THE PALAEONISCOID FISH *TURSEODUS* FROM THE UPPER TRIASSIC NEWARK GROUP

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INTRODUCTION

Up to the present time, the occurrence of palaeoniscoid fishes in the Upper Triassic Newark group has not been satisfactorily demonstrated, although several early students of the Newark fauna assigned isolated scales to various European palaeoniscoid genera. Lea (1856) identified a scale from the Lockatong formation of the Newark group at Phoenixville, Pennsylvania, as *Pygopterus mandibularis*, and Hay (1902) referred it to *P. humboldti*. In 1857 Emmons described some scales from the Triassic of North Carolina as *Amblypterus ornatus*, which Hay (1902) placed in a new species, *A. carolinae* (*nomen nudum*). These specimens cannot be located, and they must be regarded as taxonomically indeterminate. The status of *Elonichthys elegans* (Emmons), also a *nomen nudum* of Hay, 1902, has been considered recently (Schaeffer, 1951); the remains assigned to this species are definitely coelacanthid.

In 1857 Leidy described a "left dental bone with teeth" from the Lockatong formation near Phoenixville, as *Turseodus acutus*. He regarded *Turseodus* as a ganoid fish, possibly related to *Belonostomus* or *Eugnathus*. Although this genus is mentioned in several faunal lists for the Newark group (Wheatley, 1861; Lyman, 1894; Hawkins, 1914), it has received no further attention except for the opinions of Woodward (1891) and Stensiö (1921) that it is indeterminate.

About 1860 Charles M. Wheatley collected a number of isolated fish scales and fragmentary skull elements from the Reading

Railroad tunnel at Phoenixville. This collection was apparently presented to Cope and is now in the American Museum. Many of the specimens are labeled *Turseodus acutus*, presumably in Wheatley's handwriting. One lower jaw fragment is identified as "*Turseodus leptops* Cope," representing an unpublished species which the present writer has not been able to distinguish from *T. acutus*. The lower jaws in the Wheatley specimens agree in most observable characters with the Leidy type.

Along with the many hundred individuals of the coelacanth *Diplurus* discovered in the excavation for the Firestone Library at Princeton University in 1946, there are eight examples of a palaeoniscoid. The mandibles preserved in several specimens agree with the type of *Turseodus*, and the associated scales closely resemble those in the Wheatley collection. The Princeton specimens are accordingly referred to *Turseodus acutus*, and they permit, for the first time, a fairly complete description of the external morphology of this relatively rare late Triassic palaeoniscoid.

The writer is obligated to Dr. G. L. Jepsen for the opportunity to describe the Princeton material and to Dr. Horace G. Richards for the loan of the type of *Turseodus acutus* from the Academy of Natural Sciences of Philadelphia. The drawings were made by Mrs. Lois Darling, and the photographs were prepared by the Division of Photography of this museum.

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TAXONOMY AND DIAGNOSIS

FAMILY **PALAEONISCIDAE**, SENSU STRICTO[1]

GENUS **TURSEODUS** LEIDY, 1857

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Turseodus LEIDY, 1857, Proc. Acad. Nat. Sci. Philadelphia, vol. 9, p. 167.

GENOTYPE: *Turseodus acutus* Leidy.

GENERIC DIAGNOSIS: Elegantly fusiform fishes attaining a length of 15 to 20 cm. and differing from other members of the family Palaeoniscidae, *sensu stricto*, in the following combination of characters: Skull nearly one-fifth of total body length, transverse diameter of orbit about one-quarter of skull length. Rostrum moderately projecting. Postrostral bone strongly constricted at external nares. Shape and relationship of frontal and dermopterotic essentially similar to other members of the Palaeoniscidae, *sensu stricto*. Parietal about one-third of length of frontal and nearly square. Single supraorbital and dermo-

[1] See Aldinger (1937), Nielsen (1942), and Romer (1945).

sphenotic in contact with nasal. Maxillary excluded from snout, not meeting fellow below rostrum. Suspensorium oblique, pre-opercular-maxillary angle about 33 degrees. Opercular deeper than wide, twice the depth of subopercular. Dermohyal or anto-percular present. Mandible robust, with broad symphysis. Maxillary and dentary with one or more rows of conical, laniari-form teeth, alternating with more numerous smaller teeth. Dermal bones covered with low rugae or tubercles; ornamentation weakest on opercular and subopercular.

Supracleithrum broad and ornamented with low rugae. Cleithrum with attenuated dorsal extension. Pectoral fin large, horizontal, consisting of about 17 lepidotrichia which are seg-mented for about one-half of their length. Pelvic fin much smaller than pectoral, triangular, origin about midway between origins of pectoral and anal, number of lepidotrichia unknown. Dorsal fin remote, origin well behind that of anal, consisting of about 25 lepidotrichia. Anal fin long-based, nearly equal to skull length, with concave ventral margin, and consisting of about 55 lepidotrichia. Caudal fin deeply cleft, nearly equilobate, body axis extending to tip of dorsal lobe, with about 65 lepidotrichia in both lobes. Small fulcra on the anterior borders of all fins. One or more ridge scales in front of dorsal and anal fins.

Scales ornamented with low diagonal and occasionally branch-ing ridges, with prominent dorsal articular process, and with smooth posterior border. Ganoine and bony layers present, arranged essentially as in *Glaucolepis*. Cosmine layer reduced or absent.

Turseodus acutus Leidy, 1857

TYPE: The Academy of Natural Sciences of Philadelphia, Paleontology No. 14535. Incomplete mandible in counterpart with dentition. From Lockatong formation, Newark group, near Phoenixville, Chester County, Pennsylvania.

SPECIFIC DIAGNOSIS: Same as for genus.

HORIZONS AND LOCALITIES: *Turseodus* is known to occur in the Stockton and Lockatong formations of the Newark group at the following localities: A. Granton (Belmont-Gurnee) Quarry at North Bergen, New Jersey. Single dissociated specimen from unknown black shale horizon in quarry near the top of Stockton formation. B. Reading Railroad tunnel at Phoenixville, Penn-sylvania. The type may have been found in the tunnel debris,

but this is not certain. According to Hawkins (1914) the exposure of the Lockatong formation in the vicinity of the tunnel is about 1500 feet thick and consists of alternating layers of red, brown, and black shales. It is probable that the type and all the Wheatley specimens came from beds of "black shales with estheriae" which occur in the lower 200 to 400 feet of Hawkins' section. C. Firestone Library excavation, Princeton University, Princeton, New Jersey. The fish occur in a thin layer of argillite, less than 200 feet above the base of the Lockatong in association with *Diplurus* and *Redfieldia*.

REFERRED SPECIMENS: A.M.N.H. No. 8107, entire Wheatley collection, including isolated skull elements and scales, Reading Railroad tunnel, Phoenixville, Pennsylvania. A.M.N.H. No. 8108, isolated skull elements and scales, Granton Quarry, North Bergen, New Jersey.

From Firestone Library excavation, Princeton University, Princeton, New Jersey: P.U.G.M. No. 16151, incomplete specimen with dorsoventrally flattened skull. P.U.G.M. Nos. 16152a and 16152b, complete fish, badly compressed, but showing relative positions of dorsal and anal fins. P.U.G.M. No. 16153, impression of complete fish showing body form and positions of all fins. P.U.G.M. No. 16154, incomplete specimen with gular region exposed. P.U.G.M. Nos. 16155a and 16155b, complete fish, poorly preserved. P.U.G.M. Nos. 16156a and 16156b, complete specimen, badly compressed, but showing certain details of skull-roof pattern, cleithrum, and caudal fin. P.U.G.M. Nos. 16157a and 16157b, well-preserved caudal fin. P.U.G.M. Nos. 16158a and 16158b, partial specimen showing relative positions of dorsal and anal fins.

MEASUREMENTS: Because of poor preservation, only one specimen (P.U.G.M. No. 16153) has given reasonably reliable measurements. This individual is one of the smallest in the series, with an approximate dentary length of 1.75 cm., as compared with 2.60 cm. in P.U.G.M. No. 16151. The type mandible and a dentary in the Wheatley collection (fig. 5) are considerably larger. Although incomplete, it is evident that they measured over 4.0 cm. in length.

MEASUREMENTS (IN CENTIMETERS) OF P.U.G.M. No. 16153

Total length.. 14.3
Approximate length along level of lateral line to beginning of caudal inversion.. 11.5

Skull length (rostrum to posterior border of suboperculum)............... 3.0
Distance from rostrum to anterior border of dorsal fin.................... 8.45
Distance from rostrum to anterior border of pelvic fin................... 5.15
Distance from rostrum to anterior border of anal fin.................... 7.3
Approximate maximum body depth.................................... 3.2

DESCRIPTION

BODY FORM: *Turseodus* has a body outline (fig. 1) closely resembling, but more compact than, that of *Palaeoniscus*. The maximum depth, at the level of the pelvic fins, equals about one-fifth of the total body length. The skull measures somewhat less than one-fifth of the total length. The origin of the remotely situated dorsal is well behind that of the long-based anal. The pectoral fin was held in a nearly horizontal position; its area is more than twice that of the pelvic. The caudal peduncle is stout, and the tail is equilobate, deeply cleft, and completely heterocercal.

Some conclusions can be drawn from the large literature on fish locomotion regarding the possible functional significance of fin form and position in *Turseodus*. The nearly horizontal pectoral fins of the shark have been shown by Harris (1936) to furnish a lift force that neutralizes the elevating action produced by the hypochordal lobe of the heterocercal caudal fin, permitting the body to remain in a horizontal position during swimming. Westoll (1944, p. 86) has pointed out that a similar functional relationship between the pectorals and the caudal existed in the palaeoniscoids. Nielsen (1949, pp. 156, 271) notes, however, that *Australosomus* has horizontal pectorals and a symmetrical caudal with a reduced axis, while *Birgeria* has vertical pectorals and a nearly symmetrical caudal with an unreduced axis.

Affleck (1950, p. 364) states that the upturning of the axis in the caudal fin of the early actinopterygians produced a depressing force that reduced the effective lift of the hypochordal lobe. He is of the opinion that a tail having a design similar to the one in *Turseodus* will act with a resultant thrust and reaction that are horizontal and in line with the body axis. It is difficult to reconcile this conclusion with the horizontal position of the pectoral. Dr. C. M. Breder, Jr., has pointed out to the writer that the hypochordal lobe of *Turseodus* probably still provided a lifting force that required compensation by the horizontal pectorals. Although the caudal axis is upturned, its relative stiffness may have limited its action.
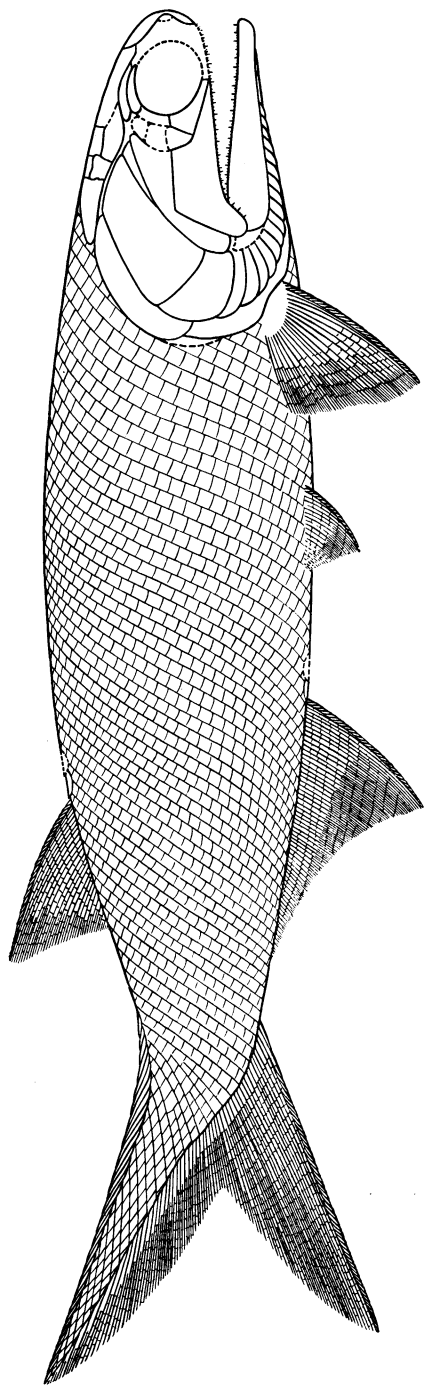
FIG. 1. *Turseodus acutus.* Reconstruction. Approximately × 1.

The apparent contradictory features in *Australosomus* and *Birgeria* suggest that changes in tail structure and pectoral fin position did not always occur at the same time or at the same rate. It is conceivable that, although the pectoral of *Australosomus* had a horizontal insertion, it may have been flexible enough to assume a nearly vertical position for a large portion of its surface, as is indicated in Nielsen's restoration (1949, fig. 55). In the case of *Birgeria*, if the pectorals were inserted vertically (the poorly ossified endoskeleton of the shoulder girdle does not prove this conclusively), either the upper lobe of the tail was flexible enough to develop the force discussed by Affleck, or the pectoral may have been warped into a more horizontal position. Perhaps horizontal swimming was maintained by a combination of the two.

The remote positions of the dorsal and anal in *Turseodus*, probably well behind the center of gravity, would provide greater stability during forward locomotion than if they were situated more anteriorly. In discussing this matter, Magnan (1929) points out that the dorsal and anal fins are always well developed when the pelvics are in front of a vertical line passing through the center of gravity. He states that if the pelvic fins are some distance anterior to the center of gravity, the anal is elongated to take the place of the pelvics in the region of this perpendicular line. Differences in the positions of the centers of buoyancy and gravity may also be related to the relative size of the dorsal and anal fins, as well as the eddying effect along the ventral surface of the body during swimming.

SKULL: The interpretation of the dermal bone pattern of the skull (fig. 3) is based on P.U.G.M. Nos. 16151 (fig. 4) and 16156. It has not been possible to determine accurately the outlines and exact relationships of all the bones, and the restored skull must be regarded as tentative in certain details.

Two extrascapular elements appear to be present on each side of the median dorsal line. They are essentially rectangular and closely approximated. The parietal is nearly square and about one-third of the length of the frontal. The frontal is narrow and meets its fellow in an undulating suture. The course of the suture between the frontal and the dermopterotic is vague. There is, however, no indication of a marked embayment in the median borders of the dermopterotic as in *Palaeoniscus* and *Glaucolepis*. The shape of this element is more nearly like that in *Cosmolepis* [*Oxygnathus*] as figured by Watson (1925). The dermosphenotic

FIG. 2. *Turseodus acutus.* P.U.G.M. No. 16153. × 1.

is narrow and suggestive of the same bone in *Glaucolepis stensioi* (Nielsen, 1942). It meets the nasal anteriorly, with the single supraorbital. The postrostral as preserved in P.U.G.M. No.
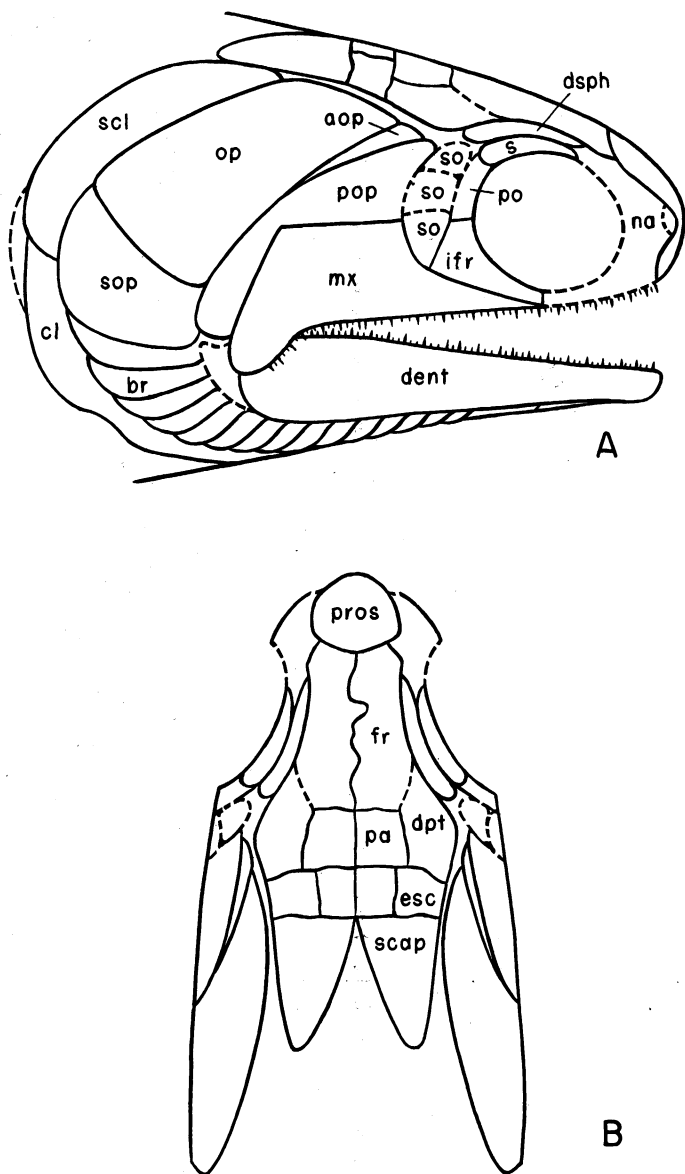
FIG. 3. *Turseodus acutus.* Reconstruction of skull. A. Lateral view. B. Dorsal view. *Abbreviations:* aop, antopercular; br, branchiostegal; cl, cleithrum; dent, dentary; dpt, dermopterotic; dsph, dermosphenotic; esc, extrascapular; fr, frontal; ifr, infraorbital; mx, maxillary; na, nasal; op, opercular; pa, parietal; po, postorbital; pop, preopercular; pros, postrostral; s, supraorbital; scap, suprascapular; scl, supracleithrum; so, suborbital; sop, subopercular.

FIG. 4.   *Turseodus acutus.*   P.U.G.M. No. 16151, dorsoventrally crushed skull. Retouched.   Abbreviations as in figure 3.   × 2.

16151 has probably kept its natural curve, indicating a round and blunt snout which is also characteristic of the other palaeoniscids.   It is markedly constricted at the level of the anterior nostrils, perhaps more so than in other palaeoniscoids for which this element has been adequately figured.   Although the exact form of the nasal cannot be determined, it is evident that the outline was very similar to that indicated in the restoration.

The number and arrangement of the suborbitals are uncertain, although there is a suggestion of three in one specimen.   The

postorbital area is occupied by a single bone as in *Glaucolepis*.
The posterior infraorbital requires no comment except to note
that it was overlapped for about one-fifth of its total length by
an anterior infraorbital. The anterior infraorbital (lacrimo-
maxillary) and the rostral are not clearly distinguishable. A
small, curved, dentigerous element is present in two specimens
in close association with the postrostral. It bears some re-
semblance to the anterior infraorbital of *Glaucolepis magma*
(Nielsen, 1942, fig. 31). Another smaller, flat bone is apparently
a snout element and may be the rostral. It is distinctively
ornamented with deep parallel grooves. An element that might
be regarded as a "premaxillary" is not in evidence.

The shape of the maxillary agrees closely with that of *Palaeonis-
cus* and *Glaucolepis*. The skull reconstruction indicates that the
maxillaries did not meet at the snout but ended under the anterior
infraorbitals. The preopercular has a gently rounded pos-
terior border as in *Glaucolepis*, without a distinct angle on this
border dividing it into anterior horizontal and posterior vertical
portions. The lower end of the preopercular is about on a level
with the ventral border of the subopercular as in *Cosmolepis* and
one species of *Glaucolepis*. The differences in this relationship
in *Glaucolepis* suggest some interspecific variation associated with
the relative size of the preopercular and the surrounding dermal
elements. Allowance must also be made for differences of inter-
pretation as expressed in the skull restorations.

The hyomandibular is partly exposed in P.U.G.M. No. 16151.
It is typically expanded in its dorsal portion and has a low opercu-
lar process. A small nodule of bone between the ventral end of
the preopercular and the maxillary may represent the displaced
symplectic. A well-defined facet on the exposed surface of this
element resembles the articular facet figured by Nielsen (1942,
fig. 42) for *Glaucolepis*.

The obliqueness of the suspensorium is reflected in the form
and proportions of all the major cheek elements and in the rela-
tive length of the maxillary and mandible. By a line drawn from
the anterodorsal corner of the preopercular to the midpoint on its
ventral border and a second line from the point on the ventral
border to the anterior termination of the maxillary, an angle is
obtained that approximates closely the inclination of the suspen-
sorium in relation to the upper jaw. In *Turseodus* this angle is
about 33 degrees, in *Palaeoniscus* about 35 degrees, in *Glaucolepis*

stensioi 32 degrees, in *Gyrolepis* 34 degrees, and in *Cosmolepis* approximately 32 degrees.

The mandible requires no comment except to note that it is broad posteriorly and has a gently concave ventral margin, as in *Cosmolepis*.

There is no conclusive evidence regarding the presence of both a dermohyal and an antopercular. At least one wedge-shaped
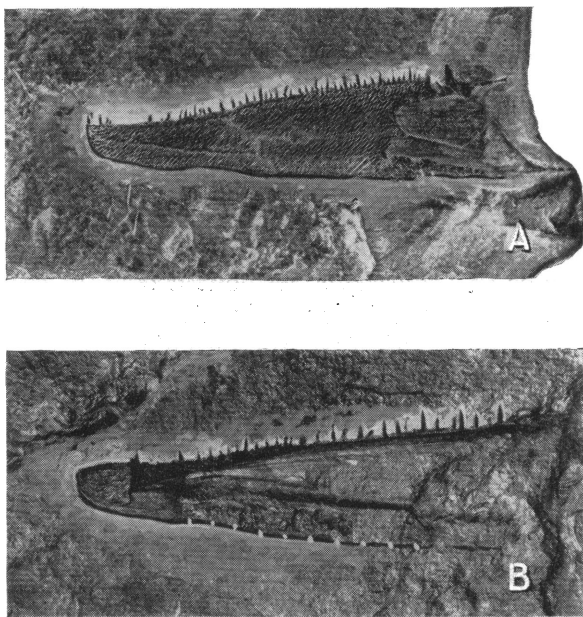

FIG. 5. *Turseodus acutus*. A. A.M.N.H. No. 8107, incomplete mandible in Wheatley collection. × 1.5. B. A.N.S.P. No. 14535, fragmentary type mandible. × 1.5. Retouched.

element is present between the preopercular and the opercular. It may be regarded tentatively as the antopercular.

The opercular is twice as long as wide. The subopercular is as broad as the lower portion of the opercular; its depth is less than half of that of the opercular. The branchiostegals number about 16.

Sensory pores have been observed on the dermopterotic and the preopercular but are otherwise not in evidence. It is probable, however, that the canals have a typical palaeoniscoid disposition.

PAIRED FINS: The suprascapular is somewhat longer antero-posteriorly than in the other palaeoniscids. It was probably not overlapped by the extrascapulars as is the case in *Glaucolepis*. The supracleithrum is a broad, nearly rectangular bone that must have been extensively covered by the opercular. The vertical portion of the cleithrum is little expanded and resembles that part in *Palaeoniscus*. The dorsal end of the cleithrum is reduced to a short, narrow process much as in *Acrorhabdus* (Stensiö, 1921). The postcleithrum and clavicle are not well enough preserved for comment.

The large pectoral fin is composed of at least 17 rays. About the first 14 are broad-based and are bifurcated for half their length. The remaining rays are more delicate and more completely divided. All are segmented for about half of their length. The fin is bordered by small fulcra.

The pelvic fin is much smaller than the pectoral. Its origin is halfway between the origins of the pectoral and the anal fins. The total number of lepidotrichia cannot be determined; 20 is a reasonable estimate. The observable rays are bifurcated distally, completely segmented, and the anterior border of the fin is fringed by very small fulcra.

MEDIAN FINS: The unusual position of the dorsal fin, with its origin well behind that of the anal, has been observed in three specimens of *Turseodus*. A similar dorsal-anal fin relationship is known to occur in only a few other palaeoniscoids: *Cheirolepis* (Lehman, 1947), *Pyritocephalus* (Westoll, 1944), and *Whiteichthys* (Moy-Thomas, 1942). Of the two genera included in the Haplolepidae, *Pyritocephalus* alone shows this condition, the dorsal of *Haplolepis* being in the more "normal" position. Should *Whiteichthys* prove to be a member of the Canobiidae (the resemblances have been pointed out by Westoll, 1944, p. 113), it will be the only genus in this family with the dorsal fin in a posterior position. In view of this possible variation in dorsal-fin position at the generic level, it would appear unwarranted to assign any higher taxonomic significance to the condition in *Turseodus*.

The dorsal fin of *Turseodus* consists of about 25 lepidotrichia which are bifurcated for about one-third of their length. The fin is bordered by delicate fulcra, preceded by one or more ridge scales. Baseosts of nearly uniform width, and similar to those of *Glaucolepis*, are present in P.U.G.M. No. 16153.

The long anal fin is a conspicuous feature of this fish. It includes

approximately 55 rays, the posterior ones being extremely short and delicate, making an accurate count difficult.   The first three or four lepidotrichia are not bifurcated.   Small fringing fulcra are present, and there is at least one ridge scale in front of the fin. The few anterior baseosts exhibited in P.U.G.M. No. 16158 are long, narrow rods, nearly half of the length of the longest anal rays.   The expanded ventral end of each rod supports about four lepidotrichia.   There is no indication of other radial ossifications
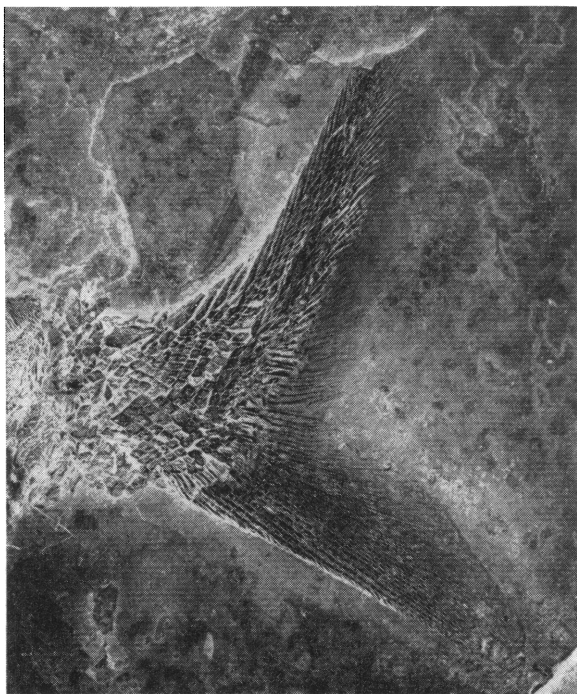

FIG. 6.   *Turseodus acutus*.   P.U.G.M. No. 161576.   Caudal fin.   × 1.5.

such as have been described for *Glaucolepis* and a few other palaeoniscoids.

The caudal fin (fig. 6) is deeply cleft and nearly equilobate. The body axis extends to the end of the dorsal lobe.   The lepidotrichia, which total about 64, are bifurcated for two-thirds of their length in the dorsal lobe.   In the ventral lobe the anterior five or six are not divided, and the remainder are bifurcated for half of their length.   The dorsal margin of the body axis is bordered by approximately 31 attenuated, unpaired fulcral scales, and the

lower border of the ventral lobe by a series of small fulcra. Along
the lower margin of the ventral lobe the tips of the first six fin
rays are interpolated between the fulcra. A somewhat similar
condition has been described for the fins of *Aetheretmon* and for
several other palaeoniscoids.

SQUAMATION: The squamation is unfortunately not completely
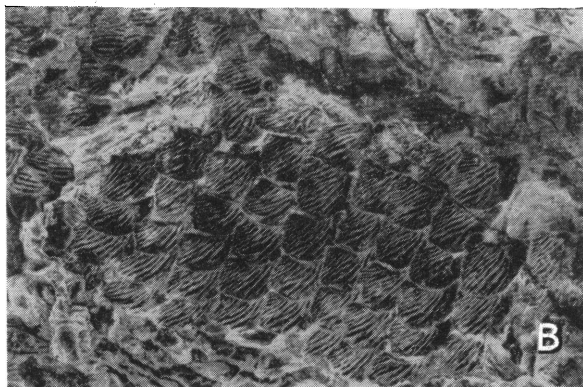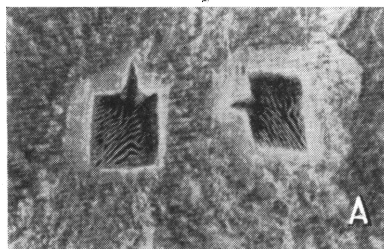preserved in any of the Princeton specimens. Patches of as-

FIG. 7. *Turseodus acutus.* A. A.M.N.H. No. 8107, isolated scales in Wheat-
ley collection. × 3. B. P.U.G.M. No. 16152b, patch of scales above pelvic
fin. × 3.

sociated scales and scale impressions from different parts of the
body are, however, present in several individuals. The tentative
reconstruction of the entire squamation (fig. 1) is based on a care-
ful plotting of these patches on a single drawing. The number
of vertical scale rows between the posterior border of the supra-
cleithrum and the beginning of the caudal inversion is thus esti-
mated to be between 50 and 55. The number of rows obtained

by dividing the same distance by the average flank scale width also falls within this range.

The exposed scale surface (fig. 7) is covered with low ridges that in general are oriented in an anterodorsal-posteroventral direction. This sort of ornamentation appears to be present on all regions of the body, although there is some variation in the number of ridges. As in *Glaucolepis*, the ridges are attenuated at each end and they may run together in the central part of the scale. The scales from the Phoenixville locality appear to differ somewhat from the Princeton examples in the curvature of the ventral ridges (fig. 7). Although this difference may indicate that two species are involved, more specimens are required for certainty.

In cross section (fig. 8), the scales show the characteristic ganoine and bony layers. The cosmine layer is not clearly differentiated, and it may be nearly absent as in *Gyrolepis* (Aldinger, 1937,

FIG. 8. *Turseodus acutus.* Vertical section of flank scale from Princeton specimen. Approx. × 48.

p. 243). Blunt lamellae projecting into the ganoine layer resemble either the cosmine lamellae of *Gaucolepis* or the bony ones of *Gyrolepis*. The presence of bone cell spaces close to the ganoine is a further indication that the cosmine layer is either much reduced or absent. The arrangement of the canal plexus cannot be determined, since the nature of the scale preservation has not favored the preparation of successful horizontal sections. Canals are present, however, immediately under the ganoine layer and well into the bony layer.

DISCUSSION

The phylogenetic relationships and classification of the palaeoniscoid fishes continue to be among the most perplexing problems in paleoichthyology. Following Aldinger's (1937) erection of six new families for certain genera formerly included in the old "catchall" family Palaeoniscidae, additional families were recognized by Moy-Thomas (1939), Westoll (1944), and Romer (1945).

Berg's (1940) classification includes a number of these families in the Order Palaeonisciformea, while certain more aberrant ones are placed in separate orders. His family Palaeoniscidae contains a number of genera placed in separate families by Aldinger, although Berg admits that it is a heterogeneous assemblage. The most recent classification, that of Romer, has 27 families in the Order Palaeoniscoidea.

At the present time, no single classification can be regarded as entirely satisfactory. The external and internal morphology of many genera is still poorly known, and the erection of some families on the basis of scale structure (Aldinger, 1937) remains questionable. The suites of characters defining a number of apparently closely related families overlap to such an extent that the allocation of new as well as many old genera has become exceedingly difficult and in many instances arbitrary. Distinguishing parallelism or convergence from true affinity in the skull-roof pattern, the cheek pattern, the form and position of the fins, the squamation, and other external characters is only beginning to be accomplished. Knowledge of endoskeletal structure is providing much additional information on some genera, but far more information of this sort is needed to be of general usefulness in palaeoniscoid classification. Undoubtedly the internal structure of many genera will never be satisfactorily known, and it will be necessary to rely on external morphology in deciding upon relationship.

In an attempt to determine the allocation of *Turseodus* in Romer's classification, only those families have been considered in which the suspensorium is usually oblique, and the body and fin form, as well as the squamation, shows some resemblance to the condition in this genus. Several of these families are without a published diagnosis, and for certain others the diagnosis is far from being reasonably restrictive. Since *Turseodus* appears to lack any specialization that would warrant the erection of a new family, its affinity with one of the more "normal" palaeoniscoid families is indicated.

There are several characters that appear to eliminate *Turseodus* from the Devonian and Carboniferous Rhadinichthyidae. The members of this family have a single supraorbital element (dermosphenotic) and a different scale structure (Aldinger, 1937, p. 202). The curious L-shaped rostral of *Rhadinichthys fusiformis* has not been described in the other rhadinichthyid genera,

but it may well be a family character (Moy-Thomas and Dyne, 1937, p. 455). Among the genera included in the Rhadinich-thyidae by Romer, some have an oblique suspensorium (*Rhadin-ichthys, Cycloptychius, Strepheoschema*), others (*Stegotrachelus, Aetheretmon*) a nearly vertical one. The lepidotrichia of the pectoral fin may be only distally bifurcated (*Aetheretmon*) or completely divided (*Stegotrachelus*). There is considerable varia-tion within the family in the development of the dorsal ridge scales and in the tendency towards equilobation of the caudal fin. The dorsal fin is remote and opposite the anal, except in *Aetheret-mon* where the origin is more anterior. The generic differences in these characters reduce their significance in a diagnosis of this family, as well as in a determination of the relationship of *Tur-seodus* to the Rhadinichthyidae.

   The family Elonichthyidae, known from the Carboniferous and Permian, has been defined by Aldinger (1937, p. 204). It in-cludes the genera *Amblypterus* and *Lepidopterus* which are placed in different families by Romer. The part of Aldinger's diagnosis dealing with the skull appears to be based largely on *Elonichthys caudalis* (Watson, 1928). The frontal is described (and so figured by Watson) as having a lateral process at about the middle of its lateral border. Behind this process, there is an embayment into which fits the anteromedian portion of the dermopterotic. This pattern has been regarded as generally characteristic of the elonich-thyids, and is presumably what Nielsen (1942, p. 276) is referring to in speaking of "the *Elonichthys*-like shape of the frontal and the supratemporo-intertemporal" in the Palaeoniscidae, *sensu stricto*. In *Elonichthys serratus* (Moy-Thomas and Dyne, 1937) the frontal-dermopterotic suture has a simple antero-posterior direction, with no indication of a frontal embayment. The pattern in the other elonichthyids is unknown. *E. caudalis* has both a dermosphenotic and a supraorbital; one (the dermosphenotic) is figured for *E. serratus*. The condition in the remaining members of the family is unknown. An antopercular (or dermohyal) is present in several species of *Elonichthys* but is not recorded in the other genera. The significance of these differences, if they are all valid, is un-certain in the present state of knowledge. *Turseodus* apparently lacks the fronto-dermopterotic relationship of *E. caudalis;* it has a dermosphenotic and a supraorbital as well as a dermohyal. It differs from *Elonichthys*, which is actually the only well-described genus in the family, in having one rather than a series of small

supraorbitals between the nasal and dermosphenotic. All the genera included in the Elonichthyidae by Romer have an inequilobate tail; the dorsal fin is always well in front of the anal. Although these characters are known to be variable in other families, their apparent consistency in the elonichthyids would appear to exclude *Turseodus*. The scales of the elonichthyids have a well-developed cosmine layer and a network of canals in both the cosmine and bony layers (Aldinger, 1937), again at variance with the condition in *Turseodus*.

The relationship of *Turseodus* to the Palaeoniscidae is considered below.

According to Aldinger (1937, p. 314), the Pygopteridae, which ranged from the Mississippian into the Triassic, resemble closely the Elonichthyidae and Palaeoniscidae except in certain features of the parasphenoid, primary shoulder girdle, endoskeleton of the median fins, and perhaps in the axial skeleton and endocranium. As these structures cannot be observed in *Turseodus*, the relationship of this genus to the pygopterids is difficult to determine. There are, however, several dermal-bone characters that may indicate absence of close affinity. The dermopterotic of *Pygopterus* and *Nematoptychius* meets the dermosphenotic in a broad transverse suture. The opercular is narrower than the subopercular in these genera and also in *Cosmoptychius*. The scale structure of the Pygopteridae is not well understood (Aldinger, 1937, p. 181). When ornamentation is absent, apparently the scale consists only of a bony layer; when ridges are present, they consist of ganoine, perhaps underlain by cosmine. There is no evidence of such variation in the scale structure of *Turseodus*. Furthermore, the scales of the Newark form are larger than in the pygopterids. Resemblances include the broad postrostral, the alternation of large and more numerous small teeth in the maxillary and dentary, the lack of segmentation in the proximal half of the pectoral lepidotrichia, the deeply cleft but inequilobate caudal, and certain other characters that are not necessarily indicative of definite relationship.

The late Paleozoic and Triassic Acrolepidae appear to be close to the Elonichthyidae, Palaeoniscidae, *sensu stricto*, and Pygopteridae. Aldinger (1937, p. 302) separates the acrolepids from the elonichthyids mainly on scale structure, the former having the ganoine layer pierced by numerous cosmine ridges. As indicated above, this condition does not occur in *Turseodus*. There

is, furthermore, no close resemblance between the dermal-bone pattern of the skull in *Turseodus* and in any of the acrolepids, including the Triassic genera *Acrorhabdus* (Stensiö, 1921) and *Hyllingea* (Aldinger, 1937). The diagnosis of the Acrolepidae by Aldinger is not precise or restrictive, as he admits (*ibid.*, p. 252). The inclusion of *Boreosomus* and *Ptycholepis* in the Acrolepidae, favored by that author and by Nielsen (1942, p. 381), increases the diagnosis difficulty; the differences in the dermal-bone pattern of the skull, and to a lesser extent in the fins and body form, are perhaps great enough to state that scale structure provides nearly the only obvious common character. The *Boreosomus-Ptycholepis* relationship as discussed by Aldinger and by Brough (1939, pp. 99–103) is convincing, but, even so, the "fundamental" relationship of some of the dermal-bone characters mentioned by Brough may be questioned.

Among the other families considered, the Mississippian Cryphiolepidae can be eliminated on the basis of the distinctive, large, thin, ovoid scales and on the relatively smaller opercular. *Cryphiolepis* does have a rather similar, long-based anal fin, but that is the only observable point of resemblance to *Turseodus*. The late Permian Boreolepidae and the Pennsylvanian Cocconiscidae differ from the Newark form in the dermal-bone pattern of the skull and in certain other characters and do not require further consideration here.

The family Palaeoniscidae has been redefined by Aldinger (1937) to include the following genera: *Palaeoniscus*, *Glaucolepis* [*Pteronisculus*], *Gyrolepis*, and *Cosmolepis* [*Oxygnathus*]. To this list Romer (1945) adds *Progyrolepis* and, with reservation, the poorly known *Agecephalichthys* (Wade, 1935). Aldinger experienced difficulty in preparing a reasonably restrictive diagnosis for this family, partly because of changes in observable characters during its history from the Permian to the early Jurassic. Nielsen (1942, pp. 276–277) has listed certain characters common to Aldinger's four genera. These are: "(1) the *Elonichthys*-like shape of the frontal and the supratemporo-intertemporal [dermopterotic], (2) the two pairs of extrascapulars, (3) the presence of two series of supraorbitals, a lateral and a medial, which are either separate or present as components in compound bones, (4) the very oblique suspensorium, (5) the large opercular, (6) the rather faint ornament on the dermal bones of the head, (7) the horizontal pectoral fin, (8) the small scales."

In regard to the *Elonichthys*-like frontal-dermopterotic relationship, *Palaeoniscus* and *Glaucolepis* are similar to *Elonichthys caudalis*. The situation in *Cosmolepis*, as illustrated by Watson (1925, fig. 30), is somewhat different and is suggestive of the pattern in *Turseodus*. The *Cosmolepis* dermopterotic is short and wide and has an irregular contact with the posterolateral portion of the frontal. The shape of these bones in the other palaeoniscids is unknown. Since the anterior portion of the *Turseodus* dermopterotic is poorly preserved in the one specimen in which this bone is otherwise distinct, no positive statement can be made regarding its contact with the frontal. The evidence indicates either a condition similar to that in *Glaucolepis*, with a rounded anterior border, or a somewhat more transverse contact as in *Cosmolepis*.

Turseodus agrees with the palaeoniscids in having two pairs of extrascapulars, both a dermosphenotic and a postorbital, a very oblique suspensorium, and a relatively large opercular. The dermal-bone ornamentation is about as prominent as in *Palaeoniscus* and *Glaucolepis*. The pectoral fin was held in a horizontal position.

The most convenient index of relative scale size (in relation to body length) is the number of vertical scale rows from the posterior border of the cleithrum to the beginning of the caudal inversion. *Palaeoniscus freieslebeni* has about 68 to 70 rows (Aldinger, 1937), *Glaucolepis cicatrosus* about 55 (White, 1933), the Greenland species of *Glaucolepis* 55 to 65 (Nielsen, 1942), and *Cosmolepis ornatus* approximately 60 to 70 (based on Edgerton's figures). Although the number of vertical scale rows for *Turseodus* cannot be accurately determined, 50 to 55 appear to be a reasonable estimate. The mean scale width is therefore somewhat greater in *Turseodus* than in the other genera, but the difference is hardly great enough to be significant.

On the basis of this discussion, it would appear reasonable to include *Turseodus* in the family Palaeoniscidae as it is now defined and delimited by Aldinger and Nielsen. Considered together, the characters listed by Nielsen as common to all members of the family probably represent as restrictive a diagnosis as can now be formulated for a group of palaeoniscoid genera that possess few, if any, known distinctive specializations. Scale structure might well be included in the diagnosis. The work of Aldinger suggests that there is a structural pattern peculiar to the Palaeo-

niscidae, particularly in the arrangement of the radial and longitudinal canals. A real distinction between the Palaeoniscidae and the apparently ancestral Elonichthyidae is, however, still difficult to make, and the separation of these families, as well as others closely related, must be regarded as tentative.

Nielsen (1942, p. 277) considers a number of structural changes in the Palaeoniscidae, *sensu stricto*, not all progressive in character, which can be observed in a series including the late Permian *Palaeoniscus*, the early Triassic *Glaucolepis*, the middle and late Triassic *Gyrolepis*, and the early Jurassic *Cosmolepis*. They are reviewed here to include, where possible, the condition in *Turseodus*.

Small dermal bones are present between the parieto-dermopterotic border and the extrascapulars in the two post-Permian genera *Glaucolepis* and *Cosmolepis*. The situation in *Gyrolepis* is unknown, and there is no evidence of these elements in *Turseodus*. Although the supraorbital is subdivided in *Palaeoniscus* and *Cosmolepis*, it is a single element in the other genera, including *Turseodus*. The statement that there is an increase in the length of the bases of the dorsal and anal fins in progressively younger forms is difficult to substantiate. The dorsal and anal of *Cosmolepis* and *Glaucolepis* are hardly, if at all, relatively longer than in *Palaeoniscus*. The anals of *Turseodus* and perhaps of *Gyrolepis alberti* have longer bases in relation to body length than other members of the family. An anterior shift in the position of the pelvic fin of the post-Permian genera to a location nearer the pectoral occurs without exception. All genera younger than *Palaeoniscus*, including *Turseodus*, have a nearly equilobate caudal fin. There is a decrease in the extent of segmentation of the pectoral fin in progressively younger genera. *Turseodus* falls roughly between *Glaucolepis* and *Cosmolepis* in this respect.

The gradual reduction in the cosmine layer of the scales in the series consisting of *Glaucolepis-Gyrolepis-Cosmolepis* has been noted by Aldinger. The situation in *Turseodus* is suggestive of that in *Gyrolepis*. A reduction in the number of ridge scales in front of the dorsal fin is characteristic of the later genera. *Turseodus* appears to have no more than two.

Nielsen regards all these changes except the erratic subdivision of the postorbital as progressive. Since the ancestor-descendent relationship of the genera themselves cannot be determined on the basis of available knowledge, the change can be regarded as pro-

gressive only in a structural sense. *Turseodus* appears to fit into this structural series at about the *Glaucolepis-Gyrolepis* stage.

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