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This volume is dedicated to Dr. Rainer Zangerl

Ptycholepis marshi Newberry, A Chondrosteian Fish from the Newark Group of Eastern North America

BOBB SCHAEFFER
CURATOR, DEPARTMENT OF VERTEBRATE PALEONTOLOGY
AMERICAN MUSEUM OF NATURAL HISTORY

DAVID H. DUNKLE
CURATOR OF PALEONTOLOGY
CLEVELAND MUSEUM OF NATURAL HISTORY

NICHOLAS G. McDONALD
DEPARTMENT OF GEOLOGY
WESLEYAN UNIVERSITY
MIDDLETOWN, CONNECTICUT

INTRODUCTION

In 1878, S. W. Loper, an inveterate collector of fossil fishes in the Triassic rocks of the Connecticut Valley, discovered several specimens of a new fossil fish at his well-known locality near Durham, Connecticut. The specimens were presented to Professor J. S. Newberry, who recognized them as a new species of the genus *Ptycholepis*, previously known only from the European Triassic and Liassic. Newberry (1878) named this species *P. marshi* and later provided a more complete description of it in his monograph on the fishes and plants from the Triassic of New Jersey and the Connecticut Valley (Newberry, 1888).

Although additional specimens were collected at Durham and other localities in the Connecticut Valley, subsequent discussions of *P. marshi* (see, for example, Lesley, 1889; Woodward, 1895; Eastman, 1905, 1911) added little to the knowledge of the species, in part because of poor preservation and inadequate preparation techniques. Between 1942 and 1949, two amateur collectors, F. M.

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Baer and W. H. Martin (1949), found some unusually well-preserved examples near Haymarket and Midland, Virginia. Further collection at these sites by D. H. Dunkle and S. P. Applegate produced additional specimens that are now in the United States National Museum of Natural History and the American Museum of Natural History. In 1970, W. B. Cornet and N. G. McDonald reopened an old Loper site at North Guilford, Connecticut, not far from the Durham locality. A number of exceptionally well-preserved examples of *P. marshi* were recovered, along with *Semionotus* and various redfieldiids.

Most of the specimens used in this study, from Virginia and Connecticut, have been prepared by the airbrasive method.

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The photographs were taken by Chester Tarka, and the drawings were made by Lorraine Meeker. The specimens used in this study were prepared by Walter Sorensen, and preliminary editing of the manuscript was done by Marlyn Mangus.

ABBREVIATIONS

AMNH, American Museum of Natural History

BM(NH), British Museum (Natural History)

MCZ, Museum of Comparative Zoology, Harvard College

NMNH, United States National Museum of Natural History

WU, Wesleyan University

YPM, Peabody Museum of Natural History, Yale University

SYSTEMATICS

Order Ptycholepiformes Andrews et al., 1967

Family Ptycholepididae Brough, 1939

Ptycholepis Agassiz, 1832

Ptycholepis Agassiz, 1832, p. 142.

Type species. — *Ptycholepis bollensis* Agassiz.

Distribution. — Middle Triassic: Italy; Upper Triassic: Austria; Upper Triassic-?Liassic: Virginia, New Jersey, Connecticut; Lower Liassic: England; Upper Liassic: Germany, France, England.

Revised generic diagnosis — Body elegantly to deeply fusiform; snout with nasals separated by postrostral bone; paired rostromaxillae in subrostral position, meeting in midline; maxilla with slight postorbital expansion in articulation with preopercular; nasal and dermosphenotic in contact above orbit; suborbitals (known in three species) numerous (8-20), narrow, and overlapping anterior border of preopercular; preopercular nearly vertical, broadest at contact with maxilla; suspensorium nearly vertical; antopercular present; interopercular absent; four to six branchiostegals, uppermost twice as wide as others; coronoid process absent; marginal teeth on maxilla and dentary small, uniform and acuminate; origin of dorsal fin about midway between snout and caudal peduncle; rays of dorsal and anal fins completely segmented; rays of paired fins segmented only distally; only dorsal rays not bifurcated; caudal fin robust, hemiheterocercal, equilobate and moderately cleft; all fins (including both lobes of caudal) with fulcra; scales rhomboidal behind shoulder girdle, elsewhere much longer than deep, with ganoine arranged in low, longitudinal ridges, frequently anastomosing; posterior borders of scales notched.

Ptycholepis marshi Newberry, 1878

Type. — AMNH 575, a nearly complete, but poorly preserved, fish from the Newark Group at the S. W. Loper locality near Durham, Connecticut.

Distribution. — Upper Triassic-?Liassic Newark Group of Massachusetts, Connecticut, New Jersey, and Virginia.

Specific diagnosis. — Differs from other species of *Ptycholepis* in having combined maximum width of parietals nearly equal to length and in having posterolateral corners of parietals extended posteriorly. Maxilla expanded postorbitally as in *P. barboi*; median

gular extending to posterior border of mandible, lateral gulars mostly covered by median gular; six branchiostegals; dermal bone ornamentation weak to strong; origin of dorsal fin at fourteenth scale row; gradual change from rhomboidal to narrow flank scales in first five vertical scale rows.

Referred specimens. — From the Shuttle Meadow Formation, Durham, Connecticut: AMNH 575 (type), AMNH 669, MCZ 6254, WU 907, WU 865. From the Shuttle Meadow Formation, North Guilford, Connecticut: AMNH 4519, AMNH 4676, AMNH 4677, AMNH 4713, AMNH 4714, AMNH 4715, AMNH 4718. From the Brunswick Formation, Watchung, New Jersey: YPM 6283. From the Brunswick Formation, Boonton, New Jersey: YPM 6272. From the ?Bull Run Shale, Midland, Virginia: AMNH 4808, AMNH 4810, AMNH 4811, AMNH 4812, AMNH 4813, AMNH 4814, AMNH 4815, AMNH 4816, AMNH 4817, USNM 21288, USNM 21289, USNM 21290, USNM 21840. From the ?Bull Run Shale, Haymarket, Virginia: USNM 18323. The specimens listed above were the most useful in this study because of their well-preserved morphological details. In addition, there are several dozen catalogued and uncatalogued specimens of *P. marshi* at various institutions.

Description. — Approximate measurements of the more complete specimens of *P. marshi* on which this description is based are presented in Table 1. The specimen sample includes fishes of relatively modest size and slender body (figs. 1, 2). An average of 28 per cent of the standard length is occupied by the head and opercular apparatus. It is not possible to obtain an accurate measurement of the maximum body depth (which occurs in front of the dorsal fin), but it is estimated to be less than the length of the head, including the opercular apparatus. The dorsal fin is triangular and originates near the middle of the body. The anal fin is slightly smaller in size, is similarly triangular, and is situated about halfway between the pelvics and the caudal. The pelvic fins arise behind the termination of the dorsal and are much closer to the anal than to the pectorals. The hemiheterocercal caudal fin, supported by a stout caudal peduncle (AMNH 4813) is robust, equilobate, and moderately cleft.

The endocranium, seen in NMNH 21289 (fig. 3B), is dorsoventrally compressed and difficult to interpret. It is typically palaeonisciform and shows no evidence of subdivision into separate centers of ossification. The ethmoid region is about twice as broad

TABLE 1. Body measurements in millimeters on various specimens of *Ptycholepis marshi*.

Specimen number	Length from snout to posterior margin of caudal body scales	Skull length (snout to posterior opercular)	Maximum depth of body	Length from snout to origin of dorsal fin	Length from snout to origin of anal fin
AMNH 8408	92.0	27.0	30.0	44.0	72.0
AMNH 4811	111.0	38.0	—	—	90.0
AMNH 4812	113.0	34.0	27.0	—	90.0
AMNH 4813	110.0	30.0	—	42.0	82.0
USNM 21288	135.0	38.0	—	72.0	98.0
USNM 21289	95.0	30.0	25.0	45.0	75.0
YPM 2608	165.0	38.0	—	—	—

FIG. 1. *Ptycholepis marshi* Newberry. A, AMNH 575, type. $\times 0.87$. B, WU 907.

FIG. 2. *Ptycholepis marshi* Newberry. Reconstruction.

as long, and its ventral surface is marked by numerous pits and foramina that indicate nerve and vascular plexi ventral to the nasal capsules. The lateral occipital fissure enters the vestibular fontanelle on either side. The ventral otic fissures extend anteriorly and somewhat medially beyond the fontanelles, but whether they have a ventromedial junction cannot be determined in this specimen. The lateral occipital fissure extends dorsally and laterally to the margins of the braincase as preserved. This fissure has not been identified dorsally, and the presence or absence of a dorsal posterior fontanelle cannot be determined. Neither can the presence of a dorsal anterior fontanelle or the size and characteristics of the fossa bridgei be demonstrated.

The dorsal aorta was enclosed in a canal in the cranial floor. A single median anterior opening and a single median posterior opening are present for the aorta. Openings for the second efferent branchial arteries are situated about equidistance between the openings for the aorta. The vagus nerve, as usual, emerged through the lateral occipital fissure, posterodorsal to the vestibular fontanelle. A faint groove traverses the wall of the endocranium in a dorsal direction, slightly anterior to the vagal opening. It is thought to have accommodated the supratemporal ramus of the glossopharyngeal nerve. Anteroventrally the groove is aligned with the rostrocaudal jugular depression and the jugular canal. The hyomandibular facet is located on the posteroventral surface of the postorbital process.

The dermal skull (figs. 4, 5, 6) is long and narrow and has a pronounced rostrum. The suprascapulars are characteristically lobate. They are not in contact with one another in the mid-dorsal line: body scales may fill the intervening space. The extrascapulars, four in number, are quadrangular and are of approximately equal dimensions. The parietals are rectangular and about half as wide as long. The frontals are twice as long as the parietals and are rather irregular in outline. They increase in width from the posterior border to the point where they are in lateral contact with the

Opposite.—

FIG. 3. *Ptycholepis marshi* Newberry. Dissociated skull bones. A, AMNH 4817. B, NMNH 21289. Both $\times 1.6$. Abbreviations: dent, dentary; dpt, dermopterotic; dptq, dermal bones of palatoquadrate; fr, frontal; hym, hyomandibular; io, infraorbital; mx, maxilla; neu, neurocranium; pa, parietal; pop, preopercular; pros, postrostral; ptq, palatoquadrate; sbo, suborbital.

anteromesial edge of the dermopterotic and with the posteromesial border of the dermosphenotic. The borders of the frontals are emarginated anteromesially to receive the postrostral; anterolaterally they are truncated for the nasals. The heavily ornamented postrostral is a robust bone with a relatively long and narrow posterior portion and a somewhat shorter, broader, and rounded anteroventral part. The flanking nasal elements are massive. Indentations in the lateral margin of the postrostral and in the anterior and posterior borders of the nasal bones mark the positions of the anterior and posterior nasal openings. The long crescent-shaped dermosphenotic is broader posteriorly than anteriorly, where it is in narrow contact with the nasal. The dermopterotic is in anteromesial contact with the frontal. It is somewhat longer than the parietal and is wider anteriorly than posteriorly.

The ovate orbit is about one-third of the total length of the skull. The mouth is barely subterminal. The mandibular symphysis is long and the suspensorium is nearly vertical. The ventral and posterior border of the orbit is formed by four narrow infraorbitals. The supraorbital bone has a long anteriorly-directed process that partly excludes the dermosphenotic from the orbital margin. The anterior infraorbitals articulate anteriorly with paired elements that are in the same position as the so-called rostro-antorbito-premaxillae (figs. 4B, 5) of *Boreosomus* Stensiö, 1921 (see Nielsen, 1942, fig. 71). These elements meet in the midline below and behind the nasals and the postrostral, and they carry several sensory canal pores. Although they form the anterior upper border of the mouth, there is no evidence that they bear teeth. Between the infraorbitals and the preopercular there is a vertical series of narrow bar-like suborbital bones that vary in number from 7 to 13. The fixed maxilla has a lobate postorbital expansion. The oral border of the maxilla is gently curved; it bears a weak internal flange to receive the palatoquadrate. The mandible is a slender element with a

Opposite.—

FIG. 4. *Ptycholepis marshi* Newberry. Reconstruction of skull. A, Dorsal aspect. B, Ventral aspect. C, Lateral aspect. Abbreviations: aop, antopercular; br, branchiostegal; dent, dentary; dpt, dermopterotic; dsph, dermosphenotic; esc, extrascapular; fr, frontal; io, infraorbital; lg, lateral gular; mg, median gular; mx, maxilla; na, nasal; op, opercular; pa, parietal; pop, preopercular; pros, postrostral; ropmx, rostro-antorbito-premaxilla; sbo, suborbital; so, supraorbital; sop, subopercular.

FIG. 5. *Ptycholepis marshi* Newberry. Skulls in lateral aspect showing variation in dermal bone ornamentation. A, AMNH 4676, $\times 2.2$. B, AMNH 4718, $\times 2.1$.

FIG. 5 (continued). *Ptycholepis marshi* Newberry. Skulls in lateral aspect showing variation in dermal bone ornamentation. C, AMNH 4715, $\times 2.0$. D, AMNH 4714, $\times 2.3$.

straight oral border and a long symphysis. The maxilla and mandible have a single row of tiny, uniformly-spaced villiform teeth. The palatoquadrate and the hyomandibular resemble their counterparts in the European species of *Ptycholepis* (Brough, 1939; Wenz, 1967).

The preoperculum is exposed in several specimens. It extends from the margin of the dermopterotic to the posteroventral extremity of the maxilla. Its posterior border is gently convex against the anteriorly concave margins of the antoperculum, operculum, and suboperculum. The anterior border is covered by the overlapping suborbitals above and by the posterodorsal border of the maxilla below. Between the two overlap areas the preoperculum is produced into a sharp, forwardly-directed spur. A perusal of the palaeonisciform restorations assembled in Schaeffer (1973) shows that this preopercular shape is frequently associated with a nearly vertical suspensorium.

The operculum is slightly deeper than long; it is somewhat closer in size to the suboperculum than it is in *P. bollensis*, *P. curta*, or *P. barboi*.

A large median gular extends from the mandibular symphysis almost to the transverse level of the angular. The lateral gulars are mostly covered by the median gular. There are six paired branchiostegal rays; the uppermost one is enlarged to nearly half the size of the suboperculum.

Ornamentation of the skull bones (figs, 5, 6) consists generally of wide enameled ridges with narrow interspaced grooves. For the most part they are rostrocaudally directed. Density of ornamentation varies from total coarse coverage near centers of ossification to wide peripheral bare areas. Invariably the ornamentation is coarsest rostrally, progressively less pronounced posteromesially and posterolaterally, and weakest ventrolaterally and ventrally.

Determination of the lateral line sensory system of the skull is dependent on the degree of ornamentation. In some specimens the course of the supraorbital canal through the nasals and frontals is indefinable; in others it may be marked by ganoine ridges higher than, but parallel to, the ornamental ridges, or by discrete pores. The three pairs of pit lines in the parietals are similarly variably observable. In some specimens they are well defined, but in others they may be only partially developed on one side and absent on the other. In one specimen (AMNH 4812) where the internal face of the

FIG. 6. *Ptycholepis marshi* Newberry. Skulls in dorsal and ventral aspect showing variation in dermal bone ornamentation. A, AMNH 4677, dorsal aspect, $\times 2.1$. B, AMNH 4813, dorsal aspect, $\times 3.0$. C, AMNH 4812, dorsal aspect, $\times 3.4$. D, AMNH 4811, ventral aspect, $\times 2.5$.

rostroantorbito-premaxilla is exposed, the ethmoidal sensory commissure can be seen. The preopercular sensory canal internally parallels the posterior margin of the preopercular bone, but emerges externally on the median vertical axis. The entire sensory canal pattern is palaeonisciform.

Scales (fig. 7B) with ganoine-covered ridges are found over the entire body. They are distinctive in their length-to-height proportions and ornamentation. They agree in all observable details with the scales of *P. bollensis* (Aldinger, 1937). Approximately 50 vertical scale rows (fig. 2) occur between the shoulder girdle and the caudal inversion. The first two rows have equilateral rhomboidal scales that are elaborately ornamented with both anteroposterior and oblique striae. Posteriorly the scales are four times as long as high. Anteriorly each vertical row includes about 50 scales, but the number diminishes to about 39 in the region of the anal fin.

The dermal elements of the shoulder girdle are incompletely known, but they seem to resemble those of *P. bollensis* (Wenz, 1967). The pectoral fin (fig. 2) consists of about 18 principal rays. The first of these is very robust, but it is only half as long as the longest ray. The second and third rays are acuminate and jointed, but unbifurcated. The fourth ray is the longest. It branches distally, as do all the succeeding rays. The first four rays are fringed by a double row of fulcral scales.

The pelvic fins are smaller than the pectorals. They originate below the fourteenth vertical scale row, and each consists of from 13 to 16 principal rays. They are fringed anteriorly by a double row of fulcra. The anterior four rays are acuminate and jointed, but not dichotomized, as are the remainder of the rays. The dorsal fin arises above the thirteenth vertical scale row. It consists of from 20 to 24 principal rays, of which approximately the first five are nonbranching and fringed by a double row of fulcra; the remaining rays are articulated and distally dichotomous. The anal fin is smaller than the dorsal. It originates beneath the twenty-fifth vertical scale row, behind the pectoral girdle. It consists of about 14 principal rays. The anterior four are acuminate and articulated; the remainder are bifurcated distally. This fin probably also possesses a double row of fulcra.

The caudal fin is equilobate (fig. 7A). The epichordal lobe consists of about 20 principal rays, all regularly articulated and distally dichotomous. The hypochordal lobe is composed of about 30

FIG. 7. *Ptycholepis marshi* Newberry. A, AMNH 4813, base of caudal fin, $\times 4.0$. B, AMNH 4715, flank scales, $\times 2.0$.

principal rays. The anteroventral rays are acuminate and jointed, but not dichotomized. The borders of both the epichordal and hypochordal lobe are fringed by a double row of fulcral scales.

Discussion. — Before considering the relationships of *P. marshi*, it will be helpful to reconsider the affinities of the genus *Ptycholepis* in terms of its presumed shared derived characters, and to discuss the status of the seven other currently recognized species in terms of both shared and unique derived characters.

On the basis of "characters-shared-in-common," Aldinger (1937) and Brough (1939) independently concluded that *Ptycholepis* is related to the palaeonisciform genus *Boreosomus*, and, in fact, that the latter is ancestral to the former. Following a detailed re-examination of *P. bollensis*, Wenz (1959, 1967) listed the following characters shared by *Boreosomus* and *Ptycholepis*: (1) completely ossified neurocranium of palaeonisciform type; (2) dermal bone pattern of cranial roof; (3) rostral (snout) pattern; (4) large orbit; (5) numerous suborbitals; (6) antopercular (dermohyal) present; (7) preopercular (sometimes) divided horizontally into two separate components; (8) mandible elongated, extending to front of snout, with mandibular canal clearly curved anteriorly; (9) hyomandibular with large opercular process and without a canal for the hyomandibular branch of the facial nerve; (10) palatoquadrate of the palaeonisciform type; (11) cranial dermal bones and scales strongly ornamented.

Wenz went on to list other *Ptycholepis* characters not shared with *Boreosomus*: (12) hyomandibular facet on braincase horizontal; (13) vertical preopercular with preopercular canal along anterior border; dorsal part occasionally covered by suborbital bones extending to anterior border of antopercular; (14) maxilla with no (or slight) postorbital expansion; (15) wide proximal hypurals; (16) hemiheterocercal tail; (17) fin rays equal in number to basals, small in number, robust and bifurcated distally.

Many of the resemblances and differences between *Boreosomus* and *Ptycholepis* that Wenz noted had previously been discussed by Aldinger (1937) and Brough (1939), who made additional comments on the opercular series, the fins, and scales.

It is now important to decide which character states previously considered to relate *Boreosomus* and *Ptycholepis* are primitive palaeonisciform ones. We regard the resemblances listed under (1), (2), (3), (4), (6), (8), (10), and perhaps (9) as primitive shared

character states that are of no value in postulating relationships. Of the characters that *Ptycholepis* does not share with *Boreosomus*, (12), (13), and (14) are involved in the nearly vertical suspensorium—a condition that certainly evolved numerous times independently among the early chondrosteans. The other unshared characters, (15), (16), and (17), are characteristic of several presumably unrelated subholostean groups.

The suborbital series has been described for three of the eight species of *Ptycholepis*. *P. marshi* has 7 to 13 of these elements. Although Brough (1939) figured four suborbitals for *P. curta* Egerton (from the Lower Lias of Dorsetshire), one specimen (BMNH 39493) actually has about 20 (*fide* Sylvie Wenz and C. Patterson). The type species of *Ptycholepis*, *P. bollensis* (from the Upper Lias of Bavaria, Yorkshire, and Yonne), has 7 to 13 suborbitals, according to Wenz (1967), rather than two, as illustrated by Gardiner (1960). It seems probable, however, that the primitive suborbital number for the palaeonisciforms was about two (Schaeffer, 1973). The high number in *Boreosomus*, *P. marshi*, *P. curta*, and *P. bollensis* may therefore be regarded as a derived condition. Unfortunately, the cheek elements are unknown in the other species of *Ptycholepis*.

The large opercular process on the hyomandibular noted by Wenz (1967) for *P. bollensis* and *Boreosomus* is also present in *P. barboi* Bassani (1939) and *P. marshi*. A robust opercular process is perhaps a derived condition, but our knowledge of the palaeonisciform hyomandibular is too incomplete to propose that such a process is shared by only these two genera.

The type of dermal bone ornamentation characteristic of *Ptycholepis* is also known in *Boreosomus* (Nielsen, 1949) and in various other palaeonisciforms, such as *Moythomasia* Gross (Jessen, 1968). It probably has little diagnostic significance except at low taxonomic levels where details of the ornamentation pattern may be derived and unique. Most specimens of *P. marshi* from Virginia and Connecticut have the typical heavy ribbing on all the dermal elements except the gulars. However, about 10 per cent of the specimens from both areas have very sparse sculpturing over the entire dermal skull. Because of this distinctive difference in ornamentation, we have considered the desirability of recognizing two species from the Newark Group. However, there is at least one specimen (AMNH 4812) from Midland, Virginia, that shows a more or less intermediate condition between heavy and sparse ornamen-

tation. Ornamentation expression is definitely not growth related, and because of the high frequency of strong ribbing, there is no basis for assuming that the differences represent sexual dimorphism. A reasonable explanation is that the Newark Group has a single species of *Ptycholepis* and that the more or less discontinuous expression of the ornamentation is an example of polymorphism (*sensu* Mayr, 1963) that is skewed, for some reason, toward greatest ornamentation density.

The characteristic narrow flank scales of *Ptycholepis* always have two to four wide, ganoine-covered ridges separated by much narrower grooves. The ridges usually anastomose near the free edge of the scale, which tends to be notched (denticulated). *Boreosomus* has much deeper scales with more numerous and more delicate oblique ganoine ridges. The free edge of the scale is also denticulated. In cross-section the ridges of both *Ptycholepis* and *Boreosomus* are seen to be composed of successive layers (generations) of enameloid separated by elevations of dentin that rise above the common dentin layer and form the floor of the grooves (see Aldinger, 1937, figs. 87, 88, 89). This histological pattern also occurs in other palaeonisciforms with similar scale ornamentation, e.g., *Acrolepis* Agassiz, *Acropholis* Aldinger, *Plegmolepis* Aldinger, and *Boreolepis* Aldinger. Apparent differences and resemblances in other aspects of the scale fine structure, such as the dentine canals, are difficult to assess. If we assume that the primitive state was one in which the enameloid and dentine layers were more or less continuous in cross section, with the horizontal and vertical canals arranged in irregular fashion, then the regular arrangement of these canals in *Ptycholepis* may be regarded as a derived condition. Although the scale architecture of *Boreosomus* resembles that of *Ptycholepis*, the resemblance is not exclusive.

Unequivocal, unique derived character states for *Ptycholepis* are few. In regard to the dermal skull pattern, the absence of a median rostral, the relatively long frontals and dermosphenotics, and the modifications in the cheek related to the vertical suspensorium are by no means unique to *Ptycholepis* and presumably evolved several times independently in other palaeonisciform groups. The numerous narrow bar-like suborbitals in *P. marshi*, *P. bollensis*, and *P. curta* may represent a unique derived condition for the genus. The suborbitals are narrower, more elongate, and more numerous in these species than in *Boreosomus*. The ornamentation of the dermal bones, when strong, as in *P.*

bollensis, *P. curta*, and most specimens of *P. marshi*, is a useful, but inconstant, recognition character that, again, is not unique to this genus.

The squamation is perhaps the most distinctive feature of *Ptycholepis*. The shape of the individual scales, their digitate posterior borders, and their few strong ganoine-covered anteroposterior ridges constitute, in our opinion, a unique derived character state (see Aldinger, 1937, fig. 85). The enlarged dorsal branchiostegal also fits into this category.

The systematic treatment of *Ptycholepis* obviously poses problems that cannot readily be resolved. We have emphasized the taxonomic isolation of this genus (which Andrews et al., 1967 implied in their recognition of the order *Ptycholepiformes*) by noting that many of the character states that *Ptycholepis* shares with other palaeonisciforms are primitive palaeonisciform ones, while others may be due to parallelism (e.g., those related to the vertical suspensorium). The alternate hypothesis, which seems less parsimonious, would favor regarding *Ptycholepis* and *Boreosomus* as sister taxa.

The relationships of *P. marshi* to the other species of *Ptycholepis* are difficult to ascertain on the basis of available information. Unique or shared derived character states for each of the recognized species are rarely evident from the published descriptions, and a revision of the entire genus is obviously necessary. The problems involved are familiar ones to anybody using the cladistic strategy for hypothesizing relationships within a group of extinct fishes.

A brief review of the species can begin with *P. barboi* Bassani (Ladinian of the south Tessin). The "distinctive" characters of this incompletely known species listed by Brough (1939, pp. 65-66) are either primitive palaeonisciform ones or are common to most or all species in the genus. We have found no unique derived character states to distinguish this species from the others. *P. avus* Kner (Carnian, Austria) remains essentially undescribed in spite of some comments by Woodward (1895, pp. 323-324). *P. minor* Egerton (Lower Lias, Leicestershire) is described by Woodward (1895, p. 323) as having feeble ornamentation on the dermal skull, but the species is not otherwise distinguished. *P. monilifer* Woodward (Lower Lias, Dorsetshire) is discussed in some detail by Woodward (1895, pp. 322-323), and later by Gardiner (1960, pp. 261-264), but aside from

being designated as the "largest known species," there are no discernible unique derived features. *P. curta* Egerton (Lower Lias, Dorsetshire), as redescribed by Brough (1939) and supplemented by some observations of Wenz (1967) and Patterson (pers. comm.) may have several unique conditions, including relatively small parietals along with elongate and posteriorly acuminate dermopterotics. A specimen (BMNH 39493) in the British Museum (Natural History) has about 20 narrow suborbitals that overlap only the anterior border of the preopercular. Accordingly, Brough's (1939) illustrations of this specimen should be revised so that the cheek area resembles that of *P. bollensis* (Wenz, 1967). *P. gracilis* Davis (Lower Lias, Dorsetshire) remains practically indeterminate in spite of Woodward's (1895, p. 320) comment that the scales differ from the anterior overlapped border." *P. bollensis* Agassiz (Lower Lias, Yonne), the type species, has been redescribed and figured by Wenz (1959, 1967). Again, there is the problem of recognizing unique derived character states. Possibly the extreme reduction of the body axis in the caudal fin may be restricted to this species.

The distribution of *Ptycholepis* during the Middle and Late Triassic and the Liassic can be readily understood in terms of the Tethys Sea and the continental seaways in existence before drift was initiated. *Ptycholepis* was a marine form that, for some reason, got into several of the Newark basins rather late in their history.

GEOLOGIC OCCURRENCE

The Newark Group of eastern North America is a gently folded and highly faulted sequence of continental and perhaps transitional marine sedimentary rocks, sheets of basaltic lava and diabase intrusives of Late Triassic and possibly Early Jurassic age. The rocks occur in a series of separate basins extending from Nova Scotia to South Carolina. Fossil fishes have been found in most of the basins, but they are particularly abundant in the Connecticut Valley and from New Jersey to Virginia.

In apparent contrast to the abundance and widespread occurrence of semionotids and redfieldiids in the Newark, *P. marshi* is numerically limited and stratigraphically restricted. Initially described by Newberry (1878, 1888) and Loper (1891) from two localities in the Connecticut Valley, *P. marshi* was not recorded elsewhere until recent decades. At present *P. marshi* is known from three widely-separated regions: the Connecticut Valley, the

Northern part of the New Jersey basin, and the Midland, Virginia, area.

Throughout most of the Connecticut Valley the Newark Group is composed of several distinct stratigraphic units: (1) a basal sequence dominated by red and gray arkose and conglomerate, with minor beds of siltstone and shale (New Haven Arkose); (2) a middle series of three basaltic lava formations separated by red and gray siltstone, shale, and coarse clastic rocks (Shuttle Meadow and East Berlin formations); and (3) an upper unit composed of coarse clastic rocks and varying amounts of red and gray shale (Portland Arkose). With a few exceptions fossil fishes in the Connecticut Valley are confined to thin layers of dark gray to black shale and limestone in the Shuttle Meadow and East Berlin formations. The absence of fishes in the red beds probably reflects inadequate conditions for preservation. The fossiliferous exposures may represent parts of one or two widespread black shale layers repeated by faulting, or they may be separate and distinct local horizons. Studies by Davis and Loper (1891) and recently by Byrnes (pers. comm.) have indicated that some black shale horizons do occur at approximately the same stratigraphic position and are, in fact, repeated by faulting. Other black shales, however, are unique to certain sections and cannot be traced or found in equivalent stratigraphic sections.

Although numerous exposures of fossiliferous strata occur in Connecticut and Massachusetts, *P. marshi* has been recorded from only three localities—all in the lower portions of the Shuttle Meadow Formation. At two of these, the Durham and Bluff Head sites (both south of the town of Durham, Connecticut), equivalent units of black shale and limestone are exposed in stream beds. Historically, the Durham locality is the most famous fossil fish locality in the Connecticut Valley and was extensively worked by Davis and Loper (1891), Eastman (1911), and others during the last century. Hundreds of plant remains, redfieldiids, semionotids, and a few examples of *P. marshi* and *Diplurus* were obtained in the years of intensive collecting. The fossiliferous limy black shale sequence at Durham is approximately 2 ft. thick and outcrops along with largely unfossiliferous thin limestone and micaceous gray shale. Stratigraphically the shale occurs at an estimated 200 ft. above the lava of the Talcott Formation. The rock is extremely black, dense, and hard, and it contains appreciable amounts of carbonate. It is well laminated and extremely brittle; it can be split easily into plates one-quarter to one-half inch thick. The Durham fishes are

usually well preserved, but it is often difficult to extract them in one piece. The beds at Durham are now largely covered over or have been removed, but there are large scrap piles of black shale in the immediate area.

Less than a mile northeast of the Durham locality, the fossiliferous black shale of the Shuttle Meadow is again exposed in a shallow stream bed. This site was discovered by Loper (1891) and was given the name "Bluff Head"; but for reasons unknown the locality remained unworked until recent years. The shale layers at Bluff Head are variably weathered—some parts crumble at a touch, others are hard and dense, like the Durham beds. The unweathered shale is dark gray to black and is very platy. The upper part of the exposure is composed of highly organic micaceous shale with occasional lenses of clay; the lower part is characterized by rhythmically bedded limy, carbonaceous shale. The entire unit is approximately 3 ft. thick and grades into a buff-brown, medium-grained quartz sandstone above. It is underlain by a light brown to white kaolinite bed. The remainder of the formation consists mainly of red siltstone and shale. The weathered shale at Bluff Head permits the removal of complete fishes. There is an extremely high concentration of fishes at this locality, and the majority are well preserved. Some 30 specimens of *P. marshi* have been recovered to date, along with well over 2,000 redfieldiids and semionotids and a single specimen of *Diplurus* cf. *longicaudatus*.

Recently a small number of *P. marshi* remains was obtained from a relatively fresh road cut on the northeast corner of Mt. Tom, near North Hampden, Massachusetts. A thick stratigraphic section of the Holyoke and presumed Shuttle Meadow formations is exposed.¹ *P. marshi* fragments, as well as more numerous semionotid and redfieldiid remains, were recovered from a well-bedded, 2 ft. thick layer of gray-black calcareous siltstone, roughly 300 ft. below the base of the Holyoke Basalt. Much of the rest of the Shuttle Meadow Formation in this exposure consists of coarse red conglomerate and finer-grained redbeds.

The fishes from Mt. Tom frequently occur in small calcareous nodules and are generally dissociated. The rock is very brittle and dense, but the specimens are usually well preserved. The specimens of *P. marshi* from this locality are the first and only examples

¹The Talcott Basalt is absent in this area. The sedimentary beds at Mt. Tom are presumably equivalent to the Shuttle Meadow Formation.

found in the northern two-thirds of the Connecticut Valley, and the only ones collected from the Massachusetts Newark.

Until a few years ago there were no recorded discoveries of *P. marshi* from the New Jersey basin, despite the high concentration and widespread occurrence of other fishes (particularly semionotids and redfieldiids). Nevertheless, recent field work has resulted in the discovery of *P. marshi* in three north-central New Jersey localities. These three localities all occur in the middle and upper portions of the Brunswick Formation, stratigraphically the youngest formation in the New Jersey basin. However, *P. marshi* is rare in New Jersey: the total number of specimens recovered is fewer than ten, and identification of most specimens is based on isolated scales or skull bones. A single complete specimen from Boonton, New Jersey, was recently found in the collection at Peabody Museum, Yale University (Schaeffer, 1952, indicated that the Boonton fishes occur in a black shale bed near the top of the Brunswick). The shale at Boonton has also yielded vast numbers of other fishes, notably semionotids. The two remaining New Jersey localities are in the thin dark shale sequences underlying the Second Watchung Basalt near the towns of Watchung and Martinsville (Olsen, pers. comm.). Here *P. marshi* is represented only by small patches of isolated scales and bones. None has yet been recorded from the sedimentary sections below the First Watchung Basalt.

Applegate (1956) noted that fishes have been found at several Newark localities in the Culpepper, Richmond, Farmville, and Danville basins of Virginia. Despite the common occurrence of fossil fishes, *P. marshi* has been recovered only from the Culpepper basin, near the towns of Midland (Fauquier County) and Haymarket (Prince William County). The fishes at Midland occur in a 2-ft. thick bed of dark gray, well-laminated silty shale and associated carbonaceous limestone that is part of a thick sequence of red and brown sandstone. At Haymarket the fossiliferous beds are a light buff, soft siltstone. Both sections are presumably in the lower portion of the Bull Run Shale (Baer and Martin, 1949).

If one views the overall distribution of *P. marshi* in the Newark basins, three significant facts emerge: (1) *P. marshi* is usually a minor constituent of the total fish fauna (the only possible exception is the Midland assemblage); (2) it occurs locally and irregularly in geographically separated regions; and (3) it appears to be restricted to certain stratigraphic horizons (the lower Shuttle Meadow Formation in the Connecticut Valley, the middle and

upper Brunswick Formation in New Jersey, and the lower Bull Run Shale in Virginia).

Since all of the European species of *Ptycholepis* are known only from marine deposits, it is suggested that *P. marshi* did not inhabit an exclusively fresh-water habitat. It is possible that it was euryhaline, and, as Schaeffer (1967) suggested, entered the Newark lowlands from the sea. Although *P. marshi* is geographically and stratigraphically restricted in the Newark basins, it occurs in sufficient concentrations at Midland, Durham, and Bluff Head to effectively rule out random introduction.

There is little doubt that many Newark sequences are terrestrial in origin, but perhaps others were transitional or even coastal marine. Byrnes (1974) and Byrnes and Horne (1974), in a detailed study of the Connecticut Valley Newark lithology and sedimentology, concluded that the rocks reflect several depositional environments, including alluvial fan, fluvial, deltaic, and tidal flat. It is reasonable to assume that marine fishes could have inhabited some of these environments, as could have certain fresh-water forms. The problem of the Newark environment cannot be solved by the occurrence of *P. marshi*, but the fact that no other species of *Ptycholepis* is known from fresh-water deposits must somehow be taken into account.

The correlation of rock sequences in the different Newark basins is difficult, as is the geochronology of the group as a whole, because of the absences of both invertebrate and vertebrate index fossils and because of the recurrence of lava flows,¹ fossiliferous dark shale units, red beds and conglomerates in geographically separated basins. Despite these obstacles, most investigators have assumed the entire Newark Group to be Upper Triassic (Carnian-Norian) in age (see Andrews et al., 1967). This assumption may prove to be not totally accurate, as evidenced by recent paleobotanical and palynological studies by Cornet et al. (1973). These authors concluded that the time-stratigraphic range of the Newark Group is greater than previously believed. In a preliminary comparison of newly-discovered Newark palynoflorules with those

¹Sanders (1963), in field studies of the Talcott Formation, and de Boer (1968), through paleomagnetic studies, have convincingly demonstrated that the lava complexes in New Jersey and in the Connecticut Valley are not stratigraphic equivalents in the manner proposed by Russell (1878) and other workers. The flows do, however, seem to represent a relatively limited period of vulcanism in Newark history.

from classic European Triassic and Jurassic type sections, they propose an upper Carnian-Norian age for the Cumnock Formation (North Carolina), the Vinita Beds (Virginia), and the upper part of the New Oxford Formation (Pennsylvania); a Carnian-basal Liassic age for the Brunswick Formation (New Jersey); a basal Liassic age for the Shuttle Meadow Formation (Connecticut Valley) and the Midland, Virginia beds; and a Liassic age for the Portland Formation (Connecticut Valley).

If it can be demonstrated that the upper Brunswick Formation, the Shuttle Meadow Formation, and the Midland beds (the only *P. marshi*-bearing deposits in the Newark Group) are contemporaneous, or nearly so, a single period of marine deposition in the Early Liassic could explain the distribution of *P. marshi*.

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