A NEW ACTINOPTERYGIAN FISH FROM THE MISSISSIPPIAN BEAR GULCH LIMESTONE OF MONTANA

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ABSTRACT. A new genus and species of tarrasiiform fish is described from the Chesterian (Upper Mississippian) Bear Gulch Limestone member of the Heath Formation, Montana, U.S.A. Among the distinguishing osteological features of the order that can now be established are premaxillae sutured in the midline, separate rostral and postrostral bones, two pairs of nasals, and a skull roof consisting of paired frontals, parietals, and postparietals. A tentative relationship is proposed with the base of the radiation of the order Palaeonisciformes.

TRAQUAIR (1881) named a most enigmatic fish from the Viséan Upper Border Group of Glencartholm, Dumfriesshire, Scotland (Lumsden *et al.* 1967), *Tarrasius problematicus*, a singularly appropriate specific name. Moy-Thomas redescribed this unique actinopterygian twice in four years (1934; Moy-Thomas and Dyne 1938) on the basis of additional but still inadequate material. It has been redescribed a third time by Jessen (1973), still without clarifying many cranial details and together with a new taxon from the German lower Upper Devonian, *Holopterygius nudus*. Jessen justifiably felt that the two species were somehow related through the common possession of a similar bladelike body form and continuous median fin, but was able to find no tangible characters linking *Holopterygius* definitively to any osteichthyan subclass.

The marine fish fauna of the Namurian Bear Gulch Limestone of Montana contains several specimens of two species belonging in the order Tarrasiiformes; one of these, described below, forms the basis of this report, while the other, far more specialized, fish will be dealt with in a subsequent paper. The osteology of the Bear Gulch tarrasiid described below reinforces as well as details the peculiar nature of this group as suggested by the previously known species. The known Tarrasiiformes are representatives of an adaptive radiation partaking of features that may have stemmed from near the origin of the Actinopterygii, and as such may have significance for interpretations of the interrelationships of the Osteichthyes.

The geological and ecological aspects of the Bear Gulch Limestone have been described elsewhere (Horner, in press; Horner and Lund, in press; DiCanzio, in press; Lowney, in press; Lund, Lund and Klein, in press; Lund, in press). In summary, however, the Bear Gulch limestone member of the Heath Formation was deposited in a small, shallow tropical bay. The water and superficial bottom sediments were well oxygenated, bottom sediments were very fine with relatively high but cyclically variable silica content (Williams 1979), deposition was quite rapid and there was no significant sessile benthic invertebrate community. Substrate for the fauna consisted of various sponges (Rigby, in press) and algae. Malacostracan crustaceans and several phyla of worms are among the more dominant aspects of the invertebrate fauna (Schram and Horner 1978; Schram 1979). There are approximately seventy species of fish currently known, including five species of coelacanths (Lund and Lund, in press), possibly two crossopterygians known from scales (Andrews, pers. comm.), about thirty-five chondrichthyan species (Lund, in press), and one acanthodian (Zidek 1980); the remaining species are actinopterygian (Lowney 1980). All but about eight species are known from holomorphs.

Specimens range in condition of preservation from scattered to excellent, although generally lacking three-dimensionality. The Tarrasiiformes, however, frequently preserve with somewhat

three-dimensional skulls and axial elements. The matrix, while technically a limestone, is not appropriate for acid preparation, and specimens are generally prepared with fine needles. The bones of some specimens or regions of specimens are sacrificed for the preparation of latex peels (Baird 1955), while in other cases the bones may be viewed through liquids, either water, alcohol, or benzene, to determine bone growth zones and the paths of the calcite filled lateral line canals. Drawings are prepared from photographic bases; photographic methods have been discussed elsewhere (Lund 1980).

SYSTEMATIC PALAEONTOLOGY

Order TARRASIIFORMES

Diagnosis. Elongate bony fishes lacking pelvic fins, and with unpaired fins continuous from near the occiput to the anus. Pectoral fins lobed, supported by few, elongate radials. Squamation may be variously reduced or absent. The bones of the skull include paired premaxillae, a rostral and separate postrostral, one or more pairs of nasals, plus frontals, parietals, and postparietals, flanked posterolaterally by supratemporals and tabulars (pterotics). A dermosphenotic is present. Cheek bones may include scales not tightly associated into a plate, plus preoperculum and a prespiracular series, or may be reduced. The operculum is small, the suboperculum is similar to the numerous branchiostegals, the more anterior of which are elongated to resemble lateral gulars. The shoulder girdle is covered by the branchiostegals and suboperculum. The ventral end of the cleithrum is overlapped anteriorly by the long thin dorsal stem of the clavicle. The braincase is composed of several ossifications.

Genus PARATARRASIUS, new genus

Diagnosis. The genus is distinguished from other members of the order by the long maxilla with a rectangular cheek expansion, a complete squamation, a downturned tail and low anterior anal fin.

Type species. Paratarrasius hibbardi, new species.

Etymology. Para, close to; and Tarrasius.

Paratarrasius hibbardi, new species

Text-figs. 1–3. Plate 50, figs. 1–5

Type specimen. University of Montana 5557, part and counterpart.

Referred specimens. University of Montana (MV) 2841, 2918, 3562, 3600, 5558, 6931, 7395. Carnegie Museum (CM) 27275, 27376, 30651, 30652, 30780, 35229–35232, 35544, 35601, 37539, 37540, 37598.

Horizon and locality. Upper Chesterian, Mississippian (Namurian E2B; Lower Carboniferous) Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Diagnosis. Tarrasioid fishes ranging in length to 136 mm; the maximum head length/total length ratio is 0·155; maximum body height total/length ratio is 0·172; the total length/snout-vent length ratio is 1·746. There are 27 to 29 precaudal vertebral arches and 68 to 73 precaudal scale rows. There are 28 to 31 scale rows above the lateral line at the anal notch and 50 to 54 rows below the lateral line. There are 27 to 28 caudal vertebral arches, disappearing at the downturn of the tail, and 78 to 81 caudal scale rows. There are approximately 4 jointed, unbranched fin rays to each vertebral arch.

Etymology. Named in honour of the late Professor Claude W. Hibbard.

DESCRIPTION

Body form. The head is approximately $\frac{1}{5}$ of the total length, with a subterminal mouth. The body is bladelike, achieving maximum height just anterior to the anal notch, from which point the dorsal margin gradually declines (Pl. 50, fig. 1). The posterior end of the tail is downturned. The dorsal fin arises behind the head, achieves maximum height relative to the dorsal body outline until shortly before the ventral downturn of the axis, and then approaches the axis more closely. The fin is continuous around the posterior tip of the axis in the midventral line, appearing to end somewhat anterior to the downturned axis but continuing forward on the ventral surface as very small fin rays to the rear margin of the anal notch. Pelvic fins are lacking. Pectoral fins are borne upon scaled lobes, about half of the body height above the ventral midline (text-fig. 2). Squamation is relatively uniform, without specialized middorsal, ventral, or anal scales, although each scale in the lateral line is perforated for a pore. The first scale row behind the cleithrum is somewhat elongated. The first 8 to 9 ventral scale rows behind the cleithrum and clavicle follow the curvature of these elements; succeeding ventral scale rows assume the same anterodorsal linearity as is typical for all flank scales. Scale rows immediately below the dorsal fin and above the anal fin consist of smaller scales and change direction to approach the vertical. This involves 6 to 9 vertical scale rows dorsally in the trunk and ventrally in the caudal region, and 13 scale rows along the dorsal margin of the caudal region (Pl. 50, fig. 5; text-fig. 3). This is interpreted to mean that the base of the median fin was borne upon a narrow, scaled extension from the somewhat more rounded body outline.

The lateral line of the body extends parallel to the axis to the point of sharp downturn, whereupon it takes a very sharp ventral bend and ends (text-fig. 3). It, therefore, does not extend into the ventral downturn. In all other well-preserved Bear Gulch actinopterygians, the lateral line extends only a short way up the dorsal lobe, and turns sharply to end at or near termination of hypochordal fin rays, or the change from regular hypochordal rays to the fin rays of the caudal flap or terminal tuft (DiCanzio, in press; Lowney 1980). We feel that, given this landmark, the downturned axis of *Paratarrasius* is actually the anatomical homologue of the upturned axis and terminal lobe of other chondrosteans. The principle webbed median fin itself therefore would represent a fusion of dorsal fin, terminal tuft, and hypochordal caudal, the anal fin being represented only by very short rays extending to the anal notch.

The blade-like body form of *Paratarrasius* is found among many recent teleostean fish that inhabit extremely sheltered, weedy environments. Propulsion is generally by continuous undulation of the median fin, with attitudinal adjustments performed by the pectoral fins. Thrust of the median dorsal particularly can generate either forward or backward motion, dependent upon the direction of wave propagation. Propulsion is thus extremely slow, with escape acceleration being provided by few strokes of the entire caudal region.

It is virtually axiomatic that all recent fishes with this particular body form and propulsive system are also weak, active low frequency electroreceptors (Bullock 1973). This unfortunately cannot be verified in extinct fish.

Cranial osteology. There are two types of ornamentation found on the head of *Paratarrasius*, the first being fine closely spaced ridges paralleling the long axis of the fish, as found on the maxilla, the lower jaw, anterodorsal expansion of the preoperculum, and the 'antorbital'. The second type, which evidently succeeds the first during ontogeny, is a smooth, glossy complete surficial covering, broken only by rows of fine nutrient foramina that are found uniformly distributed across many bones, particularly of the skull roof. Smaller specimens show that the nutrient foramina are related to the spaces between ridges of primary ornamentation on bones such as the premaxillae, and cannot be considered to be pores as found in cosmine-bearing fishes. The growth of the secondary ornamentation has the profoundest effects upon the apparent osteology of the skull roof, for it completely obliterates sutures along the dorsal midline by about 115 mm in total length (Pl. 50, figs. 2, 4). Transverse sutures, as between tabulars and postparietals, do not seem to be affected. Further, the secondary ornamentation only seems to be present, within the size range of the available specimens, upon the bones of the skull roof and rostrum. Bones of the lateral surface of the head are not affected.

The premaxillae are small, initially paired, and meet in the midline, where they fuse by ornamental overgrowth. They are dorsally overlapped by the median rostral element in loose association, and bear a strong internal shelf near their anatomically ventral but posterior edge. A single row of fluted teeth is borne upon this shelf, the teeth thus facing posteroventrally and spanning the small space between the anterior ends of the maxillae. The rostral is about the same size as the fused premaxillae, also covered with glossy ornament, and carries the ethmoid commissure across the midline without evident pores. It is notched dorsally for the reception of the anterior edge of the postrostral.

The single large postrostral has a glossy ornament. It is bordered laterally by two serial nasal bones on each side, and is notched midlaterally for the anterior naris. The anterior nasal element is somewhat expanded

anteromesially, the posterior nasals meet in the midline posterior to the postrostral, and the nares seem to be represented by lateral notches at or near the common border of the two nasals. While the lateral line canal can be seen to traverse the middle of each nasal, its relationship to the ethmoid commissure cannot be precisely determined. There are few pores for the lateral line canal. The two nasals are bordered by a single long, angled supraorbital bone.

The frontals are initially paired but fuse across the midline to form a single element dorsal to the orbit. Prominent ventral flanges project from the lateral edges of the frontal (text-fig. 1*d*). The frontal bears the supraorbital canal near its lateral edges, and shows only few, tiny, regular pores associated with the canal (text-fig. 1*b*). The frontal meets the parietals in a conspicuous suture posteriorly, and is bordered laterally by a single supraorbital element. The parietals also fuse across the midline, forming the largest bone of the skull roof. It is notched laterally for the dermosphenotic anteriorly and for the supratemporal more posteriorly and is flanked laterally anterior to the dermosphenotics by a small supraorbital. The supraorbital lateral line canal traverses the parietal to enter the tabular at the posterolateral corners, in contrast to virtually every known bony fish. A few fine, irregular pores mark the path of the supraorbital canals across the parietal, but a large pore can be seen at the parietal-supratemporal-tabular junction (text-fig. 1*c*). There seems to be no communication via a transverse supraorbital commissure (Lowney 1980; Lund and Lund, in press) with the otic canal. The supratemporals are narrow, and receive the infraorbital canals from the loose dermosphenotics. The canals continue posteriorly as the otic canals into the small, almost square tabulars. The postparietals are mesial to the tabulars and bear two discontinuous segments of a transverse pit line almost to the mid-dorsal line (Pl. 50, fig. 2; text-fig. 1*e*). The suture between postparietals is sinuous and is not generally obscured by ornamental overgrowth. The supraoccipital ossification of the braincase does not participate in the skull roof.

At least two pairs of thin, small scale-like bones closely adhere to the posterior margin of the skull roof, followed posteriorly by the paired extrascapulars and post-temporals. The otic canal passes into the extrascapulars laterally, whence the occipital commissure passes mesially. From the extrascapulars the head canal passes into the lateral edge of the post-temporals, then posteroventrally into the bone called the postspiracular in actinopterygians (Gardiner 1963; Lowney 1980).

The antorbital bone is rectangular in shape, ornamented with prominent horizontal ridges, and abuts against the rostral anteriorly, the anterior nasal anterodorsally, and the infraorbital posteriorly. It carries the infraorbital canal to the ethmoid commissure. While it appears most likely from the shapes of the bones and what is preserved of the paths of the lateral line canals that the nasal branch of the supraorbital canal (anterolateral commissure of Jarvik 1948; Stensiö 1947) joins the infraorbital canal at the antorbital, the precise position of this junction cannot be found. The infraorbital below the orbit is a strong ossification, tapering anteriorly, always tightly associated with the anterior end of the maxilla, and fitted through a curved suture to the posterior infraorbital. The latter element occupies the posteroventral quadrant of the superficial rim of the orbit, has a distinct mesially directed lamina, and usually bears fine strong, well-spaced posteriorly directed spikes along the posterior border. Occasional specimens reveal an irregularity of spacing, and one specimen bears six spikes, the dorsalmost two of which are thin and closely spaced. The infraorbital canal gives off short posterior branches that emerges to pores between the bases of the well-spaced spikes. The ventralmost two spikes are at the level of the anterior edge of the cheek expansion of the maxilla, and all spikes usually overlap the first row of cheek scales. The dermosphenotic is a strongly ossified Y-shaped element with a short ventral stem that carries the postorbital continuation of the infraorbital canal on to the skull roof.

TEXT-FIG. 1. *Paratarrasius hibbardi*, cranial bones. *a*, restoration of the external bones of the head. Based upon CM 35232, and MV 2841 and 5557. Scale in mm. *b*, partial restoration of the antorbital region of CM 35232. Scale in mm. *c*, restoration of the skull roof in dorsal view. Based on CM 35232 and CM 30583, and CM 27376, 35231, and 35544. Scale in mm. *d*, braincase, palate, and shoulder girdle in lateral view. Braincase and palate based on CM 35232. Scale in mm. *e*, braincase in occipital view, of CM 27376. Scale in mm. Abbreviations: A, angular; Ao, antorbital; C, cleithrum; Cl, clavicle; D, dentary; De, dermosphenotic; Dh, dermohyal; E, extrascapular; Ec, ectopterygoid; En, endopterygoid; Eo, exoccipital; Ep, epiotic; Et, ethmoid; F, frontal; Hy, hyomandibular; I, infraorbital; M, maxilla; Mp, metapterygoid; Nd, dorsal (posterior) nasal; Nv, ventral (anterior) nasal; O, operculum; Oc, occipitals; Op?, opisthotic?; Os, Orbitosphenoid; P, postrostral; Pa, parietal; Pc, postcleithrum; Pe, pterotic; Pm, premaxilla; Po, preoperculum; Pp, postparietal; Pr, pro-otic; Ps, parasphenoid; Pso, postspiracular; S, supratemporal; Sa, surangular; Sc, supracleithrum; So, Supraorbital; Sop, suboperculum; Sp, Suprapterygoid; St, sphenotic; Su, supraoccipital; T, tabular.
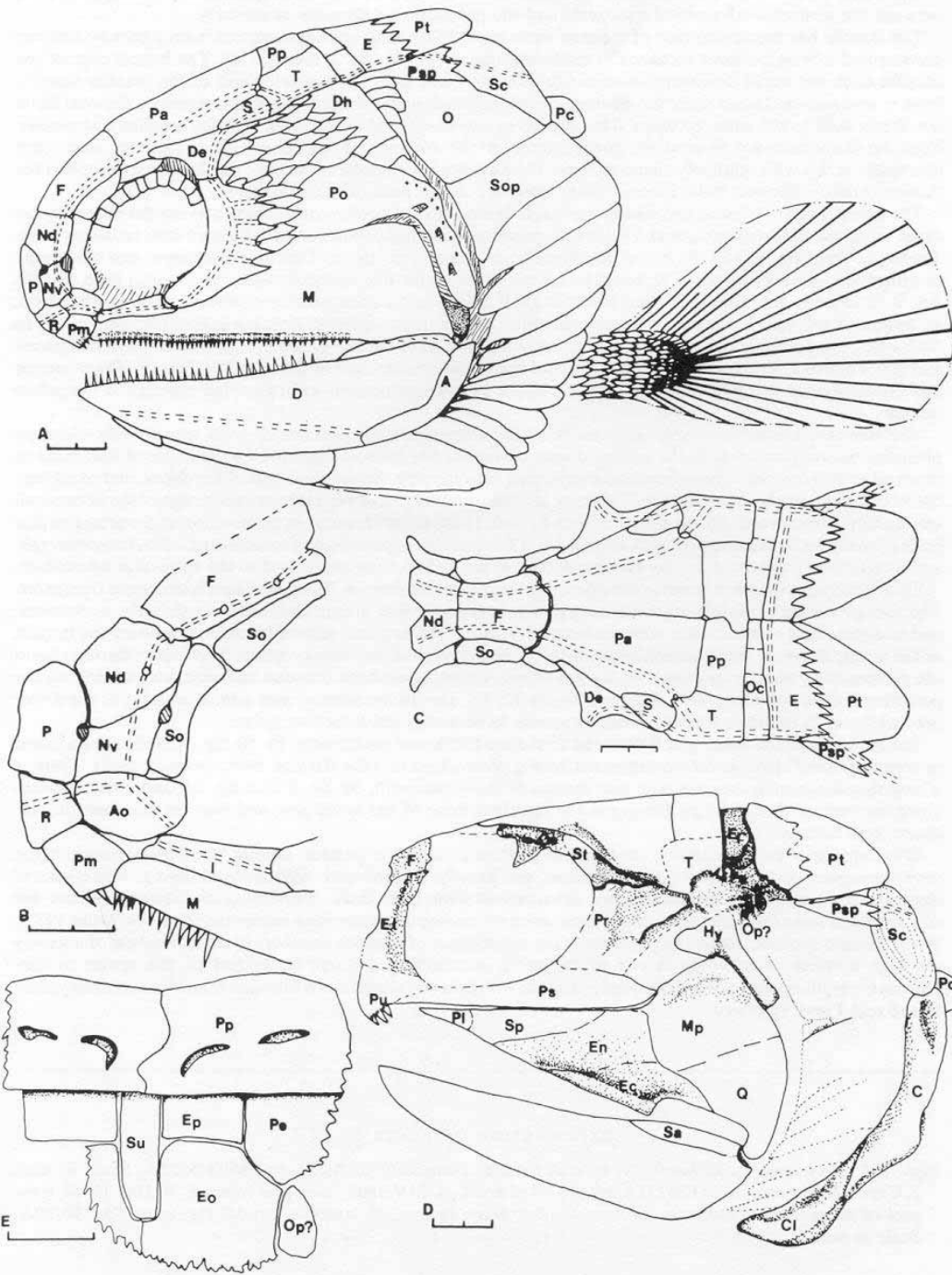
The scales of the cheek are somewhat variable, but occur in five to six anteroposteriorly overlapping rows between the posterior infraorbital anteriorly and the preopercular elements posteriorly.

The maxilla has the appearance of those of more typical Paleozoic actinopterygians, with a narrow anterior portion and a broad, almost rectangular cheek expansion (Pl. 50, fig. 2; text-fig. 1a). The buccal edge of the maxilla does not curve downward posteriorly, however, nor does the posterior end of the maxilla seem to have a shearing occlusion with the dentary. Further, judging by postmortem displacements, the maxilla is not firmly held to the preoperculum. This should not be construed as implying that the maxilla was mobile. Teeth on the maxilla are pleurodont, borne internal to the ornamented ventral margin of the bone, and occur in a single series with relatively sharp crowns. They cannot be considered 'peglike', as has been described for *Tarrasius* (Moy-Thomas 1934; Jessen 1973). There are no pit lines on the maxilla.

The preoperculum of most specimens is a single bone with a narrow ventral limb carrying the preopercular canal posterior to the maxilla, and a relatively short anterodorsal expansion ornamented with radiating lines. There is a short horizontal pit line at the junction of the two portions of the preoperculum, and there may be either few, prominent pores or possibly a quadratojugal pit line vertically upon the ventral limb (Pl. 50, figs. 2-4; text-fig. 1a). One specimen, however (MV 3600), has a preopercular of two separate ossifications, an anterodorsal and a posterior element each with distinctively different ornamentation (Pl. 50, fig. 3). In both cases, the preopercular canal occupies the posterior edge of the preoperculum, exiting through fine pores, and is not continuous to the anterodorsal part of the preoperculum, nor to the main head canal. The posterior and posterodorsal margins of the preoperculum are strongly associated with the same margins of the palate mesially.

The elements known variously as bone X or the dermohyals are a series of from one to four elements posterior to and parallel with the posterodorsal margin of the preoperculum, from the angle of that bone to the skull roof. They are strong elements, overlapped anteriorly by the last scale row of the cheek, and overlying, but not fixed to, the hyomandibular. There are several small scales between the posterior edge of the dermohyal series and the operculum (Pl. 50, figs. 2, 3; text-fig. 1a). These elements occur in the position of the prespiracular bone of coelacanths (Lund and Lund, in press) and the dorsal preoperculum of some Bear Gulch Actinopterygii, and a clear case has been made by Lowney (1980; in press) that they are related to the spiracular operculum.

There are about fourteen bones in the opercular-branchiostegal series. The operculum is small and triangular. The suboperculum is slightly expanded anteriorly, is considerably longer and narrower than the operculum, and in appearance is continuous with the branchiostegals. The first and second branchiostegals are the longest of the series; there are three branchiostegals to the ventral end of the preoperculum. The fourth through tenth are progressively shorter, posterior to the lower jaw, while the eleventh is broad and elongate, underlying the posterior half of the lower jaw. Branchiostegals 12, 13, and 14 are narrow and almost as long as the lower jaw, while the fifteenth is short and there appears to be a very small median gular.

The articular of the lower jaw is elevated above the tooth row posteriorly (Pl. 50, fig. 3), as has been found in several other Paleozoic actinopterygians with a pleurodont maxilla (Heyler 1969; Lowney 1980). There is a long thin surangular dorsal to the rear margin of the dentary (Pl. 50, fig. 2; text-fig. 1d) and a thin angular along the rear of the jaw. The dentary is the principal bone of the lower jaw, and bears a thin band of tall, sharp teeth bucally.

What appear to be the sclerotic ossifications of *Paratarrasius* are peculiar among actinopterygians in being very numerous. Further, the dorsal elements are heavily ossified and slightly overlapping, while ventral elements have not been found. All are ornamented with faint lines. Normally, all actinopterygians are considered to have four sclerotics, while dipnoans and crossopterygians have numerous elements (Miles 1977). While Miles is inclined, justifiably, to dismiss the significance of sclerotic numbers in determination of ancestry the high number of sclerotics is one of the more outstanding different characters of this group of fish. Alternatively, these may not be sclerotics but a lateral supraorbital series as is found in primitive sarcopterygians (Lund and Lund, in press).

EXPLANATION OF PLATE 50

Figs. 1-5. *Paratarrasius hibbardi*. 1, type specimen, University of Montana (MV) 5557A. Scale in mm. 2, Carnegie Museum (CM) 35232A, latex peel of head. 3, MV 3600, latex peel of head. 4, CM 35544, latex peel of head. Arrow indicates hyomandibular. Scale in mm. 5, anterior caudal region of CM 30780A. Scale in mm.

PLATE 50

LUND and MELTON, *Paratarrasius*
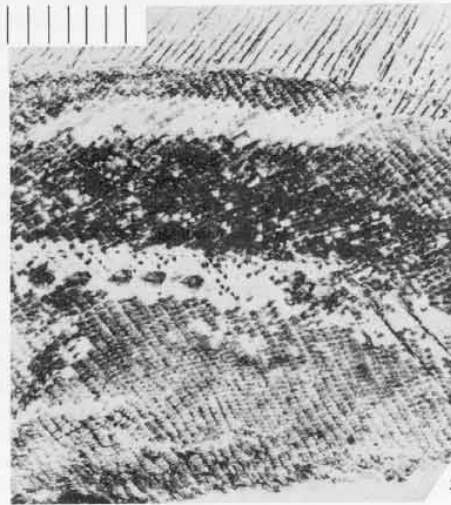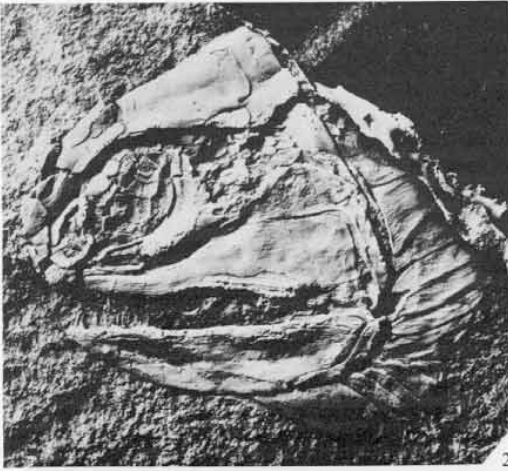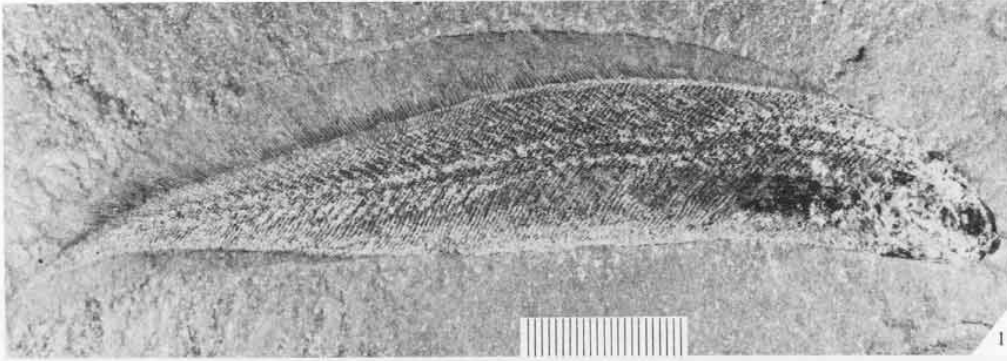
The shoulder girdle of *Paratarrasius* consists of six paired bones in dorsoventral series, including the enlarged dorsal postcleithral scale (text-fig. 1*a* and *d*) a larger number of elements than has been described for any other osteichthyan (Rosen *et al.* 1981). The otic lateral line canal runs through only the anterolateral edge of the post-temporal, and through the next elements of the series, before entering the body scales. These elements have been termed the postspiracular and supracleithrum in standard actinopterygian nomenclature (Gardiner 1963; Lowney 1980). The postspiracular has been little noted in actinopterygian studies, and while it is commonly found, it has not previously been noticed either to carry the main lateral line nor to be an element of the shoulder girdle. The name itself is singularly inappropriate. The supracleithrum dorsally overlaps the end of the cleithrum and is ornamented with strong circumferential lines. The postcleithrum is scale-like in thickness, shape, and relationships.

The cleithrum and clavicle are usually completely covered by the subopercubum and branchiostegal rays. They are well displayed only in CM 35231. The cleithrum is narrow and unornamented and ends immediately ventral to the base of the pectoral fin lobe. It is overlapped anteroventrally by the thin dorsal stem of the unornamented clavicle. There is no interclavicle; neither scapulocoracoid nor pectoral fin endoskeleton can be seen. Several problems of osteichthyan bone homologies and terminology are revealed by the tarrasiid shoulder girdle; these are discussed subsequently.

The palate is poorly displayed, and is known principally from MV 3600, CM 30780 and 35544 (text-fig. 1*d*). The palatine is very narrow, and bears a dermopalatine patch of strong, long, conical teeth. The endopterygoid appears to be long and thin, extending to about midway along the maxilla and bearing a single row of long teeth just mesial to a lateral flange contacting the maxilla. There is a thin dermal plate extending posteriorly from the endopterygoid that bears a fine shagreen of denticles. There may be a thin suprapterygoid plate along the mesial edge of the palate. The ectopterygoid continues the lateral margin of the palate, but has a strongly ossified, very marked opening for the adductor musculature between its posterolateral margin and the posteromesial end of the maxilla. The quadrate condyle is at the rear edge and only slightly below the ventral edge of this fontanelle. The metapterygoid is always almost completely covered by the preoperculum and seems to correspond with it in general outline; its posterior edge fits into a groove in the anterior edge of the short hyomandibular.

The hyomandibular is an extremely short element, obliquely articulated to the braincase with a double head at the level of the supratemporal–tabular suture and extending no further ventrally than the ventral end of the operculum (Pl. 50, fig. 4). Its contact with the palate is therefore limited to the posterodorsal edge of the metapterygoid. No other details of the hyoid arch can be resolved. The hyomandibular is essentially as illustrated by Jessen (1973) for *Tarrasius*.

The braincase is well ossified in several bones (text-fig. 1*d* and *e*). Anteriorly there is a strong ossification of the lateral wall of the ethmoid, suturing ventrally with the paired prevomers and parasphenoid. The prevomers meet in the midline and bear a prominent ventral platform upon which there are long teeth. The parasphenoid is extremely narrow in the orbital region, expanding under the braincase and apparently ending at about the level of the hyomandibular articulation. The parasphenoid bears fine granular teeth posteriorly. The lateral laminae of the parasphenoid are low, and there are no articulations between braincase and palate. The parasphenoid sutures posterodorsally with the pro-otic, and a sphenotic and small orbitosphenoid can be found (Pl. 50, fig. 3). Only a small corner of the hyomandibular facet may be borne upon the pro-otic, most of the anterior facet apparently being located upon the poorly displayed sphenotic ossification. There is a pterotic posterodorsally, although it cannot be determined whether it is co-ossified with the superficial tabular. The pterotic extends around to the posterodorsal edge of the occipital surface where it is excavated for a small post-temporal fossa (text-fig. 1*d*). There is a strong ridge, near the ventral margin of the lateral face of the pterotic, that usually marks the dorsal edge of a lateral temporal fossa in recent teleosts; this ridge is capped posteriorly by what appears to be an additional ossification in line with a ventral process of the post-temporal (text-fig. 1*d* and *e*) but further details are not available. The occipital surface slopes gently posteriad below the occipital or scale bones. On this shelf there is a narrow supraoccipital, in small part projecting between the dorsomedian ends of the exoccipitals. There is also a pair of epiotics lateral to the supraoccipital; the post-temporal fossa is small and open dorsally. The braincase, therefore, although incompletely known, is ossified in a number of parts that correspond roughly to the ossifications of the braincase of teleosts, rather than to the single unit found in Permotriassic actinopterygians (Obruchev 1967).

Axial skeleton. Neural arches are fused dorsally across the midline throughout the body, and are usually preserved in three dimensions. Neural spines are median and straight, and appear to be inserted into the dorsal ends of the neural arches. Ventral arch elements in the trunk are large and triangular. Haemal arches of the caudal region are essentially the same as the neural arches. Haemal spines are continuous with the
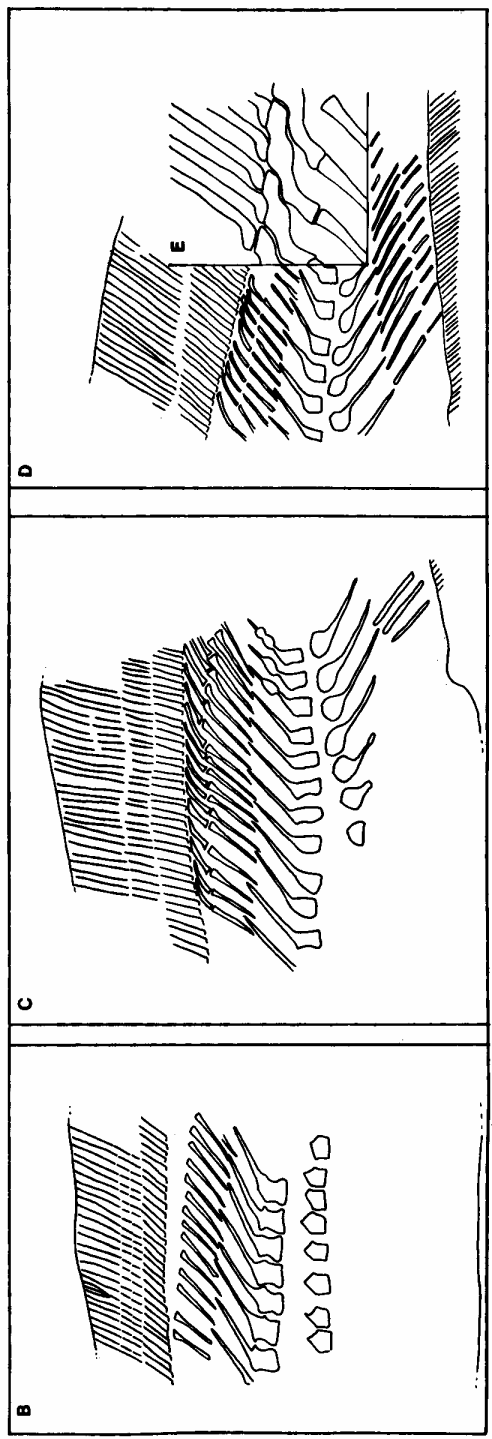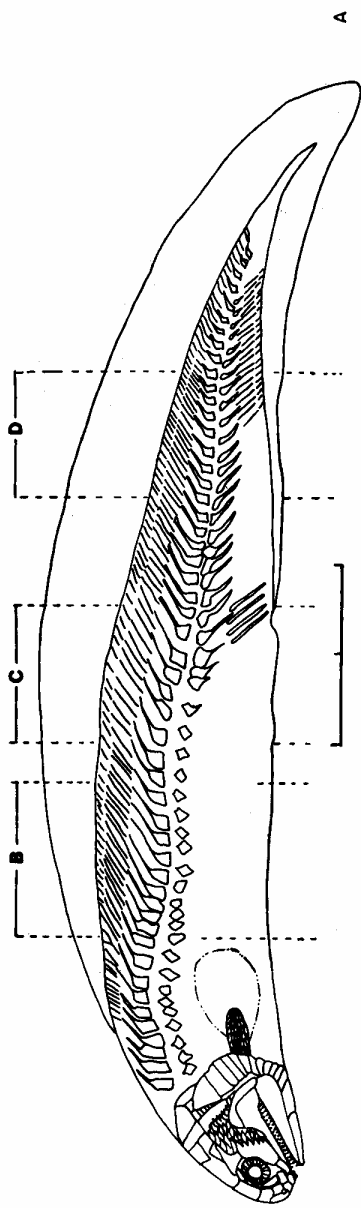
TEXT-FIG. 2. *Paratarrasius hibbardi. a*, axial skeleton. Based on MV 5557, plus. *b*, CM 37540. *c*, CM 30780. *d, e*, MC 5558, CM 37540.

arches in structure, and curve slightly posteriad distally as they taper to points. The first three or four haemal spines are closely associated with long, well-ossified epihaemals, apparently in 2:1 ratio to the spines. Only near the downturn of the caudal, where the ventral fin deepens, can there be seen two series of elements distal to the haemal spines (text-fig. 2a). There are no visible calcified centrum elements and no contact between neural and haemal arch elements.

Dorsally, each neural spine is closely associated with the ventral ends of two epineural rods, each of which, in the thoracic region, bears a small posterodorsal expansion with an articular facet for a more distal element (text-fig. 2b and c). These articulations are internal to the change in scale row orientation (Pl. 50, fig. 5). Each of the distal elements is straight anteriorly, and articulates with (usually) two fin rays. Each fin ray throughout the median fin bears an anterior process that almost contacts the fin ray next anterior. At the beginning of the caudal region the epineural-distal articulation enlarges and approaches the vertical, while the distal elements curve posteriorly and then dorsally to the bases of the fin rays (text-fig. 2d and e). At the level of the twelfth caudal segment, as the body taper becomes marked, the distal elements start becoming progressively shorter relative to the proximal segments and neural spines, where they can still be seen to be the only elements articulating with the fin rays. Neither axial nor peripheral elements are visible in the downturned caudal axis.

The two series of radials supporting the median fins may be primitive for Osteichthyes (Lund and Lund, in press), and may be homologized with axonosts and baseosts. We can find no basis, however, for Jessen's (1973) elaborate restoration of these structures in Tarrasius. As far as can be determined, the axial skeleton of Tarrasius differs principally in numbers of vertebral elements from that of Paratarrasius.

The anterior region of the peritoneal cavity often is preserved with a prominent black stain, in the position expected for a liver (Pl. 50, fig. 1).

TEXT-FIG. 3. Paratarrasius hibbardi, posterior caudal region of CM 30780 (arrow indicates the terminus of the lateral line canal). Scale in mm.

RELATIONSHIPS

Moy-Thomas's first (1934) description of the skull roof of Tarrasius was somewhat closer to the osteology of Paratarrasius than the second (Moy-Thomas and Dyne 1938). He originally described the large and unique frontals, and large supratemporal, subsequently changing the frontals to a large 'postrostral' and obliterating sutures he had, in reality, seen correctly in his original description. There is adequate reason to believe that with sufficient material the process of skull suture obliteration that characterizes both genera would have become clear to Moy-Thomas in Tarrasius. The cheek is poorly preserved, and the presence of cheek scales cannot be determined from the Glencartholm material. The maxilla is rounded posteriorly, however, and overlaps the posterior end of the lower jaw as in many other chondrostean-level actinopterygians; there is no clear evidence of pleurodonty and the teeth are called peg-like, marked differences with the Montana species. Both opercular and subopercular bones are larger, and branchiostegals are more numerous. Moy-Thomas illustrates eight elongate pectoral radials supporting the fin (Moy-Thomas 1934), an area which is obscure in Paratarrasius. Vertebral elements in the trunk of Paratarrasius are more numerous, and the median fin outlines differ dramatically, along with the termination of the body. It is not certain, however, to what degree these differences are caused by poor preservation. Again, preservational differences may account for Moy-Thomas's restoration of three rows of dorsal radials distal to the neural spines; Jessen (1973) illustrates an entirely different structure, and one

for which we could find no basis in any specimens. *Tarrasius* lacks all but lateral line scales anterior to the caudal region. If this is simply representative of an early ontogenetic stage of scale development, in a pattern typical of acanthodians and many osteichthyans (Zidek 1976; Lowney 1980, 1980*a*), then scale development of *Tarrasius* is still significantly delayed relative to the condition in *Paratarrasius*. In *Paratarrasius* all specimens from less than 90 mm preserved length have complete squamation.

Holopterygius nudus is known from one specimen that basically agrees with other Tarrasiiformes in the body form, elimination of the pelvics, and in axial skeleton, all characters that are rather inadequate ones upon which to base relationships (Jessen 1973). There is, however, also striking agreement between the shoulder girdles of *H. nudus* and *P. hibbardi*. One can judge from the three forms that experimentation with scale reduction may have been a feature of the group. *H. nudus* has interarticulating arches, not seen in either of the other species, and has apparently singularly weakly ossified skull bones. These are all features characteristic of the undescribed Bear Gulch tarrasioid. It may be suggested that *Holopterygius* is more specialized, and less closely related to either *Tarrasius* or *Paratarrasius* than they are to each other.

There are several osteological features of *Tarrasius* and *Paratarrasius* that in combination are shared by no other known Paleozoic actinopterygian. These include the serial nasals, the presence of bones that can be called frontals, parietals, and postparietals, the supraorbital canal entering not the postparietals but the tabulars, the scale rows on the cheek, and the body and fin form. The dermal shoulder girdle, however, raises the most questions.

The dermal shoulder girdle of *Paratarrasius*, and of many Paleozoic actinopterygians, consists of six paired bones, the post-temporal, 'postspiracular', supracleithrum, postcleithrum, cleithrum, and clavicle. A median interclavicle is absent. The shoulder girdle of sarcopterygians seems to lack the 'postspiracular' anterolateral to the post-temporal–supracleithrum joint, and incorporates an anocleithrum between, and overlapped by, supracleithrum and cleithrum (Andrews and Westoll 1970, 1970*a*; Rosen *et al.* 1981). The anocleithrum has been considered to be homologous to the actinopterygian postcleithral scale on the basis of topographic location and overlap relationships (Rosen *et al.* 1981) while the inappropriately named postspiracular has not previously been observed to carry a lateral line canal or to be an element of the shoulder girdle.

The tarrasiid shoulder girdle suggests several possible alternative interpretations of the dorsal bones of the series. First, the tarrasiid arrangement of post-temporal, postspiracular, supracleithrum, and cleithrum–postcleithrum may be uniquely derived among the Paleozoic actinopterygians, a remote possibility in the light of the prevalence of this arrangement (Gardiner 1963; Lowney 1980). The lateral line canal traversing the postspiracular seems to be unique, however. Second, the arrangement may be primitive for the Actinopterygii and bone nomenclature and homologies are essentially correct among osteichthyan groups, in which case the condition may also be considered primitive relative to the Sarcopterygii. Third, the tarrasiid arrangement may be uniquely derived relative to the known sarcopterygian linkage with the post-temporal and braincase. Fourth, bone homologies may not be correct; the actinopterygian postspiracular being homologous to the sarcopterygian anocleithrum, and the postcleithrum not being an element of the shoulder girdle of primitive members of either group. Overlap and lateral line relationships between postspiracular and supracleithrum do not correspond to that of the sarcopterygian supracleithrum and ano-cleithrum, strongly suggesting that these homologies cannot be demonstrated. The absence of a distinct postcleithral shoulder girdle element either in *Mimia* (Rosen *et al.* 1981), in tarrasiids, or in other Paleozoic actinopterygians suggests that there is no convincing evidence for a proposed anocleithrum–postcleithrum homology. The weight of evidence suggests that either alternative two or three are the most acceptable; that this arrangement may be either primitive for actinopterygians or uniquely derived. A median interclavicle, absent in tarrasiids, is also lacking in primitive actinopterygians (Lowney 1980) and in primitive sarcopterygians (Lund and Lund, in press, contrary to Rosen *et al* 1981), and is not a useful character in known Paleozoic actinopterygians.

Patterns of ossification of the bones of the suborbital region of the cheeks of actinopterygians are highly variable with the weight of evidence indicating that either a disorganized or fully scaled

region between the infraorbital series and the preopercular bones represents the primitive condition (Lowney, in press; 1980). Sarcopterygians as well show cheeks consisting of a large and variable number of cheek bones, although these are usually integrated into a cheek plate (Jarvik 1948; Westoll 1949). The sarcopterygian preopercular lateral line canal traverses a variable number of bones before contacting the jugal canal (Jarvik 1948; Westoll 1949); the suggestion that the single preopercular bone of tarrasiids is a derived condition relative to a large number of bones in series is reinforced by several Bear Gulch actinopterygians with two bones in the series (Lowney 1980).

The presence of a series of bones in the spiracular operculum may be regarded as a more primitive state than that of the single prespiracular bone of sarcopterygians (Lund and Lund, in press). In this case, more primitive conditions than that of the tarrasiids are known from other Bear Gulch Actinopterygii (Lund, manuscript; Lowney, in press), and no actinopterygian shows any indication of the submandibular series of certain sarcopterygians (Lund and Lund, in press). The presence of the dorsal portion of the mandibular operculum in Actinopterygii and the ventral portion of the mandibular operculum in Sarcopterygii is interpreted as reinforcing this subdivision of the Osteichthyes.

The rostral regions of sarcopterygians, where they are not fused into single solid blocks, are mosaics of many bones (Lund and Lund, in press). The rostral region of *Paratarrasius* consists of premaxillae meeting in the midline, a derived condition even among the actinopterygians; followed by a median rostral carrying the ethmoid commisure, a primitive character for the osteichthyans; followed by a separate postrostral (a derived character, several postrostrals seem to be primitive for the Osteichthyes); flanked laterally by two serial nasals, a primitive character for known Actinopterygii but derived relative to the sarcopterygian condition (Lowney 1980; Lund and Lund, in press). There is no actinopterygian that has been observed to have the 'bone' called the rostropremaxilloantorbital (Gardiner 1963, 1967) either primitively or otherwise (Lowney, in press; 1980). *Paratarrasius* and *Tarrasius* have an additional paired bone of the skull roof not found in other actinopterygians, here termed the frontals, a primitive character. This paired bone is bordered posteriorly by a conspicuous suture reminiscent of the intracranial joint of many crossopterygians, but the structure of the braincase and skull roof of *Paratarrasius* seems to preclude such a joint. In view of the gross differences of skull roofing bone patterns among the sarcopterygians (Andrews 1973; Lund and Lund, in press; Rosen *et al.* 1981) no reasonable homologies can be drawn between the tarrasiid 'frontals' and the bones of any known sarcopterygian.

It should be noted that while the occipital scale bones seem to be prevalent among Paleozoic actinopterygians, they have been little noticed in the literature (Lowney, pers. comm.). They clearly do not bear the extrascapular lateral line commisure, and their significance is not clear.

The median fin condition of two rows of serial radials supporting fin rays is shared by other actinopterygians and Dipnoi (Lowney 1980; Obruchev 1967). The endoskeleton of the pectoral fin of *Tarrasius* consists of a row of radials, again in primitive contrast to the single proximal element of the Sarcopterygii but consistent with other actinopterygians.

The Tarrasiiformes can clearly only be considered actinopterygians. Among these, however, they are primitive in retaining a separate rostral, two pairs of nasals, frontal bones, a supratemporal, scale rows on the cheek, and a portion of the spiracular operculum (Lowney 1980). Derived characters that may be useful in determining relationships include the premaxillae suturing across the midline, a Y-shaped dermosphenotic, the supraorbital canal extending into the tabular, reduction but not elimination of the supraorbital bones, a somewhat oblique articulation of the hyomandibular to the braincase, the lack of a quadratojugal bone and the presence of a single preopercular bone, pleurodont dentition on the maxilla, and reduced scale size with increased numbers of scale rows. The numerous branchiostegals may also constitute a derived condition.

Derived characters of the premaxillae and rostral along with numerous branchiostegals and reduced scales are shared with the order Palaeonisciformes, as restricted by Lowney (1980). Tarrasiiformes do not, however, share the marked palaeonisciform character trends of a strongly protruding rostrum, reduction of the suborbitals to two bones, extremely oblique suspensoriums, and reduction to elimination of the spiracular operculum.

There are a number of derived characters that the Tarrasiiformes share with a new order incorporating the Paramblypteridae, the Aeduellidae, and several Bear Gulch fish ('fatfish', 'deep belly'—Lowney, in press; Lowney 1980). These include the Y-shaped dermosphenotic, the reductions of the supraorbital series, the elevated articular and pleurodont maxilla, and, with aeduellids, the path of the supraorbital lateral line canal. The Tarrasiiformes also share a number of primitive characters in common with this group, such as the scaled cheek, the state of the spiracular operculum, and the retention of the supratemporal bone. They do not, however, share the most typical trends within this group, such as the tight premaxilla–antorbital association, the development of cervical vertebrae, and the presence of pseudocentra. Further, of the derived characters shared in common, all but perhaps the path of the supraorbital canal are characters known to have arisen independently among other Paleozoic actinopterygians. The supraorbital canal entering the tabular, further, is the only known derived character that the Aeduellidae and Tarrasiiformes share in common.

The Tarrasiiformes share no other derived characters with any other known actinopterygian. It must be tentatively concluded that this order may have diverged from the Palaeonisciformes, but close to the basal stock prior to the establishment of many of the more characteristic trends that distinguish the later members.

SUMMARY

The Tarrasiiformes incorporate a number of primitive characteristics not previously known among the Actinopterygii, such as the presence of distinct frontal bones, two pairs of nasals, and an additional canal-bearing bone in the shoulder girdle, the postspiracular. The available evidence seems to indicate a relationship with a basal stock of the order Palaeonisciformes.

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