1005β, P.3449α (in counterpart).

MANCHESTER MUSEUM: Nos. L.10751, L.10752, L.10753.

ROYAL SCOTTISH MUSEUM: No. 1886.15.8 and two unregistered specimens.

Also one specimen from Prof. D. M. S. Watson's collection and one (Westoll No. 172) from the author's collection.

This is by far the most common species at Linton, and large numbers of excellent specimens are available. In the material seen by the writer, the range in size is from *ca.* 45 mm. to *ca.* 75 mm., the majority being between 60 and 70 mm. long.

SKULL: Usually the skull roof is well preserved, the cheeks being folded in and damaged. The sagittal suture is rarely opened (figs. 15–17, 18a; cf. also pl. 3, fig. 2, pl. 4, figs. 1–7).

The frontals and dermopterotics form a large unit in the structure; there are no separate parietals, and the dermopterotics meet in the mid-line. The posterior margin of this compound roofing element is embayed to receive the extrascapulars and posttemporals, and the dermopterotics extend posterolaterally as somewhat rounded angles. The dermopterotics and frontals narrow anteriorly; the frontals have long oblique sutures with the nasals, and may or may not be notched for the postrostral. The frontals are longer than the dermopterotics, and the sutures between these two paired elements are never sinuous. In three specimens from the American Museum of Natural History (A.M.N.H. No. 980a and two unregistered separate skull roofs) there is a round area, about the middle of the interfrontal suture, which is quite distinct and very thinly ossified, if at all (fig. 16a). This is the pineal macula; the majority of specimens do not show it. The dermopterotics bear short grooves for the anterior and middle pit lines. In a few specimens (e.g., B.M.N.H. No. P.1005β, fig. 15b) there are also short grooves for the posterior pit lines.

The nasals are very broad elements, notched anteriorly for the anteromesial nasal openings; unlike typical palaeoniscids this fish has no nostril notches between nasals and postrostral. In certain specimens the nasal has a considerable notch in the orbital margin, probably for a posterior nostril. The skull roof is completed by the paired dermosphenotics, large bones roofing the orbits and extending far backwards.

The ornament of all these bones is somewhat variable but is based on a common plan. The unit of ornamentation is a broad, low, rounded tubercle, which may be elongated and fused with neighboring tubercles to produce a ridge. On the anterior parts of the postrostral and nasals there is a marked tendency for such rugae to be transversely arranged, the rugae usually swerving round the nostril notch and tending to run down to the broad anterior angle of the postrostral. Elsewhere on the nasals and postrostral the rugae and tubercles are well separated, and very sharp compared with those on other

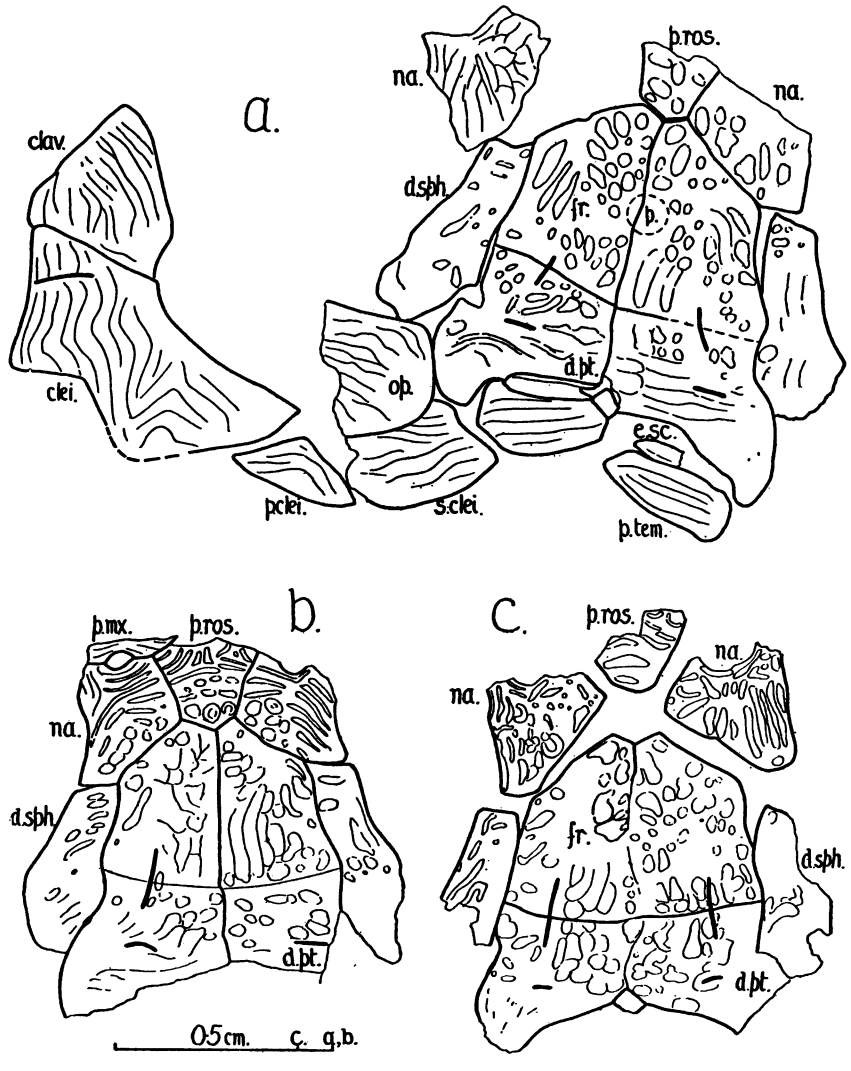


FIG. 16. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of skull. a, A.M.N.H. No. 980a; b, Manchester Mus. No. L.10753; c, Harvard, M.C.Z., unregistered.

head bones. On the frontals, dermopterotics, and dermosphenotics the ornament consists of lower, more rounded tubercles; the postero-lateral parts of the dermopterotics, however, are usually devoid of tubercles, showing only a few tiny vascular pores. There is often a tendency towards "groove-and-terrace" ornament on the posteromesial parts of the dermopterotics.

The extrascapulars are very small bones, not extending so far laterally as the larger posttemporals. In most specimens these two pairs of bones are separated in the middle line by a rhombic scale, but in A.M.N.H. No. 982G this is absent. The bones have a transverse "groove-and-terrace" ornament.

The cheek is magnificently shown in A.M.N.H. No. 447G (fig. 18a), and the details can be confirmed in many other individuals. The preopercular is an element of remarkable shape, quite unlike that of any ordinary palaeoniscoid, and consists of a stout arcuate portion with an irregular and narrow anterior projection. The maxillary has a slender suborbital part and a remarkably high and narrow expansion. There is a small quadratojugal, bearing the ventral part of the groove for the vertical pit line. The bones of the infraorbital canal are not always easy to observe; the most dorsal one, the post-orbital, is present in several specimens, and in A.M.N.H. No. 447G there is also preserved the most anterior member, intervening bones being lost. Between the postorbital and preopercular is a small suborbital, and between these last two bones and the skull

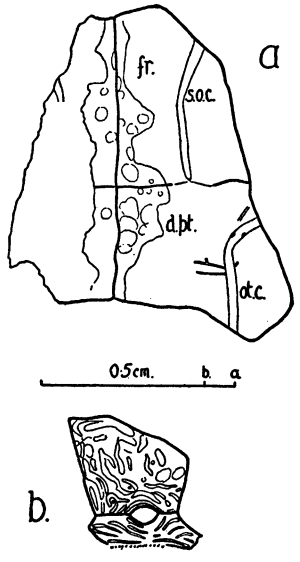


FIG. 17. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of skull. a, Skull roof of A.M.N.H. No. 992G, with bones of right side scraped to expose latero-sensory canals; b, nasal and premaxilla of A.M.N.H. No. 990G (cf. pl. 5, fig. 3).

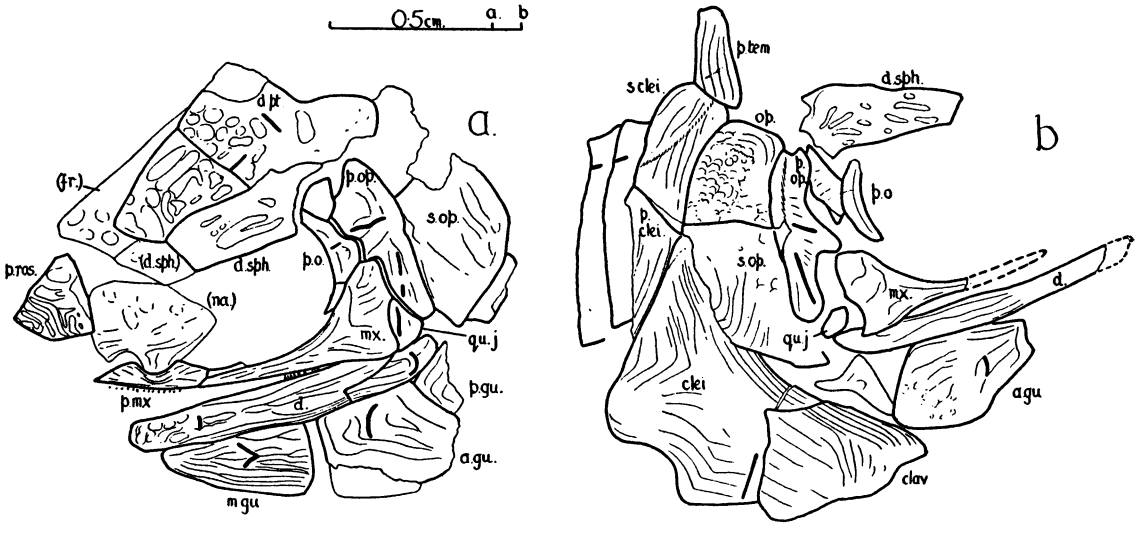


FIG. 18. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of skull. a, A.M.N.H. No. 447G (cf. pl. 3, fig. 2); b, A.M.N.H. No. 451G.

roof is a small dermal element which seems to separate the preopercular from the dermopterotic.

The ornament of the cheek bones is a little irregular and variable. The circumorbitals and the suborbital part of the maxillary are provided with strong "groove-and-terrace" ornament, and a much weaker and less consistently orientated ornament of the same kind occurs on the other bones.

The premaxillary is clearly shown, in natural relation with the maxillary and infraorbital in A.M.N.H. No. 447G (fig. 18a), and with the nasal in A.M.N.H. No. 990G (fig. 17b). It is a shallow bone, enclosing with the nasal the anteromesial nostril opening. It bears a strong ornament of rugae and almost certainly transmitted the ethmoidal commissure or anterior termination of the infraorbital canal.

The mandible is incompletely known, only the outer bones being preserved. The whole is very slender and is composed of a small angular and a larger dentary. The former carries a curved pit-line groove, the latter bears a small vertical groove for a pit line near the anterior end. The ornament of both bones consists of sharp rugae, sometimes passing into "groove-and-terrace," and arranged in a general longitudinal fashion, becoming a little irregular anteriorly.

The dentition consists of very minute teeth along the border of the maxillary, premaxillary, and probably the dentary. They are conical or peg-like, but their small size precludes any attempt at detailed description. In a few specimens there is a small free plate, probably pertaining to the palate, which bears a rather irregularly arranged group of cusps; these are not acutely conical, but fairly well rounded with pointed tips. No other ossifications of palate, mandible, etc., are known, and nothing can be seen of the endocranium.

Opercular Apparatus: The general arrangement is perfectly shown in an isolated cheek on A.M.N.H. No. 979G (fig. 19a) and can be confirmed on numerous other specimens. The opercular is about as wide as deep and is well rounded posterodorsally. There is apparently no antopercular. The subopercular is deeper and wider than the opercular. It is followed ventrally by a very remarkable series of branchiostegal or gular plates. Four small plates, lying more or less anteroposteriorly, lie below the subopercular and are followed by a paired plate lying between the posterior parts of the mandibles and meeting mid-ventrally. The series is completed ventrally by a large median gular lying between the anterior parts of the mandibular rami.

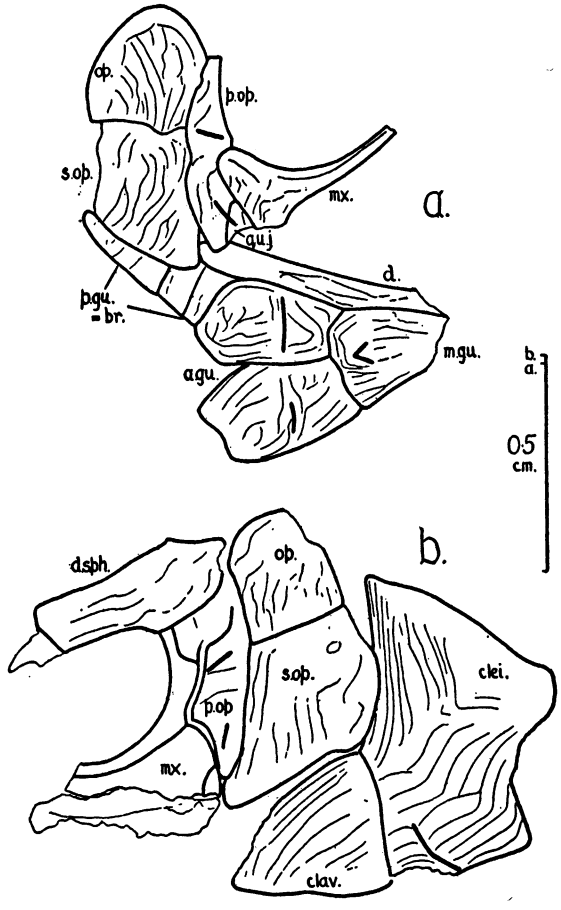


Fig. 19. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of skull. a, Separate head on A.M.N.H. No. 979G; b, B.M.N.H. No. P.1005α.

The opercular is usually ornamented with very slight, almost vertical "groove-and-terrace," but sometimes this is replaced by a reticular series of grooves (e.g., A.M.N.H. No. 451G). The ornament on the subopercular is much more irregular. On the gulars there is a marked tendency to concentric arrangement, and on the median gular the ornament becomes strongly rugose, converging anteriorly.

There is a pit-line groove with a transverse course on each of the large paired gulars, and another, more or less V-shaped, on the median gular.

PAIRED FINS: The dermal shoulder girdle is fairly robust, usually fairly well preserved. The supracleithrum, however, is not well shown in most specimens. It is a short stout bone, touching the posttemporal and dermopterotic dorsally. The anterior margin was

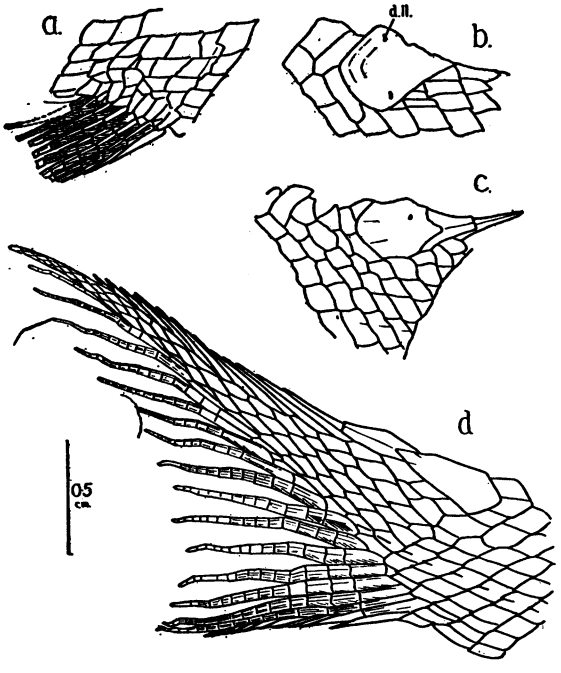


FIG. 20. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of scales and fins. a, Anal fin of A.M.N.H. No. 989G; b, scales in front of dorsal fin, Manchester Mus. No. L.10752; c, scales in front of dorsal fin, A.M.N.H. No. 975G; d, tail of A.M.N.H. No. 958G (cf. pl. 6, fig. 1).

probably partly covered in life by the opercular. There is a well-marked notch in the posterior border indicating the position of the lateral line. The postcleithrum is small and triangular. The cleithrum meets the supracleithrum only along a very short suture. It is a large element, with a broad notch at the origin of the pectoral fin. It was strongly bent during life, so that it consisted of a more or less vertical portion and a nearly horizontal part. The latter bears a pit-line groove for the ventral lateral line. The clavicles are of rounded triangular shape and were overlapped anterolaterally by the large paired gulars.

The anterior parts of the supracleithrum, cleithrum, and clavicle are ornamented in strong "groove-and-terrace" pattern parallel to the anterior margins. The rest of the bones have a feebler and more widely spaced "groove-and-terrace" ornament, more or less parallel to the hinder margins, but on the cleithrum there is often a marked zigzag arrangement.

The pectoral fins are usually poorly preserved, but a few specimens show important details. A.M.N.H. No. 448G (the holotype of "*Eurylepis granulatus*") shows the origin of the fin. The leading edge of the fin arises near the top of the notch in the cleithrum and is protected by a somewhat hemicylindrical scale. The fin rays arise from a small scale-covered lobe, and the posterior end of this lobe is somewhat more ventral than the anterior end. Several specimens convey the impression that the ventral surface of the body passed smoothly into the lower face of the scale-covered lobe; in the compressed state of certain individuals the fin and its basal lobe have been pressed against the flank, leading edge uppermost, while in others the fin is turned down with the leading edge forward. In life, therefore, the fin would form a plane directed laterally, the leading edge somewhat raised. The fin web consists of about 10 rays; the two most anterior are short and do not reach the tip of the fin. The fulcra are remarkably large, about 12 in number, and each is divided distally so that it appears to be of paired origin (e.g., A.M.N.H. No. 980a and A.M.N.H. No. 448G). They do not extend to the very tip of the fin. All the fin rays are segmented but are simple and undivided distally. The fin rays are normally well separated in the fossils, but each lepidotrich is divided into two areas by a longitudinal division. The anterior part was overlapped by the adjacent fin ray in the "collapsed" fin, and in the proximal parts of the more anterior fin rays this area is obliquely striated; this striation may have to do with the fixation of a delicate fin membrane. The posterior, free surface of the lepidotrich is smoothly covered with ganoine.

The pelvic fins arise from the ventrolateral

ridge, and, excluding the rounded scale at the origin of each fin, occupy three scale rows. Each fin consists of five or six rays similar to those of the pectorals; the leading edge is provided with about eight very large fulcra, the distal parts of which are split or deeply grooved. The fulcra do not reach the tip of the fin.

MEDIAN FINS: The dorsal fin consists of seven or eight rays of the same general type as that described above for the paired fins. The leading edge is furnished with magnificently developed fulcra. About three scale rows in front of the first true lepidotrich of the fin is an enlarged median scale. This is immediately succeeded by three large, pointed, overlapping scales, increasing in length, which reach from the dorsum up the front of the fin; the third of these reaches more than halfway to the tip of the fin. The fourth of these "fulcra" rests on the end of the short first lepidotrich, and the subsequent ones (there are about 11 in all) are borne on the second fin ray. The second and succeeding fulcra are distally split and deeply grooved, indicating a probable paired origin. The fulcra stop short of the tip of the fin. The proximal segments of the lepidotrichia are somewhat expanded and look like elongated distorted scales.

The anal fin is somewhat similar to the dorsal, but the web is not so long. It consists of about 10 rays, of which the two posterior are very small. The structure of the fin is similar to that of the dorsal; there are about 11 fulcra, the first two self-supporting, the third borne on the end of the short first fin ray, the remainder on, but not reaching the distal end of, the second ray.

The caudal (fig. 20d; pl. 6, figs. 1, 2) is a most elegant fin carried on a slender, curved, caudal lobe. The web of the fin is supported by about 16 rays and has a gently concave hinder margin, without separation of a strong ventral "lobe." The rays are of the same general type as has been described in the other fins; some of them appear to be divided distally, but this may be due only to the separation of the right and left series of lepidotrichia. The proximal segment of each ray closely resembles an elongated, distorted body scale. The first "fin ray" is small, a single segment bearing a very large fulcral scale, which may itself bear two or three smaller ones distally. About eight succeeding fulcra are borne on the second fin ray and do not reach its tip.

The dorsal fin is almost exactly opposed to the anal fin. The pelvics are slightly closer to the pectorals than to the anal, and the latter is distinctly closer to the caudal than to the pelvics.

SQUAMATION (PL. 5, FIGS. 1, 2): The body scales are covered by smooth and brilliant ganoine, in which a few tiny pits mark the openings of the vascular system of canals. The scale formula is usually

$$\frac{23\text{–}24}{7 \quad 17 \quad 26\text{–}27} \quad 29$$

The full formula could be counted in 16 specimens; the variation in position of the origins of the fins, etc., is shown below:

Pelvic fin	Scale row	7				
	No. of specimens	16				
Anal fin	Scale row	17	18			
	No. of specimens	14	2			
Caudal fin	Scale row	25	26	27		
	No. of specimens	2	6	8		
Dorsal fin	Scale row	22	23	24		
	No. of specimens	1	7	8		
Caudal inversion	Scale row	27	28	29	30	
	No. of specimens	1	4	10	1	
Change of flank scales	Scale row	14	15	16	17	18
	No. of specimens	2	4	5	4	1

There is a very considerable correlation between fin positions; if any of the median fins is nearer the head or tail than the average, the other fins tend strongly to follow its example.

There are no enlarged dorsal or median ventral scales except near the origin of median fins and along the caudal lobe. The anterior scale rows meet in the mid-line in a characteristic herringbone pattern. The most remarkable feature of the squamation in this species concerns the lateral-line scales of the flank. Anteriorly these are extraordinarily deep—6 mm. in a 70-mm. fish. These scales gradually decline in height for about half the length of the body, and then quite abruptly in the next posterior row two scales occupy the same position and area (fig. 21a–d; pl. 5, figs. 1, 2). Exceptions to this condition are

very rare, but A.M.N.H. No. 975G shows scale No. 15 "divided," No. 16 "compound," and all succeeding scales "divided." A less abrupt transition is shown in A.M.N.H. No. 980a, in which the lateral-line scales as far back as about No. 16 decline in height more markedly than usual; the lateral-line scale in row 17 is considerably shallower, but together with the next most ventral scale in that row is distinctly deeper than the lateral-line scale in row 16. This condition (which is very rare) somewhat resembles that in other species of *Haplolepis* (*sensu lato*).

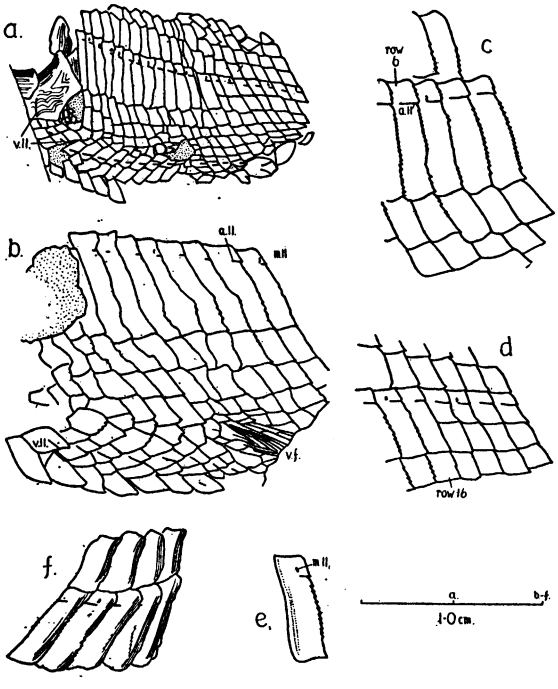


FIG. 21. *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry). Details of scales, etc. a, A.M.N.H. No. 2044 (pl. 5, fig. 2); b, anterior flank scales of A.M.N.H. No. 447G; c, d, flank scales of Manchester Mus. No. L.10752; e, separate anterior flank scale on A.M.N.H. No. 990G; f, anterior flank scales of A.M.N.H. No. 979G.

Immediately behind the skull there are two scales in each row above the lateral-line scale, each being quite deep. Traced posteriorly, the corresponding scales in other rows become less deep, and the lateral line moves down to the middle of the flank. Additional scales thus appear dorsally in the more posterior rows, until just in front of the dorsal fin there are four or five scales above the lateral-line scale. The insertion of new scales is easily studied. In the anterior trunk the right and left scale rows usually meet unsymmetrically. Occasionally a median, usually unsymmetrical, arcuate scale appears between the scales corresponding to those meeting mid-dorsally in the row in front. In the next posterior row the equivalent of the median scale occurs as a pair of scales. Behind the dorsal fin there are four or five scales in each row above the lateral line, and this is maintained as far as the caudal inversion.

The anterior deepened lateral-line scales bear traces of the lateral line only in the dorsal part; behind the sudden replacement of the deep scales by two scales in each row, the lateral line is borne by the upper scale. The depth of these lateral-line scales is gradually reduced further posteriorly until they are somewhat shallower than long on the caudal pedicle.

On the anterior flank there are usually three shallower scales in each row below the lateral-line scale; the third is succeeded by a peculiarly shaped scale lying on the ventrolateral ridge, below which the scale row is abruptly directed anteromesially on the flattened venter (fig. 21a, b). The ventrolateral paired ridges converge posteriorly from the cleithral notches and die out behind the pelvic fins; the paired fins arise near these ridges. In the most anterior rows there are two or three scales in each row between the ridge scale and the mid-ventral line; the right and left scale rows meet in "herringbone" pattern. Immediately in front of the pelvic fins the scales of the ventrolateral ridge are thickened and strongly curved. On the venter between the pelvics the arrangement of the scales is irregular (A.M.N.H. Nos. 2044, 451G). Behind the pelvics the ventrolateral ridge is less well marked, and the scale rows do not change their direction and meet in a series of narrow mid-ventral scales. At about the thirteenth or fourteenth scale row these median scales are succeeded by a much larger element extending over two or three rows and remarkably denticulated posteriorly. This scale bears deep paired grooves and is immediately followed by a pair of large scales, also denticulated posteriorly, which lie at the base of the anal fin.

Just in front of the anal fin there are about six scale rows between the lateral line and the pre-anal paired scale. There are only four scales in each row beneath the lateral line at the caudal pedicle, and this is further reduced at the caudal inversion. There are four or five scales between the lateral line and the predorsal scale, and about six between the lateral line and the middle of the base of the dorsal fin, where there are often minor irregularities in the squamation.

About three scale rows in front of the first dorsal fin ray there is a large, broad, median scale which is immediately followed by the fin fulcra. Behind that fin the scale rows meet without median elements as far as the first caudal ridge scale, of which the anterior end arises three scale rows behind the origin of the caudal fin. This scale is large, anteriorly rounded, and posteriorly drawn out and denticulated. The more posterior caudal ridge scales, which may number 15 to 18, are long, very narrow, and with their long, exposed posterior portion split into two needle-like points by a median groove; it is probable that each scale is really a paired structure. The anterior portions of the ridge scales are expanded and lie in series with the scale rows of the caudal lobe. The ridge scales appear to stop short of the extreme tip of the tail. There is a single enlarged median scale in front of the "fulcra" of the caudal fin.

The anterior flank scales are strongly denticulated on their posterior margin; each denticle is thorn-like in shape. The denticulation is most extensive on the lateral-line scales; above and below these it is limited to the lower part of the posterior margin. The denticulation normally dies out posteriorly in the neighborhood of the dorsal fin, but there is a persistent thorn-like projection at the posteroventral corner of scales on the more posterior part of the body.

With few exceptions the scales are almost perfectly smooth, with a few tiny pores in the brilliant ganoine. Some of the anterior ventral scales have many such pores, more noticeable than usual, arranged in antero-posterior rows, and some have also a slight ornament of grooves parallel to the anterior margins. Several specimens show slight indications of similar ornament of grooves parallel to the anterior and ventral margins, on some of the anterior flank and dorsal scales. (See also p. 78.)

The caudal inversion of the squamation is fairly sharp. The scales of the caudal lobe are elongated rhombs; in the anterior part of the body extension there are about five scales in each row, reduced to about three near the posterior tip.

The microscopic structure of the scales has been studied only in a few slices. It will be discussed later in this work (p. 78).

LATERAL LINES: There are three paired lateral lines on the body. The "main lateral line" runs back from the supracleithrum through the dorsal parts of the very deep flank scales, then through a series of more normal scales as far as the caudal inversion. It is marked by two sets of stigmata: on each scale of the series there is a "pit-line" groove extending over more than half the exposed breadth of the scale and reaching the posterior margin of the scale in a small notch; and on certain scales there are also lunate pores situated just above the anterior part of the groove (fig. 21a–e). The pit-line grooves can be traced behind the caudal inversion; usually the series of groove-bearing scales reaches the caudal fin near the insertion of the seventh or eighth fin ray, and, in a few specimens only, there are occasional grooves on more posterior scales adjacent to the base of the fin. These "pit-line" grooves occur on every scale row of the flank, but the distribution of the lunate pores, which must be regarded as the openings of enclosed laterosensory organs, is very irregular. In four specimens they occurred on occasional scale rows as follows:

A.M.N.H. No. 2044 . . . . . 2. 3. 5. 7. 8. 11. 12. 14. 16. 18. 19. 21—(broken)
Manch. No. L.10752 . . . . . 3. 6. 7. 8. 11. 15. 18. 21. 25. 28.
A.M.N.H. No. 447G . . . . . 1. (?)4. 9. 14. 17. 20. 24.
A.M.N.H. No. 958G . . . . . 2. 3. 7. 9. 10. 12. 13. 18. 20. 21. 24.

The enclosed lateral line is regarded as the main lateral line, the pit lines as the accessory lateral line (see p. 81).

The dorsal lateral line is shown as lunate pores opening on occasional scales above the lateral-line row. In A.M.N.H. No. 447G it

occurs on scales in the following rows: 4 (1 scale above the lateral line); 9 (3 above); 15 (3 above); 20 (4 above). In this particular specimen there is a rather close relation between the appearance of a lunate pore of the dorsal lateral line and a similar pore in the main lateral-line scale of the same row. In several individuals the pair of dorsal lateral lines can be seen to terminate posteriorly as lunate pores in the lateral parts of the enlarged predorsal scale at about scale row 22, five scales above the main lateral line (fig. 20b, c). It is thus clear that the main and dorsal lateral lines converge anteriorly.

The ventral lateral line is clearly shown in a number of individuals. A pit-line groove is developed on the lower part of the cleithrum below the pectoral fin, and a continuous paired chain of grooves of the same nature extends back between the paired fins (fig. 21a, b). Anteriorly the grooves are found on the second scale from the mid-line in each row; behind the pelvics the paired grooves converge and are responsible for the deep paired grooves on the large median pre-anal scale.

The continuation of the main lateral line in the skull is difficult to study. The bones are opaque, even when immersed in fluid and studied under powerful illumination. In a few cases it has been possible to expose the canal system in the skull roof by scraping (fig. 17a).

The main lateral line probably traverses the supracleithrum and posttemporal in the usual way, and, though there is no positive evidence, it is likely that the extrascapulars are traversed by the occipital cross-commissure. The course of the canal in the dermopterotic has been prepared; it swings laterally in a broad curve and enters the dermosphenotic, from which it certainly passes into the postorbital and infraorbital chain. Anteriorly it must have passed into the premaxillary, but the details in this region are unknown.

The anterior termination of the supraorbital canal is not known. A pore in the nasal indicates its passage through that bone, and scraped specimens have shown its flexuous course through the frontal. The enclosed canal ends at the dermopterotic suture, or just in front of it, and is continued posteriorly as the anterior pit line.

The preopercular and mandibular canals have probably their normal courses, but pores are very sparse.

Pit-line grooves are very clearly shown. On the skull roof the anterior pit line extends towards the radiation center of the dermopterotic from the posterior end of the supraorbital canal; the middle pit line is a transverse groove on the dermopterotic, and the posterior pit line is occasionally present as a very short groove lying more posteromesially on the same bone.

The pit lines of the cheek have left grooves on the preopercular and quadratojugal as shown in the text figures. A curved oralomandibular groove (continuation of the vertical pit line of the cheek) is present on the angular, and there is also a short vertical groove on the anterior part of the dentary. There is a broad V-shaped pit-line groove on the large median gular and a short transverse groove on each of the large paired gulars.

DIAGNOSIS OF *H. tuberculata:* A large species of *Haplolepis* (*sensu lato*) with no parietals, dermopterotics meeting in mid-line and bearing all pit lines of skull roof. Ornament of skull roof consisting of broad, low tubercles passing into rugae on nasals and dermosphenotics. Ornament of cheek and jaw bones of sharp, terraced rugae. Suspensorium almost vertical, preopercular of greatly modified shape, maxillary expansion very short and high. Small quadratojugal present. Dentition very weak. Opercular apparatus with remarkably modified branchiostegal rays. Dorsal and anal fins almost exactly opposed. Pelvics slightly closer to pectorals than to anal, anal distinctly closer to caudal than to pelvics. Scale formula usually

$$\frac{23\text{–}24}{7 \quad 17 \quad 26\text{–}27} \quad 29$$

Scales almost wholly devoid of ornament, very thin. Bone layer (isopedin) remarkably thin; cosmine layer with wide vascular canals; ganoine thin. Anterior lateral-line scales very deep for about 16 rows, then abruptly succeeded by two series of scales occupying the same relative position. Main lateral-line opening by occasional lunate pores, accessory main lateral line forming grooves on every lateral-line scale. Dorsal lateral line enclosed,

opening by occasional lunate pores. Ventral lateral line present as chain of grooves on cleithrum and scales of flattened venter.

Haplolepis (Parahaplolepis) cf. **tuberculata** (Newberry)

Plate 7, figure 1

One of the nodules from Mazon Creek in the Yale collection [No. 222 (4)] includes the greatly disturbed remains of a small fish which closely resembles *H. tuberculata* Newberry from Linton. Unfortunately it is not possible to decide whether or not the specimen differs significantly from that species.

SKULL: The posterior part of the skull roof is preserved in part and counterpart. Although badly preserved it can be seen to be of the "*tuberculata*" type, and the course of the sensory canals is clear. The ornament is also very similar to that of the Linton species.

BODY: The scales are apparently smooth, with the exception of a few in the anterior part of the dorsum, which may bear rows of small elongated pits as in *H. tuberculata*. At least the most anterior 12 lateral-line scales are very deep, and it is probable that the transition to the normal-sized scale is abrupt. The groove indicating the main lateral line is near the upper margin of each lateral-line scale. The posterior margin of almost every scale is hidden, but in a few there can be discerned strong denticulations.

FINS: The only fin that can with certainty be identified is the caudal, a small piece of which shows all the characters normal for *H. tuberculata*.

As far as can be judged, the specimen would fall readily into the size range of *H. tuberculata*.

Haplolepis (Parahaplolepis) anglica (Traquair)

Plate 7, figure 2; text figure 22a

The holotype is an isolated skull roof from the Ash Coal of Longton, Staffordshire, and is now in the British Museum (Natural History), No. P.7995. It consists of paired frontals and dermopterotics, without separate parietals. The ornament consists of fairly strong rugae on the frontal, less well developed on the dermopterotics. The more transverse ornament on the anterior parts of the frontals is noteworthy.

The arrangement of the latero-sensory canals is similar to that in *H. tuberculata* and *H. corrugata;* the anterior pit line extends onto the dermopterotic from the frontal suture, and the middle pit line is in its usual position.

The shape of the skull roof differs somewhat from that of other species; it is proportionately longer and narrower than that of *H. tuberculata* and *H. corrugata* and has distinctly different contours in the anterior part. The posterior margin is concave, a marked distinction from *H. corrugata*. It is uncertain how far some of these differences may be due to individual variations within the species, but they preclude reference to *H. tuberculata* or *H. corrugata*, in which, moreover, the ornament is different, particularly in *H. corrugata*. It may be concluded, therefore, that *H. anglica* represents a well-defined species, probably rather closely related to *H. tuberculata*, and much less closely to *H.*

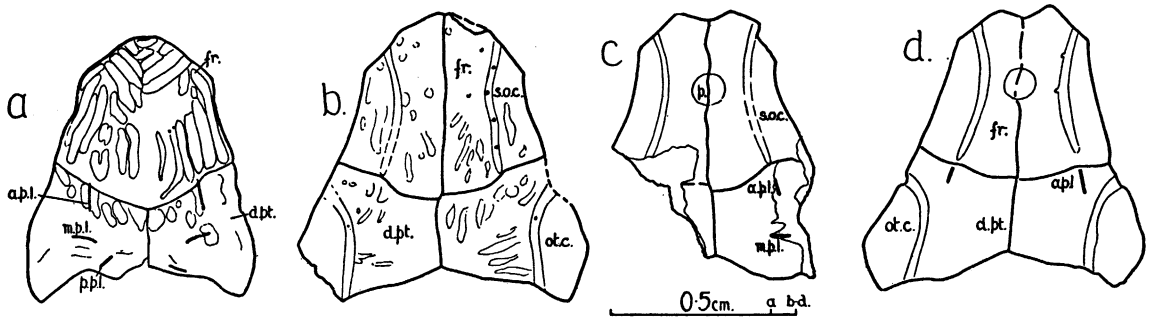


FIG. 22. a, *Haplolepis* (*Parahaplolepis*) *anglica* (Traquair). From Ash Coal, Longton, Staffordshire. Holotype, B.M.N.H. No. P.7995; b–d, *Haplolepis* (*Parahaplolepis*) aff. *anglica* (Traquair). From Low Main Cannel, Newsham, Northumberland. b, Hancock Museum, specimen B; c, d, Hancock Museum, specimen A (counterparts).

corrugata. It may confidently be placed in the subgenus *Parahaplolepis*.

Haplolepis (Parahaplolepis) aff. anglica (Traquair)

Plate 7, figures 3, 4; text figure 22b–d

Two skull roofs from Newsham in the Hancock Museum, Newcastle-on-Tyne, represent *Haplolepis* of the type without separate parietals. One of these (specimen A) is in counterpart; the other (specimen B) is represented by a skull roof seen in dorsal view, but with most of the bone material removed.

SPECIMEN A (FIG. 22c–d; PL. 7, FIG. 4): This specimen shows all the typical anatomical features of *H. tuberculata;* there is also a deep impression in the lower face of the frontals, apparently representing a thinly covered pineal foramen. The ornament is partly shown because of removal of some of the bone and is very similar to that of *H. tuberculata*. It is distinguished from that species by its greater narrowness and the less well-marked "shouldered" shape of the anterior parts of the frontal. It apparently differs from *H. anglica* in the somewhat broader proportions and the shape of the anterior part of the frontals, and in details of the ornament.

SPECIMEN B (FIG. 22b; PL. 7, FIG. 3): This specimen is probably very similar to specimen A, though not so well preserved. The latero-sensory canals are very well shown because of the removal of bone material; thus the supraorbital canal of the right side has preserved two or three tubules.

These specimens are most closely comparable with *H. anglica* and *H. tuberculata*, and will be called *Haplolepis* (*Parahaplolepis*) aff. *anglica* (Traquair).

GENUS **PYRITOCEPHALUS** FRITSCH

Pyritocephalus FRITSCH, 1893, p. 86.
Teleopterina BERG, 1936, p. 345.

GENOTYPE: *Pyritocephalus sculptus* Fritsch, 1893, pp. 86, 87.

This genus was set up by Fritsch for the reception of a small fish previously mentioned under the *nomen nudum Palaeoniscus sculptus* (Fritsch, 1879, "Fauna der Gaskohle," vol. 1, p. 30). *Pyritocephalus sculptus* Fritsch occurs in some abundance in the "splint" or cannel coal of Nýřany (Nürschan). Subsequent comments on *P. sculptus* are few. Westoll (1937b, p. 575; 1938) made mention of its peculiarities, and Moy-Thomas (1939, p. 112) has incorporated a brief statement on the remarkable skull roof in a general account and classification of the early Actinopterygii. (See also Berg, 1940, pp. 186, 405.)

Mecolepis lineatus Newberry, from Linton, Ohio, was described in 1856. In 1857 it was transferred to the new genus *Eurylepis* Newberry (*non Eurylepis* Blyth, 1854) and in 1873 was described and illustrated in greater detail. Newberry noted certain differences from other species of "*Eurylepis*" but thought that the resemblances were too clear to warrant separation. Later, in 1889 (p. 228), he remarked that the species "should be separated from that genus and probably be included in *Rhadinichthys* Traquair. . . . Whether [it] should be included in Dr. Traquair's genus *Rhadinichthys* can be decided only by a comparison of specimens, which has not yet been possible." The species is mentioned as *Rhadinichthys? lineatus* (Newberry) by Hay (1902, p. 367; 1929, p. 688) and Hussakof (1908, p. 95). In 1937 the author examined the type and other material in New York and found that it should be referred to *Pyritocephalus*.

Palaeoniscus gracilis Newberry and Worthen from Mazon Creek was described in 1870. It was later referred to *Rhadinichthys* by Woodward (1891, p. 469), Hay (1902, 1929), Eastman (1902a, 1902b, 1903, 1917), and Berg (1936). One specimen (described by Eastman, 1917) was specially studied by Berg (1936), who made it the type of a new species and genus, *Teleopterina improvisa* Berg, representing the new family Teleopterinidae. The writer has found that Berg's type specimen is somewhat disturbed and cannot be distinguished from *P. gracilis* Newberry and Worthen. This species should also be referred to *Pyritocephalus*.

A single individual from Mazon Creek is described below as a new species. The only other material which the writer would refer to the genus is a skull roof from the Low Main seam of Newsham, Northumberland, to be described below as a new species.

Certain sculptured dermal bones from the

Texan "Red Beds" were referred by Hussakof (1911, p. 173, fig. 55) to the genus *Pyritocephalus*. The bones belong to some large, thick-boned "palaeoniscid" and have no resemblance to those of the small *Pyritocephalus*. Hussakof's reference was biased by his attempt to draw a close comparison between the Texan faunas and those described by Fritsch from Bohemia.

The species at present placed in the genus are:

Pyritocephalus sculptus Fritsch . .	Nýřany
Pyritocephalus lineatus (Newberry)	Linton
Pyritocephalus gracilis (Newberry and Worthen) . . . . . (Syn. *Teleopterina improvisa* Berg)	Mazon Creek
Pyritocephalus comptus, new species	Mazon Creek
Pyritocephalus rudis, new species .	Newsham

The following short diagnosis of the genus may be attempted. Actinopterygian fishes of small size, probably rarely exceeding 70 mm. in length. Head broad and short, with very large orbit, no overhanging rostrum. Skull roof with remarkable paired fenestrations, mostly surrounded by frontals, dermopterotics, and dermosphenotics. Parietals not present, dermopterotics meeting in the midline. Extrascapular bones small. Premaxillaries (apparently dentigerous rostrals) present. Nasal openings unlike those of typical palaeoniscoids; anteromesial openings either in the lower part of the nasal, or between nasal and premaxillary, on each side. Cheek little modified from generalized palaeoniscoid type; quadratojugal present. Dentition very feeble. Opercular system much reduced, divided into distinct parts; paired opercular and subopercular flaps separated from a series of one median and two pairs of gulars between the jaws. Small triangular antopercular present. Ornament of head bones strongly developed, of fairly regularly arranged terraced rugae.

Body with flattened venter between the paired fins. Body covered with ganoine-coated scales, smooth except for a few linear grooves near the anterior margin, and without denticulations on the posterior border. Peg-and-socket articulations probably absent. Scales very thin; isopedin layer probably extremely thin. Anterior lateral-line scales may be deeper than others; anterior flank scales below the lateral line tending to be shallow and numerous. Anterior scale rows show abrupt change of direction at the ridge marking the junction of flank and flattened venter. Enlarged median scales only in front of each median fin.

Fins formed of few, well-separated rays in fan-like arrangement. Each ray fairly broad, completely segmented, and usually bifurcated once only, near the distal tip. Anterior margin of each fin with moderately stout fulcra not reaching the distal parts. Tail completely heterocercal; caudal fin more or less triangular, with slightly concave free margin and poorly developed "lower lobe," the web being about half the length of the body lobe. Dorsal fin arising behind anal. Pelvic and anal insertions are near the divisions of the pectoral-to-caudal length into thirds.

Three paired "lateral lines" with accessory main lateral line. Ventral lateral line represented by grooves on cleithrum and scales of venter as far back as anal fin. Main lateral line indicated by occasional lunate pores on the "lateral-line series" of scales and by an accessory lateral-line series of pit-line grooves. Dorsal lateral line extending from flank immediately behind supracleithrum backwards and upwards to scales immediately below dorsal fin; represented anteriorly by occasional lunate pores, posteriorly by pit-line grooves. Latero-sensory system of head modified by development of supraorbital fenestrae. "Main lateral-line" canal anastomoses with hinder end of supraorbital canal, not with infraorbital canal. Pit-line grooves very completely developed on skull roof, cheek, mandible, and gular.

Pyritocephalus sculptus Fritsch

Plate 8, figures 1–3, plate 9, figures 1, 2; text figures 23–27, 44

Palaeoniscus sculptus FRITSCH, 1879, p. 30.

Pyritocephalus sculptus FRITSCH, 1893, pp. 86–87, fig. 280, pl. 115.

Pyritocephalus sculptus WESTOLL, 1938, p. 48.

About 20 specimens of this species have been used in the present study. In many of these, remains of the very thin dermal bones and scales were present, but as no useful information could be derived from these, even in brilliant illumination under immer-

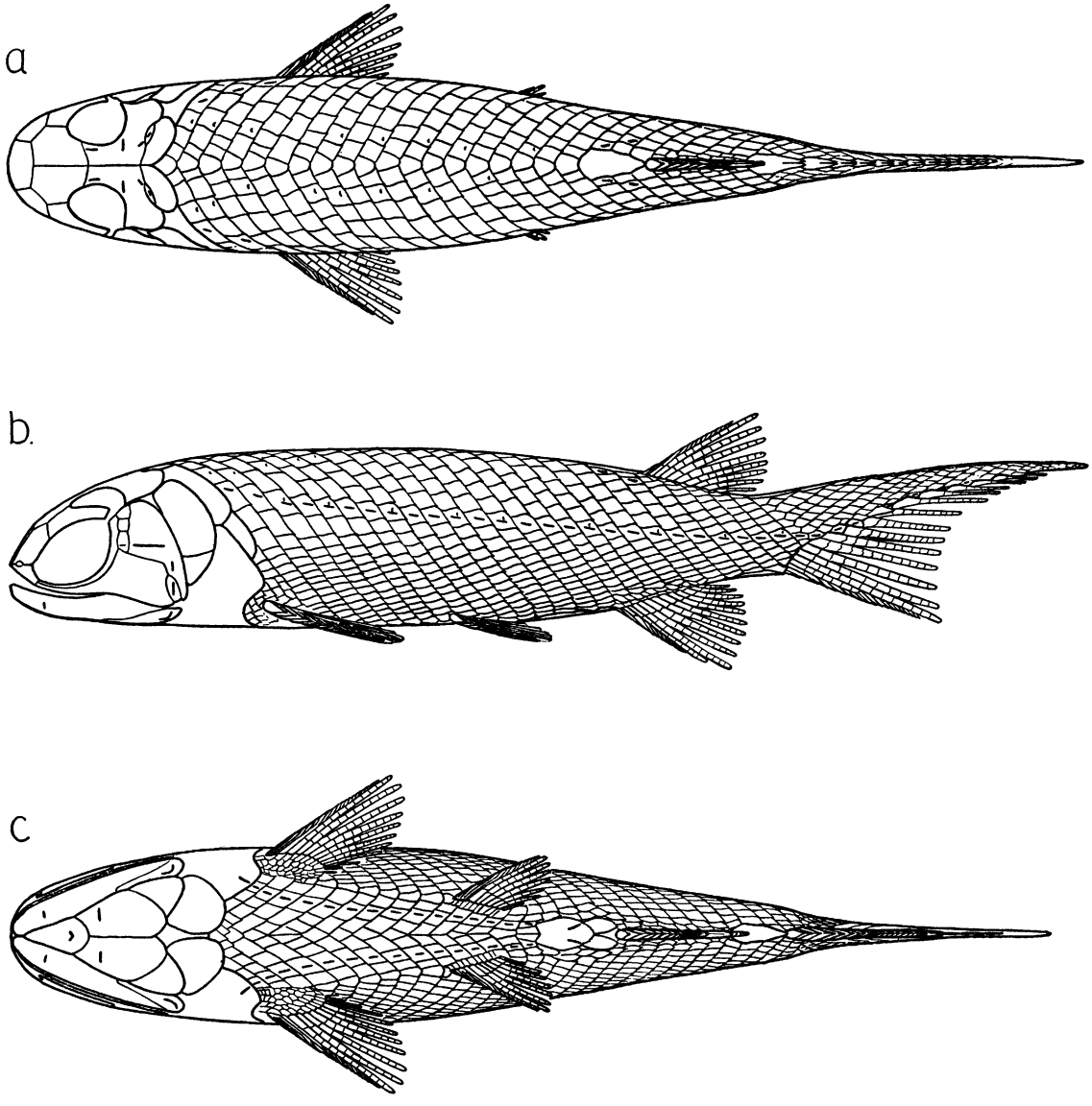


FIG. 23. *Pyritocephalus sculptus* Fritsch. Nýřany, Czechoslovakia. From a cannel ("gas-coal") of the Nýřany group, near the Westphalian-Stephanian boundary. Reconstruction of whole fish in a, dorsal, b, lateral, c, ventral views.

sion fluids, the bone was removed by the action of dilute acid; the molds thus formed are very sharp. The type material has not been examined, but Fritsch's figures show clearly that the present description is based on material properly referred to *P. sculptus*.

The species ranges in size from *ca.* 40 to 60 mm. total length in the present sample.

The hypodigm of this description of *P. sculptus* comprises the following specimens:

BRITISH MUSEUM (NATURAL HISTORY): Nos. P.8645, P.8649, P.8650, P.8672, P.8701, P.8701a, P.21989, P.21990, P.21991.

ROYAL SCOTTISH MUSEUM: Nos. 1897.96.1–4 (four specimens).

UNITED STATES NATIONAL MUSEUM: Two unregistered specimens.

Also one from Prof. D. M. S. Watson's collection, and two (Westoll Nos. 170, 171) from the author's collection.

SKULL (FIG. 24): The skull roof is a remarkable structure, with a large paired fenestration lying above the orbits and largely bounded by the frontal, dermopterotic, and dermosphenotic. There are no separate parietals, and the dermopterotics meet in the mid-line. The frontals are not easily distinguished from the dermopterotics, but the suture is visible in a few specimens. The frontals are about as long as the dermopterotics along the mid-line, but are much smaller in size; their shape and proportions will be clear from the figures. Both frontals

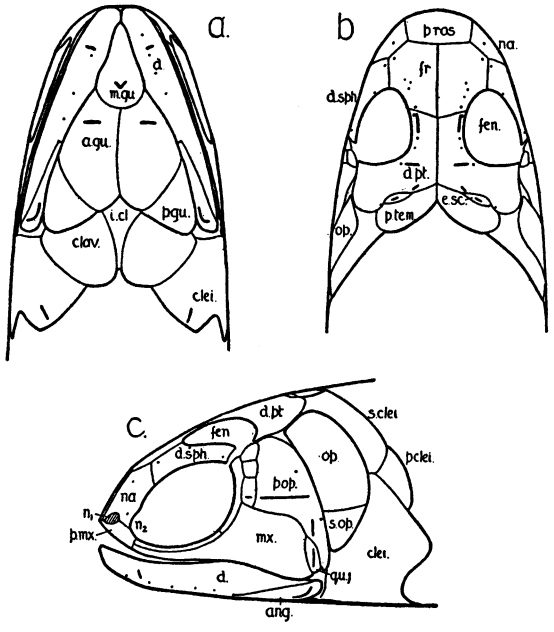


FIG. 24. *Pyritocephalus sculptus* Fritsch. Reconstruction of dermal skull and shoulder girdle in a, ventral, b, dorsal, c, lateral views. Ornament omitted.

and dermopterotics bear a rather sharp ornament of "terraced" rugae; on the frontals these have a roughly concentric arrangement, while on the dermopterotics they tend to run parallel to the posterior and lateral margins. Both bones are pierced by pores of the latero-sensory system, and there is a sharp transverse groove on each dermopterotic for the middle pit line. The anterior pit-line groove extends back onto the dermopterotic from the most posterior latero-sensory canal pore on the frontal.

The "dermosphenotic" is a large element forming a bar between the orbit and the supraorbital fenestra. It bears a strong ornament of terraced rugae arranged more or less parallel to the margins. The postrostral is a very curious, almost square element, with a very strong ornament of transverse rugae above, breaking down into elongated tubercles near the lower border. The nasals are rarely well shown; they seem to have a rounded notch in the lower border. The ornament of the bone consists of terraced rugae roughly concentric about this notch and parallel to the upper and lateral borders of the bone. A good premaxillary is shown in B.M.N.H. No. P.21989, in which it appears to close the notch in the lower border of the nasal. The two bones may actually be ankylosed, which would explain the appearance of the opening entirely surrounded by bone. No teeth can be seen on the bone, which is higher laterally than mesially.

The extrascapulars are minute paired elements, each being completely bounded by the dermopterotic and posttemporal. No latero-sensory pores have been seen on these bones, but there is sometimes a groove for the posterior pit line. The posttemporals are fairly large, meeting in the middle line. Both elements are ornamented with terraced rugae.

The cheek is well preserved in several specimens. The component bones are usually a little disturbed. The preopercular is a large element of characteristic palaeoniscoid type, with an expanded "horizontal" shank. It makes contact with the dermopterotic and bears a long groove for the horizontal cheek line of pit organs. There are two to four small suborbitals, each with one or two small concentric rugae forming a characteristic ornament. The postorbital is well shown in B.M.N.H. No. P.8650; it is an extremely slender element touching the dermosphenotic dorsally. The infraorbital is very rarely seen. There is an impression on B.M.N.H. No. P.21989 of a slender element similar to the postorbital, lying above the maxillary, which is probably the bone in question. The maxillary is of typical palaeoniscoid type with a broad cheek expansion, on which the typical terraced rugae are arranged more or less parallel to the margins. Teeth are usually not visible, but the maxillary of a specimen (Westoll No. 170) in the author's collection

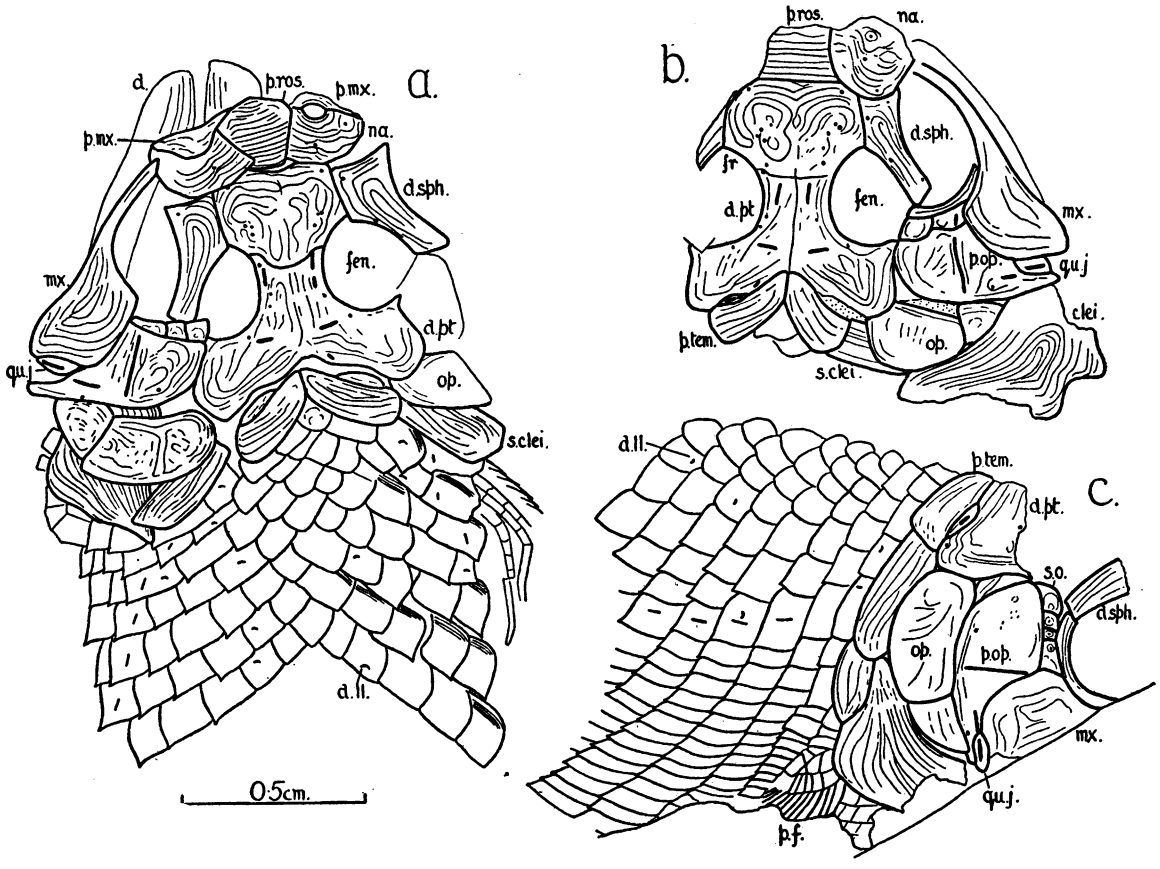


FIG. 25. *Pyritocephalus sculptus* Fritsch. Details of skull. a, B.M.N.H. No. P.21990 (cf. pl. 8, fig. 3); b, Westoll No. W.170; c, B.M.N.H. No. P.8650 (cf. pl. 8, fig. 2).

seems to have a row of very minute conical teeth. Between the maxillary and the preopercular is a small quadratojugal, which bears a groove for the vertical pit line.

The mandible is usually strongly developed, and the dermal bones in general are so thin that its impression can normally be seen even through the skull-roof elements. Only the dermal bones of the outside of the jaw are preserved; the angular and "dentary" are clearly separated. The strong, terraced ornament is arranged more or less parallel to the bone margins. There is a vertical groove on the anterior part of the dentary, probably for a pit line and a curved pit-line groove on the angular. No teeth have been observed.

The opercular apparatus is very remarkable. The opercular is distinctly deeper than wide, reaching the dermopterotic. It is followed ventrally by a smaller triangular subopercular; between this and the gulars is a considerable gap. The gular series consists of one anterior unpaired and two paired elements; there is also a small median bone between the clavicles and the gulars, which will be considered with the shoulder girdle. The posterior paired gulars are small, triangular elements; the larger anterior pair carry short grooves for pit lines. The anterior median element is smaller than the others, of an elongated pear shape, and has a V-shaped groove for a pit line. All these gular elements are strongly ornamented in the usual way, but the ornament on the operculars is much less strong. Between the opercular, preopercular, and dermopterotic is a small, triangular antopercular.

PAIRED FINS: The dermal bones of the shoulder girdle are well shown in the available material (figs. 25, 26). The supra-

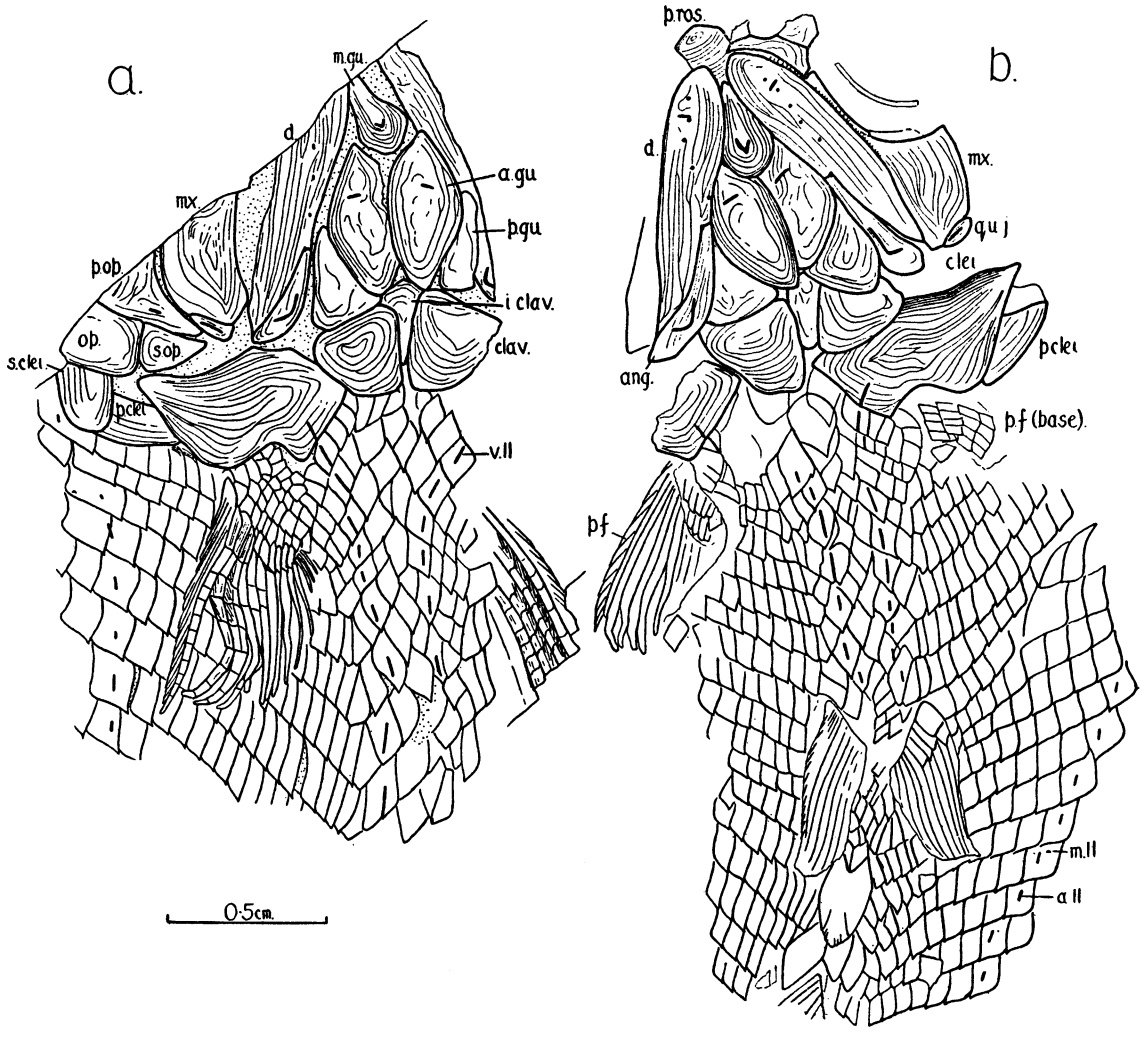


FIG. 26. *Pyritocephalus sculptus* Fritsch. Details of venter. a, Westoll No. W.171 (pl. 9, fig. 2); b, B.M.N.H. No. P.21989 (pl. 9, fig. 1).

cleithrum is an elongated element with a longitudinal ornament of the usual "terrace" type. The cleithrum is large and fairly deeply notched for the pectoral fin. The ornament is more or less parallel to the margins of the bone and of the usual type. The lower part of the bone was in life turned in at an angle to the upper shank and bears a short groove for the anterior termination of the ventral lateral line. There is a single fairly large postcleithrum. The clavicles are triangular elements, enclosing between them a curious bone, tapering posteriorly, which may be termed an "interclavicular scale" (fig. 26a, b); its nature will be discussed later (p. 77).

The pectoral fins are rarely well preserved (fig. 26a). There is a small, scale-covered lobe, probably standing out more or less horizontally in life, from which the dermal rays arise. There are about 14 separated fin rays forming a fan-like structure; the rays are segmented, and ornamented with longitudinal rugae. They show an anterior area with oblique ornament, probably overlapped in life by the next anterior ray when the fin was collapsed. The rays are segmented by somewhat sinuous divisions. They sometimes appear to be bifurcated distally. This appearance may, however, be illusory, due to the separation of the lepidotrich elements of

the two sides of the fin. There are about 15 fairly slender, greatly overlapping fulcra on the anterior margin.

The pelvic fins consist of about nine similar but shorter rays and arise from the latero-ventral body ridge. There seems to be no special enlarged scale in front of the pelvic. There are about 12 slender fulcra.

MEDIAN FINS: The dorsal fin is not well preserved in the material available. It arises behind the anal fin, and when collapsed the

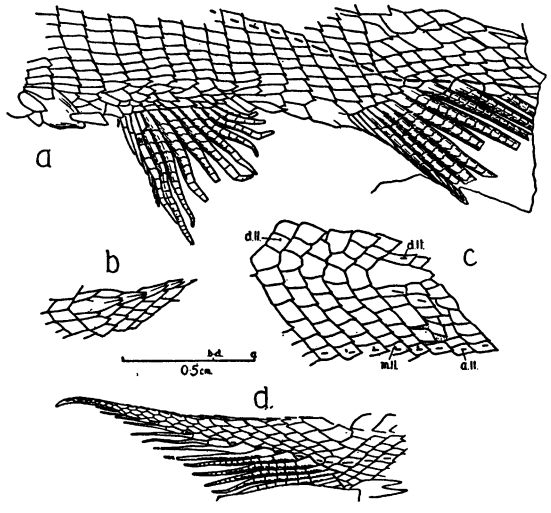


FIG. 27. *Pyritocephalus sculptus* Fritsch. Details of scales and fins. a, Anal fin and tail, R.S.M. No. 1897.96.3; b, caudal ridge scales, B.M.N.H. No. P.21990; c, scales in front of dorsal fin, B.M.N.H. No. P.21990; d, tail of B.M.N.H. No. P.8650.

fin rays extend behind the origin of the caudal. The median dorsal scales traced back to the dorsal fin become enlarged transversely, and immediately in front of the fin is a very large elongated scale, which is followed by the fulcral elements. The fin is composed of at least eight rays, which are segmented and probably undivided; the ornament consists of slightly oblique longitudinal rugae on the anterior margins, which were covered by the lepidotrichia of the next anterior ray in the collapsed fin.

The anal fin is magnificently shown in R.S.M. No. 1897.96.3 (fig. 27a; pl. 8, fig. 1), where it is fully expanded and consists of 12 rays, of which the third is the longest; the two most posterior are very thin. The rays are all segmented and are not seen to bifurcate; they are strongly ornamented on their anterior "overlapped" margins by oblique rugae. There are *ca.* 15 fulcra on the leading margin, passing anteriorly into a few enlarged median scales. Immediately in front of the origin of the fin is a large median scale with a pair of grooves marking the posterior end of the ventral lateral line (fig. 26b).

The caudal fin (fig. 27a, d) consists of about 17 similar rays, of which the third or fourth is the longest. The fin resembles that of *Haplolepis* in character, and there is no marked division into lobes. The fulcra follow an enlarged median ventral scale.

The dorsal fin arises slightly behind the anal. The origin of the anal is almost exactly halfway between those of the caudal and pelvic fins; the latter are very slightly nearer to the anal than to the pectorals.

SQUAMATION: The scale-row formula is usually

$$\frac{22}{6\text{–}7 \quad 14 \quad 23\text{–}24} \quad 25\text{–}26$$

The dorsal fin origin is nearly always at scale row 22; the pelvics arise at row 6 or 7; the anal at row 13 (3 out of 7), 14 (2) or 15 (2), and the caudal at row 22 (1 out of 9), 23 (3), or 24 (5). The inversion of directions of scale rows is almost always two or three rows behind the origin of the caudal.

There are no deepened flank scales of the type common in *Haplolepis*, but the lateral-line scales do tend to be a little deeper than the others, particularly in the most anterior rows. In the anterior part of the trunk there are no enlarged median dorsal scales, and the scale rows of the flank tend to meet *en echelon*. Farther back there is a tendency for a small scale to occur in the mid-line, from which the two flank rows originate; and at the twentieth row (in most cases) behind the nape there is the elongated scale which lies in front of the dorsal fin, and which occupies two or three scale rows (fig. 27c). Behind the dorsal fin, usually at the twenty-sixth row, there are paired elongated scales which meet in front of the most anterior caudal ridge scale (fig. 27b). The dorsal margin of the caudal lobe is protected by about 15 narrow overlapping ridge scales.

The flattened venter is marked by a change in direction of the anterior scale rows; above the ventrolateral ridge the rows extend anterodorsally, below it anteromesially (figs. 26, 27a).

In the anterior part of the body there are four or five scales between the lateral-line row and the mid-dorsal scales, and there is little change in this as far back as the caudal fin. The scales below the lateral-line series are everywhere shallow; just in front of the pelvic fins there are about 15 scales between the lateral-line series and the ridge. Between the ridge and the mid-ventral line there are about three rows. The second of these rows bears grooves for the ventral lateral line. Between the pelvic fins the squamation is not well preserved in my material; no details of the vent can be given. In the region of the anal fin there are about 13 scales between the lateral-line series and the enlarged anal scale; behind the fin the number of scales below the lateral line is reduced to about six.

The caudal inversion is rarely sharp; behind it the lateral line approaches very near the ventral margin of the caudal lobe. The caudal lobe is covered by rhomboidal scales, of which there are about five in the more anterior rows, falling to two or three near the tip. The arrangement of the ridge scales, which number about 15, is well shown in B.M.N.H. No. P.21990; each is bifurcated near the tip, and the third and subsequent scales seem to be paired elements.

In contrast with the cranial bones, the scales usually appear to be quite smooth; but careful examination of the anterior scales of the flank and dorsum shows that they are usually ornamented by three or four linear ridges close to, and parallel to, the anterior margin. Otherwise the scales have a smooth lustrous cover of ganoine. The posterior margins of the scales are free from serration, but the free posteroventral corners of the flank scales are drawn out into small thorn-like processes identical in shape with individual "teeth" of the denticulated scales of, say, *H. tuberculata*, and with the small projections on the posterior flank scales of that species.

LATERAL LINE: The main lateral line is represented by a short pit-line groove near the middle of each lateral-line scale, and by an enclosed canal opening by a more or less vertical slit-like pore above the grooves in certain scales. The placing of these pores is irregular; in B.M.N.H. No. P.8650, for example, the pores occur on all but a few of the anterior lateral-line scales and become much more sparse near the tail, while in others they only occur on occasional scales even anteriorly. There are usually about 28 scales from the shoulder girdle to the first lateral-line scale that touches the enlarged basal lepidotrichia of the caudal fin; behind this certain scales along the ventral border of the caudal lobe may also have grooves for the pit line (fig. 27a). These grooves should not be confused with the linear ornament of the enlarged basal lepidotrichs.

There is a ventral lateral line on the body, represented by pit-line grooves on the cleithrum and on scales between the ventrolateral ridge and the mid-ventral line. The paired series of grooves occurs as far back as the anal fin and terminates apparently in a pair of grooves near the tip of the much enlarged pre-anal scale.

A dorsal lateral line is also present on the body; it is of the enclosed type, opening by lunate slit-like pores, in front of the predorsal scale. The first pore is seen in certain individuals in the scale next above the most anterior lateral-line scale, and the pores are found behind this almost as far as the enlarged predorsal scale, being then usually in the scale adjacent to, or next but one to, the median scale (fig. 27c). The dorsal lateral line extends a little farther posteriorly on the scales just below the dorsal fin, but in the form of pit-line grooves (fig. 27c).

The exact course of the latero-sensory canals on the head cannot be traced, since the bone material does not allow the canals to be prepared. The system must be reconstructed from the pores and pit-line grooves for the most part. The forward continuation of the main lateral line into the supracleithrum and posttemporal has to be assumed, and there is usually no sign of pores in the extrascapulars or on the posterior parts of the dermopterotics. There is always a pore in each dermopterotic near the margin of the supraorbital fenestra, slightly in front of the middle pit-line groove; farther forward, near the same margin, there are two or three pores

behind the frontal, lying lateral to the anterior pit line. In *Pyritocephalus* the main lateral line appears to anastomose with the posterior end of the supraorbital canal, the normal forward passage into the infraorbital canal being interrupted by the development of the supraorbital fenestra. In this connection Fritsch's figure of one skull (1893, pl. 115, fig. 7) is important. The canal in the dermopterotic, "der den Gebilden des Gehororgans angehoren durfte," according to Fritsch (*op. cit.*, p. 87), is almost certainly a trace of the anterior prolongation of the main lateral line into the cranial region. (Compare *P. rudis*, new species, described below.)

The infraorbital canal leaves little or no trace of its presence, but its course through the postorbital and infraorbital into the premaxillary may be assumed.

The supraorbital canal is indicated by a group of pores in the nasal and lateral parts of the frontal (see fig. 25a, b). It is likely that it anastomoses with the anterior end of the canal in the dermopterotic, near the suture between that bone and the frontal, as there is a short groove for the anterior pit line extending backwards onto the dermopterotic from the neighborhood of the most posterior pore on the frontal.

There is usually a series of three pores on the dermosphenotic, one anterolaterally near the nasal, one about the middle of the bone near the mesial margin, and one in the narrow posterior part (fig. 25a, b). These will be discussed later.

The preopercular canal is indicated only by one or two pores near the posterior margin of the preopercular. The mandibular canal is rather better indicated; pores are present on the angular and dentary, as shown in figure 26a, b.

The lines of pit organs on the head are indicated by grooves in the ganoine-covered bones. The anterior pit line lies on the frontal and dermopterotic near their junction; the middle pit line is transversely placed near the middle of the dermopterotic. The posterior pit line may be indicated by a very short groove just in front of the mesial corner of the extrascapular in a few specimens.

The horizontal pit line of the cheek is long, extending across the most expanded part of the preopercular and sometimes onto the lowest suborbital. The vertical pit line of the cheek occurs on the preopercular and quadratojugal. On the mandible there are two pit lines: a curved groove on the angular, and a short vertical groove near the anterior end of the dentary. The anterior paired gulars bear each a short transverse groove, and the anterior median gular has a V-shaped groove. The anterior termination of the ventral lateral line of the body, a short groove on the cleithrum, has already been mentioned.

DIAGNOSIS OF *P. sculptus* FRITSCH: *Pyritocephalus* of comparatively large size, with somewhat broader head than in *P. lineatus* (Newberry). Scale formula:

$$\frac{22}{6\text{–}7 \quad 14 \quad 23\text{–}24} \quad 25\text{–}26$$

Above the lateral line there are about four or five scales in each row; below the lateral line, about 15 rows to the ventrolateral ridge in front of the pelvics, about 13 at the anal, about six at the caudal pedicle, three or four scales in each forwardly directed row between the ventrolateral ridge and the midline. Pectoral fins of *ca.* 12 rays, pelvics of *ca.* 9, dorsal of 8+, anal of 12, caudal of *ca.* 17. Dorsal slightly behind anal; anal exactly midway between pelvics and caudal, pelvics slightly closer to anal than to pectorals.

Pyritocephalus lineatus (Newberry)

Plate 10, figure 1; text figures 28–32

Mecolepis lineatus NEWBERRY, 1856, p. 96.
Eurylepis lineatus NEWBERRY, 1857, p. 150.
Eurylepis lineatus NEWBERRY, 1873, p. 353, pl. 39, figs. 7, 7a.
Rhadinichthys? lineatus NEWBERRY, 1889, p. 228.
Eurylepis? lineata WOODWARD, 1891, p. 450.
Rhadinichthys? lineatus HAY, 1902, p. 367.
Rhadinichthys? lineatus HUSSAKOF, 1908, p. 95.
Rhadinichthys? lineatus HAY, 1929, p. 688.

This American species conforms so closely in structure to the genotype that only a short comparative account is necessary. The species is, on the average, larger than *P. sculptus*, the range in size in the limited material available being *ca.* 50 mm. to 67 mm.

The hypodigm of this description of *P. lineatus* comprises the following specimens:

AMERICAN MUSEUM OF NATURAL HISTORY: Nos. 1846; 1970 and its counterpart, Newberry

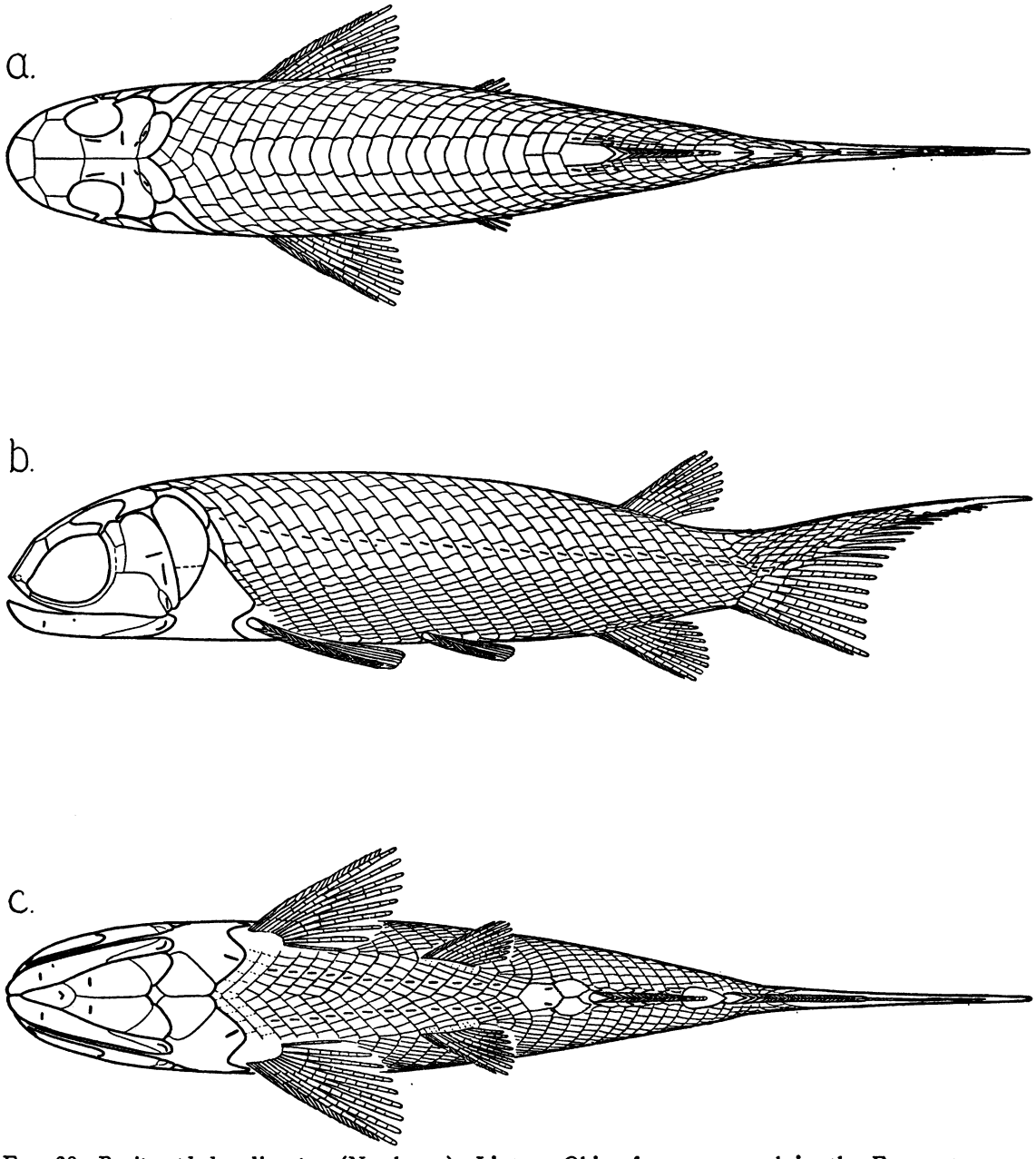


FIG. 28. *Pyritocephalus lineatus* (Newberry), Linton, Ohio; from a cannel in the Freeport group, Alleghany series, Pennsylvanian. Reconstruction of whole fish in a, dorsal, b, lateral, c, ventral views.

No. 443G; 1972 and its counterpart, Newberry No. 453G (which bears a label "Original Specimen"); and Newberry No. 454G (Newberry's figured specimen).

UNITED STATES NATIONAL MUSEUM: Nos. 4443, 4526.

BRITISH MUSEUM (NATURAL HISTORY): No. P. 7779.

SKULL (FIG. 29): The pattern of the skull bones conforms precisely to that of *P. sculptus*. The skull roof is well shown in the holotype (Newberry No. 454), in A.M.N.H. No. 1846, and Newberry No. 453G (all A.M.N.H.), in B.M.N.H. No. P.7779, and in U.S.N.M. No. 4443. The differences are

merely in slight proportions, *P. lineatus* being a little more slender than *P. sculptus*. The ornamentation is of precisely the same type, and the distribution of sensory canal pores and pit lines is practically identical on the frontal, dermopterotic, and dermosphenotic. The snout is badly preserved in the available material, but the same bones, of approximately the same shape, can be recognized.

The cheek bones are also precisely similar in plan, though there is a marked tendency for the bones to be proportionally deeper than in *P. sculptus*. The preopercular is a stout element bearing horizontal and vertical pit-line grooves; an antopercular was probably present. There is evidence of the preopercular canal in a large pore near the posterior margin of the bone just above the quadratojugal; the latter bone bears the continuation of the vertical pit-line groove. The maxillary expansion is proportionately shorter and deeper than that of *P. sculptus*.

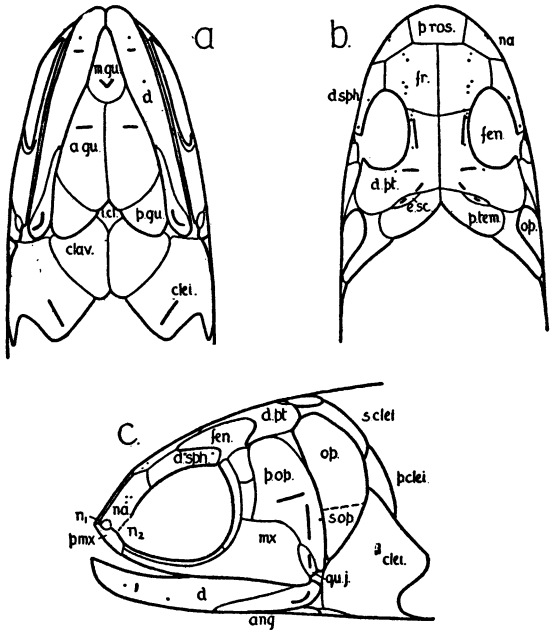


FIG. 29. *Pyritocephalus lineatus* (Newberry). Reconstruction of dermal skull and shoulder girdle in a, ventral, b, dorsal, c, lateral views.

No teeth have been observed. The ornament on these bones is slightly different from that in *P. sculptus*, the terraced rugae being more irregular in arrangement.

The suborbitals and the postorbital-infraorbital chain are not well preserved in any of the available material; as far as they can be seen they agree well with the conditions in *P. sculptus*.

The mandible shows no significant differences in the two forms, though the suture between angular and dentary is more difficult to see, and the ornament generally is stronger, in *P. lineatus*.

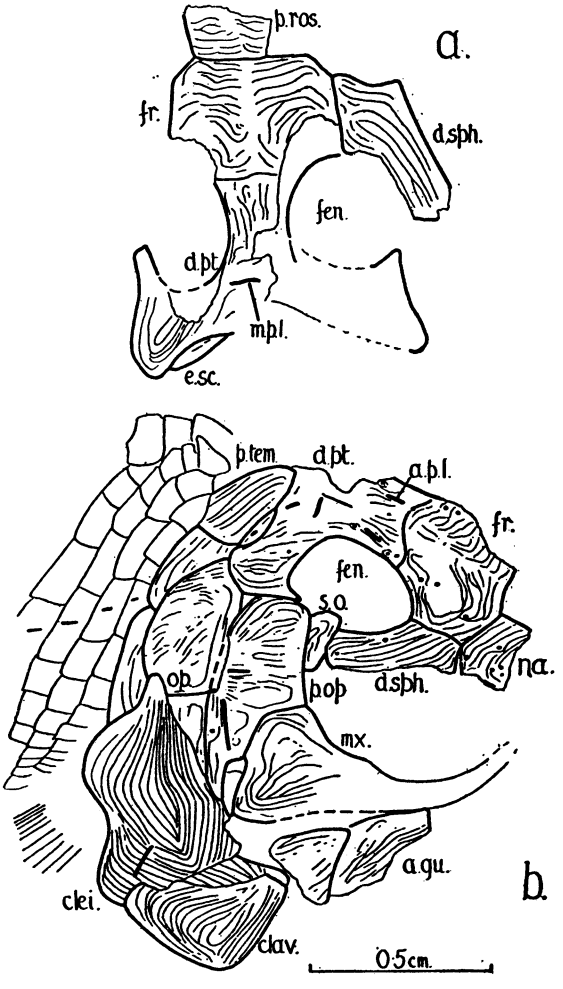


FIG. 30. *Pyritocephalus lineatus* (Newberry). Details of skull. a, A.M.N.H. No. 454G (the holotype); b, U.S.N.M. No. 4443.

The opercular apparatus closely resembles that of *P. sculptus* in every detail except minor proportions and ornament. Details of the gular region are magnificently shown in

A.M.N.H. No. 443G (Newberry collection) and B.M.N.H. No. P.7779 (fig. 31a, b). The gulars are the same in number, shape, and interrelationship in the two species, and the ornament and pit-line grooves are similar. The subopercular is not well shown in any of the available specimens, but there is no reason to suppose that it is substantially different from that in *P. sculptus*. The opercular has a much stronger ornament than in the latter species and bears irregularly curved, short, terraced rugae in most specimens.

The extrascapulars are always badly shown, but the posttemporals are usually well preserved and resemble those of *P. sculptus*.

There is a fairly large premaxillary, shown in A.M.N.H. No. 443G (Newberry collection), but no details of its sutures against the nasal and postrostral can be given.

SHOULDER GIRDLE: The dermal bones are fairly well preserved and resemble those of *P. sculptus*. The ornament is very similar in the two forms. The cleithrum of *P. lineatus* appears to be broader than that of *P. sculptus* (well shown in A.M.N.H. No. 443G); the groove for the anterior part of the ventral lateral line is well developed.

PAIRED FINS: The pectoral fin is partly preserved in several specimens, but the smaller posterior rays are never well shown. The web consists of 13 rays, well separated, but with overlap areas of the usual type. The rays are segmented, and the distal ends are bifurcated. There are stout fulcra at the anterior margin, better preserved than in the material of *P. sculptus;* in the most favorably preserved form (A.M.N.H. No. 1970, counterpart of No. 443G) there are about 18 fulcra, of which the proximal two are long and self-supporting, the next two are borne on the short first fin ray, the succeeding three on the second, the remainder on the third ray, which reaches the tip of the fin. The fin rays, especially the more anterior ones, bear a fairly strong ornament; the posterior two-thirds of the surface of each ray may have one or two longitudinal low ridges, while the anterior portion (overlapped by the next anterior ray in the collapsed fin) has a slightly oblique, more concentrated ornament. The

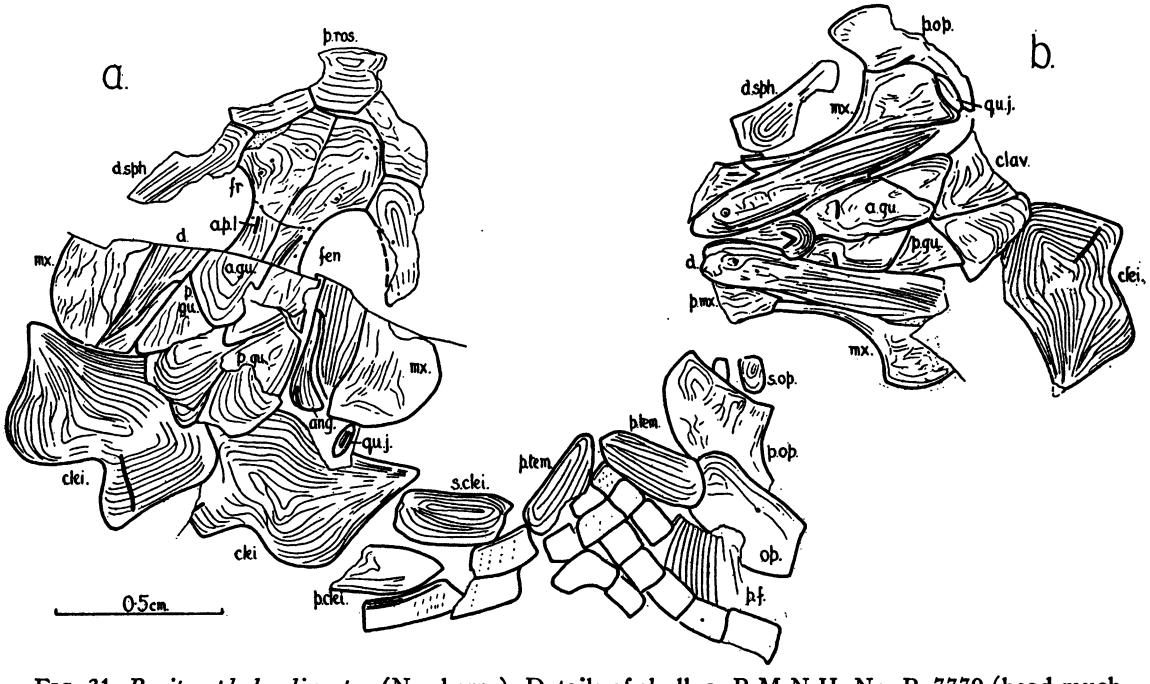


FIG. 31. *Pyritocephalus lineatus* (Newberry). Details of skull. a, B.M.N.H. No. P. 7779 (head much disturbed, anterior part of jaws and gulars split away, showing skull roof); b, A.M.N.H. No. 443G.

posterior rays are much less ornamented.

The pelvic fins are shown only in U.S.N.M. No. 4443, and partly in A.M.N.H. No. 1972. Each originates, as in *P. sculptus*, from a lateroventral ridge and consists of at least eight rays of familiar type.

MEDIAN FINS: The dorsal fin is fairly well shown in U.S.N.M. No. 4443; about seven fin rays, segmented and ornamented in the now familiar manner, are present, but the posterior rays may be hidden.

The anal fin is poorly shown in the same specimen, and consists of nine or 10 fin rays. The caudal fin is nowhere completely shown. U.S.N.M. No. 4443 shows it to consist of about 20 rays, of which about five form the very feeble, somewhat indefinite "ventral lobe."

The dorsal fin arises slightly behind the anal; the origin of the anal fin is slightly nearer to the caudal than to the pelvic origin; the latter is closer to the anal than to the pectorals.

SQUAMATION: The scale-row formula is only well shown in U.S.N.M. No. 4443, where it is

$$\frac{24}{7 \quad 16 \quad 25} \quad 28$$

The corresponding figure in *P. sculptus* is

$$\frac{22}{6\text{–}7 \quad 14 \quad 23} \quad 25\text{–}26$$

from which it is clear that the American species differs uniformly in having more scale rows. The difference in position of the pelvic fins is not significant, but the median fins all arise about two scale rows farther from the head in *P. lineatus*. This is of interest in view of the slightly greater relative distances of the anal from the pelvic in this form, and suggests the presence of one or two additional somites in the posterior trunk region as compared with *P. sculptus*.

The scales are so closely similar to those of *P. sculptus* that no extended description is necessary. The characteristic ornament of grooves separating terraced rugae on the anterior margins of the dorsal and anterior flank scales is somewhat more strongly developed and may extend a little farther posteriorly.

The anterior lateral-line scales are very slightly more vertically enlarged than is usual in *P. sculptus*. Usually the vertical scale rows of the flanks meet in short, stout, arcuate, median dorsal scales, which, however, are not particularly symmetrical (fig. 32a). At the twenty-first or twenty-second row behind the nape is the elongated scale which lies in front of the dorsal fin. Behind this fin, at the twenty-eighth row, is a pair of scales meeting just in front of the enlarged anterior caudal ridge scales (fig. 32b). The dorsal margin of the caudal lobe is protected by upwards of 15 narrow, elongated, and deeply overlapping ridge scales; the more distal members show a deep median groove and may be split near the tip.

The change in direction of the anterior scale rows at the ventrolateral ridge is shown in the holotype (A.M.N.H. No. 454), and very clearly in A.M.N.H. No. 1972 (fig. 32d). There are three scales between the lateral-line series and the mid-dorsal scales in a few anterior rows; elsewhere the number is four as far back as the caudal fin. In front of the pelvic fins there are about 14 scales between the lateral-line row and the row along the ventrolateral ridge; between this and the mid-ventral line there are about four to six scales in each row, of which the third from the ridge usually bears the groove for the ventral lateral line. The position of the vent is uncertain, probably between the posterior parts of the pelvic fins. In the region of the anal fin there are 11 or 12 scales between the lateral-line series and the enlarged anal scale, and behind the fin the number of such rows is reduced to about four or five. The caudal lobe is much the same as in *P. sculptus*.

These figures indicate that there are everywhere in the trunk region fewer scales in each row than in *P. sculptus*. Otherwise the squamation is extraordinarily similar to that of the Nýřany species, with the exception that the ornament may be stronger. The grooves on the anterior parts of the flank scales are stronger and possibly more numerous, while the scales of the anterior part of the venter have usually a few longitudinally arranged grooves and rows of elongated pits in addition.

LATERAL LINE: The arrangement of

grooves and pores for the lateral-line system of the body closely resembles that in *P. sculptus* and need not be further described. The cranial arrangements are also practically identical; the main points of interest are the clearly marked pores on the dermopterotics in U.S.N.M. No. 4443 and A.M.N.H. No. 1846, which allow the course of the sensory

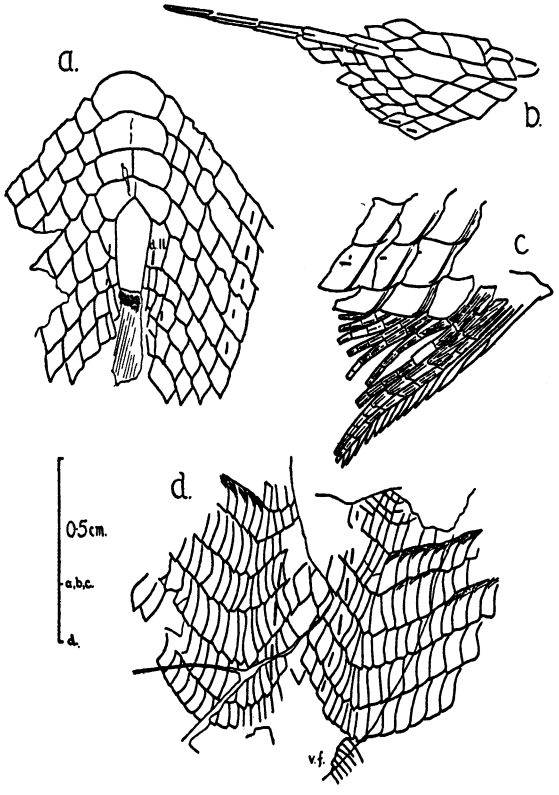


FIG. 32. *Pyritocephalus lineatus* (Newberry). Details of scales and fins. a, Scales in front of dorsal fin, A.M.N.H. No. 453G (labeled "Original Specimen (Back View)," but not the figured type); b, caudal ridge scales of A.M.N.H. No. 1970; c, pectoral fin of A.M.N.H. No. 1970; d, venter of A.M.N.H. No. 1972 between the paired fins.

canals in the dermopterotics and frontals to be completed.

DIAGNOSIS OF *P. lineatus* (NEWBERRY): *Pyritocephalus* of somewhat larger size, with somewhat more slender head, slightly shorter cheek and more vertical suspensorium than in *P. sculptus*. Scale formula:

$$\frac{24}{7\ \ 16\ \ 25}\ 28$$

Above the lateral line there are three scales to the mid-dorsal scale in the anterior trunk, elsewhere usually four; below the lateral line, about 14 scales to the ventrolateral ridge in front of the pelvics, about 11 or 12 at the anal, about four or five at the caudal pedicle; five or six scales in the more anterior forwardly directed rows between the ventrolateral ridge and the mid-line. Scales with somewhat stronger linear ornament anteriorly and ventrally than in *P. sculptus*. Pectoral fins of about 13 rays, pelvics of at least 8, dorsal of 7+, anal of 9 or 10, caudal of *ca.* 20. Dorsal slightly behind anal; anal slightly closer to caudal than to pelvics, pelvics almost midway between anal and pectorals.

Pyritocephalus gracilis (Newberry and Worthen)

Plate 10, figures 2, 3; text figure 33a–d

Palaeoniscus gracilis NEWBERRY AND WORTHEN, 1870, p. 347, pl. 3, fig. 4 (Yale No. 440).
Rhadinichthys gracilis WOODWARD, 1891, p. 469.
Rhadinichthys gracilis HAY, 1902, p. 367.
Rhadinichthys gracilis EASTMAN, 1902a, p. 97.
Rhadinichthys gracilis EASTMAN, 1902b, p. 541.
Rhadinichthys gracilis EASTMAN, 1903, p. 194.
Rhadinichthys gracilis EASTMAN, 1917, p. 274, pl. 9, fig. 4 (U.S.N.M. No. 4401).
Rhadinichthys gracilis HAY, 1929, p. 688.
Teleopterina improvisa BERG, 1936, pp. 345–347 (U.S.N.M. No. 4401).
Teleopterina improvisa BERG, 1940, fig. 70 (pp. 186, 405).

The early history of this species is straightforward; but in 1917 Eastman figured a second specimen, which was made the type of a new species, genus, and family by Berg (1936). The close relationship between Berg's species and *Pyritocephalus sculptus* was recognized by Westoll (1938), who referred it to *Pyritocephalus*. Recently a careful analysis of the writer's notes on specimens studied in America has shown him that Berg's species must be regarded as a synonym of *P. gracilis*, of which Newberry and Worthen's description is not very accurate.

In general, *P. gracilis* very closely re-

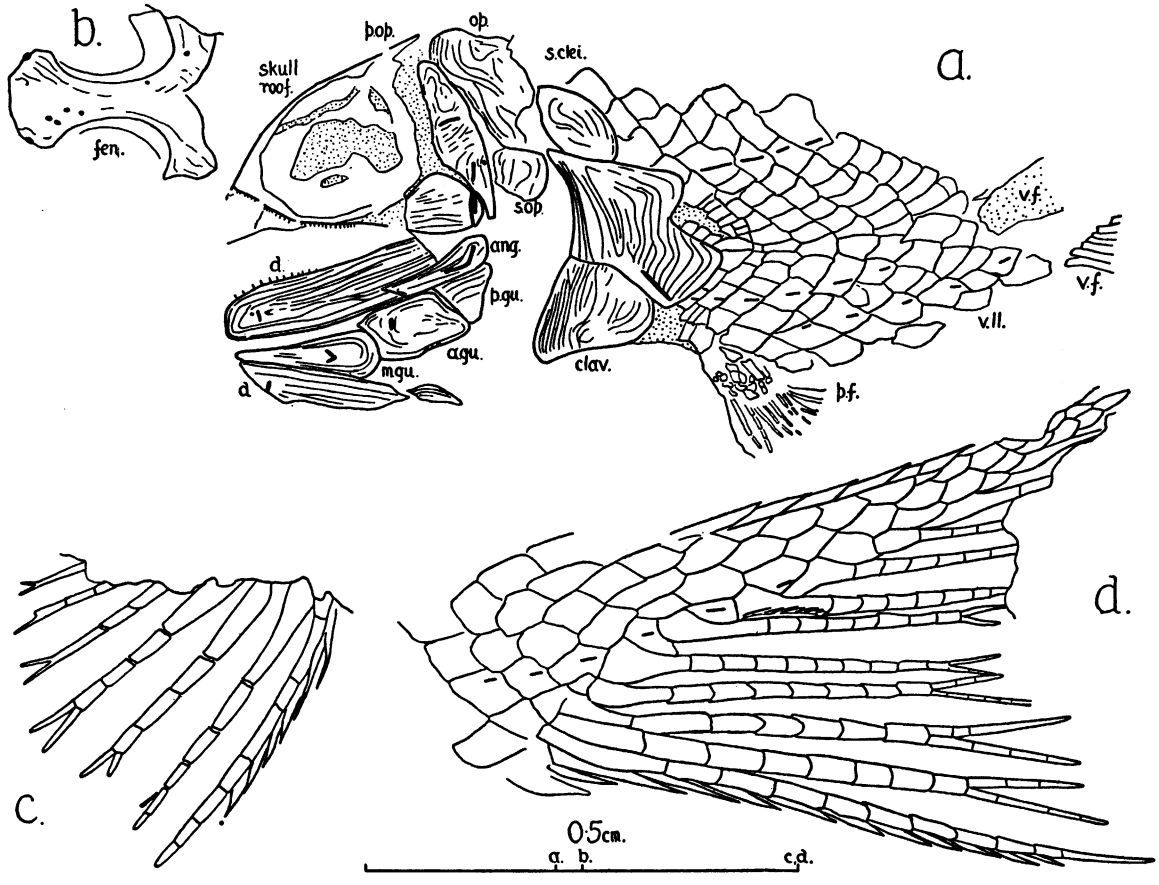


FIG. 33. *Pyritocephalus gracilis* (Meek and Worthen), Mazon Creek, Illinois; from ironstone nodules in Kittanning group, Alleghany series, Pennsylvanian. a, Specimen in Walker Museum; b, skull roof of U.S.N.M. No. 4401 (type of *Teleopterina improvisa* Berg); c, anal fin, and d, tail of U.S.N.M. No. 4401.

sembles *P. lineatus* from Linton and *P. sculptus* from Nýřany. In such characters as scale count the resemblance to *P. lineatus* is greater than that to *P. sculptus*.

The available material consisted of four specimens: the holotype (studied at Yale, No. 440), the type of *Teleopterina improvisa* (U.S.N.M. No. 4401, pl. 10, fig. 2), a very fine half nodule in the Walker Museum, Chicago (fig. 33a, pl. 10, fig. 3) and a further nodule at Yale (No. 1234). Though the writer's notes and sketches of the holotype are inadequate for full description, they leave no room for doubt that the other material is correctly referred to the species. The holotype is about 31 mm. in total length; the other individuals range from 25 mm. (U.S.N.M. No. 4401) to *ca.* 43 mm. (Chicago).

SKULL: The skull roof is partly shown in U.S.N.M. No. 4401 as a result of careful development and proves to be of the typical *Pyritocephalus* pattern (fig. 33b). The preservation is not sufficiently good to allow exact comparisons to be made, but it seems that the supraorbital vacuity is even larger than in *P. lineatus*. Some of the snout bones are fairly well shown in the same individual; the right nasal apparently encloses the nasal opening completely.

The cheek is well shown in Yale No. 440 and in the Walker Museum specimen. The maxilla has a tall expansion, much shorter anteroposteriorly than in either of the other species. The preopercular is also more anteroposteriorly compressed. The quadratojugal is present, and the pit lines and sensory canal

pores are arranged on the same general pattern as in *Pyritocephalus lineatus*. Yale No. 440 shows the suborbitals in front of the preopercular. The Chicago specimen shows the mandible very clearly; it is similar in structure, ornament, and pit-line grooves to that of *P. lineatus*. The same specimen shows that the opercular and gular apparatus corresponds exactly with that in the Linton and Nýřany species.

The Chicago specimen also shows very clearly something of the dentition (fig. 33a). The presence of teeth on the margin of the dentary or maxilla is still doubtful, but a close-set dentition of slender-pointed teeth seems to be borne on a coronoid series and on the lateral parts of the bony palate.

SHOULDER GIRDLE AND PAIRED FINS: The postcleithrum, cleithrum, and clavicle are very well shown in the Chicago specimen and bear the normal terraced ornament of the genus (fig. 33a). The pectoral fins are not well preserved in any of the material; in the Chicago specimen the proximal parts of the left fin, with its scale-covered lobe, are shown, and the fin consists of 10 (possibly 11) rays. These are of the usual segmented type, and the anterior "overlapped" portion of each ray bears a few oblique terrace grooves. In the same individuals the base of the right fin can be made out, and the way in which the scale-covered lobe passes posteriorly into the ventrolateral ridge is well illustrated.

The pelvic fin consists of about six rays of the usual type and is well shown in the Chicago specimen and the holotype.

MEDIAN FINS: The dorsal is a fairly large fin, composed of seven or eight rays. The anal is similar, composed of seven or eight rays, and is very well shown in U.S.N.M. No. 4401; the terminal portions of the anterior fin rays seem to be bifurcated (fig. 33c). The caudal is shown in the holotype and U.S.N.M. No. 4401; it has the shape characteristic of the other species and probably consists of 15 rays at most (fig. 33d).

All the fins are provided with long slender fulcra (particularly U.S.N.M. No. 4401). The dorsal fin arises above the anterior third of the anal fin. The origin of the pelvic is almost equidistant from those of the pectorals and anal; the anal is slightly closer to the pelvics than to the caudal.

SQUAMATION: Some of the features noted by Berg in his account of "*Teleopterina improvisa*" (U.S.N.M. No. 4401) are erroneous; the specimen is considerably disturbed, so that on the mold of the right side of the specimen the lateral-line scales are near the upper border. The enlarged dorsal scales of Berg's account are this row and the next most dorsal. The scales are less disturbed on the holotype and the Chicago individual, but neither is sufficiently clear for a very detailed account. Scale counts are possible on four specimens:

Holotype	7 — 23 — 16 — 25	27
Yale No. 1234	— — 24 — 16 — 25?	27
U.S.N.M. No. 4401	7 — 23 — 15 — 25	28
Chicago specimen	7 — 24 — 15 — —	27

The average is thus

7 — 23–24 — 15–16 — 25	27–28

and it may be compared with the figures for *P. lineatus* and *P. sculptus*, as follows:

P. lineatus	7 — 24 — 16 — 25–26	28
P. sculptus	6–7 — 22 — 14 — 23	25–26

There is a closer resemblance to *P. lineatus*.

The arrangement of the scales on the flanks and venter is precisely similar to that in *P. lineatus* and *P. sculptus*, but the anterior flank scales below the lateral line are far less shallow. Thus, while in *P. sculptus* and *P. lineatus* there are about 15 and 14 scales, respectively, between the lateral-line row and the anterior part of the ventrolateral ridge, in *P. gracilis* there are only six. Between the ventrolateral ridge and the midventral line there are two or three scales, of which the second from the ridge bears the ventral lateral-line groove. Between the

dorsal and anal fins there are four or five rows both above and below the lateral-line row. The anterior lateral-line scales are fairly deep, passing gradually backwards into more or less equilateral scales below the dorsal fin.

The ornamentation of the scales greatly resembles that of the other species of *Pyritocephalus;* the greater part of the scale area is covered with quite smooth, lustrous ganoine, with no more than the usual tiny pores to break the surface. The anterior flank scales, however, show marked concentric "terrace grooves" parallel to the anterior and ventral margins of the scales. They seem to differ from the scales of the other species in having these grooves continued parallel to the dorsal margin in the anterior dorsal flank scales. It should be emphasized, however, that the scale surface is only well shown in a few specimens (particularly that from Chicago).

LATERAL LINE: The distribution of the latero-sensory canals on the head can only be deduced from the position of the pores, but it corresponds with that in the other species. The pit lines on the skull roof, cheek, angular and dentary and gulars are also quite similar.

The main lateral line of the body is shown by the short grooves of the "accessory" line on the surface of the scales and also by pores opening on occasional scales as far back as the caudal pedicle. Beyond the caudal inversion the grooves are continued a considerable distance on the most ventral row on the caudal lobe.

The ventral lateral line is shown by paired grooves on the scales of the flattened venter as far back as the anal fin (fig. 33a). No useful account of the dorsal lateral line can be given.

COMMENTS: "*Palaeoniscus gracilis*" is quite clearly a species of *Pyritocephalus* and is to be distinguished from *P. sculptus* and *P. lineatus* by the following characters: shape of cheek bones, size of supraorbital vacuity (?), fewer scales on flank below lateral line, the (doubtfully) more developed scale ornament, and the smaller number of fin rays in each fin. In all these and in the scale count, the species stands closer to *P. lineatus* than to *P. sculptus*, but they are all minor features when the extraordinary structural resemblance is considered.

Pyritocephalus comptus, new species
Plate 10, figure 4; text figure 34

A small fish from the Lacoe collection in the United States National Museum (U.S.N.M. No. 4310) probably represents a new and well-defined species of *Pyritocephalus*. Unfortunately the head is very badly crushed, and there is the possibility that the fish may belong to some other genus of this closely knit family. However, in the position and character of the fins, the ornament and arrangement of the scales, and the scale count, the fish shows an unmistakable resemblance to *Pyritocephalus*.

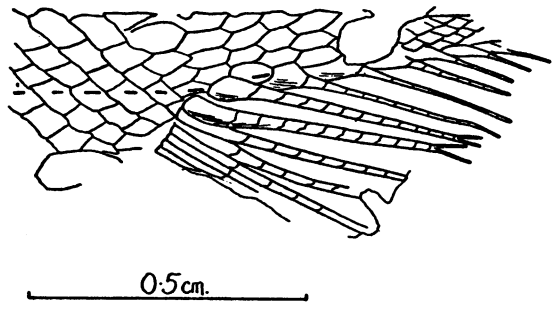


FIG. 34. *Pyritocephalus comptus*, new species, Mazon Creek, Illinois; from ironstone-nodule horizon in Kittanning group, Alleghany series, Pennsylvanian. Holotype, U.S.N.M. No. 4310. Details of caudal fin.

The squamation and the fins for the most part are well preserved. The scale count is probably

$$\frac{25}{8\ \ 20\ \ 29}\ 32$$

The anterior rows are shown only on the left side, and there may be one or more rows missing, though this is unlikely. The scales are of the usual *Pyritocephalus* type, with a few terrace grooves parallel to the anterior and anteroventral margin, sometimes also to the dorsal margin. The anterior lateral-line scales are fairly deep but are gradually reduced in height posteriorly, becoming almost equilateral beneath the dorsal fin. There are enlarged scales immediately in front of the dorsal and anal fins and on the caudal lobe, but no useful details of these are shown.

In the anterior flank regions there are about four scales in each row between the lateral-line scale and the mid-dorsal line; and about eight or nine between the lateral-line scale and the ventrolateral ridge. The ventral flank scales are quite shallow. The ventrolateral ridge marks a change in direction of the scale rows, and there are about three or four scales in each anteromedially directed row on the venter.

There is an irregularity above the anal fin; the scale rows counted as Nos. 22 and 23 are represented by only one row dorsally, a single lateral-line scale touching both rows.

The median fins are fairly well preserved, but only fragments of the pectorals and pelvics can be seen. They consist, as usual, of a few well-separated rays, which are apparently more slender than those of other species. The fulcra on one of the pelvic fins can be seen; they do not extend more than halfway to the distal margin of the fin.

The dorsal fin consists of eight slender and well-separated rays which are probably incomplete distally. The proximal segment of each ray is long and basally expanded, and there are at least nine segments in the longer rays. The fulcra extend only a little more than halfway to the distal margin of the fin.

The anal fin is very clearly shown and consists of seven rays of similar type. A small distal portion of each fin ray is bifurcated. Fulcra occur only on the proximal half of the front border of the fin.

The caudal is incomplete near the tip, but consists of 14 visible rays; there may have been one or two additional very slender posterior rays. The fin rays are of much the same type as those seen in the anal, with a small distal portion of each ray bifurcated. Fulcra occur only on the proximal part of the first ray.

On all fins the rays possess a slight ornament of grooves near the anterior margin.

The dorsal fin is almost exactly opposed to the anal, occurring only very slightly behind it. The anal origin is distinctly closer to that of the caudal than to that of the pelvic, and the pelvics are closer to the pectorals than to the anal.

Grooves for all three lateral lines of the body are preserved, in the same positions as those described in other species of *Pyritocephalus*.

COMMENTS: The nature and position of the fins are sufficient to show that this specimen should be referred to *Pyritocephalus*, and the scale ornament and shallow ventral flank scales confirm this. The species differs from the others so far described in the scale count, slender fin rays, and small development of fulcra. In these characters and in the smaller number of fin rays, it shows greater resemblance to *P. gracilis* than to *P. sculptus* and *P. lineatus*.

Pyritocephalus rudis, new species

Text figure 35

In the Hancock Museum, Newcastle-on-Tyne, is an immense mass of material from the impure cannel above the Low Main seam at Newsham. While working over this material some years ago the writer was puzzled

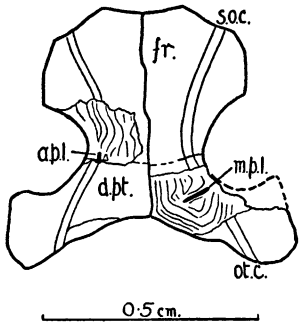


FIG. 35. *Pyritocephalus rudis*, new species, Newsham, Northumberland; from Low Main Cannel, Middle Coal Measures, Westphalian. Holotype, skull roof in Hancock Museum, showing latero-sensory canals and, where bone is lost, the external ornament.

by a small skull, for which he could find no parallel. The discovery of the curious structure of the skull roof in *Pyritocephalus* has solved the problem, and the specimen clearly represents a primitive species of the genus, in which the supraorbital vacuity remains small.

The specimen consists of the frontals and dermopterotics, which are shown mostly from the inner surface. Portions of bone have, however, been removed, so that the external

ornament is partly shown. The sagittal suture is patent, but the suture between the frontal and dermopterotic is not clearly visible and may be closed by ankylosis. Its probable course is indicated in the figure.

The shape of the bones shows a marked resemblance to the conditions in *P. sculptus*, with the exception that the whole skull roof is broader in proportion. The outline of the whole, indeed, is closer to that of the corresponding regions of *Haplolepis* (e.g., *H. tuberculata*, *H. anglica*). The sutures of the frontals against the postrostral, nasals, and dermosphenotics are very like those in species of *Pyritocephalus*. The ornament consists of rather sharp rugae separated by narrow sharp troughs, the detailed arrangement of which cannot fully be described. In general, however, it is clearly of the type familiar in *Haplolepis* (e.g., *H. anglica*) and not of the lighter, more "terraced" type distinctive of most other species of *Pyritocephalus*.

The sensory canals are particularly clearly shown. On each side an apparently continuous canal runs from the frontonasal suture backwards, running near the margin of the supraorbital vacuity, through the more lateral parts of the dermopterotic to the posterior margin. This canal seems to represent the anastomosis of the supraorbital canal with part of the cranial continuation of the "main lateral line" or otic canal. This matter will be discussed later. There is a clear groove for the middle pit line on the dermopterotic.

The relations of this species to the other members of the genus will be discussed later. The broad skull roof, comparatively small supraorbital vacuity, and the ornament of the bones may be regarded as primitive characters linking *Pyritocephalus* to *Haplolepis*.

PHYLOGENY OF *HAPLOLEPIS* AND *PYRITOCEPHALUS*

THERE CAN BE NO DOUBT that *Haplolepis* and *Pyritocephalus* include a very closely allied group of species. The structure and position of the fins, the nature of the squamation, and the anatomical structure of the head show many similarities among the species of these two genera which are not found in any other palaeoniscoids. By comparing the different species it is possible to compile a detailed account of the probable structure of their immediate common ancestor, which may be called X.

BODY FORM

Since all species of which the body is well known are fairly stout, fusiform fishes, X probably had a similar form and is unlikely to have been significantly smaller than *H. ovoidea* (45 mm. long, full grown) or larger than *H. tuberculata* (may be 75 mm. long). It must have had a flattened venter. The caudal pedicle, which is shorter in *Haplolepis* and *Pyritocephalus* than in any other palaeoniscoids, was probably intermediate in X.

CRANIAL ANATOMY

The fenestrated skull roof of *Pyritocephalus* is a specialized feature, and X must have had separate parietals and dermopterotics, since these are present in *H. ovoidea* and *H. attheyi* and in all normal palaeoniscoids. The long dermosphenotic, making contact with the nasal anteriorly, is a common character in the group. The latero-sensory canals in X must have been of an unmodified palaeoniscid pattern. The reduction and modification of the extrascapulars, marked in certain species, are less advanced in others, and it may be assumed that X possessed a single (probably narrow) pair of extrascapulars which probably reached the mid-line.

The lack of a prominent rostrum is a common character and must have been present in X. It is probable that the snout in X consisted of paired "premaxillaries" (dentigerous rostrals) and nasals, enclosing between them the mesial nasal openings, and a median postrostral which did not form part of the margin of a nostril.

The cheek shows peculiar features in each well-known species of *Haplolepis* (*sensu lato*). It may be assumed that the suspensorium in X was much less oblique than in normal palaeoniscoids but not so forwardly directed as in *Haplolepis ovoidea* and *H. tuberculata*. The cheek of X was probably composed of a moderately expanded maxillary and preopercular with a small quadratojugal. The circumorbitals must have been comparatively narrow, and there were probably two or three suborbitals.

The mandible in X was probably comparatively slender, with pit-line grooves on the anterior part of the dentary and on the angular.

The opercular system in *Haplolepis* and *Pyritocephalus* is very variable, but a general plan can be made out. The gular region in X must have been provided with an anterior median element and a large anterior and smaller posterior pair of gulars; the opercular and subopercular, probably not very dissimilar in size, may have been separated from the gulars, but it is more likely that there was a small number (two or three) of branchiostegal rays.

The ornament of the skull bones of X cannot be reconstructed with confidence; there were probably sharp rugae, tending to the "terraced" type, on the mandible, maxilla, circumorbitals, and gulars, and similar ornament was almost certainly present on the dermosphenotics and nasals and on the shoulder girdle. The skull roof may have had a tuberculate or rugose ornament.

FINS

The fin webs of all species of *Haplolepis* and *Pyritocephalus* are so similar that X must also have had the fins composed of few, well-spaced rays, probably capable of considerable movements leading to extension or collapse of the membranes. The fin rays must have been stout, articulated along the whole length, and probably bifurcated distally, since the normal palaeoniscoid fin ray is bifurcated several times, and relics of this condition persist in the single bifurcation in the fin rays of some *Pyritocephalus*.

The paired fins must have arisen from the ventrolateral ridge, and their bases probably had a similar "angle of incidence" to those assumed for *Haplolepis* and *Pyritocephalus*. It is quite likely that the insertions of the leading edges of the pectorals and anal were about equidistant from those of the pelvics. The dorsal fin must have been remote, opposed to the anal. The caudal peduncle was probably longer than in *Haplolepis* and *Pyritocephalus*, as mentioned above; in those genera the shape of the fin web of the tail is very remarkable in the small development of the ventral lobe, and it may be presumed that the tail fin in X was somewhat nearer the "normal palaeoniscid" type. The anterior fin margins must have been provided with a moderate number of overlapping fulcra, probably extending to the distal tip of the first long fin ray.

SQUAMATION

The very deep flank scales in *Haplolepis* indicate specialization; it is probable that in X the flank scales were not greatly deepened, and the anterior flank scales probably became shallow when traced towards the ventrolateral ridge.

The scales were largely smooth, but it is possible that the anterior flank scales may have been ornamented. The anterior flank scales were almost certainly denticulated, but this feature did not extend behind the front of the dorsal fin. Ornament, if present, would probably consist of grooves running parallel with the anterior and ventral margins of the flank scales, and perhaps low ridges, continuing forwards each denticulation of the hinder margin, and separately by grooves into which opened minute pores. Similar grooves were probably present on the dorsal and ventral scales.

Median scales along the dorsum and venter, except immediately in advance of the fins, were probably not developed in X.

As to scale count, it is possible to arrive at a reasonable estimate from the figures in table 2 (p. 87). It is unlikely that the ancestral forms had fewer scale rows than any of the species of *Haplolepis* or *Pyritocephalus*, because scale counts in nearly all other forms are so much higher. It is also assumed that the caudal fin was more remote in X. A fish with scale count of

$$\frac{24}{7\ \ 17\ \ 30}\ 33$$

would be suitable as an immediate ancestral form, on the somewhat doubtful assumption that a reduction in the number of scale rows in front of each fin took place during evolution.

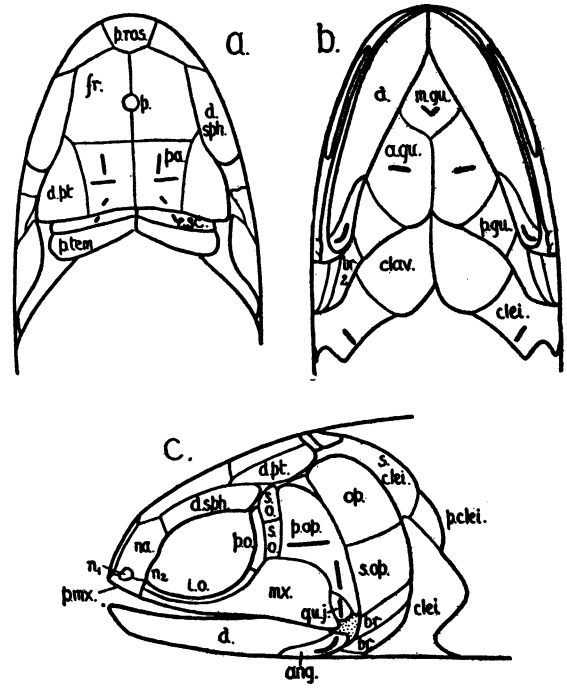


FIG. 36. Attempted reconstruction of the common ancestor X of the known Haplolepidae, in a, dorsal, b, ventral, c, lateral views. An attempt is made to show a possible transition from a "normal palaeoniscoid" to a haplolepid type of opercular system.

LATERO-SENSORY SYSTEM

The latero-sensory system of the head in X must have been close to the normal palaeoniscid pattern, except perhaps in the snout. The supraorbital canal was probably partly enclosed in the parietal, and the pit-line grooves of the skull roof were developed on that bone.

On the cheek, the horizontal pit line extended over the expansion of the preoper-

cular, and the vertical pit line traversed that bone and the quadratojugal. The pit lines of the mandible and gulars were developed as in *Haplolepis* and *Pyritocephalus*.

There were three pairs of lateral lines on the body with also paired "accessory lateral lines"; the main lateral line was enclosed, opening by pores on some (not all) of the "lateral-line series," and the associated accessory lateral line was marked by a groove in the hinder part of each scale in that series. The ventral lateral line was a series of pit-line grooves on the ventral scales and cleithrum, and the dorsal line may have been enclosed, opening by lunate pores in occasional scales.

DISCUSSION

In this way it is possible to obtain a fairly clear picture of the ancestral form. Comparison with other palaeoniscoids hitherto described shows that only one small group of genera can be considered as including close allies, viz., *Canobius*, *Mesopoma*, *Rhadinichthys*, *Rhadinoniscus*, and *Stegotrachelus*. From all these the genera *Haplolepis* (*sensu lato*) and *Pyritocephalus* show significant differences in cranial anatomy, fin structure, and proportions and should be placed in a new family, Haplolepidae. (The families Eurylepidae Moy-Thomas, 1939, and Teleopterinidae Berg, 1936, are based on synonyms, and *Pyritocephalus* is placed in the family Trissolepidae by Moy-Thomas, 1939, p. 126). The characteristic features of this family are the nature of the fins and their relative positions, the nature of the squamation, and certain features of the cranial anatomy, particularly the structure of the snout and the small number of bones in the opercular fold.

The genera listed above have the following stratigraphical distribution:

Stegotrachelus	top Middle or lowest Upper Devonian
Rhadinichthys	Upper Devonian-Upper Carboniferous
Rhadinoniscus, *Mesopoma*, *Canobius*	Lower Carboniferous

The Haplolepidae bear a remarkable resemblance to *Canobius* and *Mesopoma* (Moy-Thomas and Dyne, 1938; Moy-Thomas, 1937), particularly in the shape and relations of the dermal bones of the skull roof. These genera, however, have quite unspecialized fins, a longer caudal peduncle and more or less cleft heteroceral tail. The suspensorium in *Canobius* is markedly less and in *Mesopoma* somewhat less oblique than in the "normal palaeoniscid" cheek; the gulars are few; the rostrum is ill defined; the dorsal fin is remote, almost opposed to the anal; and in all these points the two genera form a very well-marked bridge in structure between the Haplolepidae and certain members of the broad genus *Rhadinichthys*. The species of *Rhadinichthys*, *Mesopoma*, and *Canobius* from Glencartholm (Moy-Thomas and Dyne, 1938) are particularly useful as morphological stages in this sequence.

Rhadinoniscus was set up by White (1939) for the reception of small fishes differing from *Rhadinichthys* in the fully segmented rays of the pectoral fins, the deeper caudal peduncle, and the small number of branchiostegal rays. In these characters *Rhadinoniscus* stands closer to the Haplolepidae than most species of *Rhadinichthys* and also greatly resembles *Stegotrachelus*.

There is little doubt that these fishes are really closely related and should be included in one family or a group of related families. There is a distinct tendency in many forms belonging to the five genera mentioned to develop a series of enlarged median dorsal (sometimes also apparently median ventral) scales, which are not found in the Haplolepidae, but there are species in some of those genera which are devoid of these scales, and the character may be of very minor systematic importance.

The ornament of the scales in those genera shows interesting resemblances to the conditions in Haplolepidae. Every transition from the complex ornament of the *Rhadinichthys* type, with its grooves parallel to the anterior and ventral scale margins in addition to ridges which terminate in the posterior denticulations, to the smooth ganoine surface with occasional pits can be traced within the limits of the group of genera.

It is suggested, therefore, that the Haplolepidae were derived from a lineage of relatively unspecialized palaeoniscids including stages that could probably be referred to the

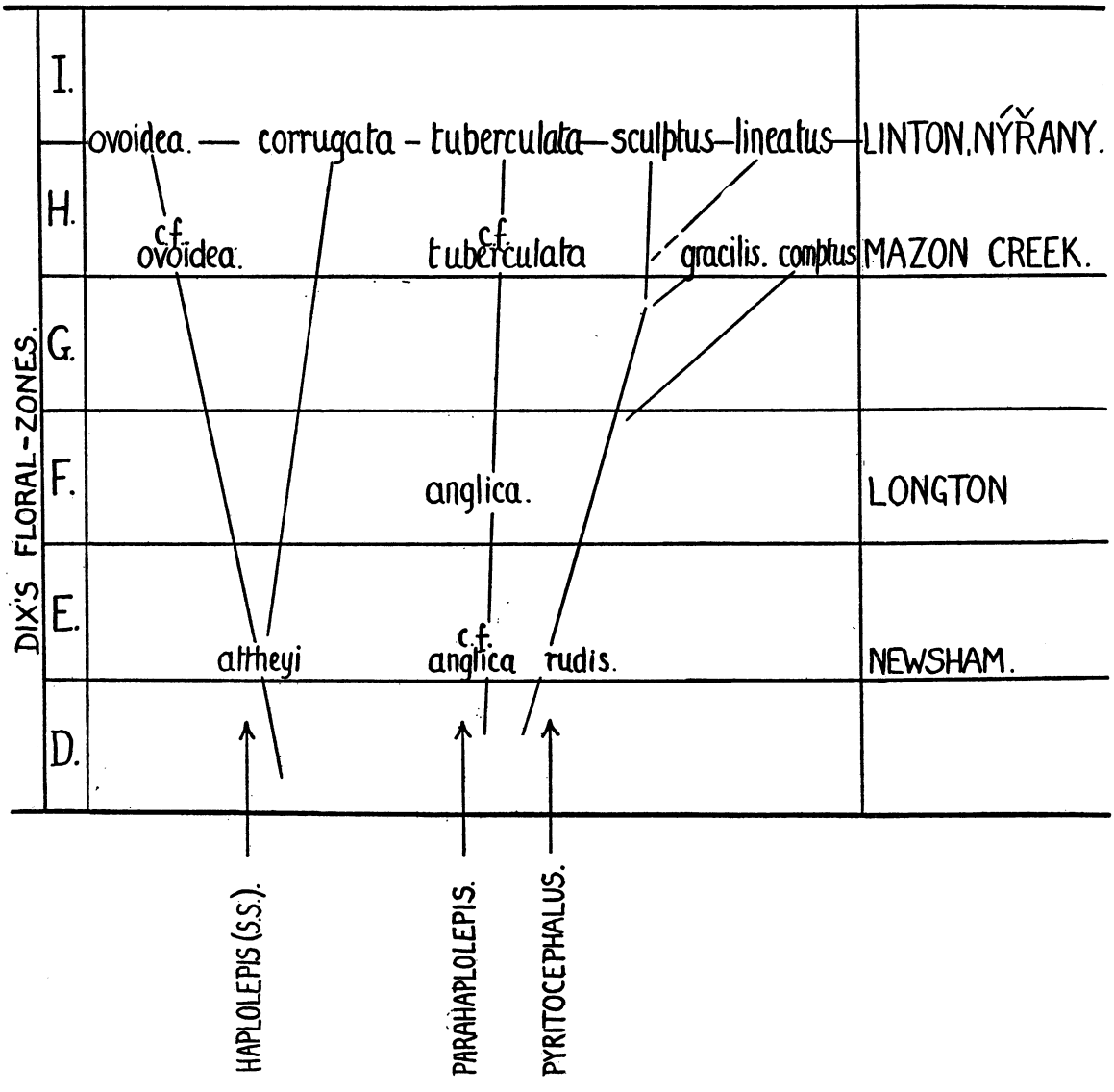
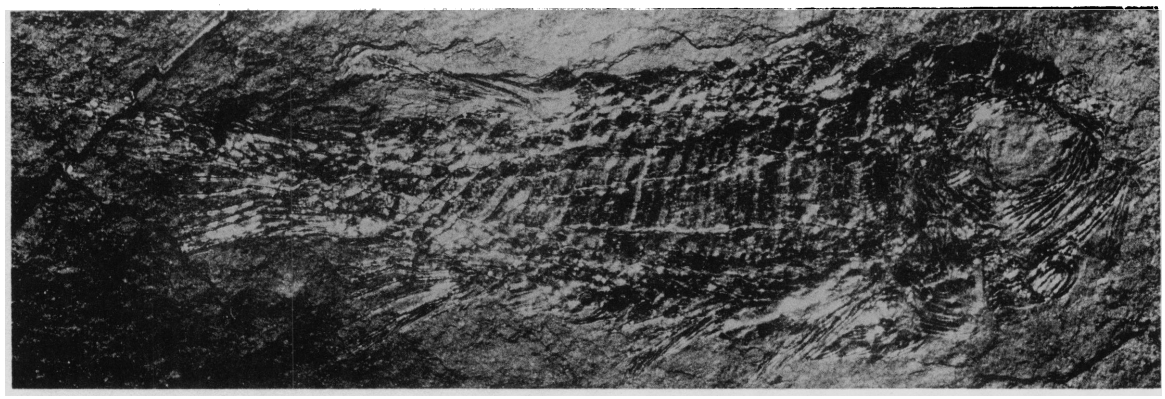


FIG. 37. Suggested relationship of the known species of Haplolepidae.

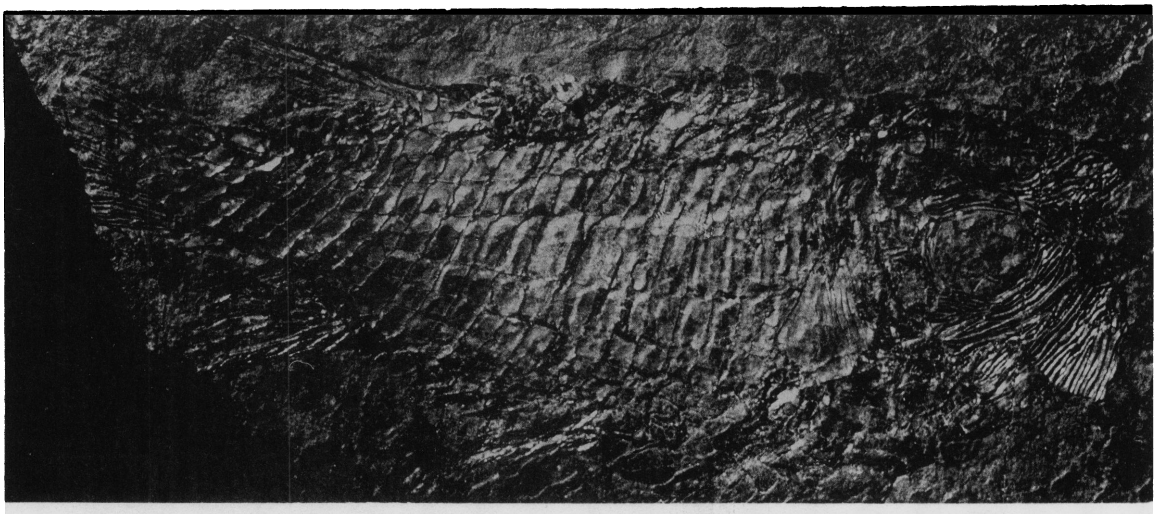
earlier genera *Canobius*, *Mesopoma*, *Rhadinoniscus* (or *Rhadinichthys*), the whole being derivable from a Devonian fish resembling *Stegotrachelus* and *Rhadinichthys*.

The evolution of the species of *Haplolepis* and *Pyritocephalus* from X was probably rapid, and since the cheek structures in several forms are peculiar, it must be admitted that the evolution took place along several distinct lines. The species of *Pyritocephalus* form a very natural and closely linked assemblage, and it is extremely unlikely that it is a polyphyletic genus in origin.

Haplolepis, however, can readily be subdivided into two subgenera in which the structure of the posterior part of the skull roof is markedly different. The cheek pattern is different in each well-known species. All these cheek patterns can be derived theoretically from a common ancestor X by the same process, namely, the forward movement of the quadrate and suspensorium. It has been



1



2

3

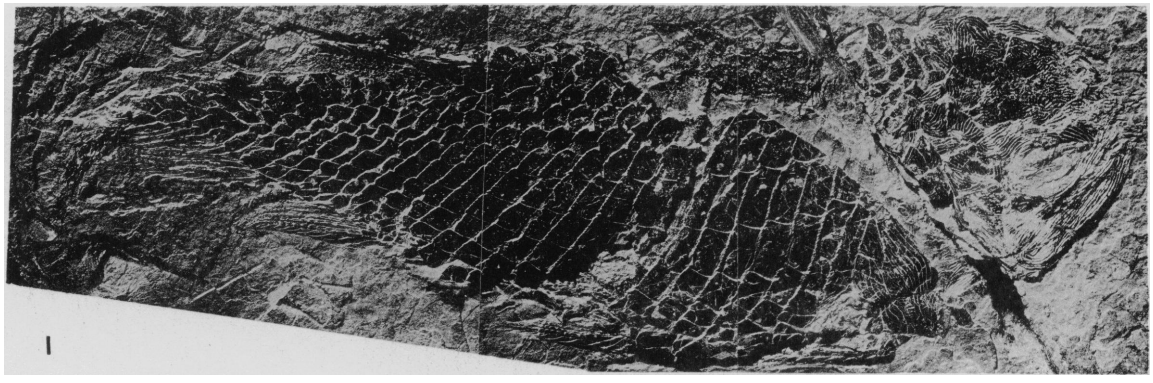
Haplolepis (*Haplolepis*) *ovoidea*

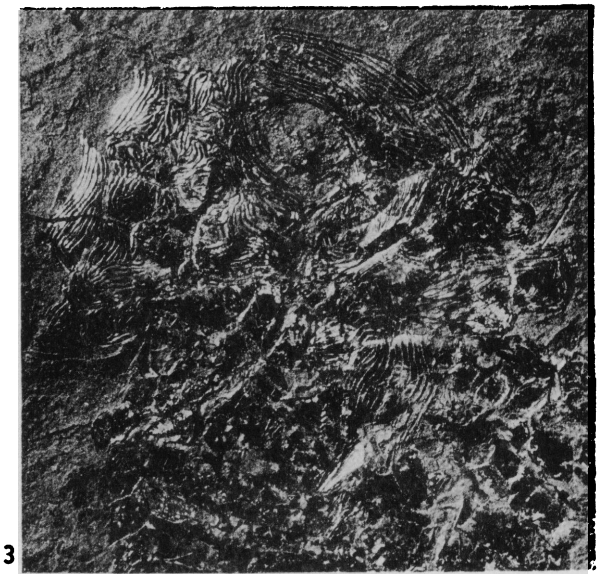
1. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry). Linton, Ohio. A.M.N.H. No. 1979 (Newberry 1024G). Holotype of *E. minima* Newberry. × 4.3.

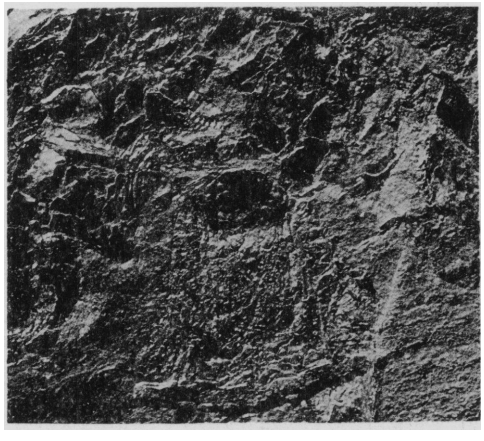
2. *Haplolepis* (*Haplolepis*) *ovoidea* (Newberry). Linton, Ohio. A.M.N.H. No. 449G. Intended holotype of *E. macrops* Newberry MS. × 4.2.

3. *Haplolepis* (*Haplolepis*) cf. *ovoidea* (Newberry). Mazon Creek, Illinois. U.S.N.M. No. 4303. × 4.8.

Lighting from top left in all cases.







Haplolepis (*Haplolepis*) *corrugata* and *attheyi*

1. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Linton, Ohio. A.M.N.H. No. 452G. Holotype of *E. corrugata* Newberry. × 2.0.

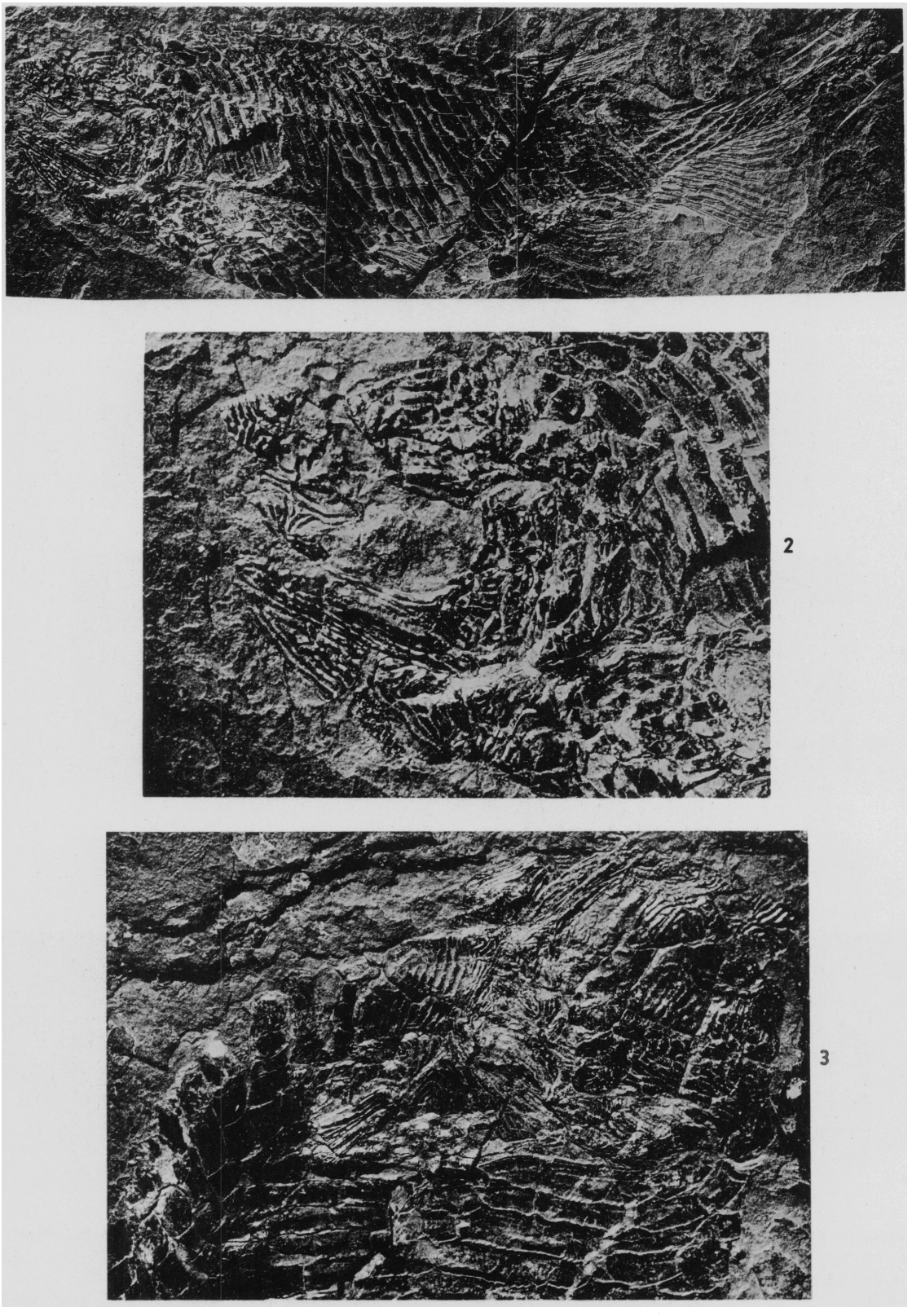
2. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Linton, Ohio. A.M.N.H. No. 452G. Holotype of *E. corrugata* Newberry. Head. × 3.7.

3. *Haplolepis* (*Haplolepis*) *corrugata* (Newberry). Linton, Ohio. U.S.N.M. No. 4496. × 3.6.

4. *Haplolepis* (*Haplolepis*) *attheyi*, new species. Newsham, Northumberland. Hancock Museum. Skull, etc. × 4.7.

5. *Haplolepis* (*Haplolepis*) *attheyi*, new species. Newsham, Northumberland. Hancock Museum. Tail, etc. × 4.7.

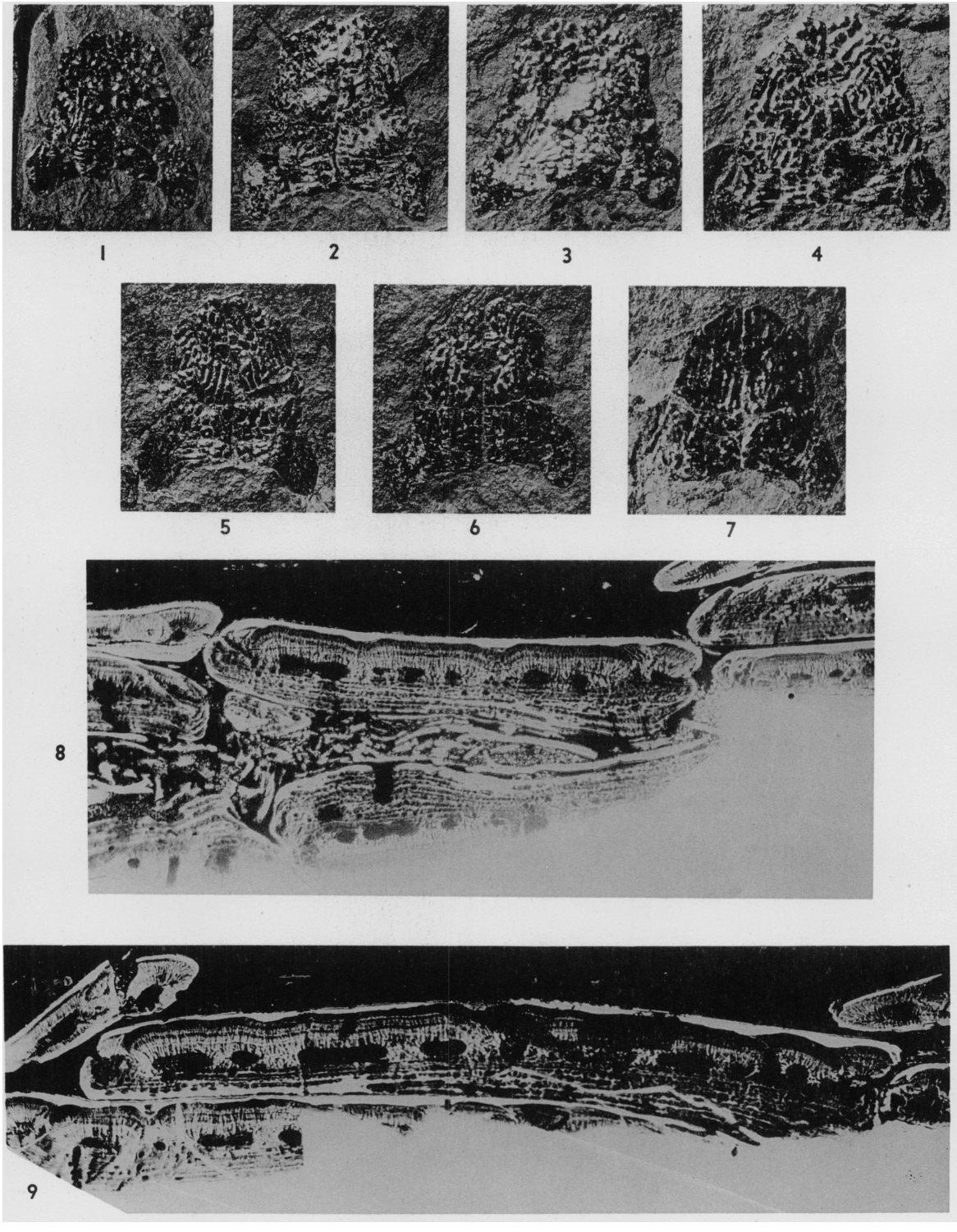
Lighting from top left in all cases.



Haplolepis (*Parahaplolepis*) *tuberculata* (Newberry). Linton, Ohio

1. A.M.N.H. No. 447G. × 2.1.
2. A.M.N.H. No. 447G. Head. × 5.0.
3. R.S.M., unregistered. Head and anterior flank scales. × 3.8.

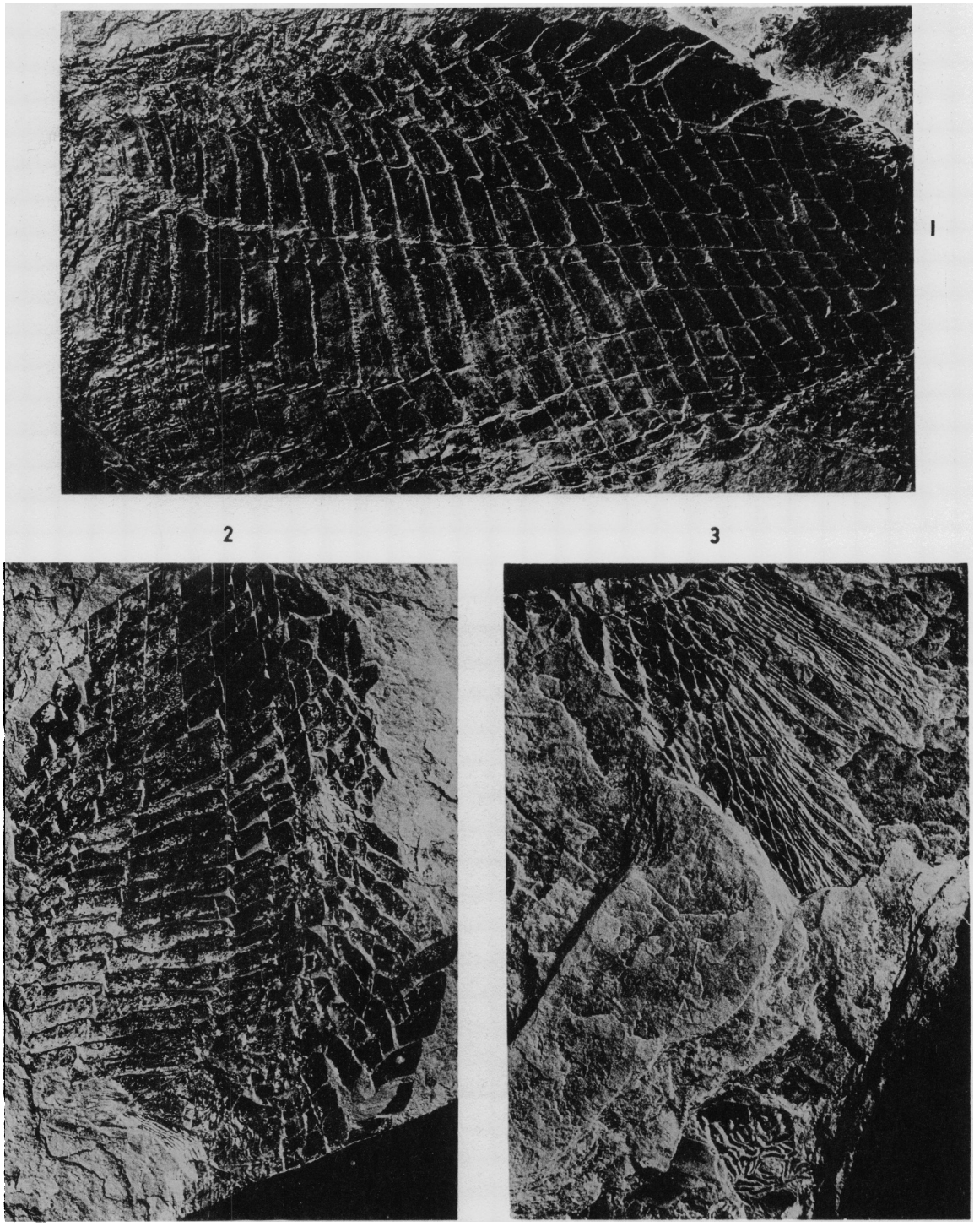
Lighting from top left in all cases.



Haplolepis (*Parahaplolepis*) *tuberculata* (Newberry). Linton, Ohio

1-7. Isolated skull roofs. Lighting from top left. 1, A.M.N.H. No. 1920, × 3.5; 2, A.M.N.H., unregistered, × 3.5; 3, A.M.N.H. No. 1001G, × 4.0; 4, A.M.N.H. No. 441G, × 4.0; 5, A.M.N.H. No. 996G, × 3.5; 6, A.M.N.H., unregistered, × 3.5; 7, A.M.N.H., unregistered, × 4.0.

8, 9. Microscopic preparations of scale structure. A.M.N.H. No. 2150. × .110.



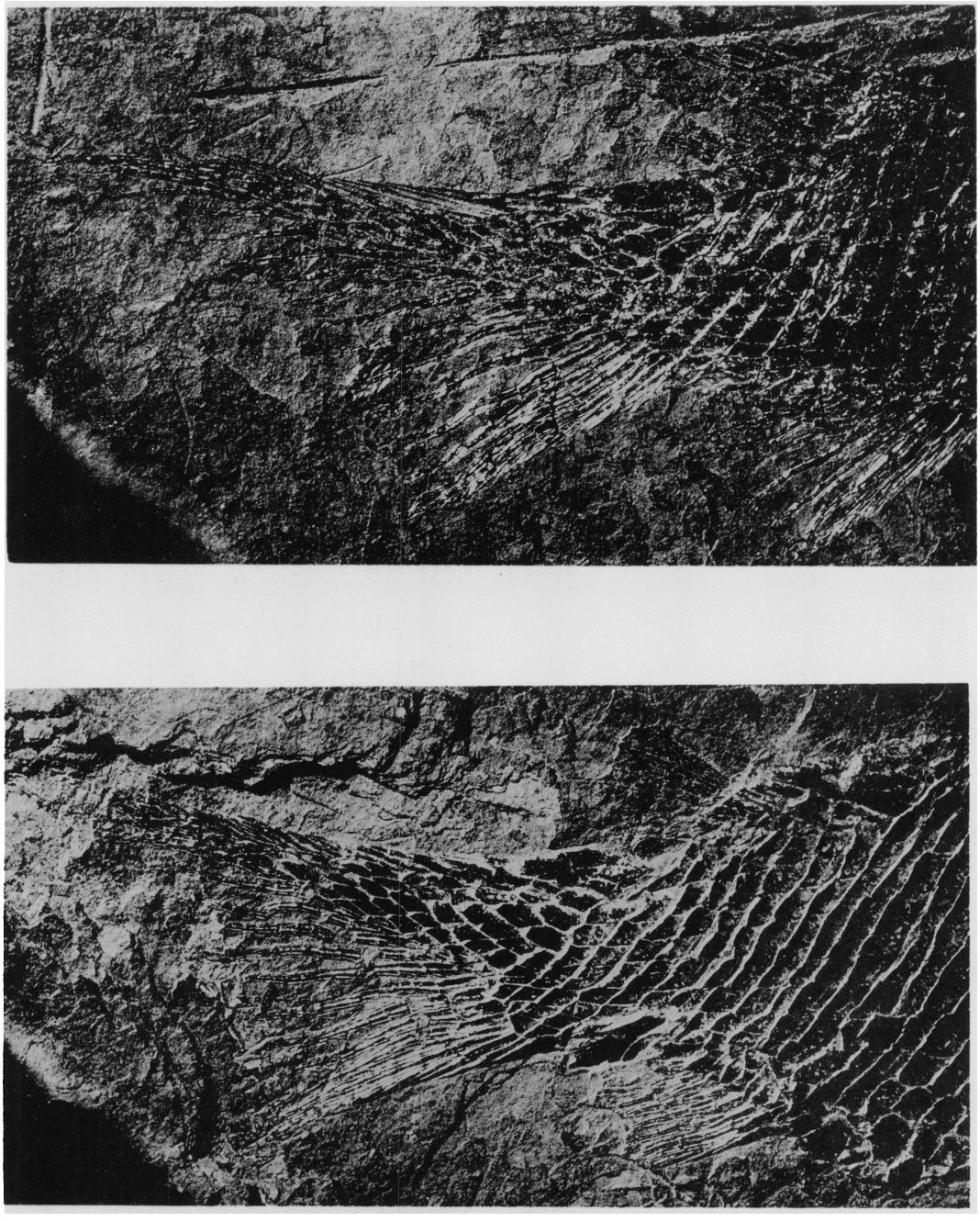
Haplolepis (*Parahaplolepis*) *tuberculata* (Newberry). Linton, Ohio

1. Anterior flank scales, showing deep lateral-line series, predorsal scale, and denticulation on hinder margins of anterior scales. Manchester Mus. No. L.10752. × 4.0.

2. Anterior squamation of A.M.N.H. No. 2044, showing nature of ventral scales. × 3.3.

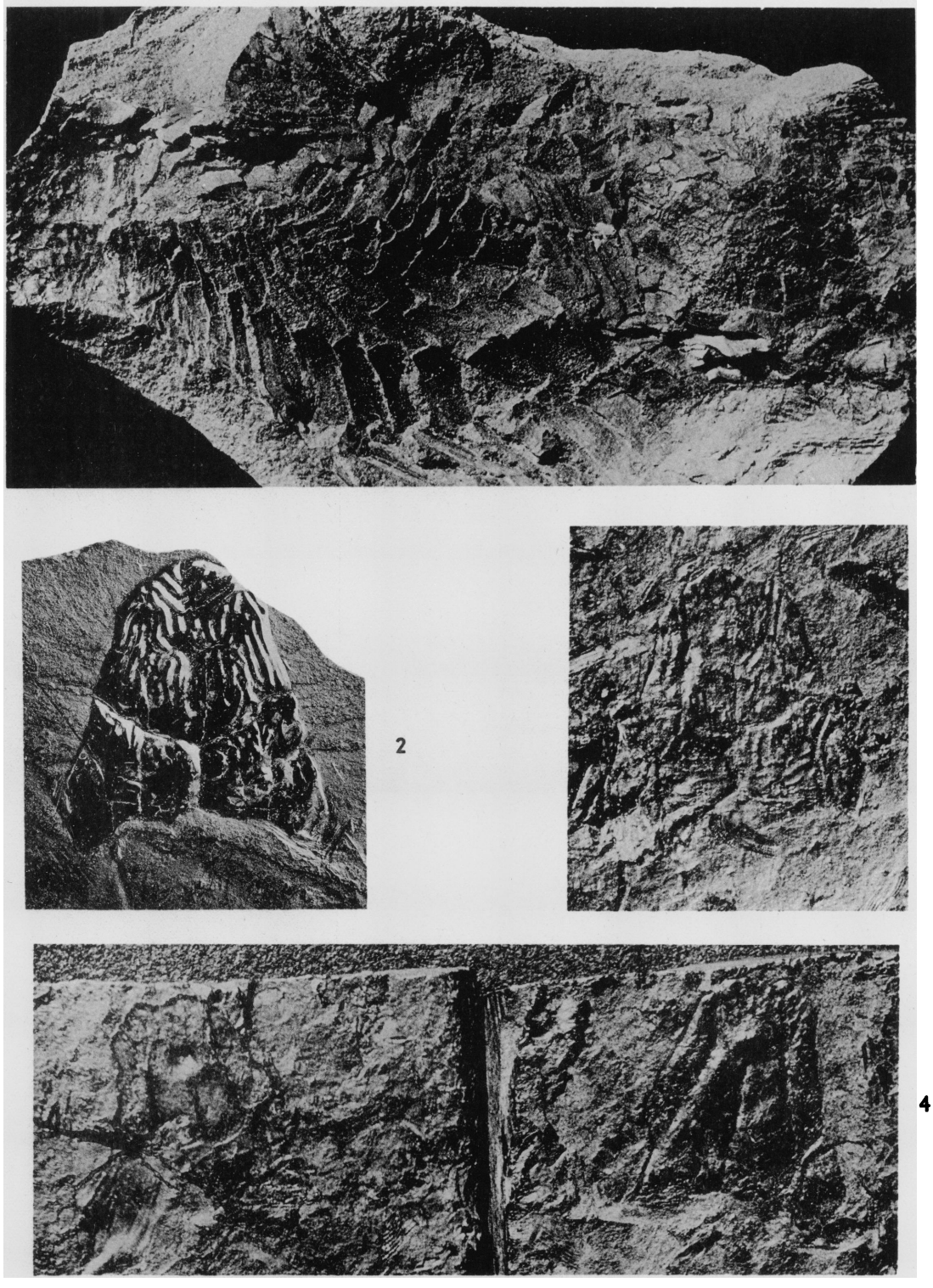
3. Separate nasal premaxilla, showing nostril opening; partial tail also shown. A.M.N.H. No. 990G. × 4.0.

Lighting from top left in 1, bottom left in 2 and 3.



Haplolepis (*Parahaplolepis*) *tuberculata* (Newberry). Linton, Ohio

1. Tail of A.M.N.H. No. 958G. Natural mold. × 4.0.
2. Tail of A.M.N.H. No. 989G. × 4.0. Lighting from top left.



Haplolepis (*Parahaplolepis*)

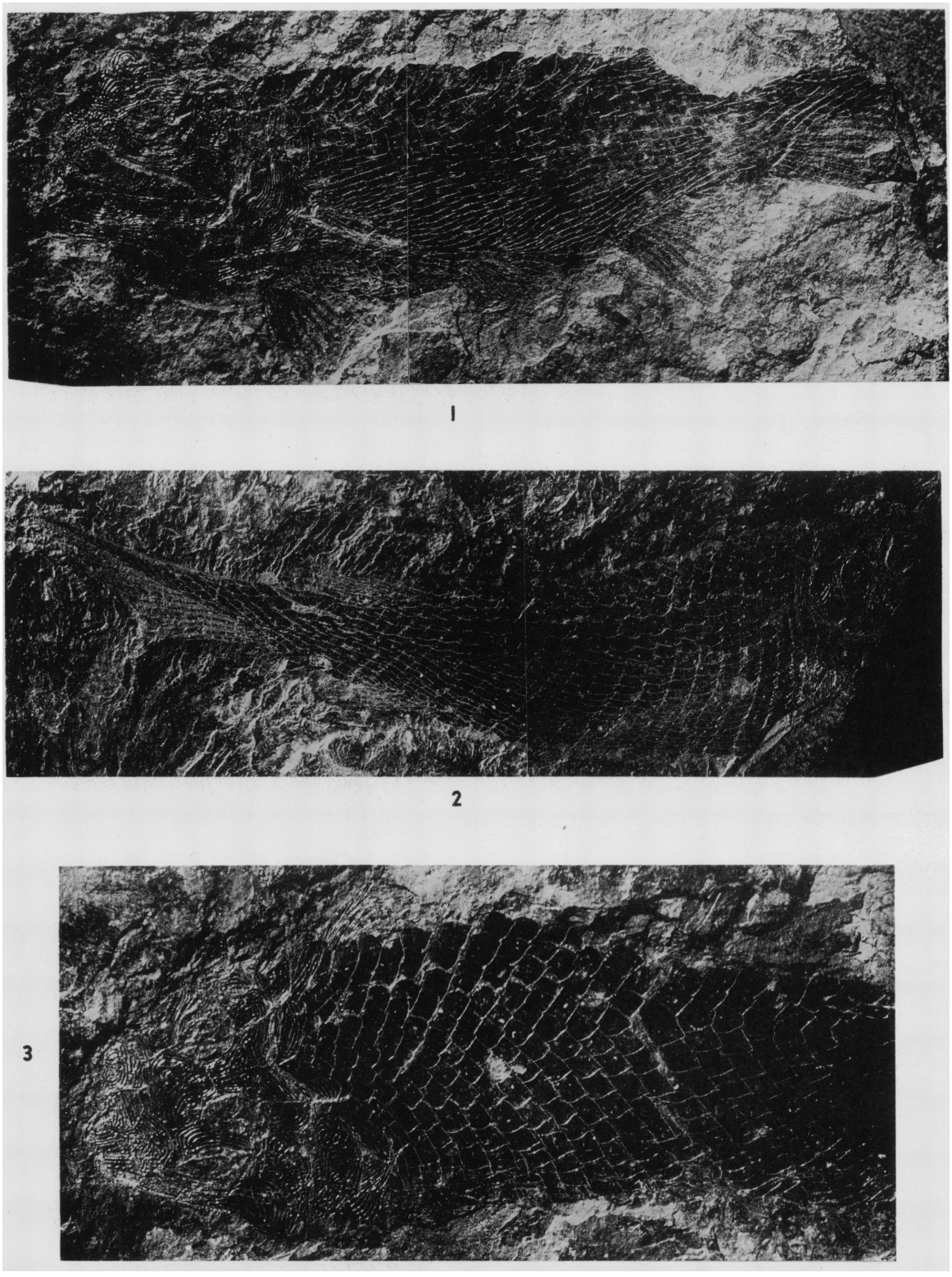
1. *Haplolepis* (*Parahaplolepis*) cf. *tuberculata* (Newberry). Mazon Creek, Illinois. Yale, Peabody Mus. No. 222. × 4.0.

2. *Haplolepis* (*Parahaplolepis*) *anglica* (Traquair). Longton, Staffordshire. Holotype, B.M.N.H. No. P.7995. × 5.7. Photograph supplied by British Museum (Natural History).

3. *Haplolepis* (*Parahaplolepis*) cf. *anglica* (Traquair). Newsham, Northumberland. Hancock Museum, specimen B. × 5.0.

4. *Haplolepis* (*Parahaplolepis*) cf. *anglica* (Traquair). Newsham, Northumberland. Hancock Museum, specimen A, in counterpart. × 5.0.

Lighting from top left in 1, 3, 4; top right in 2.



Pyritocephalus sculptus Fritsch.
Nýřany, Czechoslovakia

1. R.S.M. No. 1897.96.2. Complete fish, lateral view. × 3.0.

2. B.M.N.H. No. P.8650, showing tail. × 2.8.

3. B.M.N.H. No. P.21990. Skull and anterior squamation, dorsal compression. × 3.75. Lighting from top left.

thought better to retain the subgenera within the genus *Haplolepis* (*sensu lato*) as a recognition of this point, and to emphasize that the differences in cheek structure, though so well marked, are of an incidental nature.

The actual phylogeny of the known species can be indicated only in an extremely tentative fashion. *H.* (*H.*) *attheyi*, *H.* (*Parah.*) aff. *anglica*, and *P. rudis* are apparently the earliest species, and probably these are fairly primitive forms of the genera. *H. attheyi* resembles *H. ovoidea* in its head plan, as far as known, and in the general shape of the skull roof shows affinities also to *H. corrugata*. The palatal tooth plate resembles that seen in certain specimens of *H. tuberculata*, but this may well have been a feature common to other species. The general resemblance of *H. anglica* to *H. tuberculata* is very clear.

The characters of *Pyritocephalus*—particularly the skull roof, the extrascapulars and posttemporals, the quadratojugal, the body form, the mid-dorsal squamation, the relative position of the fins, and the distribution of the lateral lines on the body—all indicate a very close relationship to *Parahaplolepis*, and a clear distinction from the known species of *Haplolepis* (*sensu stricto*). It is considered certain that *Pyritocephalus* was derived from a primitive member of *Parahaplolepis*.

Of the five known species of *Pyritocephalus*, *P. rudis* shows the closest resemblance to *Haplolepis* in the structure of the skull roof and is regarded as extremely primitive; the absence of any remains of the body is regrettable. The other species occur in two stratigraphical levels, *P. gracilis* and *P. comptus* with flora G-H or H, *P. sculptus* and *P. lineatus* with flora H or H-I. In certain characters there is a marked distinction between these groups, e.g., the number of scales in between the lateral-line scale and the ventrolateral ridge are 6 and 8–9, 15 and 14 in order of mention.

Taking all the characters into account, a tentative "family tree" has been constructed (fig. 37).

It remains to consider the relations of the genera *Trissolepis* Fritsch and *Aeduella* Westoll to the family Haplolepidae. *Trissolepis* and *Pyritocephalus* have been associated by Moy-Thomas (1939, p. 112) in the family Trissolepidae.

Trissolepis kounovensis Fritsch, though abundantly represented in the Kounova horizon by fragments, is apparently rare as whole specimens. It is a fish about 6.5–10.0 cm. long, with a rather stoutly fusiform shape, and a large heterocercal tail with a relatively small ventral lobe. It differs markedly from any *Haplolepis* in the position of the fins (the dorsal is comparatively very anteriorly placed), the nature of the fin webs (which are made up of large numbers of rays), the nature of the squamation, and the larger number of branchiostegal rays. Fritsch's account of the head (1893, pp. 76–79, pls. 109–112) is not easy to follow; the "stirnbein" is probably the actinopterygian parietal, the "parietalia" being extrascapulars with openings of the occipital cross-commissure. The most interesting feature of the skull is the paired structure called "Orbitaleinschnitt" by Fritsch, represented as a paired vacuity between the "stirnbein" and more lateral elements. Only one skull roof has been figured (pl. 110, fig. 1), and this suggests to the present writer an entirely different interpretation. In certain heads of *Palaeoniscus freieslebeni* Agassiz, from the Kupferschiefer, and in other palaeoniscoids, otoliths are preserved in such a way that they have sharply indented the dermal bones of the skull roof (cf. also the skull of *Haplolepis corrugata*, fig. 9b). In several individuals seen by the writer the conditions almost duplicate those of Fritsch's figure; the otolith lies in a small, almost circular area of matrix surrounded by broken edges of the bones of the posterior part of the skull roof, due to the removal of the small elevations of the skull-roof bones caused by the impression of the otoliths. In any case the vacuity cannot represent the orbit. After a careful comparison of Fritsch's account, the writer thinks it likely that *Trissolepis* may be a near relative of *Sceletophorus biserialis* Fritsch (*op. cit.*, pp. 88–92, figs. 281–286, pl. 116, pl. 117, fig. 5) from the horizon of Tremosna. In Fritsch's reconstructions of these two fishes the positions of the dorsal fin do not correspond very well to the figures of actual specimens. In passing, it may

be mentioned that *Phanerosteon pauper* Fritsch [=*Gymnoniscus pauper* (Fritsch), Berg, 1936, p. 345] (*op. cit.*, pp. 92–94, fig. 287, pl. 117, figs. 1–4), a small fish 33 mm. long, without flank scales, is almost certainly the young of *Sceletophorus*, as was actually suggested as a possibility by Fritsch. The tail of the only figured specimen is incomplete and perhaps distorted. The main differences from *Sceletophorus* noted by Fritsch, lack of flank scales and paired nature of the median scales behind the dorsal fin, are exactly what would be expected of a young form.

It may be accepted, therefore, that *Trissolepis* is quite distinct from *Pyritocephalus*, that the alleged fenestrations in its skull roof are very doubtful, and that the peculiar characters of *Trissolepis* and its relation to other fishes are in need of revision.

Aeduella blainvillei (Agassiz) was described in some detail by Westoll (1937b). It is a small fish, usually less than 15 cm. long, occurring in great numbers in the Lower Permian shales of Muse, near Autun. In the structure of the cheek it shows considerable approach to "holostean" conditions, and the preopercular and maxilla are much modified from the normal palaeoniscoid pattern. The head resembles that of Haplolepidae in certain features such as the lack of a rostrum, the probable modification in position of the nostrils, the large eye, the great breadth of the head, and the small number of branchiostegals or gulars. In addition, the anterior pit line shows an abnormal course. The differences in structure of the broad snout, the cheek pattern, the extrascapulars, and the type of ornament are, however, quite enough to show that *Aeduella* is sufficiently different from genera now placed in the Haplolepidae for it to be reasonable to suppose that the "holostean" characters have been acquired independently in different forms; this tentative conclusion (Westoll, 1937b, p. 576) can now be reaffirmed on far stronger grounds.

COMPARATIVE MORPHOLOGY

THE DETAILED STUDY of a group of closely allied fishes, such as the community of fin structure, body shape, and basic head pattern shows the above assemblage to be, is likely to yield much information concerning both the evolutionary process of differentiation within the group and the nature of more or less similar changes in other phylogenetic lines. It is proposed to discuss certain morphological features from this aspect, but a preliminary general note on bone nomenclature seems necessary.

In this paper the simplest names for dermal bones are generally used, with their customary modern meaning. In some cases names are used which are noncommittal as regards certain current controversies. For instance, "dermopterotic" is used throughout for the bone generally called "supratemporal," which is believed by certain workers, following Stensiö (1921, p. 138), to be a compound "supratemporo-intertemporal." In the use of the simple terms "preopercular" and "maxilla," however, the writer affirms his strong belief that there is no element in the actinopterygian cheek corresponding to the squamosal of crossopterygians and tetrapods.

The bone here called "dermosphenotic" is of greater interest. It is often termed "postfrontal." Stensiö and his followers would regard it as the product of fusion of a "dermosphenotic" and supraorbital elements; the writer regards it as a "dermosphenotic" growing forward so that supraorbitals cannot appear. The use of the term "postfrontal" is questionable; the term should be restricted to bones demonstrably equivalent to the postfrontal of tetrapods, and this particular problem of nomenclature is the subject of very diverse views (Säve-Söderbergh, 1932, 1936; Westoll, 1936, 1937d, 1938a, 1940).

In the skull roof as a whole there is great difficulty in the application of such terms as "parietal," "frontal," and "nasal." Strictly, these terms should only be applied to the certain homologues of the similarly named dermal bones of tetrapods. This matter has been mentioned by the writer in previous papers (1938a, 1938c) and will be more fully discussed on a later occasion. For the moment it is sufficient to state that these bones in Actinopterygii are *roughly* equivalent to those usually given the same name in osteolepid fishes, but that the homologues of these osteolepid bones are *not* the correspondingly named elements of tetrapods. It is thus necessary to point out that these bone names are used here in their well-understood sense in actinopterygian fishes.

The case of the premaxillary is of greater interest and is dealt with in greater detail below.

In the mandible the simple form "dentary" is used without prejudice to the argument that the bone includes splenial elements.

SKULL ROOF

Of all the Palaeozoic Actinopterygii so far described, only *Canobius* (Moy-Thomas and Dyne, 1938, pp. 440–445, esp. figs. 2, 6) has a very close resemblance in its skull roof to the most generalized species of *Haplolepis*. This resemblance extends to the shape of the bones as a whole (not including the snout bones) and in particular to the large dermosphenotic and the narrow extrascapulars, which may not reach the mid-line (e.g., *C. ramsayi*, *op. cit.*, fig. 2). It is interesting that the cheek also in this genus is not unlike that of *Haplolepis*. *Canobius* is clearly related in general structure to *Mesopoma*, which forms an excellent link with certain species of *Rhadinichthys* (described by Moy-Thomas and Dyne, *op. cit.*). There is thus an excellent series of morphological stages linking *Rhadinichthys* (e.g., *Rh. fusiformis*, *Rh. canobiensis*) with a generalized *Haplolepis* such as *H. ovoidea* or *H. attheyi*, by way of *Mesopoma* and *Canobius* (cf. fig. 38). Since many other features change quite harmoniously with this arrangement, it may be accepted provisionally as a reasonable approach to the earlier history of the group. *Rhadinichthys* or closely allied forms occur in the Upper Devonian, and there is, therefore, the possibility that the evolutionary line now under consideration was, from the very early times, separate from other "palaeoniscoids."

It is necessary to accept the skull-roof pattern of *H. ovoidea* and *H. attheyi* as more

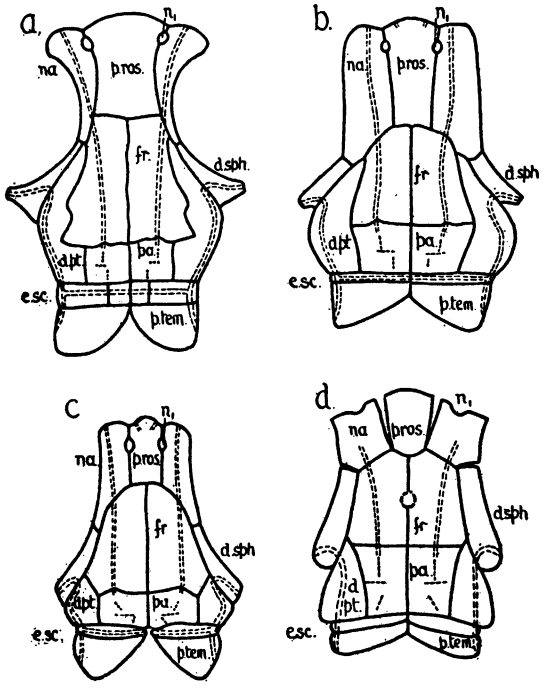


FIG. 38. Skull roofs of a, *Rhadinichthys canobiensis* Traquair; b, *Canobius elegantulus* Traquair; c, *Canobius ramsayi* Traquair (all after Moy-Thomas and Dyne), compared with X.

"primitive" than those of other species because of the presence of parietals. In all other members of *Haplolepis* and *Pyritocephalus* the parietals are absent and the dermopterotics meet in the mid-line. This modification seems to have occurred independently at least twice, in *Haplolepis* (*H.*) *corrugata* and in *Parahaplolepis-Pyritocephalus*. An explanation of this change involves an analysis of the latero-sensory canal system.

In such "normal" palaeoniscoids as *Rhadinichthys* the supraorbital canal is continued from the frontal into the parietal and enclosed for some distance in that bone before passing back into the surface "anterior pit line." The same conditions hold in *Mesopoma* and *Canobius*. In these fishes, therefore, it may be assumed that during development one or more sensory organs of the supraorbital series became infolded into a canal and so localized a stimulus for dermal bone formation, resulting in the separate parietal (cf. fig. 39).

It is a remarkable fact that the posterior part of the supraorbital canal in many groups of fishes shows a progressive "degeneration," the sensory organs fail to become infolded in canals or gutters but remain at the surface as small pit organs. In *Haplolepis* and *Pyritocephalus* this process is already marked, and the closed canals usually terminate in the most posterior parts of the frontal. According to the hypotheses developed by Westoll (1937a, pp. 378–379) this "degeneration" should result in the gradual loss of the stimulus for the formation of a separate parietal. In *Haplolepis*, two species (*H. ovoidea* and *H. attheyi*) retain separate parietals and, therefore, retain a more "primitive" arrangement; but in other species of *Haplolepis* and in *Pyritocephalus* the enlarged dermopterotics, meeting in the mid-line, indicate the completion of the process.

The "degeneration" of the posterior part of the supraorbital canal is found in numerous other groups of fishes and is frequently associated with the loss of separate "parietal" elements. Thus in certain Teleostei (e.g., *Macrodon*, *Hydrocyon*, and *Carassius*, figured by Allis, 1904, pls. 12, 13) the "parietals" seem to have been replaced by anterior extensions of the extrascapulars. In *Polypterus* and *Calamoichthys* the dermopterotics have invaded their area. The conditions in the Dipnoi, in which the changes are very clearly shown, will be described in another place if present circumstances permit. In the Crossopterygii the "degeneration" of the posterior part of the supraorbital canal seems to have been very nearly complete in all known members. "Parietals" are still present in general in the Osteolepida, but in occasional specimens of *Osteolepis* and *Megalichthys* and in the holoptychiids and coelacanths, separate "parietals" are absent and the more lateral sensory canal bones ("intertemporals," or "supratemporals," or both) have grown to the mid-line.

It is noteworthy, however, that a bone may continue to appear for some time phylogenetically, apparently after the removal of the sensory canal stimulus. In *Haplolepis* the loss was quite quick, as will be shown later, and the same is true, in part, of Dipnoi, and probably of holoptychiids and coelacanths. Many other fishes retain the "parietals" in

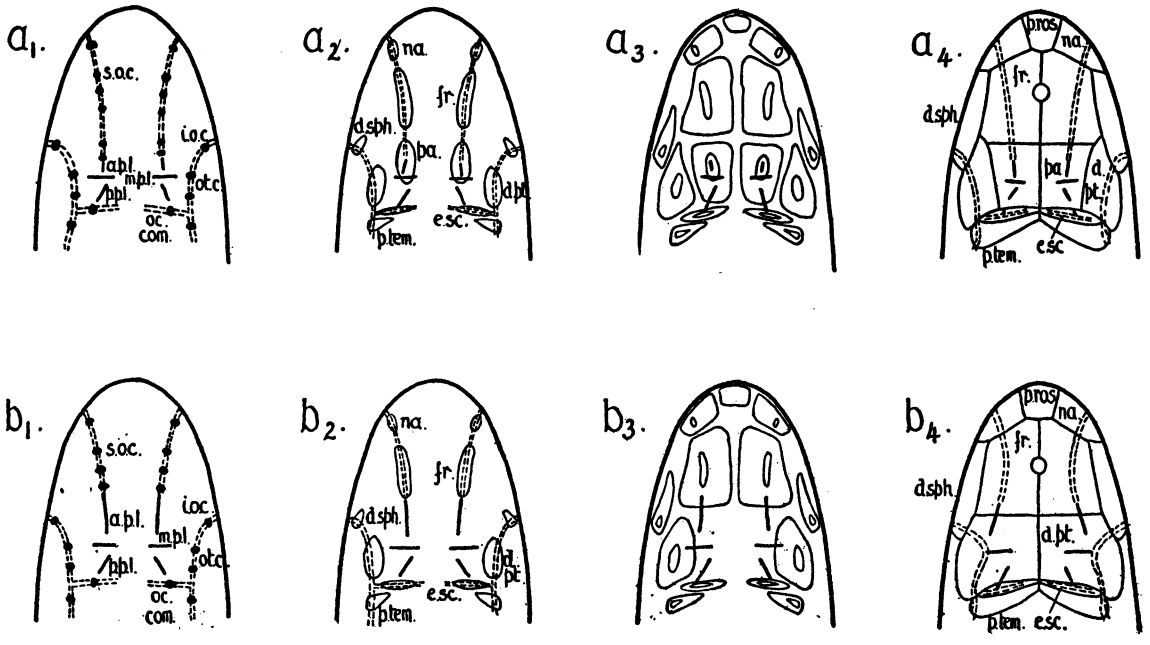


FIG. 39. Explanation of the loss of the parietals, growth of the dermopterotics, and capture of pit lines consequent on the reduction of the posterior part of the supraorbital canal. a_1–a_4 Represent stages in the development of the dermal bones of a primitive type in relation to the latero-sensory canals. In a_1 the rudiments of the dermal bones are shown as mesodermal condensations associated with the latero-sensory organs; in a_2 these have fused to provide rudiments of the definitive bones; in a_3 a later stage is shown, with the new growth since a_2; in a_4 the dermal bones and latero-sensory system of the adult are shown. b_1–b_4 Represent similar stages where the posterior latero-sensory organs of the supraorbital canal show progressive failure to develop and to be associated with bone growth. No account is taken of the changes in shape of the head during growth.

similar circumstances. The case of *Aeduella blainvillei* (Agassiz) (Westoll, 1937b) is particularly interesting because of the clear demonstration of the retention of the parietals; the anterior pit line passes actually onto the dermopterotic. This problem has previously been discussed (Westoll, 1937a, pp. 378–379; 1937b, pp. 571–572); it is necessary to point out that no attention was paid in those works to the possibility of analysis of the problem along genetical lines. It is hoped to return to this matter on another occasion.

The fenestration of the skull roof in *Pyrito-*

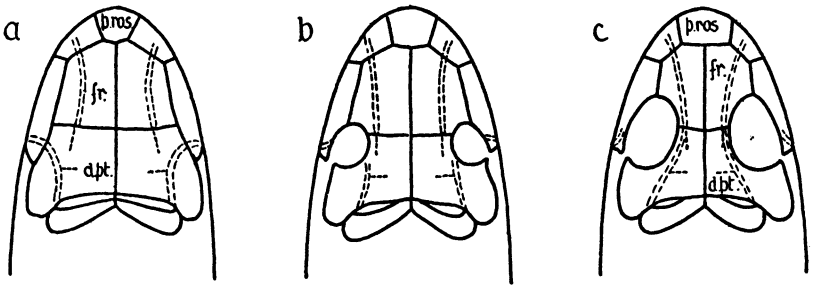


FIG. 40. Suggested phylogeny of the skull roof of *Pyritocephalus*, showing interference with bone growth and course of otico-infraorbital canal, producing fenestration and modification of pattern of latero-sensory canals.

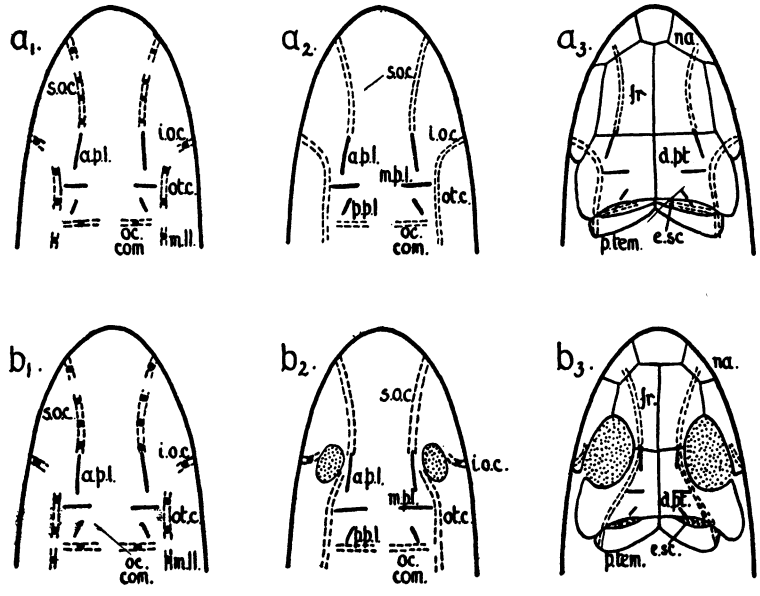


FIG. 41. Explanation of modified course of latero-sensory canals in *Pyritocephalus*. a_1–a_3 Represent conditions in a *Parahaplolepis*. In a_1 the early development of the system is indicated; short sections of tissue derived from placodes show differentiation of latero-sensory organs; in a_2 the main lateral-line, otic, and infraorbital sections anastomose, and the adult structure is shown in a_3. b_1–b_3 Represent similar stages in growth of *Pyritocephalus*. In b_2 the interference with growth is shown by stippling, and it is suggested that the otic section anastomoses with the most posterior pore of the supraorbital canal to produce the adult pattern shown in b_3.

cephalus is open to simple analysis. The conditions can be derived from those of *Haplolepis*, such as *H. tuberculata*, by some process which involves interference with bone growth near the junction of the dermosphenotic, frontal, and dermopterotic (fig. 40). The fenestration recorded in *Trissolepis kounovensis* (e.g., Fritsch, 1894, p. 76, pl. 110, fig. 1) has been given a different interpretation above. Moy-Thomas (1939) has noted this apparent resemblance and unites *Pyritocephalus* and *Trissolepis* in the family Trissolepidae. Close relation between the genera, however, is quite unlikely when attention is paid to other features of their anatomy, and the fenestration of the skull roof of *Trissolepis* is highly questionable and is not accepted here (above, p. 65). It is still less likely that the fenestrated dermal skull of *Polyodon* indicates any genetic or structural relationship to *Pyritocephalus*. Woodward (1917, p. 387) has drawn special attention to a small paired "supratemporal" vacuity in the dermal skull roof of certain pycnodonts such as *Coelodus* and *Pycnodus*. The vacuity is bounded by the frontal, "supraoccipital," and "parietal" and is thus morphologically considerably posteromesial to the place of the fenestration in *Pyritocephalus*. Woodward compares the pycnodont structure with that of the living teleost family Zeidae and shows that both may be due to the anterior migration of the insertions of the lateral trunk muscles on the cranium. The probable position of the fenestration in primitive *Pyritocephalus* was somewhere near the front of the fossa bridgei, which is a depression on the dorsal aspect of the endocranium receiving extensions of the body musculature. The original fenestration may, therefore, have been caused by the further encroachment of muscles, but in the well-known species the fenestrae extend so far forward that they overlie the orbits. It is thus possible that the whole fenestration may be due to structures associated with a proportionately large eye-

ball, or that such structures increased the importance of fenestration primarily due to other causes.[1]

The remarkable changes in the laterosensory canals of the head in *Pyritocephalus* may be regarded as based on the same causes as those responsible for the fenestration. It is suggested that these causes, whether due to the extension of the body musculature or structures related to the huge eye or to other causes, brought about interference with all the structures near the dermosphenotic-frontal-dermopterotic junction of more primitive forms, and it is likely that this disturbance was present in quite young fishes, before the full adult development of the laterosensory canals. It is usual in fishes for these canals to be formed by the end-to-end anastomosis of shorter sections, and in *Pyritocephalus* it is likely that the otic section related to the dermopterotic was prevented from joining up with the section of the infraorbital canal related to the dermosphenotic. As a secondary result there was formed a new anastomosis between the anterior terminal pore of the otic canal in the dermopterotic and the most posterior tubule of the supraorbital canal. The conditions are illustrated diagrammatically in figure 41. The dorsal end of the infraorbital canal seems to have been turned forward in the dermosphenotic.

The existence of the anterior, middle, and posterior pit lines on the dermopterotic would be held, by some palaeontologists, to be evidence of the "compound" nature of that bone, which would then be called a parieto-dermopterotic, or parieto-supratemporo-intertemporal. It is proposed briefly to extend and illustrate the short discussions of this problem already published (Westoll, 1937a, pp. 379–380; 1937b, p. 572). In *Amia calva* (Pehrson, 1922, p. 45; Westoll, 1937a, p. 375) the postorbital bones develop as rudiments in association with sensory organs of the infraorbital canal; from the rudiments of the lower postorbital a lamella grows backwards and comes to have a secondary, casual relation to the cheek lines of pit organs. In *Amia* the grooves for these pit lines lie at some distance from the radiation center of the bone, and the secondary nature is apparent. The conditions in *Haplolepis* and *Pyritocephalus*, however, resemble those in the intertemporals of coelacanths and *Holoptychius*, because the pit line, which there is reason to suppose is secondarily related to the bone, lies on or across the radiation center. This can only be explained by considering early growth stages. Should the growing bone lamella very quickly surround the nerve supply of the pit line, the latter will be "anchored" to the bone, and since the growth of the bone is peripheral, the pit-line groove will come in time to be restricted to the middle of the surface (see figs. 39, 41). In *Haplolepis* such as *H. tuberculata* and *Pyritocephalus* the middle pit line lies above and mesial to the course of the sensory canal in the dermopterotic, which indicates that the bone lamella grew mesially in "capturing" the pit line. This is in accord with the other suggestions made above.

The presence of a pineal foramen in Palaeoniscoidei has been recorded by Berg (1939) in the Lower Carboniferous *Gyrolepidotus*, and the writer has observed it also in Devonian and Carboniferous "*Rhadinichthys*." It is not otherwise known in normal actinopterygians, though fenestrations near the appropriate position occur in such forms as *Polyodon* and several teleosts; these are clearly secondary developments. Berg's comments (1939, p. 635) on the writer's discussion based on *Elpistostege* (1938a, 1938c) would be pertinent if the pineal foramen had been the only key used in homology, but the position of the pineal is only incidental to a much more far-reaching correspondence of parts.

CHEEK

Haplolepis shows very clearly the effects of a change in the suspensorium from the "normal palaeoniscid" type to an almost vertical arrangement. Even *Pyritocephalus*, though it retains much more clearly the familiar bent preopercular and the maxillary

[1] Another possibility is that the fenestra may be comparable with the rather similarly placed supraorbital fontanelle of *Polypterus*, which is roofed by the frontal. Allis (1922, p. 191) has shown that this structure is related to the origin of the "temporal" division of m. adductor mandibulae. It seems on the whole very unlikely that the *Pyritocephalus* condition is really comparable.

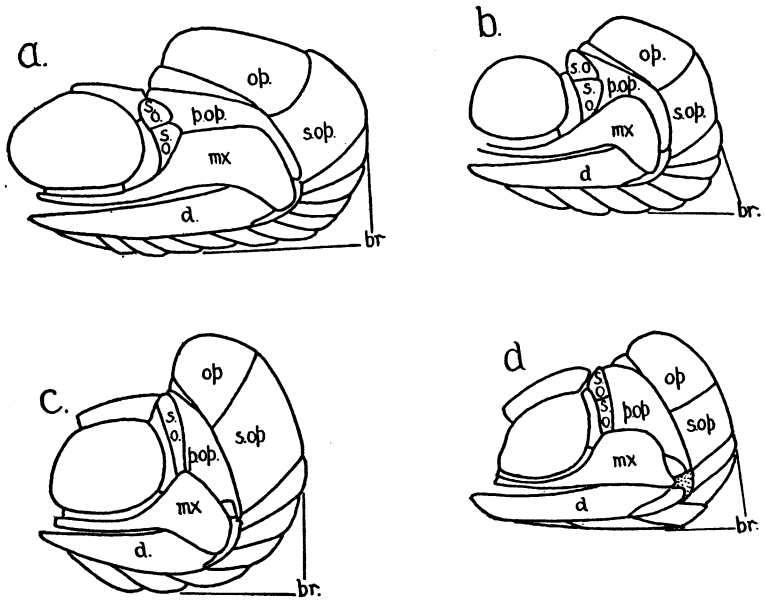


FIG. 42. Cheek bones of a, *Rhadinichthys canobiensis* Traquair; b, *Mesopoma pulchellum* Traquair; c, *Canobius ramsayi* Traquair (all after Moy-Thomas and Dyne; c, with quadratojugal added) compared with d, the cheek of X.

expansion, has a suspensorium distinctly less oblique than that of most palaeoniscids (fig. 42).

The remarkably different patterns produced in the haplolepid species of which the cheek is well known form an unexpected novelty. The very close resemblance in fins, body structure, and even in basic skull-roof pattern are at first sight out of harmony with the marked differences in cheek pattern. The different patterns are, however, all capable of being derived from a "normal palaeoniscid" type by the more vertical inclination of the suspensorium and the associated forward movement of the quadrate. In this way the bones covering the cheek would have less room to grow between the opercular apparatus and the eye, and it might be expected that the maxillary expansion would become very short, and that the preopercular would have its familiar two-shanked appearance much modified; in addition the suborbital series should be much reduced. These expectations are realized, but the importance of these fishes is that they show that the shortening of the cheek must have taken place independently, since the division of the stock into several lineages. The *Pyritocephalus* cheek is least modified, with its still recognizably "palaeoniscid" maxilla and preopercular, the suborbitals between preopercular and postorbitals, and the separate quadratojugal. The cheek of *Haplolepis tuberculata* could be derived from such a "palaeoniscid" type by forward movement of the lower end of the suspensorium, so that the maxillary expansion became high and narrow, the preopercular attained its curiously compressed shape, and the suborbitals were cut off from the maxilla; the quadratojugal was retained. In the line leading to *H. corrugata* the quadratojugal was lost, and the suborbital series much modified; but the preopercular and maxilla retain considerable expansions and cover the cheek as broad plates. In *H. ovoidea*, however, the shortening has been extreme, so that the preopercular is most oddly shaped (though still with recognizable equivalents of the "horizontal" and "vertical" shanks), and the maxillary expansion has lost its individuality; the suborbitals are again reduced, and the quadratojugal is lost.

Each of these cheek patterns seems to have been formed independently from the others, and in view of the great similarity in other anatomical features it is very likely that the

changes took place comparatively rapidly.

The presence of the small bone regarded as a quadratojugal is one of the most interesting features of the cheek of *Haplolepis tuberculata* and *Pyritocephalus sculptus*. Since the cheek in these forms is still recognizably "palaeoniscid," in nature, it is presumed that the bone is inherited from a more generalized ancestor. The presence of a quadratojugal in *Cheirolepis* was indicated with some doubt by Watson (1925, p. 821) and Westoll (1937a, p. 368, fig. 4a, "Qu.j?"). In other palaeoniscoids there is little evidence from published

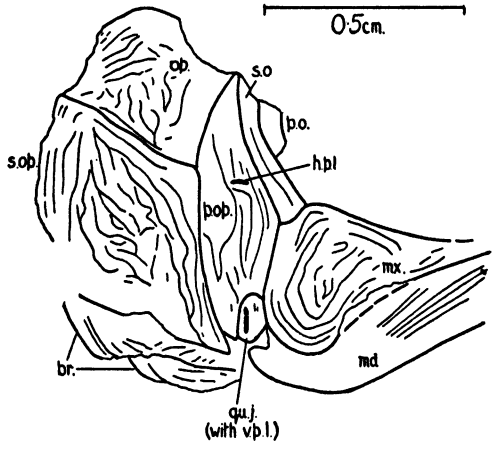


FIG. 43. Cheek bones of *Canobius ramsayi* Traquair, Manchester Mus. No. L.10448, showing the probable existence of a quadratojugal.

figures of the general presence of a quadratojugal, but in material of *Glaucolepis* and *Palaeoniscus* described by Nielsen (1936, p. 38, figs. 17, 19) the bone is clearly developed. A careful examination by the author of material of *Palaeoniscus freieslebeni* Agassiz from the Marl Slate and Kupferschiefer has shown that the bone is probably absent in most individuals but occurs in some cases. I wish here to withdraw my earlier (1937a, p. 370) interpretation of the quadratojugal of *Saurichthys*. It is not improbable that systematic search would demonstrate its more general occurrence in palaeoniscoids.[1]

[1] In another place I hope to present evidence that the two small bone plates lying below the great cheek plate in *Polypterus* (e.g., Allis, 1922, pl. 5) represent the maxillary and quadratojugal of earlier Actinopterygii.

The published reconstructions of *Canobius*, *Mesopoma*, and *Rhadinichthys* do not show any sign of the bone, but the ornament would tend to mask the suture, and the bone was found by the writer in one specimen of *Canobius ramsayi* Traquair (fig. 43).

A most remarkable feature is the degree of resemblance in cheek pattern between *Haplolepis corrugata* and certain Perleididae, between *H. tuberculata* and *Peltopleurus lissocephalus*, and between *H. ovoidea* and a generalized holostean (fig. 44). In the first-named group, the triangular maxilla and preopercular are quite closely similar, and in the last the shape of the maxilla of *H. ovoidea* suggests that the freeing of that bone and the transformation of the preopercular could easily be accomplished from such a condition. It is of course not suggested that these species of *Haplolepis* are ancestral to Perleididae, Holostei, etc., but the occurrence of such remarkable developments in closely allied fishes indicates forcibly that changes of a kind and degree necessary for the production of holostean and subholostean characters might happen rather quickly in certain "palaeoniscoid" groups, and, moreover, that apparently remarkably different patterns of cheek bones might be produced from a narrowly defined but unstable stock of fishes.

SNOUT

A most important feature of *Haplolepis* and *Pyritocephalus* is the absence of the overhanging rostrum characteristic of most "palaeoniscids." This is correlated with a marked change in the shape of the postrostral bone; in "normal palaeoniscid" snouts the bone is strongly convex and forms the most curved part of the rostral surface. The genera *Rhadinichthys-Mesopoma-Canobius-Haplolepis* form a regular series showing this change in form of the bone (fig. 45). The presence of the highly convex form of the postrostral is a major feature distinguishing the "palaeoniscid" snout from that of any "holostean" or most "subholosteans," but a holostean-like modification has been described previously in the Lower Permian *Aeduella* (Westoll, 1937b), and is characteristic also of the "platysomids" in general.

The change in the dermal bones is, how-

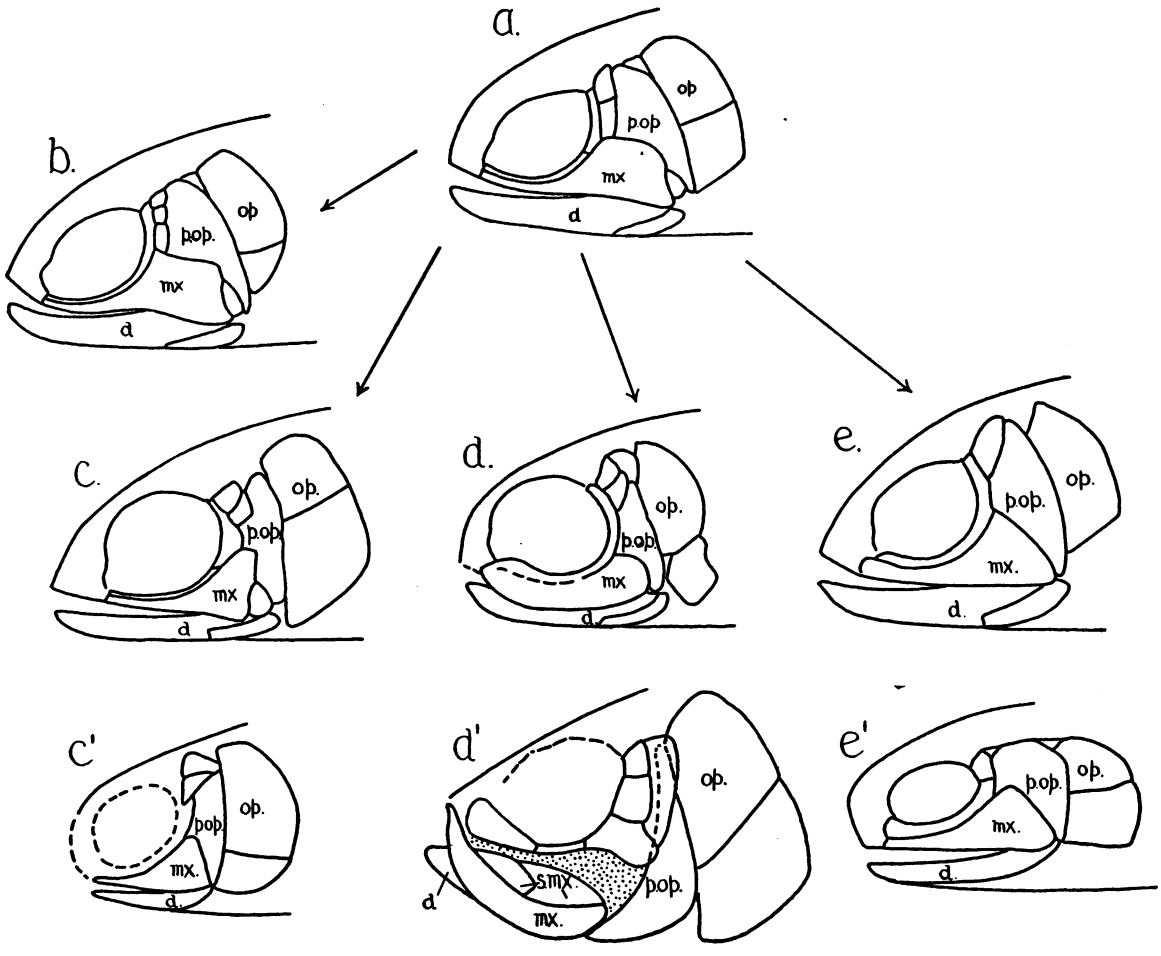


FIG. 44. Derivation of different haplolepid cheek patterns from X, with examples of convergent structure in later Actinopterygii. a, Cheek of X; b, *Pyritocephalus sculptus* Fritsch; c, *H.* (*Parahaplolepis*) *tuberculata* (Newberry); d, *H.* (*H.*) *ovoidea* (Newberry); e, *H.* (*H.*) *corrugata* (Newberry); c^1, *Peltopleurus lissocephalus* Brough (after Brough); d^1, *Leptolepis bronni* Agassiz (modified after Rayner); e^1, *Perleidus madagascariensis* (after Piveteau).

ever, less unexpected than the change in position of the nostrils (fig. 46). Typically the palaeoniscids seem to have had two pairs of nostrils, one indicated by a paired opening between the postrostral and each nasal, the more lateral pair by a notch in the orbital border of each nasal or by a groove on the inner side of that bone (e.g., *Palaeoniscus*, Westoll *in* Aldinger, 1937, p. 95, fig. 25; *Pygopterus*, *op. cit.*, p. 135, fig. 94; *Cornuboniscus*, White, 1939, fig. 1). In most *Haplolepis* (e.g., *H. ovoidea*, *H. tuberculata*) the more mesial pair is found between the nasals and premaxillaries (rostrals) and the more lateral pair probably opened immediately lateral to the nasals; in *Pyritocephalus* the mesial pair seems to have been surrounded, in some individuals, entirely by the nasals. In *Aeduella* (Westoll, 1937b) the shape of the postrostral shows that the palaeoniscoid arrangement has also been modified, perhaps similarly, but details are unknown. There is a very remarkable resemblance between these changes and those which must have occurred during the evolution of the holostean and subholostean fishes. Piveteau (1934, p. 74, fig. 51) has already commented on the structural changes of the snout region

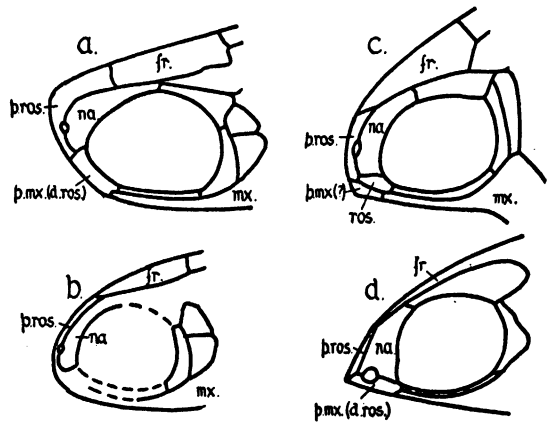


FIG. 45. Snout regions of a, *Rhadinichthys canobiensis* Traquair; b, *Mesopoma pulchellum* Traquair; c, *Canobius ramsayi* Traquair (all after Moy-Thomas and Dyne) compared with d, *H.* (*Parahaplolepis*) *tuberculata* (Newberry), to show progressive loss of rostral prominence. Too much reliance cannot be placed on the exact outlines, since the rostral region is normally very difficult to reconstruct.

in many Triassic forms. *Haplolepis* and *Pyritocephalus* actually show a condition further removed from the presumably primitive "palaeoniscid" arrangement than that

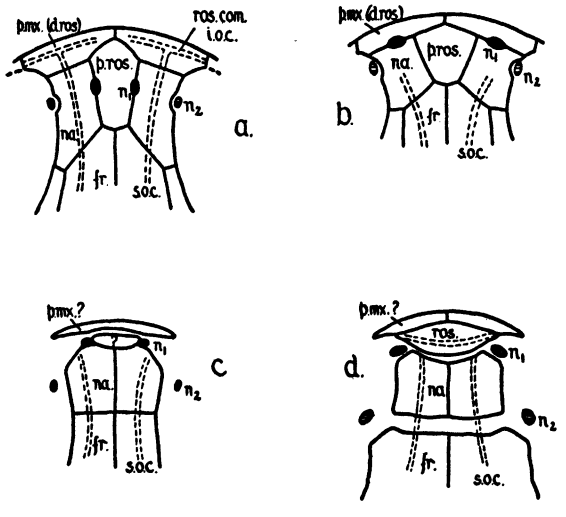


FIG. 46. Diagram to show relation of anterior (n_1) and posterior (n_2) nostril openings to snout bones in a, a primitive member of the *Rhadinichthys-Canobius* group; b, *H.* (*Parahaplolepis*) *tuberculata* (Newberry); c, a parasemionotid (adapted from Piveteau); d, *Amia*.

of *Perleidus* and of almost all other "advanced" Triassic groups and resemble very greatly the parasemionotids. Without a much more certain knowledge of the course of the more anterior part of the supraorbital laterosensory canal a detailed comparison with "holostean" fishes such as *Amia* is impossible. It is useful, however, to consider this change in relations of the nasal openings with reference to the structure of the snout as a whole.

In "palaeoniscids" of normal type the two nasal openings on each side were separated by the nasal and generally speaking were in front of, and a little below, the middle of the orbit as defined by the dermal bones. In *Haplolepis* and *Pyritocephalus* and in many post-Palaeozoic derivatives of "palaeoniscids" (*sensu lato*), much the same can be said, and it is most likely that the loss of the projecting rostrum and the other changes in the snout have come about by the same process —the reduction of the "underhung" portion of the snout and the upward movement of the premaxillary region. It is possible to link this change with another that occurred simultaneously in several groups showing the same loss of the rostrum (e.g., *Haplolepis* and *Pyritocephalus*, *Aeduella*, platysomids, parasemionotids, Holostei): that is the change in attitude of the maxilla, palate, and suspensorium.

These changes can be correlated by the simple operations shown in figure 47; the suspensorium becomes more vertical and may actually be forwardly directed, and the palate and maxilla are tilted up anteriorly. The "palaeoniscid" palate has been described by Watson (1925, 1928); the anterior part, underneath and in front of the eye, is remarkably deep and arched upwards towards the mid-line, and the course of the parasphenoid was across the lower part of the orbit and directed towards the snout slightly below the rostral prominence. In *Haplolepis* the palate was certainly deeper posteriorly than in a "normal" palaeoniscid of similar size and almost certainly much shallower anteriorly. The diagrams show how it would be possible to derive a holostean type of cheek, snout, and palate from a palaeoniscid one by this comparatively simple form change, affecting only the angle of the suspensorium and the

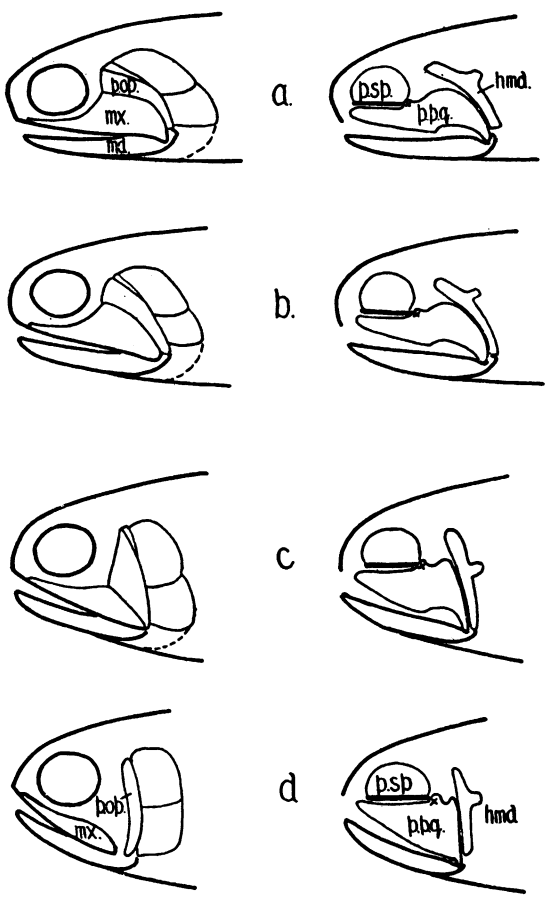


FIG. 47. Diagram to show interrelation of three progressively changing characters in the evolution of a holostean structure: the loss of the overhanging rostral prominence, the change in attitude of the suspensorium, and the change in proportions of the palate.

reduction of the ventral parts of the snout.

If such a suggestion could be confirmed it might be possible to make more definite statements about the evolution of the snout region, and particularly the "premaxillaries," of the higher Actinopterygii; clearly, a great change of mechanical functions in the snout region would be indicated. The problem concerning the true nature of the premaxillary bone of Holostei and the "higher" Actinopterygii has already been raised and discussed by Westoll (1937b, pp. 569–571). More recently, important new material has been described by White (1939) and Moy-Thomas and Dyne (1938). Four types of "palaeoniscoids" may now be identified on the basis of the bones which form the outer arcade of the upper jaws.

A. A group with the maxillaries meeting in the mid-line, with canal-bearing rostral bones above them, e.g., *Cornuboniscus* (White, 1939).

B. A group in which the maxillaries either do not meet in the mid-line or are covered externally by the rostrals, which bear teeth, e.g., *Palaeoniscus* (Westoll, *in* Aldinger, 1937), *Elonichthys*, *Rhadinichthys*, *Canobius* (Moy-Thomas and Dyne, 1938), and many others.

C. Certain fishes in which this retreat of the maxillaries is even more pronounced, so that teeth are also found on the most anterior infraorbital, e.g., *Glaucolepis* (Nielsen, 1936).

D. A problematical group with a "premaxillary" separate from both maxillary and rostrals. Many palaeoniscids were originally described with this structure, but examination has shown that they are referable to one of the other groups. A premaxillary of this type is doubtfully distinct in *Cheirolepis*, but the only well-documented cases so far described are the curious triangular median tooth-bearing bone of *Canobius ramsayi* Traquair (Moy-Thomas and Dyne, 1938, figs. 1, 40, p. 477) and the somewhat similar element of the aberrant Triassic form *Birgeria* (Stensiö, 1932, p. 113).

Haplolepis and *Pyritocephalus* belong to the second group. The previous analysis (Westoll, 1937b, p. 569) is thus largely confirmed, but the exact mode of derivation of the "premaxillary" of, say, *Amia* (where it is quite distinct from a rostral series) remains quite uncertain, but that this bone is homologous with the tetrapod premaxillary seems quite impossible.

OPERCULAR APPARATUS

In "normal palaeoniscids" the opercular apparatus consists of paired operculars (with or without antoperculars) and suboperculars, and a comparatively large number of branchiostegal rays or lateral gulars on each side, with an anterior median gular that is comparatively small. In *Haplolepis* and *Pyritocephalus*, on the other hand, the number of lateral gulars or branchiostegal rays is very

much smaller, and in many cases there is a much enlarged median gular. Moreover, in all species in which the dermal bones of the opercular folds are well known there is a marked division which may even be an actual discontinuity between the subopercular and the gulars, and the normal palaeoniscid pattern of branchiostegals or lateral gulars following in series after the subopercular is not found in any member of the group. This feature is a sharp distinction between *Haplolepis* and *Pyritocephalus* and any palaeoniscids so far described; the arrangement of the gulars in all known members of these two genera is so similar that it is probable that their immediate common ancestors had a similar pattern.

Several "palaeoniscids" have much reduced gulars; *Canobius* (Moy-Thomas and Dyne, 1938, figs. 1, 4), *Rhadinoniscus* (White, 1937, p. 418) and *Aeduella* (Westoll, 1937b) may be instanced. In each case the suspensorium is more nearly vertical than in "normal palaeoniscids," and there is little doubt that the reduction in number of the gulars is directly correlated with this forward movement of the quadrate. The similarity in the basic pattern of the gulars of *Haplolepis* (both subgenera) and *Pyritocephalus* suggests strongly that these fishes diverged from a common ancestor in which the forward movement of the quadrate was already well advanced. The structure of the cheeks shows just as clearly that there has been much more forward movement since the time of divergence.

The great reduction in the number of dermal bones of the opercular fold found in certain groups of palaeoniscoid derivatives (e.g., Catopteridae, see Brough, 1931, etc.) is also associated with a forward movement of the quadrate. One of these groups (Catopteridae) is interesting because the branchiostegal rays (gulars) seem to be completely missing with the occasional exception of the most dorsal member; at least the opercular and subopercular are separate from ventral members of the series. A separation of the bones of the opercular series into a dorsal and a ventral group is found also in *Holoptychius* (Westoll, 1937a, fig. 1c, p. 364; 1937c, fig. 9c), the coelacanths, the saurichthyids, and in *Polypterus* (which has a most remarkable resemblance to coelacanths in many features). It is not clear whether or not all these cases can be ascribed to similar causes operating in each group. The *Holoptychius* cheek is distinctly longer, with a more oblique suspensorium, than the cheek in the more "normal" osteolepids, while in each of the other groups it is much shorter than in the presumed "normal" ancestors. Although a single mechanical basis for this condition of the opercular system seems to be made unlikely by these facts, one functional aspect seems to be of interest. Certain groups of these fishes may have lived generally in comparatively poorly oxygenated waters. It is possible that modification of the opercular apparatus may be due to the presence of accessory respiratory structures in the pharyngeal or branchial region, either external gills or respiratory diverticula in which bubbles of air could be used. Many recent fishes living in poorly oxygenated waters have such structures (see Carter and Beadle, 1931). This matter will be considered in a later section.

SHOULDER GIRDLE[1]

The most important comparative features of the dermal shoulder girdle are the presence of a lateral-line groove on the cleithrum and the peculiar median "interclavicular scale" of *Pyritocephalus*. The lateral-line groove (the anterior end of the ventral lateral line) is apparently the first to be recorded in an actinopterygian. The "interclavicular scale" is also apparently unique in actinopterygians. It has almost certainly no comparative value and must be regarded as a chance resemblance to the characteristic amphibian interclavicles. It may be significant that enlarged median scales occur between the posterior parts of the clavicles in some species of *Haplolepis*, but there is no evidence to show how a body scale could be "inserted" between the clavicles.

BODY FORM

The excellent preservation of the squamation in *Haplolepis* and *Pyritocephalus* has allowed the clear recognition of a flattened

[1] See also discussion of pectoral fins, page 83.

ventral region in the body. A pair of ridges running through the pectoral and pelvic fin bases and converging in front of the anal fin separated this flattened venter from the flanks. The clavicles and gulars continued this flattened region forwards.

In most palaeoniscids the squamation is much disturbed ventrally, and there is little evidence of a similar flattened venter. In *Pyritocephalus* and *Haplolepis* the change is marked by the different directions of the scale rows dorsally and ventromesially of each ridge. Similar conditions have been described in *Acropholis stensioei* by Aldinger (1937, pp. 32, 37); the "lateralen Bauchkanten" of his descriptions are not shown in his reconstruction (fig. 4), which also gives no indication of the change of direction of the scale rows shown in his plate 5 and plate 8, figure 1. An examination by the writer of several genera has shown that there is a more or less pronounced break in the direction of the anterior scale rows in *Palaeoniscus*, *Rhadinichthys alberti*, and certain Upper Carboniferous *Elonichthys*. It is quite likely, therefore, that the flattened venter was a common character of palaeoniscids, where it was probably correlated with the keel-like nature of the paired fins. This matter has already been mentioned in a discussion of the shape of the palaeoniscid cleithrum (Watson, 1925, p. 825).

SQUAMATION

The scales of all species of *Haplolepis* and *Pyritocephalus* are for the most part quite smooth, with only a few tiny pores, the openings of the system of vascular canals within the scales. In the few instances where ornament is present it is of two kinds: (a) a series of aligned pores or grooves, directed roughly parallel to the anteroposterior axis of the fish; and (b) sharp grooves running parallel to, and normally restricted to the neighborhood of, the anterior and ventral margins.

The author has been able to make very few microscopical preparations of the scales of Haplolepidae; the only satisfactory slices are from *Haplolepis* (*Parahaplolepis*) *tuberculata* Newberry, A.M.N.H. No. 2150. The scales are always extremely thin, and films and small crystals of pyrites affect many individuals.

The histology of the scales of palaeoniscoids was studied by Williamson, later by Goodrich, and recently in considerable detail by Aldinger (1937). Three main elements are present: a basal (inner) layer of laminated compact bone or isopedin, an external layer of shiny ganoine (often discontinuous, forming ribs, etc.), and an intermediate layer of dentine tissue known as cosmine (this may occasionally be replaced later by osteodentine). Aldinger has used the precise details of the scale histology and particularly of the arrangement of vascular canals in the cosmine layer as an important factor in an attempted detailed classification of the palaeoniscoids. It is now known that, in general, growth of each scale takes place apparently in stages; a new layer of bone is formed internally, a new strip of cosmine is added to the margin of the cosmine layer, and a new layer of ganoine forms externally. The external ganoine may be pierced by pores or separated by areas of cosmine, in which case new cosmine growth also takes place around ascending vascular canals, which pass up through the pores, etc., and presumably supplied the epidermis and other very superficial tissues.

These structures can be seen very well in the sections of *H. tuberculata*. The bone layer or isopedin is remarkably thin, and the ganoine layer is quite thin, as compared with the well-developed cosmine layer. The isopedin is laminated, is traversed by a very few ascending canals of wide lumen, and shows poorly preserved remains of bone cells.

Occasional indications of bundles of Sharpey's fibers were found. The cosmine is clearly composed of bands which may be concentric strips anteriorly and ventrally, but are longitudinal in the middle of the scale (fig. 48b); these are usually sharply delimited, and each strip is apparently traversed longitudinally by a large canal from which the cosmine tubules radiate outwards. There may also be important cross canals. The cosmine is often clearly banded parallel to the external surface. There is evidence that resorption of preexisting tissues (bone, cosmine, and ganoine) preceded the deposition of new tissues. The external ganoine, which is unusually thin, shows few details, but its deposition in periodic layers

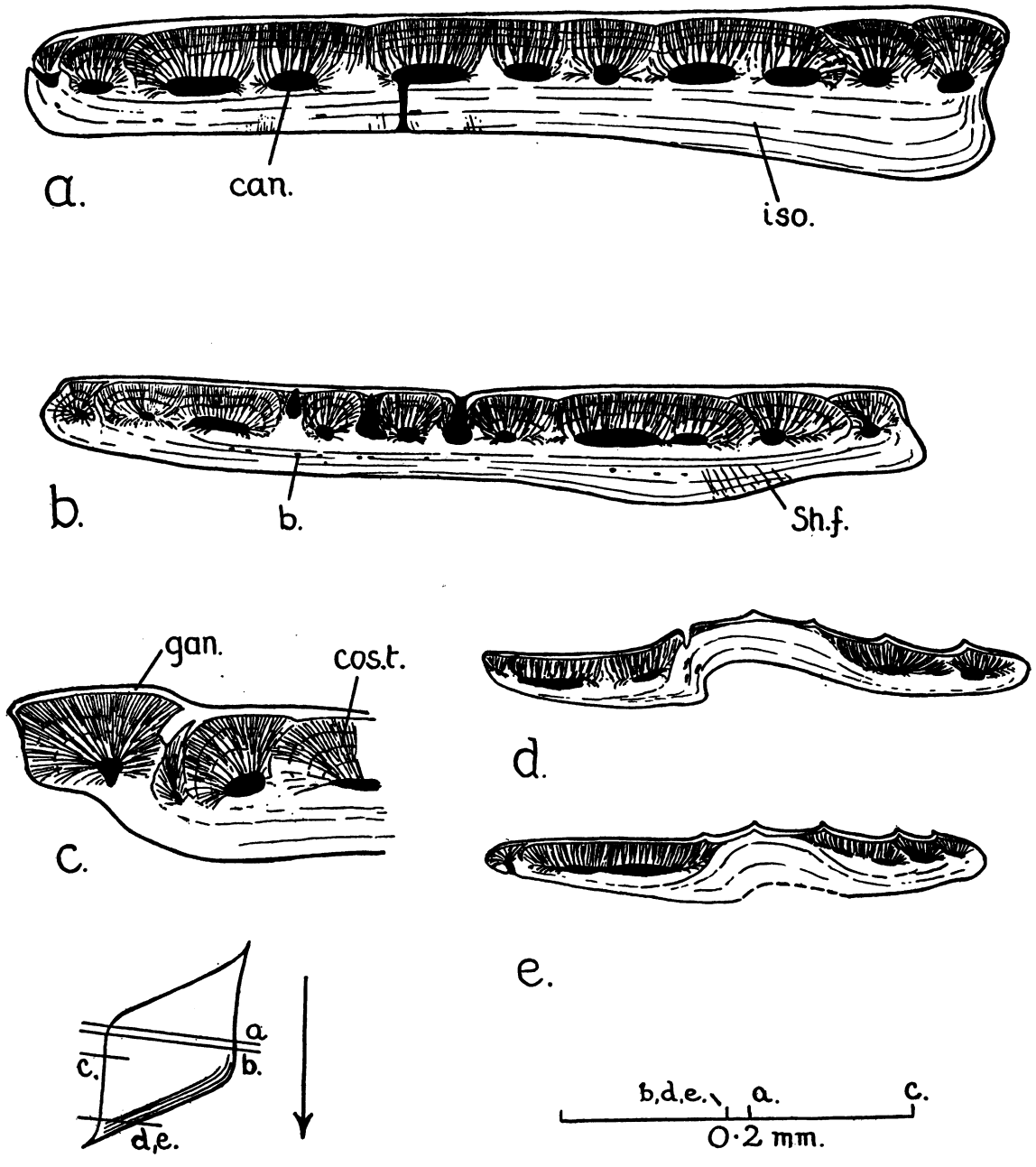


FIG. 48. Scale histology of *H.* (*Parahaplolepis*) *tuberculata* (Newberry) from sections cut approximately dorsoventrally through squamation of A.M.N.H. No. 2150. The scale consists of a remarkably thin layer of laminated isopedin (iso), including bone cells (b); a middle layer of cosmine (cos) laid down in (partly concentric) strips, each strip having wide vascular canals (can) from which cosmine tubules (cos.t.) radiate outwards, each cosmine unit showing a marked layered effect; and an external layer of ganoine (gan), laid down as very thin lamellae when each cosmine strip was formed. a, Semidiagrammatic, composite; b, through rather posterior part of scale, showing several surface pores and the longitudinal cosmine ridges (Sh.f = traces of Sharpey's fibers); c, detail to show relationships of newly formed to older cosmine and ganoine; d, e, sections through anterodorsal corner of scale, showing thickening of isopedin layer and the nature of the sharp surface ridges. Inset is a diagram to show approximate position of each section of a scale; arrow points anteriorly.

is clearly shown. No lamination can be traced in the ganoine.

Occasional scale sections show very unusual features (fig. 48d, e). These sections are apparently vertical sections through the anterodorsal corner of the scale and show a remarkable thickening of the isopedin layer, the cosmine being almost entirely reduced. It is probable that the thickened isopedin marks the base of the slight anterodorsal projection which is the sole special link between scales of the same vertical row in the absence of the normal palaeoniscoid peg and socket. It cannot represent lateral-line structures since several occur in the same section of an undisturbed squamation. The sections also demonstrate the nature of the sharp ridge-and-terrace ornament parallel to the anterior scale margin. They are caused by sharp ridges of ganoine, which in appropriate sections (fig. 48d) can be seen to be related to the bands of new growth of cosmine.

While the scales of *Haplolepis* are of normal palaeoniscoid histology, they are quite remarkable in the proportionate thinness of the isopedin and the ganoine compared with the cosmine, and can be compared with few of the forms figured by Aldinger. Only in *Amblypterus* are somewhat similar conditions known, and there the details do not very closely correspond. It is unfortunate that practically nothing is known of the scale histology of *Rhadinichthys*, *Mesopoma*, and *Canobius*. It may well be that in those palaeoniscoids that remain small the proportions of the elements which build up the scale are somewhat different from those which are found in larger fishes, such as most of those figured by Aldinger.

It may, therefore, be accepted that the series of aligned pores or grooves which are found on some scales were related to ascendant vascular canals between the strips of cosmine (fig. 48b), and that the sharp grooves found near, and parallel to, the anterior and ventral margins of the scales in some species may be connected with the concentric arrangement of the strips of cosmine, which affects the overlying ganoine. It is important that certain species of *Rhadinichthys*, *Mesopoma*, and *Canobius* have scales ornamented in much the same fashion as in *Haplolepis* and *Pyritocephalus*. Certain species of *Rhadinichthys* (e.g., *Rh. macconochii* Traquair) have the anterior and ventral grooves very well developed on the anterior flank scales. Without a very much more detailed knowledge of the fine structure of the scales of other palaeoniscids with smooth scales it would be dangerous to place too much reliance on these resemblances, but the facts are at least in harmony with the view that *Haplolepis* and *Pyritocephalus* are descended from *Rhadinichthys* through *Mesopoma*-like and *Canobius*-like forms. The evidence of relationship given by the scale counts will be considered later.

The presence of very deep lateral-line scales in the anterior flank is highly characteristic of most species of *Haplolepis*, but *Pyritocephalus* shows more normal conditions. This variability is proof that deepened flank scales are not in themselves a satisfactory character on which to base discussions on taxonomic relationship (cf., Westoll, 1937b, p. 575, footnote). Certain species of *Haplolepis* (*H. ovoidea*, *H. corrugata*) have very deep anterior lateral-line scales, with the lateral-line grooves and pores near the superior margin, passing back gradually into almost equilateral scales with the lateral-line traces near the middle. In *H. tuberculata*, on the other hand, the lateral-line scales of the anterior flank (about the first 16 rows) are very deep indeed and appear to correspond to two series of scales in more posterior rows. There is no evidence of late fusion of scales to provide these elongated plates, but the possibility of earlier fusion cannot be ignored. There seem to be two possibilities to account for the presence of these deep scales: (a) each is the product of fusion of the lateral-line scale or its rudiment with that next beneath; or (b) each is the result of more vigorous growth of a single-scale rudiment, probably of the lateral-line scale.

Neave (1936) concluded, from his studies of salmonid scales, that the pattern of the scale rows is dependent on growth from centers underlying the lateral-line organs. From these, strands of tissue extend dorsally and ventrally, and the individual scale pockets arise from localized condensations in these strands. The subsidiary dorsal centers mentioned by Neave may possibly be related to remnants of the dorsal lateral line. These

observations are in agreement with the conditions in young specimens of *Brookvalia* (Wade, 1935, p. 27) and other fishes, where the body squamation spreads during ontogeny from the lateral line. It is possible, therefore, that the conditions set out by Neave may apply generally or widely among Actinopterygii. In the case of *Haplolepis tuberculata* and similar fishes, the part of each strand that would be expected to give rise to two scales has in fact produced only one, but whether by amalgamation or obliteration of rudiments it is impossible to say.

The fact that in other species of *Haplolepis* the anterior lateral-line scales are also deep suggests strongly that these scales (which are usually first formed on the flanks during ontogeny) may have a tendency to enlarge and may have grown so rapidly in early stages that the scales which should have appeared immediately below were not able to develop as separate entities before their territory was invaded.

Similar deep scales along the lateral line are found in other forms, e.g., *Rhadinichthys hancocki* (Atthey) (Traquair, 1911, p. 147, pl. 33, figs. 1, 2), *Phanerorhynchus* (Gill, 1923), and *Eurylepidoides socialis* Case (1935), among palaeoniscoids, and *Pholidopleurus*, *Luganoia* (Brough, 1939, p. 40), *Australosomus*, *Saurichthys*, and other forms among the Triassic actinopterygians. The conditions in *Luganoia* are particularly close. Aldinger (1937, p. 344) has suggested that such forms are closely related, but this is highly questionable. It is much more likely that the deep flank squamation may eventually be shown to have some functional significance in the control of rigidity in the swimming fish.

The very thin scales of Haplolepidae are not often seen from the mesial aspect, but the writer has not found the normal palaeoniscoid peg-and-socket articulation between scales of the same vertical row. The anterodorsal corner in most flank scales is drawn out and lies along the anteroventral margin of the next scale above; this process is less well marked in the dorsal region. It is this process that is apparently responsible for the peculiar conditions noted in some thin sections (cf. fig. 48d, e). The loss of the peg-and-socket articulation in many groups of higher Actinopterygii is noteworthy; here again the Haplolepidae show an interesting parallel development.

LATERAL LINES OF THE BODY

Haplolepis and *Pyritocephalus* are of considerable interest because they have provided the first known examples of the presence of three paired series of lateral-line organs (with the additional paired accessory lateral line) in actinopterygian fishes. Dorsal and accessory lateral lines have long been known in living fishes (e.g., in *Amia*, Allis, 1889) and have been described in part in fossil material (in *Aeduella*, Westoll, 1937b). The discovery of a ventral lateral line brings the Actinopterygii into line with Dipnoi, Crossopterygii, Amphibia, etc., and provides striking evidence in favor of the suggestion that three pairs of lateral lines are to be regarded as a generalized feature of primitive aquatic vertebrates.

The nature of the latero-sensory lines is important. Along the flanks are traces of the "main lateral line." This consists of a presumably enclosed lateral-line opening by occasional lunate pores, and a surface series of pit-line grooves. The enclosed canal is apparently the true main lateral line, the pit lines representing the accessory lateral line of *Amia* (Allis, 1889, pl. 30, figs. 1–3; pl. 31, figs. 4–6; pl. 32, figs. 8–9). Somewhat similar conditions are recorded by Säve-Söderbergh in *Osteolepis* and seem to exist in several other fossil fishes (e.g., of those described by Brough, 1939, *Meridensia meridensis*, *Placopleurus besanensis*, and *Eoeugnathus megalepis*). In his description of *Polypterus*, Allis (1922, p. 251, pl. 3, fig. 1) described conditions not unlike those in Haplolepidae. The main lateral line in external view appears as a series of longitudinal grooves, and slightly dorsal to these are short, irregular, transverse pit-line grooves representing apparently the accessory lateral line. The dorsal lateral line also consists of pit-line grooves.

The dorsal lateral line of Haplolepidae is usually an enclosed canal opening by pores, but in some species it passes into the pit-line condition near the dorsal fin. The ventral lateral line is entirely in the pit-line condition.

It is deduced from the study of the latero-sensory system of the cranium that "enclosed" latero-sensory canals opening by tubules may become degenerate in phylogeny so that they are replaced by pit lines which merely leave grooves on the surface layers of the bones and may altogether disappear. The ventral lateral line, entirely represented by pit-line grooves, is thus probably more "degenerate" than the dorsal lateral line. The form of the ventral lateral line, curling up round the front of the pectoral fin, can be compared with that in certain Amphibia (Escher, 1925, figs. 10, 22, etc.).

Graham-Smith (1936) has discussed the lateral lines of fishes with reference to their relation to the fins. The conditions in *Haplolepis* and *Pyritocephalus* in this respect are interesting; the main lateral line approaches the lower border of the body lobe and in some species is continued posterodorsally along the lower margin of the body lobe. This arrangement is found also in *Cornuboniscus budensis* (White, 1939) and is characteristic of the most generalized fin in Graham-Smith's scheme (that of Acanthodii), though it is not shown in his figures of fossil Actinopterygii (*ibid.*, figs. 28–30, 32, 33). It may be mentioned for completeness that a similar extension is clearly marked in some *Osteolepis* (Crossopterygii) in the author's possession. The courses in Haplolepidae of the ventral lateral line (mesial to the paired fins, and onto the enlarged scales in front of the anal) and the dorsal line (rising from the main lateral line to the dorsal fin) are in full agreement with conditions in other groups of fishes. If the terminology of Graham-Smith be applied, the ventral lobe of the tail fin, though ill defined, is the caudal fin (*sensu stricto*), the remainder of the fin being the ventral longitudinal fin. The dorsal longitudinal fin is represented only by the dorsal ridge scales, as there is no epichordal lobe.

STRUCTURE OF FINS

Perhaps the most characteristic feature of *Haplolepis* and *Pyritocephalus* is the nature of the fin webs, which are composed of few stout rays which are segmented, but only bifurcated, if at all, once (in the distal parts). In these features they differ notably from all palaeoniscids hitherto described (though *Phanerorhynchus* shows certain resemblances). The reduction in number of fin rays is a feature very characteristic of a number of holostean and subholostean groups, e.g., certain Perleididae, Semionotidae, etc. The type of ray in the Carboniferous genera indeed specifically recalls that seen in the perleidid *Manlietta* (Wade, 1935, p. 58, pl. 9, fig. 1).

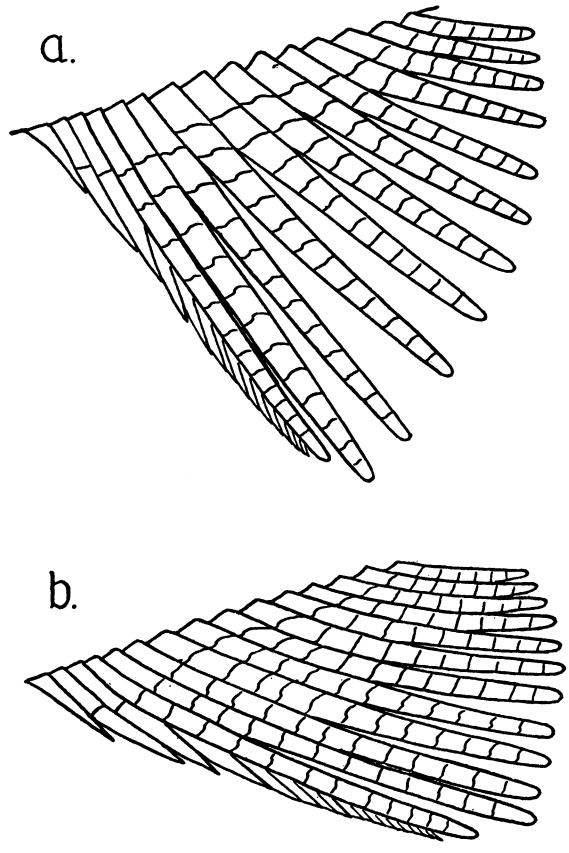


FIG. 49. Fin rays of a haplolepid median fin in "erect" and "collapsed" conditions.

The dermal fin rays in *Haplolepis* and *Pyritocephalus* present one important feature. The anterior portion of the proximal part of each ray is rather sharply marked off from the posterior and is considerably beveled. This anterior portion of the lepidotrich also bears a peculiar "ornament" of ridges running obliquely to the axis of the fin ray. It is suggested that the detailed structure of the

fins is as follows: the lepidotrichia are a "paired" series of ossifications lying along opposite faces of each endoskeletal fin ray. Each lepidotrich overlapped the beveled anterior part of that immediately behind when the fin was collapsed. It is quite possible that the "ornament" on the overlapped area is some indication of the attachment of the fin membrane. The general impression derived from this comparison is that the fins of *Haplolepis* and *Pyritocephalus* were capable of much greater variation in effective area as a result of relative movement of the rays than those of normal palaeoniscids, and in this they resemble fins of many groups of "higher" fishes (fig. 49).

The fin fulcra deserve brief comment. There is good reason to believe that they (and the dorsal ridge scales of the tail) are paired in origin, and their relations to one another, to the somewhat enlarged scales in front of the fin insertions, and to the lepidotrichia of the fins are such as to show very strikingly that the fulcra and lepidotrichia are only modified scales, and that the fulcra should be regarded as parts of the system of lepidotrichia, greatly modified at the leading edge or "cut-water" of each fin (cf. White, 1927, pp. 262, 285, figs. 10–12).

There is clear indication in *Pyritocephalus* and certain species of *Haplolepis* that the fulcra are not present distally. This may be an early stage in the reduction of fulcra, a process again very characteristic of certain groups of "higher" fishes.

The tail fin shows little sign of reduction of the body lobe, which is such a marked feature of Triassic palaeoniscid derivatives.[1] The relations of the fin to the main lateral line have been mentioned above. The peculiar shape of the fin web is very characteristic of these two genera; its functional significance will be analyzed later.

POSITION OF FINS

In both *Haplolepis* and *Pyritocephalus* the position and carriage of the paired fins are shown only in few specimens, but there is good evidence that the fins had fairly extended bases, from which the rays gradually diverged. The paired fins are inserted approximately along the ventrolateral ridges which bound the flattened venter, and in both pectorals and pelvics the anterior insertion of the fin is very slightly higher than the posterior. The pectoral fins have narrow scale-covered lobes.

Traquair's admirable reconstructions of palaeoniscids are well known, and most modern restorations follow the same convention in displaying the fins. The pectoral fin is shown in these drawings as though inserted in quite a different way, with the leading edge (with fulcra) facing downwards and forwards, and the line of insertion of the rays rising more or less steeply up the flank from the anterior insertion. This method is, of course, very useful in showing the character of the fin in a reconstruction, but there is no evidence that this position was actually characteristic of the living fishes. The writer has made a careful examination of favorably preserved material of *Elonichthys*, *Palaeoniscus*, and *Rhadinichthys* of various species and finds that the pectoral fins are inserted in the same manner as those of *Haplolepis* and *Pyritocephalus*. Watson (1925) has shown that the long-based pectoral fin with a nearly horizontal insertion is to be considered as a primitive feature of the Actinopterygii. He has figured (*ibid.*, fig. 4) a shoulder girdle of *Amblypterus latus* in which the almost horizontal attitude of the glenoid surface is well displayed.

Aldinger (1937, figs. 27, 44, 84, pp. 108, 161, 283) has figured developments of the primary shoulder girdle in *Palaeoniscus freieslebeni*, *Pygopterus nielseni*, and *Acrorhabdus bertili*, and in all of these he finds a more or less vertical "margo radialis" against which he assumes the fin radials articulated, and in the case of *Pygopterus nielseni* he indicates a fossa lying above the margo radialis. This he describes as "die Fossa glenoidalis, in welcher vermutlich der erste Strahl der Pectoralflosse mit dem Schultergürtel gelenkt" (p. 163). This seems to imply that the preaxial margin of the fin was tilted up so that it articulated with this fossa glenoidalis, but this conclusion would make quite untenable Aldinger's description (in legend of fig. 44, p. 162) of the cavity, below the level

[1] In well-preserved caudal lobes the number of scale rows across the distal part is, however, greatly reduced.

of the fossa glenoidalis, as "Hohlraum zwischen Cleithrum und primärem Gürtel für die dorsale Flossenmusculatur." In fact, there is no evidence to suggest such a remarkable position of the pectoral fins in the fishes described by Aldinger, and it must be concluded that the relation of the fins to the endoskeleton of the shoulder girdle requires a very full investigation. In any case, Aldinger's reconstruction of the endoskeleton suggests that the "first ray" (presumably the most anterior, or preaxial) articulated with the shoulder girdle above and behind the other rays, while his reconstructions of the body form of all the palaeoniscids described by him show the pectoral fins held in an equally unlikely position with the leading edge inserted anteroventrally to the posterior margin.

Comparison with other actinopterygian shoulder girdles suggests that Aldinger's identifications of structures are not correct. The "fossa glenoidalis" and "margo radialis" of his descriptions seem to be part of the supraglenoid buttress of Romer's terminology (1924), and the "processus radialis" (Aldinger, 1937, fig. 27) is the most important part of the glenoid surface, as is shown not only by comparison with living forms but actually by the fossil evidence figured by Aldinger himself (fig. 84, pl. 24, fig. 2, etc.). It is clear from the study of his figures alone that the pectoral fin was carried low on the flank in palaeoniscoids, the leading edge slightly raised (cf. in particular *Acropholis stensioei*, pl. 5, pl. 8, fig. 2). The illustrations of *Palaeoniscus freieslebeni* (pl. 24, fig. 2) show the right pectoral fin turned downwards (cf. fig. 50c of this work) but still probably in natural relationship with its shoulder girdle. It seems quite certain that the dorsomedial fin musculature had its origin along the "margo radialis" and "processus glenoidalis" and on the mesial face of the primary shoulder girdle lateral to the mesocoracoid arch, and was inserted on the dorsal face of the radials of the laterally directed pectoral fins. The ventrolateral musculature probably passed back to the fin through the cavity between primary and dermal shoulder girdles determined by Aldinger as "für die dorsale Flossenmuskulatur."

This problem has also been reviewed by White (1939) who described a vertically held fin in *Cornuboniscus budensis*. In his account the preaxial margin is shown to lie above the postaxial, so that the scale-covered lobe met the body along an almost vertical line behind the cleithrum. A similar paddle-like fin has been figured by Moy-Thomas (1934, fig. 4) in *Tarrasius* and resembles that of living *Polypterus*. The attitude of the pectoral fin of *Aeduella*, which has also a scale-covered lobe, was probably wrongly restored by Westoll (1937b, fig. 1).

In the case of *Polypterus* and *Tarrasius* there is good reason for the shape of the pectorals, but in *Aeduella* and *Cornuboniscus* it is most unlikely that the fish could ever have functioned with the scale-covered lobe held in the positions in which they are restored by Westoll and White, since the powerful upward drive of the heterocercal tail would not be capable of being counterbalanced. The writer has decided, on reconsidering the evidence, that the pectoral fin in *Aeduella* was probably held with the scale-covered lobe almost horizontal, the anterior edge perhaps slightly raised. White realized the difficulties in the way of accepting his reconstruction of the posture of the fin in *Cornuboniscus* but suggested that this fish provides a case in which "form preceded function," and that the "development was probably orthogenetic" (1939, p. 57). In view of the extremely close correlation between form and function in the fins of fishes, this explanation seems highly unlikely. The writer has been able to study a number of paratypes of *C. budensis* belonging to the British Museum (Natural History), thanks to the friendly kindness of Dr. E. I. White. Examination of this material has suggested to the writer an alternative explanation. The fishes are preserved in small concretionary nodules and are often somewhat disturbed, so that maceration must have been somewhat advanced before entombment. The pectoral fin is very variously preserved. Out of six specimens studied (five in counterpart), two pectorals were too disturbed for detailed comparison; three fins are in the position figured by White; two are turned up on the flank so that the upwardly directed margin of the fin is almost parallel to the dorsal shank of the cleithrum; three are so preserved that the fin cannot have been

applied to the flank; and one shows the fin web turned down so that it lies apparently in the position favored in the older "orthodox" reconstructions of palaeoniscoid pectoral fins. It seems rather probable, therefore, that the fin was in life held out from the body and that the conditions found in the fossils are due to post-mortem changes in the body form. It is interesting that in B.M.N.H. No. P.20986 the (right) pelvic fin is also folded up against the flank. A cast of B.M.N.H. No. P.20988 apparently offers confirmatory evidence. There is a distinct ridge lying behind the cleithrum which corresponds almost exactly to the glenoid surface in a specimen of *Amblypterus* described by Watson (1925, fig. 4, pp. 824–826). This ridge is slightly more inclined to the horizontal than in *Amblypterus*. The actual conditions visible in the fossils may be explained in a diagram to show the effects of different crushing (fig. 50). In passing, it may be mentioned that the following specimens of *C. budensis* appear to show lateral crushing so that the fin rays are bunched and twisted together: B.M.N.H. Nos. P.24551, P.21000, P.16168, P.20986. Against this view may be set the comparative frequency with which palaeoniscids preserved in nodules show the natural position of the fin; but *Cornuboniscus* was, in comparison with most forms, laterally compressed in life, and the gentle curvature of the cleithrum seems to show that a flat venter was not well developed. These factors must have had great influence in determining the attitude of entombment and the nature of the collapse of squamation, etc., during maceration. Whatever may be the conditions in *Cornuboniscus*, a large number of "palaeoniscids" show the two positions of preservation of the pectoral fin web in different individuals—folded down, and folded flat against the flank. *Haplolepis* and *Pyritocephalus* show this very clearly (fig. 50).

The pelvic fins were placed on the ventrolateral ridge, and again the point of insertion of the leading edge is a little higher than that of the trailing edge. It is most likely that the pelvic fins were also held out from the body as "keels." Probably the "drooping" position in which they are customarily restored in palaeoniscids is misleading.

The posterior position of the dorsal fin

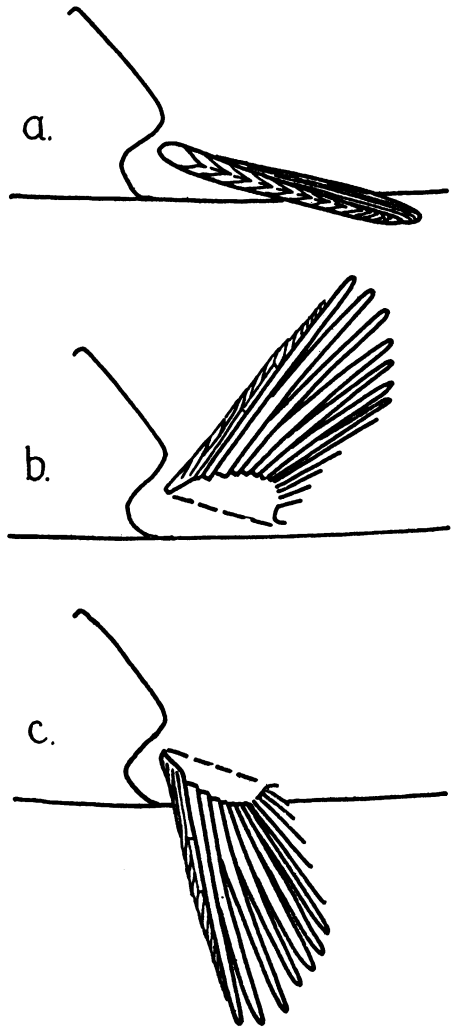


FIG. 50. Pectoral fin of a haplolepid in lateral view; a, normal position; b, turned up against flank; c, turned downwards. The embedding of the individual in sediment after death may result in preservation in any of these positions, which may be modified by crushing.

with respect to the anal is a noteworthy feature of *Haplolepis* and *Pyritocephalus*. The dorsal is almost opposed to the anal in several palaeoniscid genera, e.g., *Cheirolepis*, *Rhadinichthys*, *Canobius*, some species of "*Amblypterus*," *Nematoptychius*, and *Pygopterus*, but it is rare for the dorsal to arise behind the anal, as it does in *Pyritocephalus*.

The caudal fin is markedly inequilobate and not deeply cleft. In this it differs from the majority of palaeoniscids, though there is

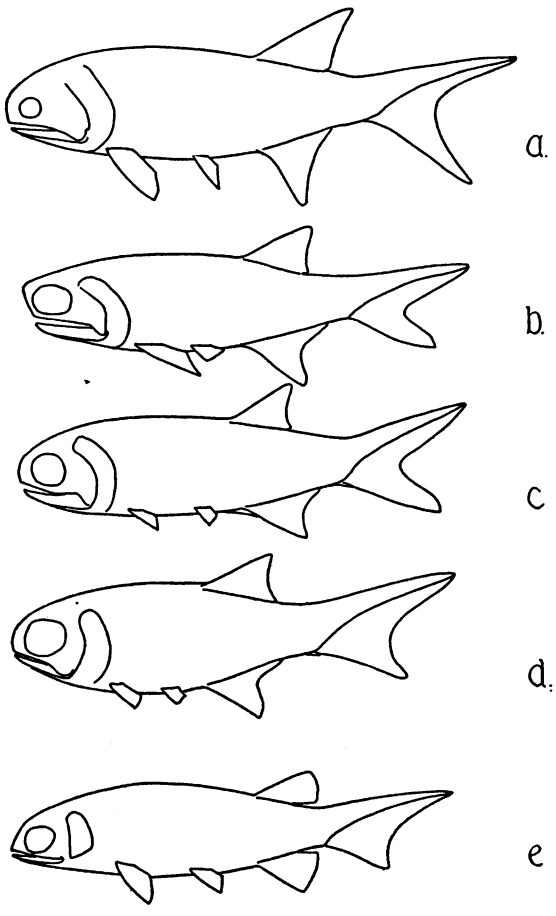


FIG. 51. Outlines of palaeoniscoids in the approximate phylogeny of Haplolepidae. a, *Stegotrachelus finlayi* Woodward and White (Devonian, after Woodward and White); b, *Rhadinichthys fusiformis* Traquair; c, *Mesopoma pulchellum* Traquair; d, *Canobius ramsayi* Traquair (all lower Carboniferous, after Moy-Thomas and Dyne); e, *Pyritocephalus sculptus* Fritsch. The earlier reconstructions are inaccurate as regards depth of body. As a compromise, a–d have been made slightly more slender, e, slightly deeper, than in the original reconstructions.

great diversity in the actual form of the heterocercal tail within that group. The most unusual feature in *Haplolepis* and *Pyritocephalus* concerns the extreme shortening of the caudal peduncle. This can be seen by comparing the shapes of entire fishes (fig. 51) and also by counting the scale rows.

The sequence *Rhadinichthys-Mesopoma-Canobius-Haplolepis-Pyritocephalus* may be accepted as a close approximation to the phylogeny of the two last-named genera. Species of the three first named have recently been described by Moy-Thomas and Dyne (1938) in some detail, and the following figures for the scale count may be given (table 2).

While it is obvious that the true ancestral forms of *Haplolepis* and *Pyritocephalus* are unlikely to be represented in the list of species given above, the general aspect of the scale counts is indicative of a reasonably close relationship. If the counts above are compared with those of palaeoniscids outside the immediate relations of *Haplolepis* a striking difference is to be observed, e.g., *Elonichthys serratus* gives

$$\frac{47}{25 \quad 50 \quad 73}$$

Palaeoniscus freieslebeni,

$$\frac{40}{25 \quad 42 \quad 68}$$

(these two are fairly closely related); *Aeduella blainvillei*,

$$\frac{23\text{–}24}{7 \quad 23\text{–}24 \quad 33\text{–}34}$$

The general trends in the scale counts are noteworthy; the number of scale rows on the body as a whole tends to be reduced in the approximate "phylogeny" of haplolepids, but the most striking differences are to be observed in the numbers of scale rows intervening between D (dorsal), A (anal), and C (caudal) fins. This is another expression of the shortening of the peduncle. The other figures show no significant change with time. The dynamical significance of this will be discussed later.

MECHANICAL SIGNIFICANCE OF FINS

It is now well established that a heterocercal tail of the type seen in palaeoniscoids is a propelling fin; when it is sculled from side to side it transmits to the fish a powerful forward thrust and a strong lift (see in particular Grove and Newell, 1936). Since the lift is applied behind the center of gravity it would cause a powerful pitching moment if it were not counterbalanced by an upward thrust in front of the center of gravity. This

TABLE 2

			V-A	V-D	A-D	D-C	A-C
Stegotrachelus finlayi	26 / 11 20 43	47	9	15	6	17	23
Rhadinichthys canobiensis	28 / 11 21 44	47	10	17	7	16	23
Rhadinichthys fusiformis	27 / 10 19 38	41	9	17	8	11	19
Mesopoma politum	25 / 10 19 40	42	9	15	6	15	21
Mesopoma pulchellum	19 / 7 14 30	33	7	12	5	11	16
Canobius ramsayi	21 / 8 14 31	34	6	13	7	10	17
Canobius elegantulus	20 / 6 13 30	34	7	14	7	10	17
Pyritocephalus gracilis	23–24 / 7 15–16 25	27–28	8–9	16–17	8	1–2	9–10
Pyritocephalus lineatus	24 / 7 16 25–26	28	9	17	8	1–2	9–10
Pyritocephalus sculptus	22 / 6–7 14 23	25–26	7–8	15–16	8	1	9
Haplolepis tuberculata	23–24 / 7 17 26–27	29	10	16–17	6–7	3	9–10
Haplolepis corrugata	20 / 6–7 15 22–23	25	8–9	13–14	5	1–2	7–8
Haplolepis ovoidea	18 / 6 13 21	23	7	12	5	3	8

was attained in palaeoniscoids by the action of the "aerofoil" (in this case, of course, a "hydrofoil") formed by the pectoral fins, of which the leading edge is somewhat higher than the trailing edge.

Another possible factor is the overhanging rostrum, which might cause a smaller upward thrust at a greater distance from the center of gravity. In itself this might provide a significant pitching moment, but it is likely that the other surfaces presented by the head would greatly reduce the effect. The mechanical significance of the tail and pectoral fins is thus easily explained; the case is similar to that of the dogfish, investigated by Harris (1936, 1937, 1938).

Harris (1938) found that the result of amputating the pelvic fins of dogfish was very slight; those fins play little or no part in the rolling stability in dogfish, and they play a smaller part in the lift, in spite of their angle of attack, than would be expected from their size. Harris concludes that the "downwash effect" produced by the more anterior "aerofoil" (hydrofoil in swimming) of the pectoral fins is sufficient to account for the deficiency of lift, and notes that the bilge-keel action of the pelvics (i.e., the ability to

prevent rolling) is apparently insignificant in the dogfish. In *Mustelus*, however, the broad keels of the pectorals and the expanded anterior dorsal fin are no doubt the main stabilizing structures against rolling movements. In such fishes as palaeoniscids there is only one dorsal fin, set behind the paired fins, and it is probable that the pelvics play a larger part in the stability against rolling.

The posterior position of the median fins points to a great directional stability, i.e., to conditions such that the fish would not, during gliding, suffer "yawing" movements without immediate correction. During active swimming the ability to flex the body in the lateral plane would allow the production of large yawing moments, which would be controllable to some extent by change in area of the median fins. Thus if the fin rays of the dorsal and anal fins were to be "collapsed" the instability to yawing moments would be increased.

A third type of swimming mechanism is possible in these fishes, namely, hovering as a result of undulating movements of the fin webs. This is difficult to analyze, and no attempt is made here to discuss it.

Thus if the movements of the body be analyzed into the usual three components, *Haplolepis* and *Pyritocephalus* show the following conditions:

DURING GLIDING

A. Rolling movement: neutral equilibrium.

B. Yawing movement: stable equilibrium, slight control by collapse of fins.

C. Pitching movement: unstable equilibrium, with great powers of control by varying the angle of incidence of the paired fins.

DURING ACTIVE SWIMMING

A. Rolling movement: neutral equilibrium; position could be controlled by unilateral variation of incidence of pectoral fins.

B. Yawing movement: probably very highly controlled by lateral flexure of body and ability to expand or close the median fin webs.

C. Pitching movement: unstable equilibrium, controlled by varying the angle of incidence of the pectoral fins.

During active swimming, the lift, due to the action of the heterocercal tail and the "hydrofoils" of the paired fins, was considerable. The presence of the strongly heterocercal tail is evidence that the fishes were of greater specific gravity than the water in which they lived (Grove and Newell, 1939); hence passive gliding would result in slow fall through the water. Possible effects of undulatory movements of the fin webs have not been considered, but some slight degree of hovering may well have been attained.

The application of these results to the ecological study of the fishes is reserved till a later section.

Meanwhile it may be as well briefly to summarize the essential differences between this type of palaeoniscid and the group with the dorsal fin almost apposed to the interval between the anal and the pelvics. This latter group includes the larger, obviously rapacious types such as *Elonichthys*, *Acrolepis*, *Pygopterus*, and *Namatoptychius*. In these fishes the control of size of the fin webs was probably less well developed. The rolling and pitching would not be affected, but the more anterior position of the dorsal fin would affect the stable equilibrium of the yawing moments and might even result in conditions of neutral equilibrium. That is to say, the directional control during rapid swimming would be greater than that of such fishes as *Haplolepis*, and the efficiency of the fish as a predator would be enhanced.

BEARING ON HOLOSTEAN EVOLUTION

THE HAPLOLEPIDAE have undergone an evolution from a palaeoniscoid ancestor which is similar in many respects to that undergone by various palaeoniscoid derivatives usually classified as Holostei and Sub-Holostei. It is one of the most remarkable achievements of the last two decades of the palaeontological study of fishes that the old group "Palaeoniscidae" has not only been shown to include a large number of evolutionary lines but has also been shown to be the root stock of many groups of derivatives, some of which show a striking degree of "parallel evolution." Certain generalized changes (e.g., in the skull roof, snout, cheek, and braincase; in the opercular apparatus; in the structure of the fins; in the nature of the tail; in the histology of the squamation) are found in several groups of fishes, mostly of Triassic age; and lately there has accumulated much evidence which tends to show that many of these families were derived quite independently from different palaeoniscoid ancestors. In this study the fundamental contributions have been those of Stensiö (1921, 1925, 1932), Brough (1931, 1933, 1934, 1936, 1939), White (1932, 1933), Piveteau (1934), Wade (1935, 1940, 1941), Nielsen (1936), Rayner (1941), and Berg (1941).

The clearest result of this work is to show that many different stocks within the palaeoniscids suffered a series of profound changes during (or immediately before) Triassic times, and that in many cases these changes trend towards a "holostean" structure of skull, fins, tail, or squamation. This very remarkable development of new forms has naturally focused attention on the Triassic fish faunas. The wealth of new families appearing at that time is certainly significant, as will be shown below; but the pre-Triassic "palaeoniscoids" include several forms which are probably of equal morphological distinctness, but which for the greater part retain a heterocercal tail. The earliest known actinopterygian, *Cheirolepis* (Middle Devonian, Watson, 1925), differs in several ways from all other members of the group. Besides the various families of "normal palaeoniscids" that can be distinguished in Lower Carboniferous deposits there are at least three side branches, represented by *Canobius*, *Holurus*, and *Tarrasius* (which may be related to *Holurus*), which show various evolutionary potentialities of the group, in addition to deep-bodied derivatives retaining a fairly generalized structure. In late Carboniferous times there appeared such peculiar developments as *Phanerorhynchus*, the Haplolepidae, and various forms from Bohemia described by Fritsch, each of which foreshadows to some extent structures of more "advanced" forms. In the early Permian occurred *Aeduella*, of which the structure has previously been described (Westoll, 1937b), and a whole series of little-known, greatly modified forms from Czechoslovakia; the late Permian form *Acentrophorus* is already a fully developed holostean (Gill, 1923), and the truly remarkable *Dorypterus* (Gill, 1925; Westoll, 1941) shows certain features of startling modernity.

The order Sub-Holostei was proposed by Brough (1936) for a group of (mainly Triassic) families. With more recent additions the following families can be recognized:

1. Catopteridae
2. Perleididae
3. Parasemionotidae
4. Cleithrolepidae
5. Pholidopleuridae
6. Saurichthyidae
7. Platysiagidae
8. Cephaloxenidae
9. Peltopleuridae
10. Luganoiidae
11. Aethodontidae
12. Pytcholepidae
13. ?Pycnodontidae (Woodward, 1939)

The other palaeoniscoid derivatives of present interest comprise the "Holostei" (and Teleostei), "Chondrostei," and Polypterini. It will be shown later that the actinopterygian fishes derived from palaeoniscoids are best considered as a diverging sheaf of many lines of evolution, some of which passed through several "grades" of structural development. The importance of the Haplolepidae is that they show certain structural

features parallel to those evolved in later fishes, and thus may give information bearing on the evolution of "Holostei." These features may be considered under separate heads.

SKULL ROOF

The most significant feature of the haplolepid skull roof is the normal reduction of the parietals, so that the dermopterotics reach the mid-line. This is a specialized feature within the group; it may be compared with

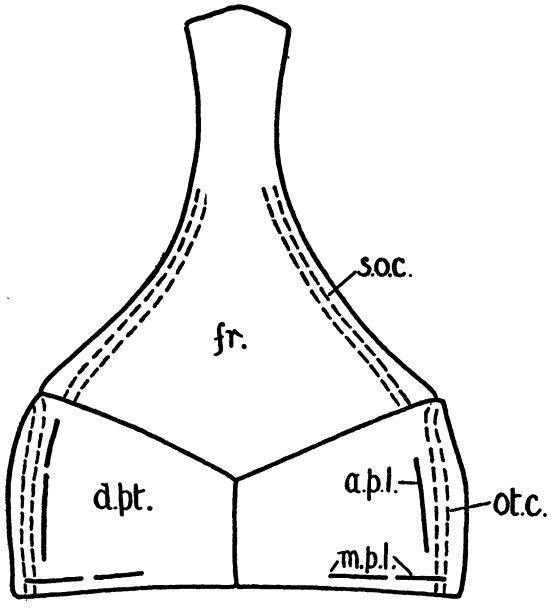


FIG. 52. Skull roof of *Luganoia* (composite, from several species), after Brough. Reinterpretation of structure of skull roof and of latero-sensory system.

the conditions in *Polypterus* (cf. Allis, 1922) and depends on the progressive reduction of the posterior part of the supraorbital sensory canal to the pit-line condition (see above, pp. 67–69). Conditions resembling those of the Haplolepidae are rare in fishes, but the skull roof of *Luganoia*, from the marine middle Trias of Lombardy, shows points of resemblance, and Brough's account (1939, pp. 39–49, figs. 15, 17, 19) can be re-interpreted (fig. 52). It seems likely that the parietals have disappeared with the reduction of the canal, just as in *Haplolepis tuberculata*, etc., and that the dermopterotics have grown to the mid-line and captured the anterior pit line. The grooves in the dermopterotics (="parietals" of Brough's account) represent the anterior and middle pit lines. Though the results of the reduction of the supraorbital sensory canal may be peculiar in the Haplolepidae, "degeneration" of the hinder part of the supraorbital canal to a pit line, often with the production of a secondary anastomosis of the supraorbital canal with the "infraorbital canal," is a characteristic of the higher Actinopterygii. On this point a short note seems necessary. The anastomosis of the two canals has taken place quite independently in a number of groups of fishes (Dipnoi, Crossopterygii, besides many "higher" actinopterygians), and it is by no means a reliable character for systematic studies. A palaeoniscoid, *Oxygnathus*, in which the anastomosis has taken place has been figured by Watson (1925, fig. 30) and in the "holostean" Semionotidae particularly, the writer has observed most variable conditions. The primitive "palaeoniscoid" arrangement occurs in several species as late as the early Cretaceous, sometimes only in a proportion of the individuals of a single species.

The Haplolepidae thus anticipate the later reduction of the posterior part of the supraorbital canal, but the results of this process are peculiar to the family and can only be paralleled in a few later forms. *Aeduella* (Westoll, 1937b) also shows this reduction.

CHEEK

The Haplolepidae show a marked tendency to adopt a forwardly displaced suspensorium of the jaw. A similar change is eminently characteristic of the Triassic derivatives of the palaeoniscoid stock and is shown in a few pre-Triassic palaeoniscoids such as *Holurus*, *Tarrasius*, and *Aeduella* and apparently also in several of the Stephanian and early Permian fishes from Bohemia figured by Fritsch (1893). The change must have involved considerable adjustment of the jaw musculature, but so little is known of the detailed structure of the cranium, palate, and mandible in Palaeozoic Actinopterygii that the possibility of an analysis along these lines seems remote. It is probable that the change involved a gradual modification of the method of taking or ingesting food, but one thing is

certain—the fishes must have been functionally efficient, at all stages of the process.

The importance of the Haplolepidae lies in the diversity of the patterns of the cheek bones in different forms. The dermal bones formed a firm plating outside the adductor-mandibulae musculature, and the shape of the whole of the cheek shows only minor differences. But in the shape of the individual bones certain species are remarkably similar to much later Triassic derivatives. Thus the triangular preopercular and maxillary expansion of *H. corrugata* resemble the corresponding elements of many Perleididae; the curious preopercular of *H. tuberculata* is not unlike that of certain species of *Peltopleurus*, and the whole cheek is quite like that of *P. lissocephalus* as figured by Brough (1939, fig. 11A). The conditions in *H. ovoidea* are most remarkable because the maxilla has lost all trace of its cheek expansion, and only a little modification would be necessary to free the bone altogether from the preopercular, when a thoroughly "holostean" condition would result (fig. 44).

The Haplolepidae thus show extremely clearly that the evolution of apparently very distinct cheek patterns could be carried out very quickly, without much modification of other structures. To the fishes themselves, as functional organisms, the differences in pattern were probably unimportant, because the bones concerned covered the cheek rigidly, and there can have been little difference in the structural effectiveness of different patterns. But the changes are clearly correlated with the forward migration of the suspensorium, and continuation of that tendency might result in such modification of the functions of various elements that the cheek bones would be freed from their earlier duty of providing a rigid part of a girder system to take some of the stress of muscle action. In such circumstances differences in the cheek pattern would result in very different characters in the derivative.

Similar topics have already been discussed in the previous description of *Aeduella* (Westoll, 1937b).

SNOUT

The resemblance of the Haplolepidae to much later Actinopterygii is nowhere more clearly shown than in the snout. The typical "palaeoniscid" overhanging rostrum is replaced by a profile more characteristic of semionotids and other Mesozoic higher Actinopterygii, but the most striking feature is the position of the notches which mark the anteromesial nasal openings. Somewhat similar conditions are probably present in *Aeduella* (Westoll, 1937b). Indeed many of the well-established groups of Triassic Sub-Holostei have gone less far in this direction towards a typical holostean condition. The Perleididae and Catopteridae are more palaeoniscid in snout structure than the Haplolepidae, and in most of the other Sub-Holostei the detailed anatomy of this region is unknown. It is only in the Parasemionotidae (including Ospiidae, Stensiö, 1932, pp. 225, 183; Piveteau, 1934, p. 54, and particularly p. 74, fig. 51) and in certain Holostei that the conditions show any considerable resemblance to the Haplolepidae, and in the Triassic family the postrostral has altogether disappeared. In the relations of the nasal apertures a few other forms besides *Aeduella* show a slighter degree of resemblance, e.g., the very peculiar catopterid *Atopocephala* (Brough, 1934, fig. 3), in which the nasal opening is apparently enclosed between the nasal, postrostral, and "rostral." Possible correlations between the structure of the snout and other cranial features have been mentioned above (figs. 46, 47).

OPERCULAR APPARATUS

The Haplolepidae show a remarkable tendency to possess a discontinuous series of dermal ossifications in the opercular folds. In most species the opercular and subopercular are completely separated from the ventral gular series, consisting of two pairs of bones and an anterior median element; only in *H. tuberculata* is there any trace of other dermal bones, but the elements found between the subopercular and the gulars in that species are remarkably different in arrangement from the normal "branchiostegal rays." These conditions at once suggest comparison with the catopterid condition; in the Catopteridae, Brough (1931, 1934) has shown that the opercular series consists of opercular and subopercular (in *Catopterus redfieldi*), with the usual addition of one (*Helichthys*, *Atopo-*

cephala) or two (*Daedalichthys*) large plates lying immediately below the subopercular. In some cases there may be signs of a small median gular, but normal branchiostegals are never found. Similar conditions have been described in Australian material by Wade (1935). These similarities may well be due to adaptational changes of similar kind, because it is most unlikely that any close relationship can be established between catopterids and Haplolepidae; the conditions must have been evolved independently. This matter has been reviewed above, and its bearing on possible air-gulping habits discussed.

It may be no coincidence that there is a disturbance of the opercular ossifications near the angle of the jaws in so many palaeoniscoid derivatives. In Haplolepidae, Saurichthyidae, Catopteridae, and Polypterini this is indicated by a marked discontinuity. In other forms, e.g., Parasemionotidae, the uppermost branchiostegal ray is apparently drawn out of position and forms an incipient interopercular. It is not yet possible to give reasons why these changes should have occurred in certain forms with forwardly shifted suspensoria and not in others.

FIN STRUCTURE

The Haplolepidae are sharply distinguished from normal palaeoniscids in the small number of lepidotrichia in each fin web. The fins of typical palaeoniscids are composed of numerous rays, usually articulated, which divide distally to produce a fine fringe; the lepidotrichia are much more numerous than the endoskeletal fin supports. It is one of the best-known characters of the "Holostei" that the lepidotrichia are usually equal in number to the endoskeletal fin supports, and the small number of fin rays in several groups of Sub-Holostei suggests that similar conditions may have held there. Such a change from the palaeoniscid type probably signifies a much greater degree of control of fin shape and, therefore, of maneuver. In Carboniferous fishes the tendency towards reduction of the number of fin rays is seen only (as far as is known) in Haplolepidae and in the remarkable specialized form *Phanerorhynchus* (Gill, 1923), but in these the conditions are no less "advanced" than in most Triassic groups of palaeoniscoid derivatives.

SQUAMATION

It has long been known that various groups of bony fishes have scales of different histological structure. Goodrich (1908) gave clear definitions of the main types of bony scale found in Actinopterygii, and Aldinger (1937) has initiated the detailed study of palaeoniscoid scales. Brough (1931, 1936) has studied the transition in Triassic fishes from the palaeoniscid type (with cosmine) to the lepidosteid type in which cosmine is lost. The scales of Haplolepidae are very thin and almost completely smooth. Their microscopic structure is still unknown in all but one species, but there can be little doubt that the structure is similar throughout the group. The cosmine layer is thick, the ganoine layer very thin, the bony layer extremely thin in *H. tuberculata*. In view of the widely held opinion that evolution of the scales in many palaeoniscoid derivatives is marked by a reduction of cosmine, this is the reverse of what might have been expected in very thin scales. It will be shown later that the reduction of cosmine is a very variable process in various lines of descent and is not a useful character in taxonomic studies. Comparatively few palaeoniscoids have smooth, unornamented ganoid scales, but that description is applicable to many Mesozoic Actinopterygii.

The absence of the normal palaeoniscoid peg-and-socket articulations in the dorsally directed scale rows of Haplolepidae has already been commented upon (p. 81). The loss of this apparently primitive character in later Actinopterygii has often been mentioned (e.g., by Berg, 1940, p. 384).

The deep flank scales of certain species of *Haplolepis* have their counterparts in several other groups, particularly *Phanerorhynchus armatus*, *Rhadinichthys hancocki*, and certain Triassic derivatives. Brough (1939) has recently described several groups of Triassic actinopterygians in which the lateral-line scales of the flank are excessively deep, e.g., Peltopleuridae, Luganoiidae. The conditions in *Luganoia lepidosteoides* Brough are of particular importance, for there are 14 or 15 deep flank scales, the most posterior of which is

abruptly succeeded by two or three scales, in the same manner as in *Haplolepis tuberculata*. It is entirely unlikely that there is any close blood relationship between *Haplolepis* and the Peltopleuridae, Luganoiidae, Pholidopleuridae, Saurichthyidae, and other Triassic groups with deep flank scales, and *Haplolepis* is sharply distinct from such fishes as the late Carboniferous *Rhadinichthys hancocki* Traquair, *Phanerorhynchus*, and *Eurylepidoides socialis* Case (from the late Carboniferous or early Permian of Texas). It is difficult to conceive of any functional use of deep flank scales except as a means of providing greater stiffness against dorsoventral flexure, and it seems most feasible to regard this feature as a parallel development in many different groups of species.

DISCUSSION

In this short discussion emphasis has been laid on a number of characters common to the Haplolepidae and various later palaeoniscoid derivatives. These common traits are not to be found in any one family of the latter, which are mostly of Triassic age, and there is no difficulty in separating members of the various families concerned. It is, therefore, necessary that the validity of certain conceptions of the classification of Actinopterygii, based on these characters, should be examined; this is particularly true of Brough's usage of the category "Sub-Holostei" for the reception of many Triassic forms. The existence of such pre-Triassic fishes as *Tarrasius*, *Canobius*, the Haplolepidae, *Phanerorhynchus*, *Aeduella*, etc. (to make no mention of deep-bodied forms) indicates a considerable aptitude for variation in the "Palaeoniscoidei," and it is difficult to justify their separation from the heterogeneous "Sub-Holostei" except on the grounds of tail structure.

The nature of the transition from the palaeoniscoids to more "advanced" actinopterygians is still very poorly known from actual observation, but some general conclusions can be drawn. The early palaeoniscoids of later Devonian and early Carboniferous age already show a considerable diversity in detail of skull structure and body form, though the general structural pattern is similar. It has long been suspected that these early palaeoniscoids include a number of evolutionary lines, which in favorable circumstances can be separated with more or less ease and regarded as families, and recent works by Aldinger (1937) and Moy-Thomas (1939) have begun the development of this analysis. Certain of these lineages were apparently sterile, dying out without suffering any noteworthy morphological change; the latest of these persisted into the Cretaceous period. Very many lineages, however, underwent changes of such magnitude that their separation from the central body of the palaeoniscoid assemblage is easy. The degree of morphological modification in these branches is very variable. Some (e.g., the platysomids) merely become very deep bodied, retaining most of the structural characters of the palaeoniscoids. In other groups changes may affect the structure in the following characters, among others: (a) skull-roof pattern; (b) snout structure; (c) cheek pattern; (d) opercular pattern; (e) scale histology; (f) shape of tail; (g) nature of paired fins; (h) nature of fin web and fin supports; and (i) extent of ossification of exoskeleton and endoskeleton.

The living representatives of these derivatives comprise the following:

A. *Acipenser* and other sturgeons, closely related

B. *Polyodon*

These two groups retain the palaeoniscoid heterocercal tail and show considerable resemblances in their internal skeleton, but they differ markedly in their cranial anatomy, and their palaeontological history shows them to have been long separate.

C. *Amia*

D. *Lepidosteus*

These genera have lost the heterocercal tail form, and the palaeoniscoid head pattern is considerably, though differently, modified in both.

E. (?) *Polypterus* and *Calamoichthys*

These closely related genera are still of uncertain systematic relations.[1]

F. The "Teleostei"

[1] I hope to discuss this group elsewhere. *Polypterus* is a palaeoniscoid derivative preserving some remarkably archaic characters amid a host of specializations.

This extremely numerous and varied group of fishes is usually regarded as an order.

The customary recognition of "orders" Chondrostei (embracing sturgeons and *Polyodon*), Holostei (including *Amia* and *Lepidosteus*), Polypterini, and Teleostei is largely determined by the accident that little is generally known about the palaeontology of the Actinopterygii. Even if it could be accepted that *Amia* and *Lepidosteus* form a natural, narrowly restricted, and monophyletic group, which is certainly not the case, it would be wrong to impress on extinct forms a grouping into categories based on the characters of well-separated, phylogenetically long independent forms which are the scattered remnants of once abundant and diverse fishes.

The living fishes classified together as "Holostei" are *Amia* and *Lepidosteus*. They share the following modifications of palaeoniscoid characters: (a) the more forwardly directed suspensorium; (b) the narrow preopercular; (c) the reduction of the maxilla; (d) the modification of the course of the supraorbital latero-sensory canal; (e) the presence of an interopercular; (f) the scale histology, in so far as there is a reduction of the complex palaeoniscoid type; (g) the nature and support of the fin web; and (h) the loss of the heterocercal tail. All these differences can be found in various combinations among the families of the Sub-Holostei, and it may at once be suspected that they may be an arbitrary selection. There are, indeed, very marked differences between the two genera, e.g., the structure of the circumorbital region, the nature of the maxillary region,[1] the nature of the gular or branchiostegal plates, the fin fulcra, the scale histology, and the nature of the vertebrae, to mention the more outstanding. It is, therefore, necessary to examine the geological history of these and related fishes.

The living and fossil derivatives of the Palaeoniscoidei, excluding the Sub-Holostei, may be shown in the following tabular form. The arrangement of "Holostei" is based on that of Rayner (1941) with the addition of Wade's new family Promecosominidae (1941) of the Pycnodontidae (doubtfully placed here), and of superfamily designations for the three largest groups.

"HOLOSTEI"

GROUP 1. AMIOIDEA
?Promecosominidae
Eugnathidae
Amiidae
Macrosemiidae

GROUP 2. SEMIONOTOIDEA
Semionotidae
Lepidosteidae

GROUP 3
Pachycormidae

GROUP 4
Aspidorhynchidae

GROUP 5. PHOLIDOPHOROIDEA
Pholidophoridae
Oligopleuridae
Leptolepidae (leading to the Teleostei)

GROUP 6. ?
Pycnodontidae

CHONDROSTEI

Chondrosteidae
Acipenseridae
Polyodontidae

POLYPTERINI

Polypterus
Calamoichthys

It is probable that future investigations of Mesozoic faunas will amplify this list and may result in some modifications of the arrangement, but it shows well our present understanding of the groups concerned. Rayner (1941, p. 234) has discussed the monophyletic or polyphyletic origin of the "Holostei" and concludes that the evidence is indecisive; against the various differences between the groups she sets the similarity of endocranial structure. There are certainly important points of resemblance in skull roof and endocranium between most of the groups of the "Holostei," but to the present writer the polyphyletic nature of the "Holostei" is clearly indicated. The best evidence is provided by the Amioidea and Semionotoidea.

[1] The chain of tooth-bearing latero-sensory canal elements customarily regarded as fragmented maxillary elements in *Lepidosteus* do not include any homologues of the maxillary; the true maxillary was long ago figured by Agassiz, and more recently by Hammarberg. *Polypterus* shows a remarkable parallel development.

Brough (1939, p. 89) has shown that the Amiidae are derived from the Eugnathidae, which almost certainly developed from a parasemionotid (i.e., subholostean) stock in, probably, Middle or Upper Triassic times. *Promecosomina*, from the non-marine Middle and Upper Triassic of New South Wales, has recently been shown by Wade (1941, p. 381) to be probably an immediate parasemionotid derivative, and it has significant resemblances to *Eoeugnathus*. The earliest semionotid (*Acentrophorus*), from the Upper Permian, differs very markedly from the Parasemionotidae; the actual palaeoniscoid ancestors of this group cannot yet be indicated with certainty, but there is strong evidence (Westoll, unpublished) suggesting derivation from that group of palaeoniscoids which includes *Elonichthys*. Very obvious differences between the Parasemionotidae and the Semionotidae are: (a) the pattern of the circumorbital and cheek regions; (b) the structure of the snout, as far as it is known; (c) the method of reduction of the ancestral heterocercal tail to a hemi-heterocercal condition. Taken in conjunction with the time difference of first appearance of these fishes, these points are amply sufficient to demonstrate that the two groups are derived independently from palaeoniscoids and strongly suggest that the palaeoniscoid ancestors were not particularly closely related within that group. If this be accepted, the similarly constituted endocrania merely indicate retention of similar generalized ancestral conditions. In all "normal" adult palaeoniscoids so far described the endocranium in the postorbital region is apparently a single ossification. Only in an apparently juvenile individual (see Watson, 1928) have discrete, paired, and unpaired ossifications been described, but the writer has evidence of more than one ossification in *Cheirolepis*. It may be suspected that the "single" adult ossification of the palaeoniscoid endocranium developed first as discrete rudiments or centers of ossification, which normally became fused. In most Holostei the homologues of some or all of these separate ossifications remain visibly separate during life. It is particularly noteworthy that in those Parasemionotidae of which the endocranium is known (e.g., Stensiö, 1932, pp. 228, 268; Nielsen, 1936, p. 47) the palaeoniscoid condition is retained, and it is, therefore, very highly probable that the semionotoid and amioid patterns have developed independently. If this be once granted, the main reasons for considering these and the other groups of "Holostei" as monophyletic have vanished.

There are, therefore, two clearly marked groups within the Holostei which are not monophyletic, and the status of the other groups may now be considered. The endocranial resemblances noted by Rayner do not necessarily indicate close relationship between the groups, if the above analysis be correct. The Pholidophoroidea are peculiar in having an autopterotic in the endocranium. As far as their dermal skull is concerned, they may be nearest akin to the Amioidea. The Pachycormidae are a very isolated family, as pointed out by Rayner (1941, p. 228), and cannot profitably be discussed. The Aspidorhynchidae also occupy an isolated position; the writer suspects relationship between them and the Triassic Saurichthyidae and Pholidopleuridae. The pycnodonts afford an extremely instructive case. They were at one time brigaded with Platysomidae and removed when the broad division of the Actinopterygii on the basis of fin structure was instituted. The family was later regarded by Traquair and Woodward as related to Semionotidae, but Woodward (1939) has recently shown that they may more readily be derived from Sub-Holostei such as Bobasatraniidae, which in turn may have evolved from Platysomidae, and some confirmatory evidence has been provided by Westoll (1941). Again, the Jurassic species of *Ptycholepis* were for long regarded as holosteans of the family Eugnathidae, but Brough's account of Triassic species reveals important differences, so that he regards the whole family as of subholostean affinities. Both Brough (1939, p. 98) and Aldinger (1937, pp. 286, 301) have shown that *Ptycholepis* is derived from palaeoniscoid fishes closely related to, or including, the Lower Triassic *Boreosomus* (*Diaphoragnathus*). It appears, therefore, that the "Holostei" is not a "natural" order but comprises several groups of fishes which have been derived from more than one palaeoniscoid family, and have independently acquired those characters of jaw, cheek, oper-

cular apparatus, and tail which are the "uniform" of the "Holostei." Moreover, there are several other groups of Mesozoic fishes which it is very difficult to exclude from the "Holostei," e.g., *Ptycholepis*, pycnodonts, etc., and it seems fairly clear that the characters used in defining this "order" merely represent a grade of evolutionary development which was reached several times independently. Attention is drawn, therefore, to the functional, as distinct from the genetical and hereditary, significance of these evolutionary changes.

Brough's use of the term "Sub-Holostei" is open to the criticism that it appears to imply relationship to "Holostei" (though Brough's definition is more explicit) and seems to carry the assumption that the Holostei are a more or less homogeneous group. The foregoing analysis strongly suggests that the fishes referred to the "Order Holostei" are polyphyletic, ultimately palaeoniscoid derivatives which happen to share certain characters of cheek pattern, fin-web structure, and tail conformation, each of which can also be matched in one or more Triassic or Palaeozoic "Sub-Holostei" or palaeoniscoid derivatives.

This conclusion is somewhat unfortunate, since the great merit of Brough's work has been to emphasize the periods of dominance of his classificatory groups, the "Order Palaeoniscoidea" being dominant in the late Palaeozoic, the "Order Sub-Holostei" in the Triassic, the "Order Holostei" in the Jurassic and early Cretaceous, the "Order Teleostei" in late Cretaceous and subsequent times. From this aspect Brough's usage of the terms is advantageous, but the use of the term "Order" to indicate progressive grades of evolution is not in accord with the views of most vertebrate palaeontologists. Brough has briefly discussed these points (1939, p. 109) and remarks that classifications are necessary, "if only for convenience in discussion, and all classification must somewhere cut across phyletic lines." But no classification in palaeontology can be of much use unless it pays some regard to phylogeny, and it is an object of this discussion to show that the "Orders" Sub-Holostei and Holostei not only cut across phyletic lines, but are based on characters which are of adaptational nature. It seems far better to regard *all* Actinopterygii which notably differ from palaeoniscoids in structure as forming a fringe of evolutionary twigs and branches around a central compact bush, in which we may hope some day to distinguish the origin of each derivative group. Within this fringe it is legitimate to recognize close and similar groups, to which handy names such as Teleostei may be given but of group names now in use neither Holostei nor Sub-Holostei can be considered satisfactory. The former certainly covers polyphyletic forms, and the fishes grouped in the latter are not only polyphyletic, in all probability, but are arbitrarily marked off from pre-Triassic fishes which have at least a very remarkably similar degree of specialization. If the change in form of the tail fin be disregarded, it would be difficult to exclude certain species of *Haplolepis* and such forms as *Aeduella* from the groups of now recognized Triassic derivatives. Comparison of various published accounts shows clearly that many fishes now placed in the "Sub-Holostei" are far less removed from palaeoniscoids in cranial structure than Haplolepidae, *Aeduella*, and many other pre-Triassic forms. This is true of genera of the following "subholostean" families:

Perleididae
Catopteridae (in many features)
Cleithrolepidae
Platysiagidae
Peltopleuridae
Ptycholepidae (Triassic forms)
Saurichthyidae

Since the most important remaining character used in the customary classification is the nature of the tail, attention is thus focused on the changes in the fins, and it seems likely that these changes can be correlated with other events in the history of the dynamic adaptations of Actinopterygii. In order to place these changes in a proper perspective, a brief account of the history of Actinopterygii in Palaeozoic and early Mesozoic times will be attempted, special reference being made to probable conditions of life.

GENERAL REMARKS ON THE EVOLUTION OF THE ACTINOPTERYGII

THE EARLIEST, MOST PRIMITIVE Actinopterygii are fusiform fishes with a distinct overhanging rostrum; eyes of moderate to large size set far forwards; oblique suspensoria; keel-like, long-based paired fins; and a strong heterocercal tail in which the hypochordal lobe, though large, is not usually so long as the body extension. They are known in Middle Devonian and later times and until the end of the Carboniferous suffered comparatively little change. The vast majority of forms of Devonian, Carboniferous, and early Permian age are found in rocks which there is good reason to believe were laid down in continental fresh waters. A mere handful of species exist rarely in truly marine rocks, and others have been found in rocks of debatable origin. In general, it seems reasonable to suppose that these "marine" species were either washed into the sea after death, or that they represent the few species that had been able successfully to change their environmental relations. Traquair has demonstrated, in a series of publications, the great differences between the marine fishes of the Carboniferous (mostly Elasmobranchii) and the "estuarine" fishes, consisting largely of palaeoniscoids and Crossopterygii. These "estuarine" faunas (better regarded as deltaic) were certainly not for the most part entombed in marine environments, but one of the largest and best-known early Carboniferous faunas is that from Glencartholm in Eskdale (Moy-Thomas and Dyne, 1938), and this at first sight offers difficulties. The Glencartholm fishes occur in a thin belt of shaly sediments among the Glencartholm volcanic group, and the other fauna includes not only scorpions and plants, but also a number of marine invertebrates such as *Orthoceras*. However, Peach and Horne (1903), in their excellent account of these deposits, make these illuminating comments: " . . . the fishes are usually found underneath a band in which *Orthoceras* is a conspicuous fossil. The scorpions and plants usually occur together in a separate bed, while the crustaceans are found in association with the fishes" (p. 845). In fact, there is no true intermingling. Peach and Horne also conclude (p. 845), "In view of the evidence regarding the conditions of entombment of the organic remains, it is highly probable that the Glencartholm shales may have been deposited in a muddy creek, shut off at intervals from the open ocean." The present writer feels that the Glencartholm occurrence is not enough to overthrow the generalities advanced above.

Most of these early forms seem to have been fairly heavily ossified, at least compared with certain later forms. Without any compensatory device, therefore, they might be expected to sink fairly rapidly in fresh waters; it is probable that the air bladder functioned mainly as a hydrostatic balancing device, enabling the specific gravity of the entire fish to be controlled within certain limits. The heterocercal tail has a great importance in this respect; it has been shown above that the action of such a fin will produce in the swimming fish not only a propulsive force, but also an upward thrust applied to the fin web. The pitching moment of this upward force about the center of gravity is normally balanced by an opposite pitching moment produced by the forward movement against the water of inclined surfaces at the anterior end of the body, in particular by the action of the pectoral fins. Ability to control the angle of incidence of these fins would provide a most delicate control of pitching movement during swimming, but the net effect must have been to drive the fish up towards the surface. It is, therefore, entirely reasonable to view the nature of the paired fins and the tail as necessary structural devices for the maintenance of active, comparatively heavy forms.

These fishes lived in continental fresh waters, cruising in the upper layers as a rule, and were normally active, predaceous fishes. These waters were often reasonably well oxygenated, as may be deduced from the occurrence of rich benthonic faunas; but sometimes in the Old Red Sandstone and more often in the Carboniferous and early Permian (especially in coal-swamp regions), the nature

of the sediments, no less than the limitations of the fauna, indicate that the waters were de-oxygenated to a great extent, and probably with a high CO_2 content. In these conditions other means of respiration besides gills, e.g., branchial and pharyngeal pouches, diverticula of the gut, etc., may have been necessary, and it is not unlikely that the air bladder in at least some forms was a functional lung. This must have resulted in still greater necessity of control by the fins in the hydrostatic balance of the swimming fish.

This type of body form remains standard for early Actinopterygii as late as the middle of the Permian. Even before that time, however, various remarkable modifications of structure are known. *Tarrasius* (Moy-Thomas, 1934; Moy-Thomas and Dyne, 1938) is particularly instructive from this point of view. The structure of the head shows it to be a fairly normal actinopterygian, and yet the body is almost of larval simplicity, without any great differentiation of median fins from a continuous fin fold extending from the nape to the tip of the body and halfway forward along the ventral side. This type of median fin would not be used for producing a lifting and propelling force of the kind noted above, but would probably be used for propulsion by the transmission of rippling undulations along the length of the fin. This method of progression would not need a balancing upward drive from the incidence of the pectoral fins, and it is very satisfactory to find that these fins, which are fully described by Moy-Thomas (1934), were held in about the same position as those of the living *Polypterus*, that is, with the web of the fin more or less parallel to the flanks. This structural pattern implies a lack of the lifting force of normal palaeoniscoids, and this can at once be explained by the fact that *Tarrasius* is far less ossified than most forms; scales are found only on the caudal region. It may, therefore, be assumed that *Tarrasius* was of approximately the same bulk specific gravity as its environment. The modifications of pattern noted in *Phanerorhynchus*, Haplolepidae, *Aeduella*, etc., do not seem to imply any noteworthy change from the "standard" type of swimming mechanism, although the changes in skull anatomy may be very considerable. The deep-bodied palaeoniscoid derivatives, e.g., *Platysomus* and *Amphicentrum*, which existed in Carboniferous and Permian times, are also provided with heterocercal tails, and it is likely that they controlled their bodily rise and fall, as well as their pitching movements, in a manner comparable with that deduced for "palaeoniscids."

It is evident that this considerable unity of dynamic structure contrasts exceedingly with the well-known fish faunas of late Permian and Triassic age. In many members of these faunas the heterocercal tail is greatly reduced, either by thinning, or by shortening, of the caudal extension of the body; hemi-heterocercal or practically homocercal tails become common at this time. This remarkable change in the whole aspect of the actinopterygian faunas has been used by Brough as the essential basis of his separation of the "Order Sub-Holostei." It is legitimate to consider this change as a mark of widespread functional changes, and the study of the geological background provides a very convincing proof of this assumption.

The chief theaters of evolution of the bony fishes in Devonian and Carboniferous times included what are now parts of northeast Europe, Spitzbergen, Greenland, and other Arctic lands, and the Appalachian and Acadian regions of North America. Devonian and early Carboniferous fish faunas of the same type are known in Australia and Antarctica, but the subsequent glaciations in those continents must have broken the continuity of evolution there. In the northwest European, Arctic, and American regions the dominating physiographical *motif* of Devonian and early Carboniferous times was the denudation of the mountain chains formed during the Caledonian (*sensu lato*) and Acadian orogenies. The débris first filled in the main basins, then by late Carboniferous times had in places spread as immense piedmonts almost at sea level, the sites of the extensive coal swamps. In the fresh, or at any rate non-marine, waters of these continental basins and later in the sluggish or stagnant waters of the coal swamps, the early actinopterygians flourished. Towards the middle of the Carboniferous, crumpling forces increased in magnitude, and by the middle Permian another great orogenetic period had passed its climax and resulted in the Appalachian,

Armorican, and Hercynian mountain chains. In western Europe this resulted in the delimitation of a great area enclosed between the remnants of the Caledonian chain and the Armorican-Hercynian front, and this area was invaded by the Permian seas in which were laid down the Kupferschiefer and Marl Slate and the Zechstein and Magnesian Limestone. It is an important point that the fish fauna of the Marl Slate and Kupferschiefer includes the descendants of late Carboniferous genera of coal-swamp habitat. *Palaeoniscus* is closest to *Elonichthys*, *Pygopterus* is a very close relative of *Nematoptychius*, *Acrolepis* and *Platysomus* are little changed from Carboniferous species, and *Globulodus* is probably a large amphicentrid. The available evidence tends to show that these Marl Slate-Kupferschiefer fishes were of lagoonar habitat, and no doubt the influx of salt water was so gradual that succeeding generations were able to acquire a control of the different physiological environment. Indeed, these Permian fishes are on the average larger in size than a comparable Coal-Measures association. It is further important that close relatives of some of these fishes persist in early Triassic truly marine faunas: *Glaucolepis* is very similar to *Palaeoniscus* and occurs in Madagascar, Spitzbergen, and Greenland, while *Pygopterus* is recorded from Spitzbergen. Moreover, this clear indication that fresh-water Carboniferous fishes gave rise to marine late Permian and Triassic forms is borne out by our knowledge of several other groups. Thus Woodward (1910, p. 5) and Moy-Thomas (1935, p. 223) have noted that the Eotriassic species *Coelacanthus madagascariensis* is generically indistinguishable from the late Carboniferous fresh-water forms recently referred by the latter (1937b) to the genus *Rhabdoderma*. Again, it is now generally accepted, after the investigations of Brough (1935) and Moy-Thomas (1936), that the marine Mesozoic hybodont sharks are the direct descendants of late Carboniferous forms allied to *Petrodus* and descended from early Carboniferous ctenacanths; and the marine Mesozoic Holocephali are now regarded as derivatives of late Carboniferous bradyodonts similar to *Helodus*, which flourished in fresh waters.

This change in fish faunas is indeed even more remarkable than has been indicated. The different conditions in Permian times of areas which had been richly populated with fishes of fresh-water habitat are shown by the extinction in the early Permian of acanthodians, many bradyodonts, and rhipidistian Crossopterygii, and also by the considerable change in the tetrapod faunas. The Phyllospondyli, Adelospondyli, and Lepospondyli die out, while at the same time the rise of reptiles and terrestrial Stegocephalia during the Permian is very marked.

Taking these factors into consideration, it is a reasonable deduction that a very important series of environmental changes mark the Permian period, and the nature of the changes suggests very strongly that a comparatively restricted area was the theater of evolutionary activity among the aquatic vertebrates in late Carboniferous times. This at first dominantly continental region was in part desiccated, in part invaded, by Permian seas, and only the more adaptable members of the existing vertebrate faunas were able to change over to terrestrial or to marine habitats.

This new adaptation implies considerable modifications of physiological activities of various kinds, but one result is very important. In exchanging fresh for marine waters the fishes had entered a medium of higher specific gravity. This means that a good deal of the lift previously necessary for keeping fishes from sinking would now no longer be required. In such circumstances it seems that two changes might be effected: (a) modification of the gross specific gravity of the fish by means of increased ossification or reduction of the air bladder, or (b) loss of the structural devices for providing "lift."

It is likely that some palaeoniscoids were able at first to struggle on, without change of form, by reduction of the air bladder, but this would reduce the range of hydrostatic balance very dangerously. Increase in gross specific gravity, too, is a very doubtful factor in this adjustment, since extensive ossification would demand great changes in the calcium metabolism in an environment probably less rich in calcium salts than the fresh waters of Carboniferous times. It is, therefore, a very simple matter to deduce a probable reduction in the heterocercal tail, and perhaps also a change in function of the pectoral fins, in

several stocks of fishes which survived the change over with little diminution in vigor. Apart from *Tarrasius*, the structure of which can be adequately explained, the earliest actinopterygian fish with a notable modification of the tail is *Acentrophorus*, from shallow-water, marine, Upper Permian rocks, and the subsequent enormous decrease of fishes with the old heterocercal tail has been well expressed in diagrammatic form by Brough (1931, fig. 19). Recently Brough has suggested that the great Triassic change in the Actinopterygii is due to mutation of equivalent genes in closely related fishes, thus producing parallel evolution (see also Wade, 1941, p. 395). In so far as the morphology of the adult fish may be viewed as the result of the operation of the gene complement, this may be partly true, but the rise to dominance of the "advanced" forms of Actinopterygii found in the early Triassic can only mean that they were at least as successful in competing with their environment as the palaeoniscoids were in the late Carboniferous fresh waters, and it seems more reasonable to regard the "parallel evolution" as a result of a widespread adaptation to change in environment.

It is necessary to insist that the "parallel evolution" noted by Brough is largely confined to the nature of the tail; even there it may be urged that the different methods of reduction of the body lobe are an indication of a "functional" rather than a "mutational" explanation of the change. In the cranial structure particularly, the Triassic "Sub-Holostei" are very divergent, and it is almost certain that the Semionotidae and Parasemionotidae, to take two examples of palaeoniscoid derivatives, were derived at very different times from quite distinct groups of palaeoniscoids. The difference in time of origin must be measured in millions of generations, and parallel evolution of a gene complex after such a lapse of time will hardly commend itself as a satisfactory explanation. If the tail form be regarded as a feature largely correlated with change of hydrodynamic function, so that many groups of Actinopterygii could suffer similar changes at the same time, it cannot be regarded as a satisfactory classificatory character. We are, therefore, free to regard the "Sub-Holostei" and "Holostei" as extremely diverse groups of polyphyletic origin. In spite of this the stratigraphical use of the terms "Sub-Holostei" and "Holostei" is considerable, since they represent the transition stages from heterocercal to homocercal tails, which were only of limited duration.

The general impression derived from summary reading of the literature and from Brough's diagnosis of the "Order Sub-Holostei" is that certain cranial characters are closely correlated with tail form. The most important of these is the more forwardly directed suspensorium. But is this really true? Forms such as *Canobius*, *Haplolepis*, *Aeduella*, and probably many of the late Stephanian and early Permian forms from Bohemia described by Fritsch have developed this character quite as much as the majority of early Triassic "Sub-Holostei." Our knowledge of Permian, and especially of Lower Permian, fish faunas is so slight that only a weighted guess can be made as to their constitution, but it is very likely that the palaeoniscoids, which already included many diverse types in the Carboniferous, underwent still further differentiation in the skull pattern before the great Triassic change in body form. The diversity of cranial structure in many of the species from the Lower Permian described by Fritsch (1893) is significant from this point of view.

The change in scale histology has also been adduced as an example of the parallel evolution of a character in Triassic forms. The evidence for this is extremely slender, since the scale histology of many groups of palaeoniscoids is unknown, and, moreover, Aldinger (1937) has demonstrated the extraordinary variety of scale structure in palaeoniscoids. Gross (1935, p. 48, etc.) has also demonstrated the presence of remnants of the dentine layer in *Lepidotus minor* (a late Mesozoic "holostean") and the Jurassic *Ptycholepis hollensis*, which is a very interesting case, since it is almost a full "holostean," of which the "subholostean" and even perhaps the palaeoniscoid ancestors can be indicated. There is no doubt that the loss of the dentine layer from the scale is widespread in Mesozoic ganoids, and it certainly took place in many phylogenetic lines, but much more knowledge of scale histology in these fishes as well as in

palaeoniscoids is necessary before a satisfactory general account of the changes can be given. Moreover, the Triassic palaeoniscoid *Gyrolepis* (Aldinger, 1937, pp. 241–245) has apparently lost its cosmine.

The post-Permian history of the Actinopterygii remains to be considered. No late Permian or very early Triassic fresh-water faunas with abundant Actinopterygii have been described, but abundant collections have been made from marine rocks of these ages in the following areas:

LATE PERMIAN

Marl Slate of England
Kupferschiefer of Germany
East Greenland, Kazan, Kungur of Russia

EARLY TRIAS

East Greenland
Madagascar
Spitzbergen

The earliest "holostean" (*Acentrophorus*) occurs in the Marl Slate and Kupferschiefer, but the bulk of late Permian forms are still palaeoniscoids. In early Triassic times the palaeoniscoids are fewer, and "subholostean" families become important. In the marine Middle Triassic faunas of the Muschelkalk and Besano (Alpine Trias) palaeoniscoids are uncommon, but a remarkable variety of "subholostean" and holostean families imposes a characteristic aspect on the faunas. During the late Triassic and very early Jurassic, as Brough (1939) has shown, the "Sub-Holostei" become unimportant and are replaced by the "holostean" families Semionotidae, Eugnathidae, and Pholidophoridae as dominant elements of the actinopterygian fauna.

In the seas of Triassic times, therefore, a very rapid evolution of palaeoniscoid derivatives may be discerned. But Triassic fresh-water deposits have also yielded actinopterygian faunas, and a consideration of these is of much interest. The following are the important faunas:

LOWER TRIASSIC (UPPER PART)	MIDDLE TRIASSIC	LATE TRIASSIC
Gosford, New South Wales Woodward, 1890 Wade, 1940	Bekker's Kraal, South Africa (lower *Cynognathus* zone) Brough, 1931, 1934 Brookvale, New South Wales (Hawkesbury Sandstone) Wade, 1935	St. Peters, New South Wales (lowest Upper Trias) Woodward, 1908 Wade, 1941 Newark beds, United States Eastman, 1904, 1911, 1914 Brough, 1931 Keuper of Germany and Britain: occasional finds

The extraordinary abundance of individuals in some of these faunas is contrasted by the small variety. Few families of Actinopterygii are developed; the number of genera (and species) in each is indicated.

	LOWER TRIASSIC	MIDDLE TRIASSIC		UPPER TRIASSIC
	Gosford	Bekker's Kraal	Brookvale	Newark
Palaeoniscoidei	2 (3)	2 (3)	6 (9)	—
Catopteridae	1 (3)	3 (7)	7 (9)	2 (3)
Perleididae	4 (7)	1 (1)	2 (2)	—
Cleithrolepidae	1 (2)	2 (3)	1 (2)	—
Saurichthyidae	1 (2)	—	1 (2)	—
Pholidopleuridae	—	—	1 (2)	—
Ptycholepidae	—	—	1 (1)	1 (1)
Semionotidae	—	—	—	1 (many)

It is further remarkable that these faunas show great conservatism. The latest-known developments of several of these families are in Triassic fresh-water rocks, and Brough has drawn attention to this phenomenon. It is further interesting that the faunas are extraordinarily cosmopolitan in appearance. This appearance is perhaps most remarkable in the case of the Catopteridae, which are unknown in marine faunas. However, all the families listed above, with the exception of Catopteridae and Cleithrolepidae, are known from marine faunas of earlier date than their first appearance in fresh waters, and there is probably no valid objection to the view that the marine late Permian and Triassic actinopterygian fishes were largely shallow water, often lagoonar forms which could easily enter fresh waters again. Wade (1941, p. 395) has commented on the immigrant nature of the Australian Triassic fresh-water faunas. The Catopteridae and Cleithrolepidae have been discussed by Brough (1931, 1934, 1936). The latter family is shown by Brough to be probably a deep-bodied perleidid derivative; it would not be surprising if this were true, because for a short period, about the Middle Trias, the Perleididae appear to have been among the commonest Actinopterygii. The history of the Catopteridae is quite obscure, but in view of the probability that all the other families of these fresh-water middle and late Triassic actinopterygian fishes must be regarded as derivatives from forms found abundantly in certain marine strata of somewhat earlier age, it seems possible that this eminently fresh-water family should also be a derivative from marine fishes of late Permian or early Triassic age. Any discussion of the subsequent history of actinopterygian fishes would be quite outside the scope of this paper. It is believed, however, that a good case has been made out for the following conclusions.

1. The early Actinopterygii are rarely found in normal marine deposits. The main theater of actinopterygian evolution in late Devonian, Carboniferious, and early Permian times included the continental fresh waters of northwest Europe, and the Appalachian region of North America.

2. These early Actinopterygii are characterized by their heterocercal tail structure and are usually known as the Palaeoniscoidei.

3. The Palaeoniscoidei comprise numerous evolutionary lines, and some of these become progressively more distinct. In particular, several Carboniferous and Permian types show a forward movement of the suspensorium. The heterocercal tail, however, imposes a uniform appearance on these various lineages.

4. Important earth movements in later Carboniferous and early Permian times were followed by progressive desiccation, and there was in the late Permian a widespread shallow marine invasion of parts of Europe and Greenland.

5. These factors account satisfactorily for the decline and extinction of several groups of Carboniferous and early Permian vertebrates.

6. Several groups of Actinopterygii successfully adapted themselves to the new conditions. Important faunas are known from several localities in marine rocks of late Permian and early Triassic age. In many cases it is very highly probable that elements of these faunas have been derived from fresh-water forms of earlier age.

7. These marine faunas were probably at first largely of shallow-water, often lagoonar, habitat. They were capable of greater migrations and seem in turn to have colonized several continental areas of dominantly fresh-water sedimentation in the middle and late Triassic (e.g., in South Africa, Australia, northeast United States). In these fresh-water faunas are found late members of stocks, mostly short lived, known from earlier marine horizons.

8. The main subsequent evolution of Actinopterygii was in the sea and led finally to the dominance of the Teleostei. Minor groups have succeeded in existing to the present day and comprise the sturgeons and *Polyodon*, *Amia*, *Lepidosteus*, and perhaps the Polypterini. The majority of these occur in fresh waters, which are often regarded with good reason as a retreat for certain fishes faced with intensive competition from other, more successful, forms.

ECOLOGICAL NOTES

THE PHYSICAL ENVIRONMENT OF HAPLOLEPIDAE

THE HAPLOLEPIDAE, as far as they are known, are restricted to the Coal Measures of late Carboniferous age. They occur in deposits of the following types: (a) "cannel" coals, e.g., Linton, Nýřany; (b) very carbonaceous canneloid shales closely associated with coal seams, e.g., Cannelton, Newsham, Longton; (c) ironstone nodules, e.g., Mazon Creek.

The origin of cannel and allied coals has been the subject of considerable speculation; there is now little doubt that these peculiar sediments were formed in shallow, stagnant water as accumulation of organic (mostly plant) débris. The cannels are rarely extensive and sometimes occupy areas which strongly suggest that they were formed in a temporary pool, such as an abandoned or occasional channel of one of the sluggish drainage ways of the coal swamps. This is clearly shown in many of the American occurrences described by Ashley (1918, see especially pp. 31–34), and in the case of the famous vertebrate-yielding seam of Jarrow Colliery, Kilkenny, Ireland (Hallisey, 1939, p. 333). Certain cannels of this type include very abundant remains of fishes and amphibians.

The carbonaceous shales from many Coal-Measures localities which yield vertebrate fossils are essentially impure cannels, with a greater admixture of very fine-grained sediments. The conditions of sedimentation were probably not greatly different from those necessary for the formation of the true cannels.

Ironstone nodules, such as those found at Mazon Creek, are generally believed to have been deposited in stagnant shallow waters (Twenhofel, 1926, pp. 351, 584). They occasionally pass laterally into carbonaceous shales (blackband ironstones). The Mazon Creek flora is abundant and well preserved, and there can be little doubt that the nodules were formed in shallow waters in close proximity to thick growths of the usual Coal-Measures vegetation.

In each case, therefore, the Haplolepidae occur in rocks that can be regarded as having been formed in stagnant shallow waters, into which an abundance of organic material was constantly being transported. It is surprising that sediments laid down in such conditions should contain so many fossils, because the waters would be almost entirely de-oxygenated. It is always possible that the fauna did not actually live in such waters, but that either remains were carried in, or fishes entering the area were killed off. On the other hand, numbers of fishes live today in somewhat similar environments (e.g., the Gran Chaco swamps, see Carter and Beadle, 1930, 1931), and the amphibians which accompany the fishes from the cannels, etc., would be little affected by de-oxygenated waters.

Carter and Beadle (1930, 1931) have given a very convenient account of the environment and respiratory adaptations of a number of fishes living in the stagnant swamps of the Paraguayan Chaco. No fewer than six independent types of aerial respiration were distinguished by these writers in seven genera studied: (1) pharyngeal diverticula; (2) diverticula of the branchial chamber; (3) branchial chamber filled with air; (4) epithelium of pharynx respiratory; (5) air bladder and lung; (6) stomach and intestine modified for respiration. It is impossible to be sure of the occurrence of any such structures in Haplolepidae, but the modified opercular apparatus may be of significance in this respect.

The conditions in the Paraguayan Chaco swamps are of some interest for comparison with the environment deduced for the Haplolepidae. The South American swamps occupy shallow east-west valleys, being thus narrow in proportion to their length. The surrounding country is very little higher and forms open grassy plains. A considerable vegetation grows in the swamps. The water is rarely more than 3 or 4 feet deep. The bottom is everywhere a black mud, 2 or 3 feet thick, containing much gas, and resting on several feet of clay passing down into many hundreds of feet of silt. The waters of the swamps have a very low oxygen content; the stagnant conditions necessary for this are maintained by

the absence of such diurnal temperature changes as would mix the waters, by the protection against disturbance afforded by the vegetation growing above the water, by the lack of abundant phytoplankton owing to the opacity of the water, and by the energetic bacterial decay in the bottom waters and the mud. In some pools the water may be sufficiently clear for the photosynthetic activity of a large phytoplankton, and in such cases there may be more oxygen in the water and a more abundant fauna. The waters of the swamps have a very great content of CO_2 (average, 50–70 cc. per liter), a pH on the acid side of neutrality (average, say, 6.6), and an extremely low oxygen content; the deeper waters are greatly impoverished in oxygen, and values below 0.2 cc. per liter were found to be common. Only in the thin (1 or 2 inches) surface layers did Carter and Beadle ever find the oxygen content to be of the order of 2 or 3 cc. per liter, and even here the value often fell almost to zero. It is probable that these conditions are not very different from those obtaining in the shallow cannel pools of the Coal Measures. Carter and Beadle (1930, p. 257) suggest "that similar conditions will be found to occur in other tropical waters which resemble those of these swamps in the following respects:

"1. A small phytoplankton either on account of the opacity of the water or its unsuitable chemical composition. [Note: A large phytoplankton will produce much oxygen; opacity of the water reduces the penetration of ultraviolet light and thus the rate of photosynthesis.—T.S.W.]

"2. The absence of disturbance.

"3. The presence of much aerial plant-life in and around the water."

The black muds of the Paraguayan swamps, in the due course of geological time, would be capable of being transformed into carbonaceous fine-grained rocks very similar to some of the shaly cannels or splint shales of the Carboniferous.

It is interesting to consider the adaptation of Haplolepidae to conditions of this kind. The strongly hetercercal tail and the carriage of the pectoral fins would combine to drive the fish towards the surface while swimming; the low dorsal fin could probably be collapsed, allowing the fish to skim the under surface of the water. It is possible that in such a situation the instability of the swimming fish to yawing moments would be increased, and the control of quick lateral turning would then be much increased. Such sub-surface swimming would demand a very nice control of pitching movements; this was probably achieved by varying the angle of incidence of the pectoral fins. It is possible that the very high flank scales found in some species of *Haplolepis* were of structural use in preventing too easy flexure of the body in the vertical plane, and thus controlling the strong pitching moments experienced by an actively swimming fish very flexible in that plane.

A strongly heterocercal tail form has recently been shown by Grove and Newell (1939) to be correlated with the high specific gravity of the fish with regard to its swimming medium. In fishes of the form of *Haplolepis* the center of gravity must have been far forward in the trunk, and it is very likely that there was developed an air bladder of the usual actinopterygian type. In living Actinopterygii the air bladder functions mainly as a means of hydrostatic control; in the fishes such as *Haplolepis*, which lived in very poorly oxygenated waters, the air bladder may have fulfilled important respiratory functions. In this connection the great reduction in the opercular plates in Haplolepidae may be significant as an indication that the gills were of less importance in respiration. These small fishes seem to be admirably suited to take bubbles of air at the surface, and the absence of the typical palaeoniscoid snout must have made this easier.

Another possibility which cannot at once

PLATE 9

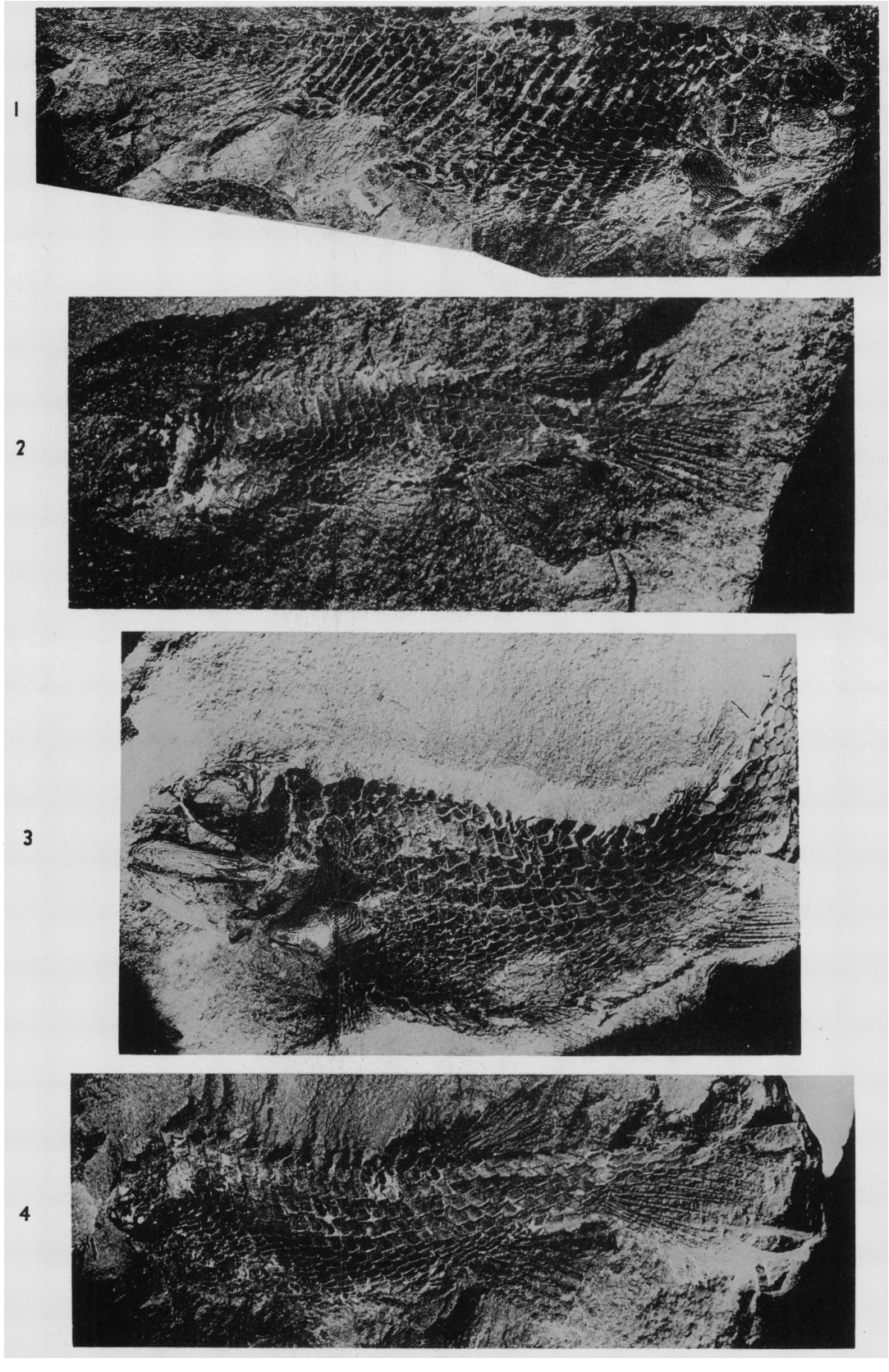
Pyritocephalus sculptus Fritsch. Nýřany, Czechoslovakia

1. B.M.N.H. No. P.21989. ×4.5.
2. Westoll collection No. W.171. ×4.5.

Both are impressions of the ventral structures of the head and squamation. Lighting from top left.

1

2


1
2
3
4

be dismissed is that these small fishes had developed external gill filaments. The peculiar division of the opercular fold could then be regarded as an adaptation necessary for the functioning of such gills, which might be very useful to fishes swimming so much in the somewhat better oxygenated surface waters. Powers (1932) has discussed certain physicochemical problems presented by the swim bladder of teleost fishes considered as a respiratory organ. He concludes that there are great difficulties in the simultaneous use of the swim bladder and gills. The blood from the swim bladder (presumably enriched in oxygen) passes through the capillaries of the gills before reaching the tissues, so that the oxygen would be lost there unless the gills could be excluded from contact with the poorly oxygenated waters outside by closure of the mouth and gill cover. But if this is done, elimination of CO_2 by the gills will be inhibited (*op. cit.*, p. 462). This would seem to make it unlikely that an air bladder would be used for respiratory purposes in a fish with external gills. Powers concludes (p. 463) that it seems more reasonable to suppose "that fishes with pneumatic ducts that 'break' in water low in oxygen swallow the air, and both swim-bladder and gills perform the function of gaseous exchange as do lungs, unless the gills are cut off entirely by closure of the opercula. In that case the gills would be obsolete, and the swim-bladder would act entirely as lung." Hence unless some remarkable modification of the vascular supply of the swim bladder be assumed it is probable that the Haplolepidae had *either* auxiliary respiratory structures such as lung-like air bladders or branchial diverticula, *or* external gills. In view of the nature of the snout and the probable ability of Haplolepidae to take bubbles of air, the possession of external gill filaments is considered to be unlikely.

ASSOCIATED FAUNAS

It is very difficult to offer a complete list of the associated vertebrate and invertebrate life in the waters which were the home of the Haplolepidae. Lists covering the known faunas of most of the localities have been available for many years, but in spite of recent revisions of parts of the tetrapod faunas there are many difficulties in assessing the affinities of even the tetrapods, and the lists of fishes are frequently highly unreliable. An attempt is made in the adjoined tables to present the main elements of the faunas. Some forms are omitted; others are in such obvious need of revision that they are indicated only with doubt. In spite of this, some very remarkable features are at once obvious. A number of peculiar, specialized, and recognizable forms accompany the Haplolepidae in almost every fauna except those of Cannelton (which is very sparse indeed, and related to that of Linton, Ohio) and Mazon Creek. The important members of this associated faunal assemblage are the nectridians *Urocordylus* (including *Sauropleura*) and *Keraterpeton* (with its allies *Batrachiderpeton*, *Diceratosaurus*); the aistopods *Ophiderpeton* and *Dolichosoma* (with its close relative *Phlegethontia*); and loxommid and anthracosaurid Embolomeri.[1] In a few localities some of these forms are missing. This may be explained, at least in part, by the very unequal opportunities of collecting, but it may also

[1] Nopcsa (1934, p. 71) has already given an incomplete account of these resemblances.

PLATE 10

American *Pyritocephalus*

1. *Pyritocephalus lineatus* (Newberry). Linton, Ohio. U.S.N.M. No. 4443. ×2.4.
2. *Pyritocephalus gracilis* (Meek and Worthen). Mazon Creek, Illinois. Holotype of *Teleopterina improvisa* Berg, U.S.N.M. No. 4401. ×4.5.
3. *Pyritocephalus gracilis* (Meek and Worthen). Mazon Creek, Illinois. Chicago, Walker Museum. ×3.1.
4. *Pyritocephalus comptus*, new species. Mazon Creek, Illinois. Holotype, U.S.N.M. No. 4310. ×3.9.

Lighting from top left.

TABLE 3

OCCURRENCE OF CERTAIN FISHES IN HAPLOLEPID-YIELDING STRATA AND AT JARROW

	Newsham	Longton	Jarrow	Nýřany	Linton	Mazon Creek
Acanthodes, Acanthodepsis	x	x	x?	x		x
Pleuracanthus	x	x		x	x	x
Euctenius	x	x		x	x	
Ctenodus	x		x	x	x	x
Sagenodus	x			x?	x	x
Megalichthys	x	x	x		x?	
Coelacanthus	x	x			x	x
Elonichthys	x				x	x
Platysomus	x					x
Amphicentrum	x	x			x	x

N.B. All these forms are widely distributed in Coal-Measures faunas.

TABLE 4

OCCURRENCE OF TETRAPODS IN HAPLOLEPID-YIELDING STRATA AND AT JARROW

	Newsham	Longton	Jarrow	Nýřany	Linton	Mazon Creek
Nectridia						
Urocordylus			x	x		
Sauropleura					x	
?*Lepterpeton*			x	x?		
Scincosaurus				x		
Batrachiderpeton	x					
Diceratosaurus					x	
Keraterpeton	x	x	x			
Aistopoda						
Ophiderpeton	x		x	x	x	
Dolichosoma			x	x		
Phlegethontia					x	
Adelospondyli						
Cocytinus					x	
Pleuroptyx					x	
Cephalerpeton						x
Microbrachis				x		
Hyloplesion				x		
Loxommoidea						
Loxomma		x		x		
Orthosauriscus	x				x	
Macrerpeton					x	
Anthracosauroidea	x	x	x	x	x	x
Rhachitomi				x	x	
Phyllospondyli				x	x	x
Reptilia				x	x	

indicate real differences in faunas due to absence of certain elements by reason of physical or physiological barriers in migration. Leaving out of account the Embolomeri, members of a very widespread group, it is a remarkable fact that these genera are practically confined to the haplolepid-yielding localities (except Cannelton and Mazon Creek) and to Jarrow, Kilkenny. At the latter place they are accompanied by a badly known fish fauna and by several undescribed Amphibia (Huxley and Wright, 1867). Hap-

lolepidae are not recorded from Jarrow but might easily escape attention or recognition.

Other elements of the tetrapod faunas show little correspondence and are either of more widespread distribution (e.g., Rhachitomi) or seem to be peculiar to single faunas (e.g., *Ricnodon*). The case of the adelospondyls is interesting, because *Cocytinus* (from Linton) is clearly ancestral to *Lysorophus* of the Stephanian of Illinois and the early Permian of Texas. The relations of the coal-swamp faunas to the "red-beds" faunas will be discussed later. However, the Adelospondyli described from other localities do not seem to be closely related.

It is quite remarkable to discover that the Nectridia and Aistopoda, including the most curiously specialized among Carboniferous tetrapods, should accompany the Haplolepidae so frequently and should occur practically nowhere else in Westphalian sediments. It suggests, indeed, that these form together part of a "facies fauna" which it is now proposed to consider. Comparison of all the fish faunas shows that only about 10 genera can be considered from this point of view, all others being too restricted in distribution among the localities considered and too widely distributed elsewhere. Of these 10, only the Dipnoi, *Megalichthys*, *Coelacanthus*, *Euctenius*, and *Pleuracanthus* are found in a majority of the faunas, and all are so widely distributed in Coal-Measures faunas that they need hardly be considered further. They form part of a generalized coal-swamp vertebrate fauna, together with labyrinthodonts (in the sense of Temnospondyli), phyllospondyls, varied "Adelospondyls," and (in the higher Westphalian and later beds) rare early reptiles. The presence of the haplolepid-nectridian-aistopodan group imposes a very characteristic appearance on the fauna. However, it is as well to point out that isolated genera of this group may be represented in other faunas, but very rarely. The only examples known to the writer are from the Stephanian of Kounova, west of Prague (?*Keraterpeton* and *Ophiderpeton*), from the topmost Stephanian of Kostalov (*Urocordylus*), from the early Permian of Olivetin, south of the Riesengebirge (*Palaeosiren*, said to resemble *Ophiderpeton* and *Dolichosoma*), from the early Permian (Wellington) of Orlando, Oklahoma (*Crossotelos* and *Cricotillus*, Nectridia), and finally *Diplocaulus*, a late specialized nectridian from the United States (from the middle of the McLeansboro [Lower Stephanian] of Illinois, and the uppermost Stephanian and early Permian of Texas and Oklahoma). All these occurrences are of later date than those studied here, and it is very reasonable to regard them as the last straggling survivors, in changing conditions, of a characteristic Westphalian assemblage.

It is also necessary to insist on the fact that the members of this "facies fauna" of haplolepids, nectridians, and Aistopoda are present in varying concentration in the faunas studied. Thus at Newsham and Longton they are quite outnumbered by the other vertebrates, while at Nýřany and Linton they form at least a great part of the material that has been collected. In spite of these numerical differences, the groups must be regarded as part of a single "facies fauna" adapted to very strictly limited physiological and physical conditions, as may be inferred from the sporadic nature of their occurrence. The implications of this in the broader study of late Palaeozoic environments will be discussed later.

From this group of occurrences the Mazon Creek fauna stands quite apart. The fish fauna includes many widespread Coal-Measures genera, e.g., *Pleuracanthus*, *Acanthodes*, *Ctenodus*, *Sagenodus*, *Coelacanthus*, *Elonichthys*, *Platysomus*, and *Amphicentrum*, and, with these, rare Haplolepidae. The tetrapods have been monographed by Moodie (1916), but his descriptions are not adequate for comparative purposes, and I am indebted to Prof. D. M. S. Watson for information on the fauna which is incorporated in the following notes.[1]

1. *Amphibamus grandiceps* and *Miobatrachus* are closely related: they have phyllospondyl neural arches and intercentra and pleurocentra.

2. *Micrerpeton* and *Eumicrerpeton* are also probably phyllospondyls.

3. *Cephalerpeton* is an adelospondyl with a deep, triangular, pointed head.

4. *Amphibamus thoracatus* is not related to *A. grandiceps*. This form, with the two species

[1] Recently a full account has been published (Watson, 1940).

of *Mazonerpeton*, *Erierpeton*, and *Erpetobrachium*, is indeterminable for the purpose of comparison.

5. *Spondylerpeton* is an embolomere. (It is noteworthy that the neural arch is borne entirely by the pleurocentrum; this is a "reptilian" condition shared by anthracosaurid embolomeres.)

Clearly there is nothing in this fauna to suggest the presence of the nectridian-aistopodan element. It is probably significant that this locality is the only one in which the fossil-bearing stratum is not a carbonaceous shale or cannel. Although certain features of the sheet of water in which the animals lived were similar (e.g., comparative shallowness, probable de-oxygenation, etc.), it is quite certain that the difference in rock type indicates some differences in other aspects of the physicochemical, and in turn the biological, environment of the vertebrate faunas. This is another confirmation of the view that the haplolepid-nectridian-aistopodan assemblage is a "facies fauna," members of which strayed but rarely into other than a narrowly restricted environment.

FOOD RELATIONS

One of the most remarkable features of the thin, vertebrate-yielding strata that have been mentioned above is the almost complete lack of invertebrate remains. Case (1917; 1919, p. 199) has discussed the environment of the Linton fauna, and his observations can be paralleled in some of the other cannel localities. There are few more invertebrates recorded from Nýřany: Fritsch lists two species of the myriapod *Julus*, *Estheria (tenella?)*, *Gampsonychus krejcii*, and insect wings. Only at Mazon Creek does there appear an invertebrate fauna outnumbering the vertebrates, and it has already been shown that this locality is quite separate in its nature from all the others.

In these circumstances only the most tentative views concerning the food relations of the fishes can be entertained. That the small Haplolepidae, so common at Linton and Nýřany, formed a large part of the food of the rapacious larger fishes and Amphibia admits of no question. It is probable that other small fishes (such as acanthodians) and small Amphibia, such as some of the Aistopoda and Nectridia, formed another part of this ecological stratum. But while it is easy to account for the food of the larger rapacious fishes (such as *Elonichthys*, *Megalichthys*, etc.) and Amphibia, it is difficult to arrive at any certain conception of the food of the smaller species. The sharply conical teeth of the smaller Amphibia most strongly suggest a diet of young forms and of small invertebrates, but the very poor dentition of most Haplolepidae makes their food source more problematical. The conical teeth of *H. corrugata* indicate some ability to deal with larvae and small invertebrates. This character is not shared by other species, which have very slender, tiny, marginal teeth and, at least in some forms, low, more or less rounded teeth on the bones of the palate. It may be surmised that these species fed largely on the planktonic life that must at times have been abundant in the surface waters of the swamp, but which was so preyed upon, both alive and dead, as to leave little trace of its presence and which may have been poorly provided with hard parts capable of preservation. It is always possible that eggs and newly hatched young forms made up a large part of their food supply at certain seasons.

Many recent writers on the dietary ecology of fresh-water fishes have stressed the opportunism shown in the feeding, and there can be little doubt that most fishes will eat, within wide limits, whatever happens to be available. This is clearly shown, for example, in recent works on *Salmo* by Neill and Carpenter. Neill studied a small area of the Aberdeenshire Don in which there was no overhanging vegetation, and found a very small part of the stomach contents of the brown trout to be of subaerial origin, less than 2 per cent (1938, p. 508). On the other hand, at certain seasons, salmon parr, from stretches of the Cheshire Dee which were well shaded by trees and shrubs, had taken more than 70 per cent of their diet from subaerial organisms (Carpenter, 1940, p. 86). It is possible that subaerial organisms from the ecological environment of the marginal re-

gions of the Coal-Measures cannel pools contributed largely to the diet of these smaller fishes. It is necessary, however, to recall that the majority of the subaerial elements in these studies of present-day ecology are small insects belonging to groups which have no known representatives in the Carboniferous, though there may well have been other small organisms in analogous environments.

Haplolepid scales occur very frequently in coprolite-like masses and as scattered scales at Linton; one of the former was figured by Newberry (1873, pl. 38, fig. 5) as the "tail of a crustacean."

There can be little doubt that the Haplolepidae occupied a similar position in the ecological pattern of the other localities—Newsham, Longton, Mazon Creek—but their position was there more precarious because of the greater abundance of predaceous forms.

DISTRIBUTION OF THE HAPLOLEPIDAE

The haplolepid-nectridian-aistopodan faunas which have been described above have a significant bearing on certain problems of palaeogeography. These small vertebrates, which must have lived in a most strictly defined fresh-water swamp habitat, occur in rocks of Westphalian (perhaps also early Stephanian) age in Ohio, Ireland, England, and Bohemia. It is thus certain that these regions must then have enjoyed such physiographical conditions that free migration of the vertebrates was possible. The nature of the coal swamps in which the animals lived is now fairly well understood. Vast areas in northwest Europe and eastern North America were effectively extended piedmonts stretching in front of the partly degraded mountains resulting from the Taconic, Caledonian, Acadian, and (in part) early "Hercynian" orogeneses. These great areas were never far from sea level. Across them meandered numerous streams, no doubt braided and sluggish, and at times thick swamp vegetation was widespread. It was in the almost stagnant fresh waters of such a region that the fish and amphibian fauna of the Coal-Measures cannels and ironstones dwelt.

Their physiological environment has been analyzed above. It was certainly a very peculiar one, with its low oxygenation, high CO_2 content, pH probably <7, etc., and it seems quite inconceivable that the haplolepid-nectridian-aistopodan assemblage could have migrated between Ohio and Bohemia by passing downstream to the sea and passing along the littoral in very different physiological surroundings. In particular, the highly vascular auxiliary respiratory structures which, it has been shown above, were probably present in Haplolepidae would make osmotic regulation alone a great barrier to any successful migration *via* the seas. It is quite feasible to account for fairly long migrations by way of the braided streams and extensive standing waters of the coal swamps. This is perhaps the most convincing evidence for the nonexistence of the North Atlantic basin during late Carboniferous times.[1] The great similarity in the Coal-Measures floras and faunas of northwest Europe and North America is well known, but the presence of such closely related, highly specialized fishes implies a free and not very circuitous connection between the coal swamps of the two areas. There are other good indications of such continental continuity in middle and late Palaeozoic times. To give only two examples, the continental Old Red Sandstone fishes of Britain have remarkable links with Canada and Greenland (e.g., the distribution of *Phlyctaenaspis*, *Cheirolepis*, *Eusthenopteron*), and in late Carboniferous and early Permian times near relatives of some very characteristic tetrapods of Texan "Red Beds" occur also in Europe.

Evidence of land communications between North America and Europe from Devonian and earlier times at least as late as the Cretaceous has accumulated over many decades.[2] Much of the evidence merely indicates some kind of land communication, however indirect, but in late Palaeozoic and Mesozoic times there are many occurrences which seem to indicate a close and direct means of migration. It is unnecessary in this paper to deal at length with the diverse theories and hypotheses that have been set forth to ac-

[1] Cf. Nopcsa, 1934.

[2] Nopcsa (1934) has given an important review of this evidence.

count for the migrations. They may be divided roughly into two groups: those which postulate more or less unchanging relative positions of continental masses, with emergence and submergence of some kind of land bridge, and those based on some variety of intercontinental movement such as continental drift.

The case of the Haplolepidae can offer no decisive evidence in favor of either of these alternatives, but in the writer's opinion it is less easy to understand the distribution on the basis of "land bridges" than by accepting continental drift. The great circle distance between Nýřany (latitude approximately 49° 30′ north, longitude 13° east) and Linton, Ohio (latitude approximately 40° 30′ north, longitude 81° west) is about 62° 30′, roughly 6900 km. On the basis of the continental apposition with very loose fit advocated by Du Toit (1937, fig. 18), the great circle distance may be calculated as roughly 50°, or 5500 km., and with the much closer apposition of the continental masses favored by other "driftists" this distance may be shortened by anything up to 500 km. The difficulties in visualizing the migration of these specialized forms over the Coal-Measures swamps are much greater, the greater the distance of migration. The Haplolepidae, therefore, not only demonstrate the direct connection between the Coal-Measures swamps of Europe and North America, but provide another small factor in favor of continental drift.

FATE OF THE HAPLOLEPID FACIES FAUNA

Some of the effects of the changes in physiographical conditions in northwest Europe and North America have been discussed in a previous section (pp. 98–102). The new conditions are indicated by the increasing importance of terrestrial vertebrates, by changes in the nature of the flora, and by progressive changes in sedimentation. The new conditions of sedimentation are implied by the disappearance of coal-swamps sediments and the wide distribution of red beds. There has been much controversy about the nature of red beds, but it seems probable that a lowering of the water table was an important factor, with greater aeration of the soils and sediments. A certain amount of uplift and increasing aridity are indicated. Such conditions appear at notably different horizons in different places, as has already been emphasized by Case and by Romer (1934). It is, indeed, one of the most instructive examples of the non-synchronous nature of change of facies.

It is to be expected that highly specialized organisms restricted to a certain range of habitats in Coal-Measures times would be very unlikely to survive physiographical changes of such magnitude, and this certainly seems to be true of the haplolepid-nectridian-aistopodan facies fauna discussed above. The change begins in Europe north of the Hercynian-Armorican (i.e., Variscan, *sensu lato*) front before it affects the intermontane basins of France and Bohemia, so that it is not remarkable that we find stragglers (Nectridia and Aistopoda) in the Stephanian and early Permian of Bohemia. In North America a few Amphibia (Nectridia such as *Crossotelos* and *Diplocaulus*) persist into the true red beds. But there is at present no indication that any members of the Haplolepidae survived later than early Stephanian times. The Amphibia such as *Diplocaulus* which occur in the red beds were almost certainly semi-aquatic creatures, and presumably were much better able to withstand changes that would be physiologically insupportable to Haplolepidae.

SUMMARY

A GROUP OF late Carboniferous actinopterygian fishes is described and referred to the genera *Haplolepis* Miller, 1892 (syn. *Mecolepis* Newberry, 1856, *Eurylepis* Newberry, 1857—both preoccupied), and *Pyritocephalus* Fritsch, 1893 (syn. *Teleopterina* Berg, 1936). They are from six localities, of which the stratigraphical horizons can be stated by reference to Dix's succession of Coal-Measures floras. *Haplolepis* is divided into two new subgenera, *Haplolepis* (*sensu stricto*) and *Parahaplolepis*. The following species are described:

Haplolepis (*Haplolepis*) *ovoidea* (Newberry), Linton, Ohio, Zone H–I
(Syn. *Mecolepis ornatissimus* Newberry
Eurylepis minimus Newberry
Eurylepis macrops Newberry MS
?Mecolepis serratus Newberry)
Haplolepis (*Haplolepis*) cf. *ovoidea* (Newberry), Mazon Creek, Illinois, Zone H
Haplolepis (*Haplolepis*) aff. *ovoidea* (Newberry), Cannelton, Pennsylvania, Zone H
Haplolepis (*Haplolepis*) *corrugata* (Newberry), Linton, Ohio, Zone H–I
(Syn. *?Eurylepis striolatus* Newberry)
Haplolepis (*Haplolepis*) *attheyi*, new species, Newsham, Northumberland, Zone E
Haplolepis (*Parahaplolepis*) *tuberculata* (Newberry), Linton, Ohio, Zone H–I
(Syn. *Mecolepis granulatus* Newberry
Mecolepis insculptus Newberry)
Haplolepis (*Parahaplolepis*) cf. *tuberculata* (Newberry), Mazon Creek, Illinois, Zone H
Haplolepis (*Parahaplolepis*) *anglica* (Traquair), Longton, Staffordshire, Zone F
Haplolepis (*Parahaplolepis*) aff. *anglica* (Traquair), Newsham, Northumberland, Zone E
Pyritocephalus sculptus Fritsch, Nýřany, Bohemia, Zone H–I
Pyritocephalus lineatus (Newberry), Linton, Ohio, Zone H–I
Pyritocephalus gracilis (Newberry and Worthen), Mazon Creek, Illinois, Zone H
(Syn. *Teleopterina improvisa* Berg)
Pyritocephalus comptus, new species, Mazon Creek, Illinois, Zone H
Pyritocephalus rudis, new species, Newsham, Northumberland, Zone E

In several cases it has been possible to make very detailed reconstructions of the dermal bones and the body, but remains of the endoskeleton are too bad for description.

The fishes are shown to be closely related and sharply marked off from all other known Carboniferous Actinopterygii; the new family, Haplolepidae, is set up for their reception. It is shown that the family was probably derived from the lower Carboniferous *Canobius*, which in turn is derived through *Mesopoma* from a series of "normal" palaeoniscoids allied to *Rhadinichthys*. The family was thus well separated from most Carboniferous evolutionary lines within the palaeoniscoids. It is shown that *Aeduella* Westoll is not a close relative of the Haplolepidae and that the resemblances are largely due to parallel evolution; and that *Trissolepis* Fritsch, of which the skull roof has been described as fenestrated in a manner similar to that of *Pyritocephalus*, is probably of normal palaeoniscoid structure with an entire skull roof. The subgenera of *Haplolepis* and *Pyritocephalus* are separate throughout their known range, but *Pyritocephalus* was certainly derived from an early *Parahaplolepis*.

The comparative anatomy of the dermal bones, the body, and the fins is discussed in detail. Peculiar modifications of the skull roof and cheek, some of them independently undergone in different members of the group, are demonstrated. The development and significance of the paired fenestrations in the skull roof of *Pyritocephalus* are discussed. Attention is given also to the remarkable modifications of the snout, external nares, and opercular apparatus; to the presence of a flattened venter between the paired fins, associated with a modified course of the scale rows of the body; to the frequent development of very deep scales on the anterior flank; to the modifications leading to the extreme thinness of the scales; to the laterosensory system, which is very fully developed, and includes main and accessory, together with dorsal and ventral, lateral lines, the last described for the first time in an actinopterygian; and to the significance of the structure and nature of the dermal fin rays and of the relative positions of the fins.

Many of the characters demonstrated in Haplolepidae are to be found also in some

members of the "Holostei" and "Sub-Holostei." A critical discussion of the status of these unnatural groups leads to a general statement of a new hypothesis of the evolution of the "holostean" condition, in which it is shown that the characteristic modification of the tail fin has happened independently in different lineages and is correlated with a great change in habitat and environment. This section is based largely on a consideration of the fish as a swimming organism.

The geographical distribution of the Haplolepidae is remarkably extensive for so specialized a family. In particular, the highly specialized *Pyritocephalus sculptus* from Bohemia is extremely similar in all details to the contemporaneous *P. lineatus* from Ohio. An analysis of the probable conditions of deposition of the rocks yielding the fossils leads to the conclusion that the Haplolepidae were fresh-water fishes thoroughly adapted to life in stagnant swamps, and almost certainly incapable of migration by sea. The implications of such conclusions in the understanding of the distribution and nature of Coal-Measures swamps and on the theory of continental drift are considered. The faunas associated with Haplolepidae are shown to include certain peculiar Amphibia, the distribution of which is extremely closely correlated with that of the fishes. The fate of this "facies fauna" is described, and the food relations of the various members are briefly noted.

ADDENDA

OCTOBER 23, 1942

J. A. MOY-THOMAS (1942, p. 738) has described an interesting fish from strata of Carboniferous age in east Greenland. *Whiteichthys greenlandicus* is almost certainly a member of the group ancestral to Haplolepidae, though it is probably somewhat divergently specialized. The structure of the skull is extremely similar to that deduced for the immediate ancestor X (cf. fig. 36 of this paper, and Moy-Thomas, 1942, fig. 2). The resemblances extend to the nature and relations of the postrostral, the absence of nostril openings between the postrostral and nasals, the pattern of the skull roof (a dermosphenotic was probably present in *Whiteichthys*), and the bones of the opercular series. According to Moy-Thomas's figures there is no quadratojugal, but in poorly preserved material this bone is very rarely observed, even if present. There are also apparently no "suborbitals."

The body form is immediately comparable with that of Haplolepidae. The origin of the dorsal fin somewhat behind the anal and the shortness of the caudal pedicle are significant, and the "not very deeply cleft" tail is an interesting resemblance. The scale count, from Moy-Thomas's figure 1, is

$$\frac{31}{7 \quad 22 \quad 39}\ 45$$

The formula suggested for the *immediate* ancestor of haplolepids (p. 62) was

$$\frac{24}{7 \quad 17 \quad 30}\ 33$$

and it was noted above (pp. 86, 87, table 2) that the number of scale rows had probably decreased during the evolution of haplolepids. The extended pelvic and anal fins are points of difference from the Haplolepidae and probably indicate that *Whiteichthys* and Haplolepidae are divergently specialized from their probable common ancestry. This feature may indicate that there has been intercalation of myomeres in the trunk region of *Whiteichthys* compared with the probable ancestral group.

The ancestors of *Whiteichthys* can be sought only among the *Rhadinichthys-Mesopoma-Canobius* group, and the structure of the cheek compares most closely with that of *Canobius* and *Mesopoma*. The reduction of the branchiostegals is also closely comparable with that seen in *Canobius*. The scale formula in known canobiids is (average)

$$\frac{20\text{–}21}{7 \quad 13\text{–}14 \quad 30\text{–}31}\ 34$$

Comparison with *Whiteichthys*

$$\left(\frac{25}{7 \quad 16 \quad 33}\ 39\right)$$

seems to be very close.

The scales of *Whiteichthys* are briefly described by Moy-Thomas. Their histological structure is unknown. There seems to be nothing in their ornament to oppose the relationships suggested above.

These observations are significant in trying to assess the age of the strata yielding *Whiteichthys*. The fish is considerably less advanced than the Westphalian Haplolepidae and is probably derived from a form showing very close relationship to the Dinantian canobiids (probably zone C_2S_1 = Mississippian). The *Whiteichthys* horizon may be regarded as of late Dinantian or Namurian age (i.e., late Mississippian or earliest Pennsylvanian).

MARCH 20, 1943

A magnificent new work by Nielsen (1942) contains the most detailed descriptions yet attempted, in many particulars, of "palaeoniscoid" fishes. Certain matters discussed above call for brief comment in the light of his monograph.

NOMENCLATURE OF BONES

Nielsen adopts a number of compound names for elements observed in *Glaucolepis* and *Boreosomus*. No discussion of many of these names is desirable in this brief note. The use of the terms "rostro-antorbital" and "rostro-antorbito-premaxillary" follows a tendency that has led already to much confusion in bone nomenclature. The "antorbital" part of the name reflects what may be a false homology with the antorbital of *Amia;* the snout of *Coccocephalus wildi* (Watson, 1925, fig. 6) is too disturbed for certainty in reconstruction. The "premaxillary" part, and

the "maxillary" component of the "lacrimo-maxillary," depend largely on the fact that the bones in question bear teeth. I have dealt with this matter elsewhere (Westoll, 1936, p. 165). In *Glaucolepis stensiöi*, Nielsen figures small separate premaxillaries not related to the latero-sensory canals. In the text (p. 136) he says that the presence of these is "not quite certain"; the bones are not known in other species of *Glaucolepis*, but according to Nielsen a space for them exists in the reconstructed snout region. No separate premaxillary exists in *Boreosomus*. These points have a bearing on the discussion in the present paper (p. 76) on the premaxillary region. I feel unable to agree wholeheartedly with Nielsen's assumption that a once-separate premaxillary component has fused with other elements in most palaeoniscoids. In *Cheirolepis* I have seen the premaxillary as a bone bearing the ethmoidal commissure; only in the cases of *Canobius ramsayi*, possibly in *Glaucolepis*, and much more doubtfully in *Birgeria* (where the snout region is still very badly known) is there any indication among many palaeoniscoid genera of a separate tooth-bearing bone in this region. The plates and figures of *Glaucolepis* suggest that the "rostro-antorbital" and the "premaxillary" have been displaced somewhat by being driven beneath the nasal and postrostral. No teeth were apparently noted in the "premaxillary." Nielsen (p. 139) says that no independent rostral was present in *Birgeria;* presumably the "premaxillary" of this form (Stensiö, 1932, p. 113, fig. 41, pl. 26, fig. 1) is part of a canal-bearing bone. I can, therefore, see no reason to believe that a separate premaxillary element is a fundamental character in primitive actinopterygians; the problem of the homology of the large and complicated separate premaxillary (without rostral component) in the higher actinopterygians remains. The presence of small separate elements in these few forms suggests rather that they may be new formations. (In *Glaucolepis* the maxillary has retreated posteriorly.)

In the supraorbital region Nielsen uses the terms "supraorbito-dermosphenotic" and "supraorbito-postorbital" for the elements usually called intertemporal (Aldinger's "epitemporale") and dermosphenotic (or postfrontal), respectively. The main reasons for this are that in *Palaeoniscus freieslebeni* the present writer (*in* Aldinger, 1937, pp. 97, 231) has recorded two series of postorbitals, as in *Oxygnathus* (Watson, 1925, fig. 30; 1928, fig. 10); and Nielsen considers that in *Glaucolepis* the lateral series has fused with the "dermosphenotic" ("postorbital" of Nielsen), the medial series with the "intertemporal" ("dermosphenotic" of Nielsen). However, in *Palaeoniscus* the "intertemporal" does not meet either set of supraorbitals, and the "dermosphenotic" is in series with the medial supraorbitals. The supraorbitals of *Palaeoniscus freieslebeni* are very variable in number and shape. Without much more comparative work, the homology of all these elements must remain uncertain, but I can see no good reason for Nielsen's usage, especially as in *Glaucolepis magna* the "supraorbito-dermosphenotic" is very variable and may be very short. The bone here called intertemporal is very large in *Cheirolepis traili*, but is usually absent in *C. canadensis* (author's observations), where it is probably incorporated in the dermopterotic. It seems to have had a similar fate in many palaeoniscoids (including Haplolepidae). The dermosphenotic of this monograph seems to be homologous with the "supraorbito-postorbital" of Nielsen's account. The separate supraorbitals of such forms as *Palaeoniscus* may actually result from "fragmentation." Until more is known of this region I prefer a simple nomenclature; the compound form used by Nielsen expresses no more than geographical extent and disguises the possible effects of invasion of territory.

The Use of Pit Lines in Homology

Nielsen (p. 203) notes that some so-called pit-line grooves may actually represent narrow shallow canals and suggests that pit lines in primitive actinopterygians may have been less superficial than in recent forms. He quotes short résumés of a work by Pehrson (1940) which has not been available to me: "the parietal and the gular plate in *Amia* have developed independently of the pit-organs in the very superficial pit-lines overlying these bones, while the canal bones in *Amia* always develop in association with canal organs." He points out also that the

gradual degeneration of enclosed sensory canals to pit lines might leave a bone-forming stimulus for some time. These statements are in very good agreement with previous discussion by the writer (1937a, p. 378; 1937b, p. 571). The pit lines cannot be of more than conditional value in homologizing dermal bones. The discussion above (pp. 68, 69) clarifies a number of Nielsen's points of difficulty.

Opercular Region

The presence of dermohyal and antopercular elements in *Glaucolepis* is fully discussed by Nielsen. In *G. magna* there may be either one or two antoperculars. The example of *Haplolepis ovoidea* with the antopercular apparently incorporated in the operculum (above, p. 19, fig. 4b) derives new interest from this fact of individual variation.

Shoulder Girdle and Pectoral Fins

Nielsen gives very full and complete accounts of the paired fins and girdles in both *Boreosomus* and *Glaucolepis*, and these allow much more to be made of Aldinger's descriptions (1937) of the pectoral endoskeletal girdle in *Palaeoniscus*, *Pygopterus*, and *Acrorhabdus* (the last is probably a fairly close relative of *Boreosomus*—cf. above, p. 83, etc.). *Nielsen* shows that in *Glaucolepis* the margo radialis is nearly horizontal and the fin must have been of the type sketched in figure 50 above. The *Palaeoniscus* shoulder girdle is comparable in detail with that of *Glaucolepis*, and Aldinger's reconstruction, with the margo radialis nearly vertical, is certainly wrong (cf. Nielsen, p. 228; the fins are normally preserved in such a way that a vertical margo radialis is an impossibility). In *Boreosomus*, on the other hand, the margo radialis is steeply uptilted, and the pectoral fin must have lain nearly parallel to the flank, preaxial margin uppermost, in a manner typical of the higher Actinopterygii. *Pygopterus* offers difficulties. In Aldinger's figures the margo radialis is nearly vertical, but the shape of the cleithrum is most improbable for this part of the flank. My own observations on *Pygopterus* show that the endoskeletal shoulder girdle was much lower down than seems to be shown by Aldinger, and the margo radialis seems to have been somewhat, though not excessively, uptilted. The position of the pectoral fin, as preserved in nearly all the specimens I have seen, is comparable with the specimen figured in King (1850, pl. 23). For such a fin a vertical or highly upturned margo radialis is impossible.

Change in Function of Fins

Boreosomus, with its nearly vertical margo radialis, is a fine test case for the theory advanced above (pp. 99, 100) concerning the change in function of the pectoral fins. There can be no doubt that *Boreosomus* is in the "Subholostean" grade, since Nielsen has shown (p. 370) that the caudal lobe does not reach the tip of the tail. The reduction in lift forces during swimming, therefore, correlates well with the change in attitude of the pectoral fins.

Systematic Position of *Boreosomus*

The reduced caudal lobe and the different orientation of the pectoral fins suffice to differentiate *Boreosomus* from true Acrolepidae. *Boreosomus* should certainly be referred to the family Ptycholepidae (Brough, 1939), and *Acrorhabdus* should no doubt go with it. Both these early Triassic fishes may be considered as "Subholosteans." In *Acrolepis* (above, p. 83) the pectoral fins are of normal palaeoniscoid type, and the tail is fully heterocercal. The Ptycholepidae may have been derived from the Acrolepidae but are quite distinct from them. *Boreosomus* is a very primitive member of the family.

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ABBREVIATIONS USED IN TEXT FIGURES[1]

a.gu., anterior paired gular
a.ll., accessory lateral line
ang., angular
a.op., antopercular
a.p.l., anterior pit line

br., $br._1$, etc., branchiostegal rays

clav., clavicle
clei., cleithrum

d., dentary
d.ll., dorsal lateral line
d.pt., dermopterotic
d.ros., dentigerous rostral
d.sph., dermosphenotic

e.sc., extrascapular

fen., fenestration in skull roof
fr., frontal

h.md., hyomandibular
h.p.l., horizontal pit line

i.clav., "interclavicular" element
i.o., infraorbital bone
i.o.c., infraorbital canal

m.d., mandible
m.gu., median gular
m.ll., main lateral line
m.p.l., middle pit line
mx., maxilla

n_1., anterior paired nostril
n_2., posterior paired nostril

na., nasal

oc.com., occipital commissure
om.pl., oralomandibular pit line
op., opercular
ot., otolith
ot.c., otic canal

p., pineal foramen or macula
pa., parietal
pal.t., palatal tooth plate
p.clei., postcleithrum
p.f., pectoral fin
p.gu., posterior paired gular
p.mx., premaxilla
p.mx.?, so-called premaxilla of higher fishes, not a dentigerous rostral
p.o., postorbital bone
p.op., preopercular
p.p.l., posterior pit line
p.p.q., palato-pterygo-quadrate
p.ros., postrostral
psp., parasphenoid
p.tem., posttemporal

qu.j., quadratojugal

ros., rostral
ros.com., rostral commissure

s.clei., supracleithrum
s.mx., supramaxilla
s.o., suborbital
s.o.c., supraorbital canal
s.op., subopercular

v.f., pelvic fin
v.ll., ventral lateral line
v.p.l., vertical pit line

x., position of basipterygoid articulation

[1] In certain cases the lettering is in parentheses, e.g., (na). This signifies that the bone is an impression or differently preserved from the rest of the specimen.