AN EARLY TRIASSIC FISH ASSEMBLAGE
FROM BRITISH COLUMBIA

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ABSTRACT

A Lower Triassic (Sulphur Mountain Forma-
tion) marine fossil fish assemblage from the
Wapiti Lake area, British Columbia, is described.
It includes the following taxa: cf. *Palaeobates*,
Chondrichthyes, *incertae sedis*, *Pteronisculus* sp.,
Birgeria sp., *Boreosomus* sp., *Bobasatrania
canadensis*, cf. *Perleidus*, *Australosomus* sp.,
Saurichthys sp., Parasemionotidae, *incertae sedis*,
Albertonia cupidinia, and *Whiteia* sp.

Most of these forms, or close relatives, are also
known from the marine Lower Triassic rocks of
East Greenland, Spitzbergen, and Madagascar.

Although the Wapiti Lake specimens have not
added significantly to our knowledge of the
morphology and systematics of marine Scythian
fishes, the assemblage has helped us understand
their paleozoogeographic distribution around the
periphery of Pangaea.

INTRODUCTION

The discovery of fossil fishes in the Lower
Triassic Sulphur Mountain Formation of the
Wapiti Lake area, British Columbia, was made
during the summer of 1947 by L. R. Laudon
(then at the University of Wisconsin) and a group
of graduate students. Because of transportation
difficulties, none of the specimens was collected.
The following year Charles M. Sternberg visited
the area and collected specimens for the National
Museum of Canada. In 1957 Imperial Oil Enter-
prises, Ltd., acquired several dozen fossil fishes
during exploration in this same region. However,
no effort was made to obtain a representative
fossil fish collection until the 1960s, when two
expeditions organized by Bobb Schaeffer of the
American Museum of Natural History and Loris
S. Russell and Wann Langston, Jr., both then of
the National Museum of Canada, were sent to
Wapiti Lake.

The first joint American Museum-National
Museum of Canada expedition was made during
July and August of 1961. The field party
included Gilbert F. Stucker of the American
Museum, who headed the expedition, and Harvey
Champagne of the National Museum of Canada,
who acted as assistant. Their success, despite
trying field conditions, prompted a second trip in
August and September of 1962. In all, more than
140 fish specimens (as well as a number of
ichthyosaur fragments, invertebrate remains, and
rock samples) were collected. This material has
been divided between the two museums and is
now part of the permanent collections of these
institutions.

Since 1962 various other workers, including
B. R. Pelletier of the Geological Survey of
Canada, J. R. Nursall of the University of Alberta,
and Alan McGugan of the University of Calgary,
have collected fossil fishes from the Lower
Triassic rocks of western Canada.

The fishes obtained by the joint AMNH-NMC
expeditions of 1961 and 1962 form the basis of
the present paper. The collection donated to the
National Museum of Canada by Imperial Oil
Enterprises, Ltd., about 45 specimens, has also
been incorporated. Although no attempt has
been made to survey all the marine Lower
Triassic fishes from western Canada, reference
has been made to material obtained by L. M.
Lambe in the early part of this century and by C.
M. Sternberg, B. R. Pelletier, and Alan McGugan.
Note has also been made of two specimens from
Ellesmere Island found in 1962 by E. T. Tozer of
the Geological Survey of Canada.

Our purpose is to document the first impor-
tant Lower Triassic marine fish assemblage
reported in the Western Hemisphere. Because of
generally poor preservation (with a few ex-
ceptions) identification has been challenging and
frequently frustrating. The authors therefore
regard their taxonomic treatment as realistic
rather than simply conservative. At least 12 taxa
of fossil fishes are now known from Wapiti Lake.
They include a hybodont, an undiagnosed
chondrichthyan, three palaeonisciforms, a boba-
satranid, a perleidid, a pholidopleurid, a saur-
ichthyid, two or more parasemionotids, and a
coelacanth. Many of the recognized genera (or

families) also occur in Lower Triassic marine rocks of Greenland, Spitzbergen, and Madagascar. The relatively good preservation of the specimens from these localities has provided much essential information on the morphology of various taxa, particularly the palaeonisciforms, "subholosteans," parasemionotids, and coelacanths. Unfortunately, the specimens from Wapiti Lake add little to our knowledge of anatomy or systematics, but they do provide new data for paleogeographical consideration. In addition, several endemic forms (those known only from the Sulphur Mountain Formation) are of particular interest.

Diagnostic information on skull morphology has been obtained from some specimens by removing the bone fragments with dilute hydrochloric acid and making "smooth-on" peels. The peels often reveal details that are not observable in the original material.

ABBREVIATIONS

AMNH, the American Museum of Natural History

GSC, Geological Survey of Canada

IP, Institut de Paléontologie, Muséum National d'Histoire Naturelle (Paris)

MCZ, Museum of Comparative Zoology (Harvard University)

NMC, National Museum of Canada

PIUU, Paleontologiska Institutionen, Uppsala University

UAM, University of Alberta Museum
UC, University of Calgary

GEOLOGIC OCCURRENCE

Most of the fossil fishes described in this paper were collected in the vicinity of Wapiti Lake, British Columbia, in the Ganoid Range, approximately 100 air miles southwest of Grande Prairie, Alberta (lat. 54° 32′ N., 120° 45′ W.; GSC loc. 48236; see fig. 1). The Ganoid Range is one of the eastern ranges of the northwest-

southeast trending ridges comprising the Canadian Rockies, which are underlain for the most part by Paleozoic rocks. The local structure is a minor expression of the widespread overturning and overthrusting in the Canadian Rocky Mountain System (Irish, 1968). The remarks that follow are made only in reference to the area in which the AMNH-NMC expedition collections were made.

Two of the fossil localities (locs. 1 and 2) occur in the cirque just above Fossil Fish Lake (fig. 2), where the Mississippian Rundle Formation
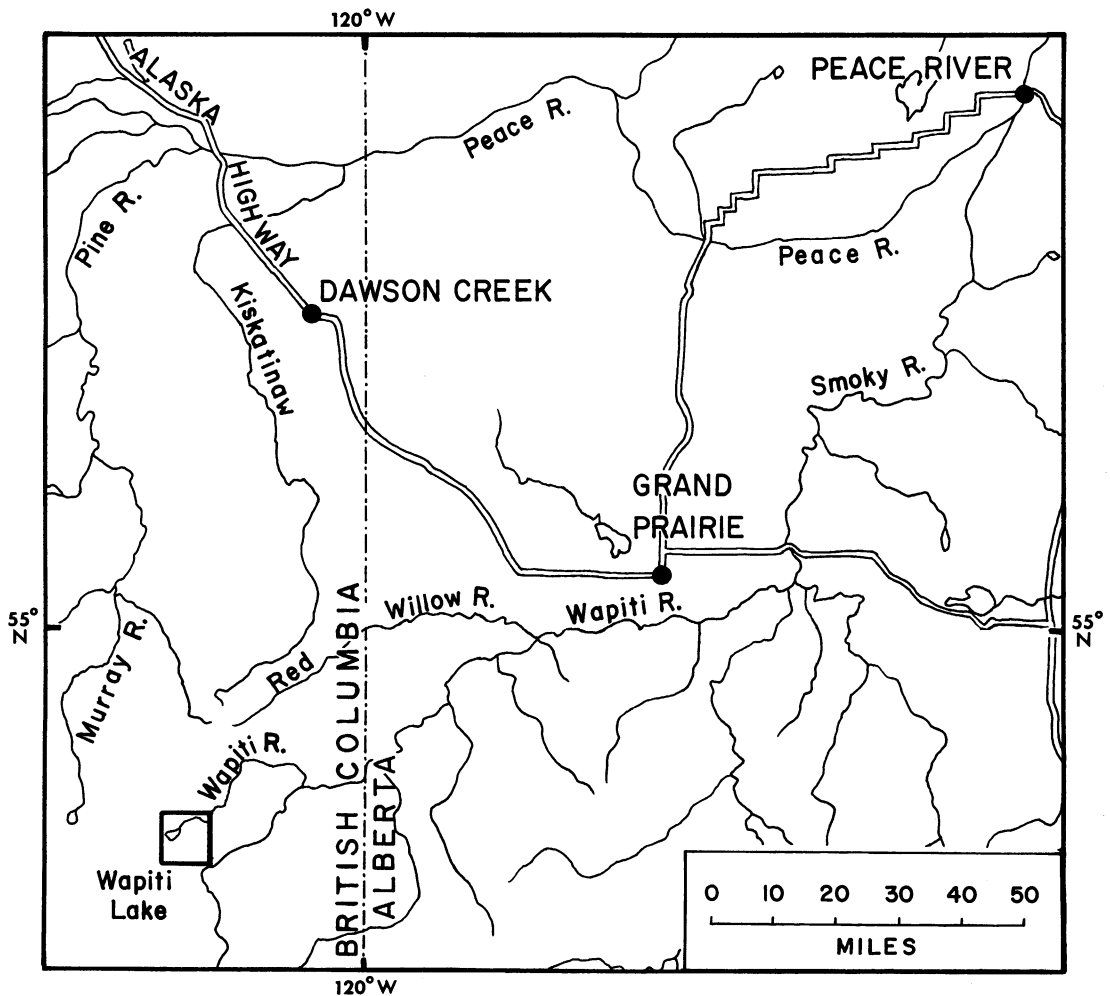
FIG. 1. Map showing location of Wapiti Lake, British Columbia. (Detail inside heavy square shown in fig. 2.)
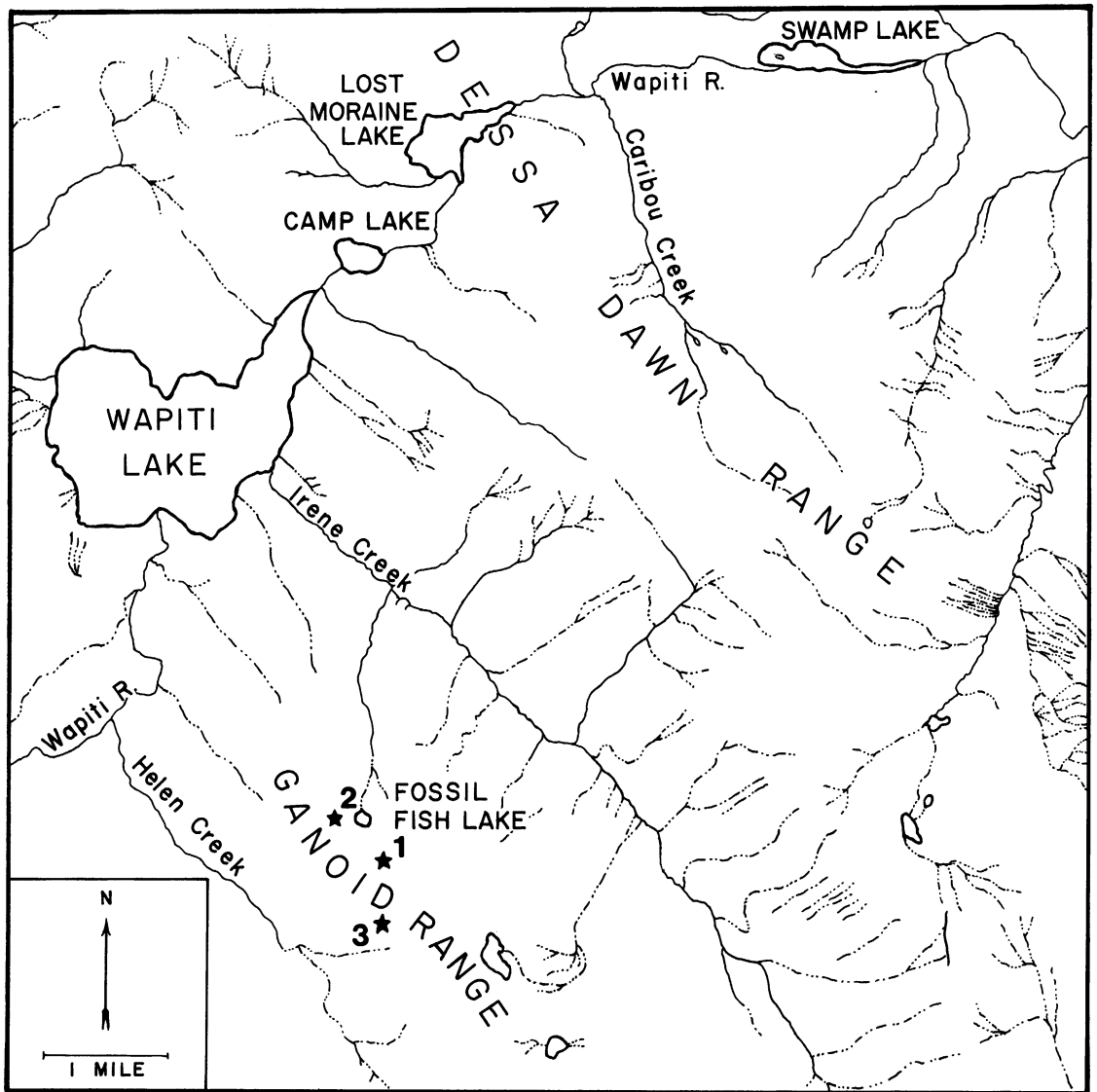
FIG. 2. Detailed map of Wapiti Lake area, British Columbia (heavy square of fig. 1), with the three major fish-bearing localities indicated by stars. (After Laudon et al., 1949.)

overlies the Triassic Sulphur Mountain Formation in a reversal of the normal sequence. The inversion of the strata, along with a 48-degree dip to the southwest along the contact between the two formations, indicates an overturned fold. Thrusting, which is most prominent along a major fault cutting diagonally across the cirque face, further accounts for discontinuity, displacement, and repetition of the beds. Locality 1, which produced most of the specimens, is a dislocated block found just below the fault, about 400 feet below the Rundle-Sulphur Mountain contact. On the opposite side of the cirque, at locality 2, fish were recovered from the talus. A third locality (loc. 3) was discovered on the southwest slope of the Ganoid Range, where the

stratigraphic sequence is intact. Here the fish horizon occurs about 135 feet above the Rundle-Sulphur Mountain contact.

Lithologically the Triassic section begins with a chert breccia, but it consists predominantly of black shales. The shales grade upward into thickly laminated black siltstones, and these, in turn, into blocky and massive siltstones that fracture black and weather to a light brown. Concentration of the fossil material occurs in the upper part of the thickly laminated siltstones and continues into the blocky siltstones. The fish remains extend through a vertical range of about 30 feet, but nearly 90 percent of the specimens *in situ* were found in the lower 5 feet of this section. All the invertebrates found *in situ* occurred above the main fish zone. A thin silt-stone lens, persistent throughout the area above the 30-foot fish zone, yielded *Listracanthus*-like spines.

The fossil-bearing Triassic rocks at Wapiti Lake belong to the Vega-Phroso Siltstone Member (Gibson, 1972) of the Sulphur Mountain Formation (fig. 3) and can be dated as Smithian (Tozer, 1967; Silberling and Tozer, 1968). The name Vega-Phroso is a combination of the names of two distinct members of the Sulphur Mountain Formation in the area around Jasper, Alberta, to the south. The equivalents to the north (in the Sikanni Chief-Pine Pass area) are the Grayling Formation and the lower part of the Toad Formation.

Invertebrate material collected *in situ* at locality 1 was identified by E. T. Tozer (personal commun., 1962, 1963, 1974) as *Posidonia mimer*, *Pseudomonotis occidentalis*, *Xenoceltites* sp., and *Trigonodus* ? sp.; material found as float was identified as *Xenoceltites* cf. *hannai* and *Juvenites* ? sp. According to Tozer the best age indicator among these invertebrates is *Pseudomonotis occidentalis*, which suggests an upper Smithian age (*Wasatchites tardus* Zone). Gibson (1972) collected *Posidonia mimer* and *Xenoceltites* sp. at Wapiti Lake and indicated that they came from the *Euflemingites romunderi* Zone, which is lower Smithian. On the basis of this information and in view of the fact that all the invertebrate material found *in situ* by the AMNH-NMC field parties occurred above the main fish zone, we will not attempt to date the fish-bearing beds more precisely than Smithian.

SYSTEMATICS

CLASS CHONDRICHTHYES

SUBCLASS ELASMOBRANCHII

ORDER SELACHII

FAMILY HYBODONTIDAE

PALAEOBATES VON MEYER, 1849

Type Species. Palaeobates angustissimus (Agassiz).

Distribution. Lower Triassic of Spitzbergen and possibly British Columbia; Triassic of Europe and Soviet Central Asia.

Diagnosis. See Stensiö, 1921, page 34 ff.

Cf. *Palaeobates*
Figure 4

Referred Specimen. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: NMC 9980, a nearly complete but poorly preserved specimen.

Description and Discussion. Palaeobates is known only from teeth, dermal denticles and parts of the visceral skeleton. The Wapiti Lake hybodont (NMC 9980; fig. 4A), was assigned to *Hybodus* Agassiz, 1837, by Gardiner (1966, p. 44). It lacks the anterior part of the skull, the dentition, and the dorsal fins. The dermal denticles (fig. 4B) resemble those of *P. polaris* Stensiö, 1921 (fig. 4C). Stensiö (1921) did not compare the denticles of *P. polaris* with those of the several other species of *Palaeobates*, but he did state that they differ from the denticles of *Hybodus* and *Acrodus* Agassiz, 1838, in having their three or four lateral ridges extended as posteriorly directed acuminate processes. Actually, the dermal denticles of *Hybodus dela-bechi* Charlesworth, 1839, figured by Woodward (1889, pl. 8, figs. 4, 5), are similar to those of

FIG. 3. Correlation chart of some Lower Triassic rock units discussed in text.

STAGES	S.E. BRITISH COLUMBIA	ALBERTA Jasper area	IDAHO Bear Lake	EAST GREENLAND	SPITZ-BERGEN	MADAGASCAR North	MADAGASCAR South
SPATHIAN	Spray River Group — Vega-Phroso Siltstone Member	Sulphur Mountain Formation — Vega Siltstone Member	Thaynes Formation	Pingo Dal Formation	Sassendalen Group / Sticky Keep Formation — Kaos-fjellet Mem.	Iroro Sh.	Bed 6
SMITHIAN					Isk-letten Mem.	fish beds	Bed 5
DIENERIAN		Phroso Siltstone Member	Woodside Formation	Wordie Creek Formation	Vardebukta F. — Siksaken Mem.	Claraia beds / Sakamena Gr.	Sakamena Gr.
GRIES-BACHIAN			Dinwoody Formation		Selman-eset Mem.		

LOWER TRIASSIC

(Gibson, 1972) (Gibson, 1968) (Reeside et al., 1957) (Perch-Nielsen et al., 1974) (Buchan et al., 1965) (Anderson, 1973) (Anderson, 1973)

Palaeobates, except that the bases of the former appear to be relatively larger than those of the latter.

NMC 9980 lacks centra, as do other hybodontids, but calcified neural spines are evident in several areas. The badly compressed and incomplete head region includes some fragments of calcified cartilage that probably represent parts of the scapulocoracoid, and there are some rodlike structures that may be portions of visceral arches.

The body proportions of NMC 9980 are similar to those of *Hybodus*. The base of the posterior dorsal fin spine is represented by a mold that shows a few well-spaced, delicate ridges just above the embedded portion. The first dorsal fin is entirely missing. There is little evidence as to the shape and size of the anal and caudal fins, which are represented mostly by displaced patches of dermal denticles.

CLASS CHONDRICHTHYES, *INCERTAE SEDIS*
Figure 5

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6282, slab with 10 spines; AMNH 6283, spine; AMNH 6284, spine; AMNH 6285, spine; AMNH 6286, spine; AMNH 6287, spine; AMNH 6288, spine; AMNH 6289, spine; NMC 10124, three spines; NMC 10125, spine; NMC 10126, spine; NMC 10127, two spines; NMC 10128, spine; NMC 10129, two spines; NMC 10130, block with several poorly preserved spines; NMC 10131, spine; NMC 10132, spine; NMC 10133, spine; NMC 26200, spine; NMC 26201, spine.

From the Toad-Grayling Formation, Needham Creek-Graham River-Horn Creek area, British Columbia: NMC 26211, spine.

From either the Toad Formation or the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, 10 miles north of Wapiti Lake, British Columbia: NMC 26212, spine.

Description and Discussion. As noted in the section on geologic occurrence, *Listracanthus*-like spines (fig. 5) occur at Wapiti Lake in a siltstone lens above the main fish layer; they are not found in direct association with any of the other fish remains. The spines range from 4 to 6 cm. in

height, and they have an expanded base that is 1 to 2 cm. wide. The fine parallel grooves and ridges on the lateral surfaces gradually disappear toward the apex. The apex is slightly expanded, and the few apical ridges have a tuftlike arrangement. The denticles along the anterior convex margin are relatively short and thornlike. The denticles on the concave posterior margin are elongate, fringelike, and regularly spaced.

These spines resemble those called *Listracanthus* Newberry and Worthen, 1870, more closely than they resemble the spines of any other known chondrichthyans. In fact, the resemblance is so close that the Wapiti Lake form could be regarded as a new species of *Listracanthus* if it were not for several complicating factors. The problem of identification is compounded by the fact that *Listracanthus* spines occur with the menaspoid holocephalan *Deltoptychius* Morris and Roberts, 1862 (see Patterson, 1965); they have also been found with patches of *Petrodus* McCoy, 1848, denticles (from the Mississippian Black Shales of Indiana), aligned in rows and undoubtedly in place with respect to each other (Zangerl and Richardson, 1963). Even more confusing is the occurrence of *Petrodus*-like scales on the head and trunk of *Deltoptychius*.

For the present it does not seem advisable to allocate the Wapiti Lake spines to any category lower than the class Chondrichthyes. More precise identification depends on the discovery of more complete remains and the resolution of the *Petrodus-Deltoptychius* problem.

CLASS OSTEICHTHYES

SUBCLASS ACTINOPTERYGII

ORDER PALAEONISCIFORMES

FAMILY PALAEONISCIDAE

PTERONISCULUS WHITE, 1933

Acrolepis (in part): Lambe, 1916a, p. 42.
?*Gyrolepis* (in part): Stensiö, 1918, p. 77.
Glaucolepis Stensiö, 1921, p. 200 (preoccupied name)
Glaucolepis: Stensiö, 1932, pp. 119-121.
Pteronisculus White, 1933, p. 118.

Type Species. Pteronisculus cicatrosus White.
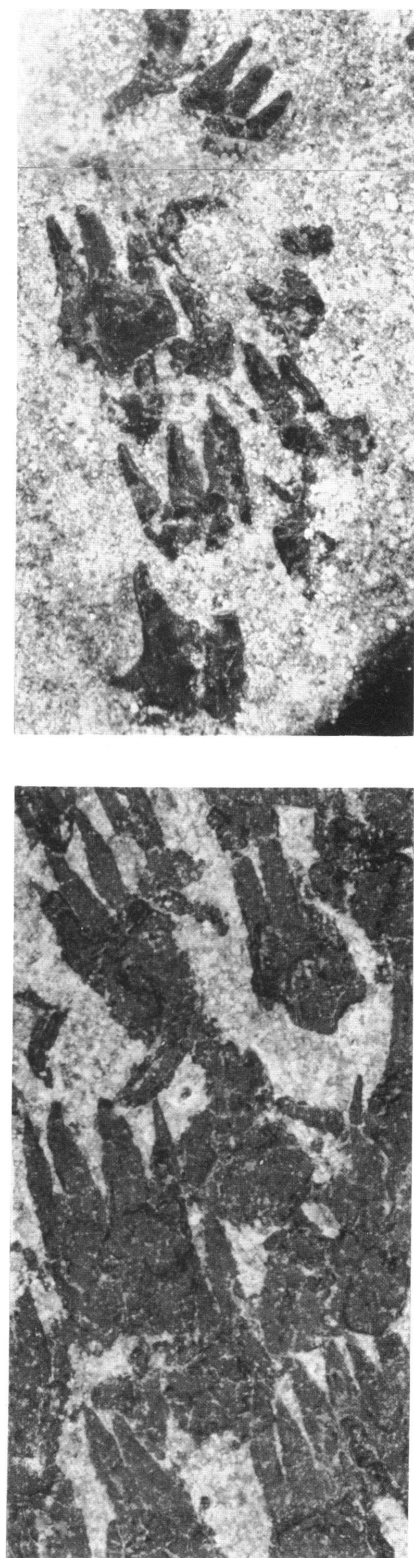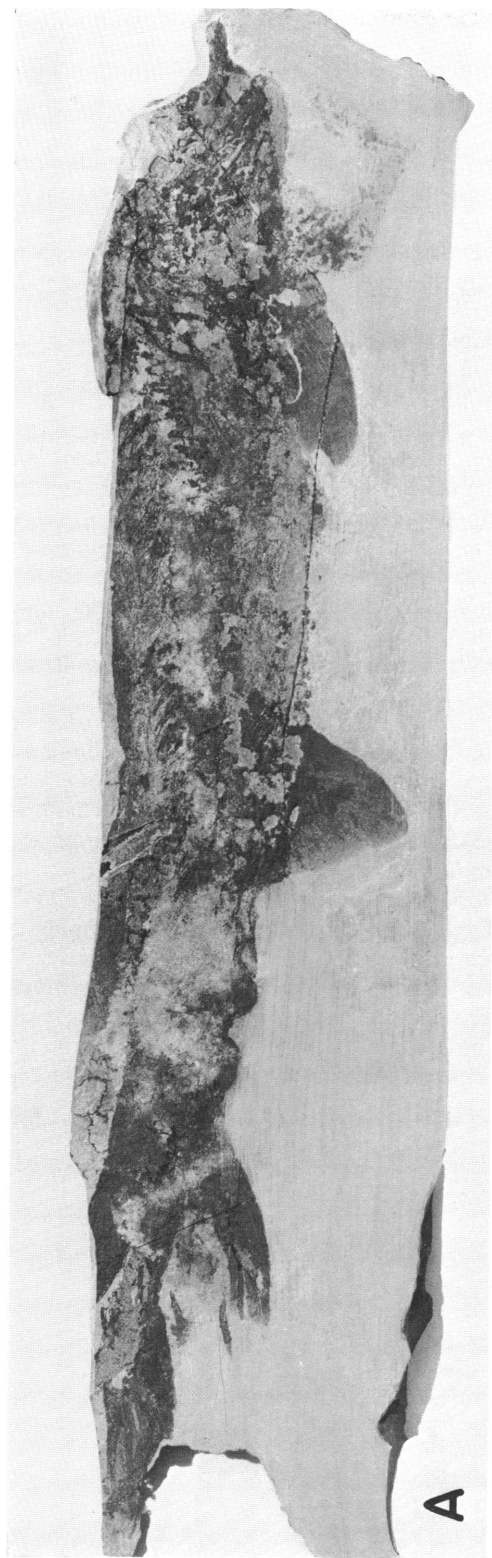
FIG. 4. A. Cf. *Palaeobates*, NMC 9980, specimen lacking part of caudal fin and both dorsal fins, from Wapiti Lake. *Ca.* ×0.18. B. Dermal denticles of cf. *Palaeobates*, NMC 9980, from Wapiti Lake. *Ca.* ×28.00 C. Dermal denticles of *Palaeobates polaris*, PIUU P107, from Lower Triassic of Spitzbergen. *Ca.* ×28.00.

Distribution. Lower Triassic of Madagascar, East Greenland, Spitzbergen, Alberta, and British Columbia; Middle Triassic of Spitzbergen.

Diagnosis. See White, 1933, pages 118-120; Stensiö, 1921, page 200; 1932, pages 119-120.

Pteronisculus sp.
Figure 6

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6264, skull and anterior body; NMC 12324, partial fin with scale patch.

Discussion. Two specimens, AMNH 6264 (fig. 6) and NMC 12324, have been identified as *Pteronisculus* sp. mainly on the basis of the relative size and ornamentation of the scales, the shape of the maxilla, and the number of branchiostegals. Because no complete specimens have been found, it is impossible to make a specific determination.
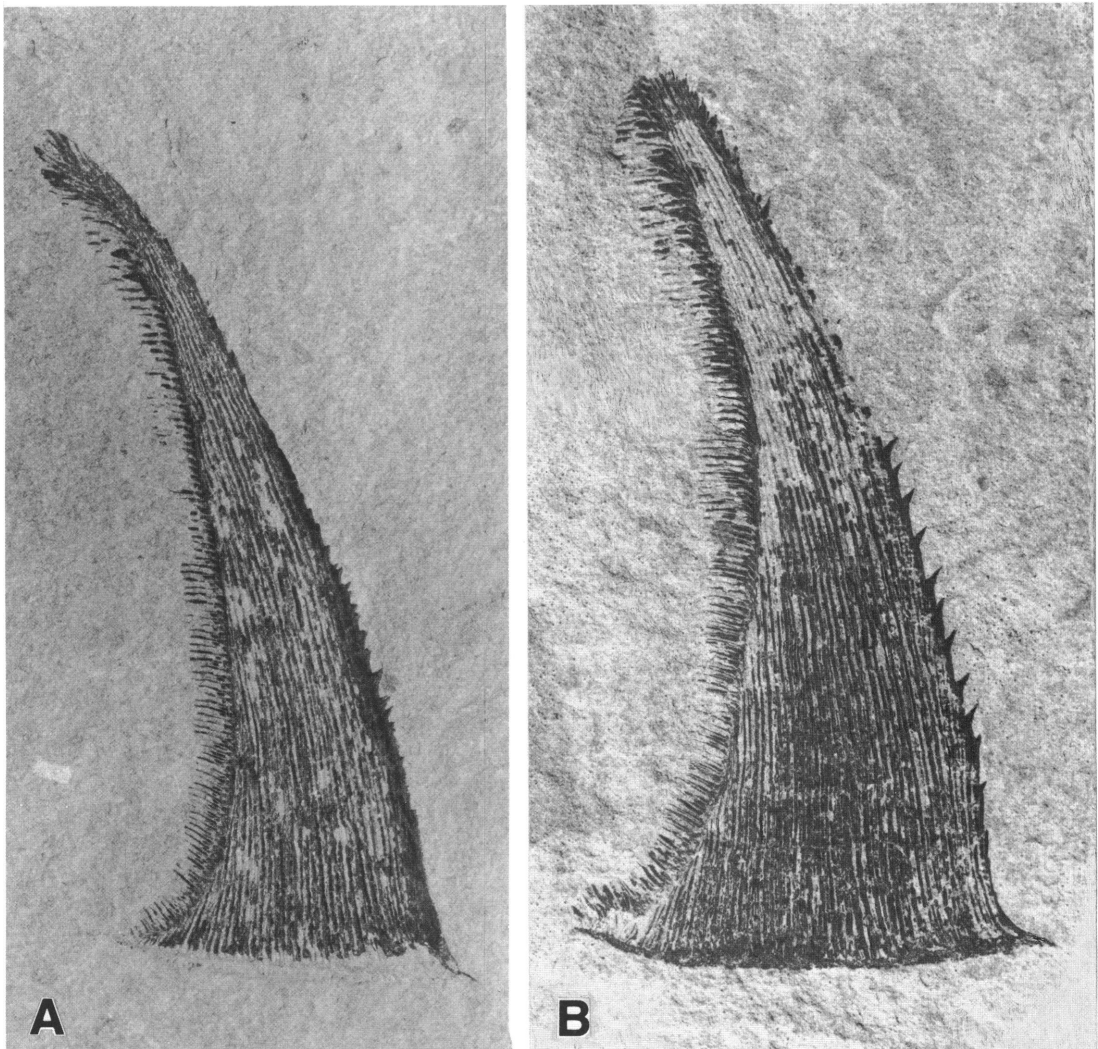
FIG. 5. Chondrichthyes, *incertae sedis*, from Wapiti Lake. A. NMC 10133, spine. *Ca.* ×2.80. B. NMC 10132, spine (photograph reversed). *Ca.* ×2.82.
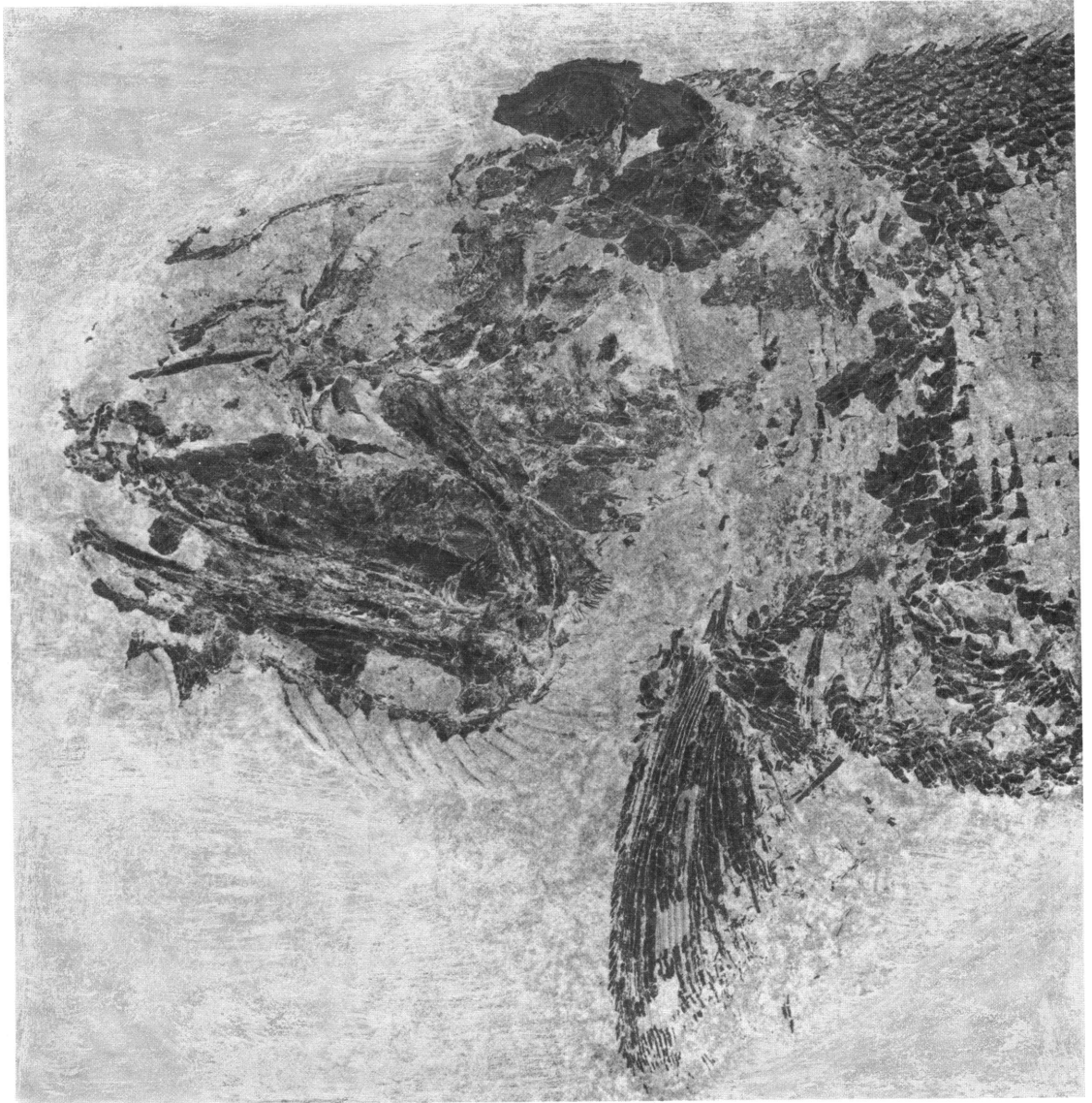
FIG. 6. *Pteronisculus* sp., AMNH 6264, weathered skull and pectoral fin, from Wapiti Lake. *Ca.* ×2.21.

Pteronisculus ?laetus (Lambe)

Remarks. Lambe (1916a, p. 42) erected the species *Acrolepis laetus* for a single specimen from the Spray River Group near Banff-Massive, Alberta. The specimen (NMC 755, 755a) consists of an imperfect trunk in part and counterpart.

Stensiö (1921, p. 149) noted that the specimen probably does not belong to *Acrolepis*. Gardiner (1966, p. 64) later referred it to *Pteronisculus ?laetus*. Its specific status is questionable, and it cannot be determined whether it is conspecific with the specimens of *Pteronisculus* from Wapiti Lake.

FAMILY BIRGERIIDAE

BIRGERIA STENSIÖ, 1919

Saurichthys (in part) Agassiz, 1834, p. 85.
Xenestes Jordan, 1907, pp. 120-121 (*nomen dubium*).
Birgeria Stensiö, 1919, pp. 177-181.

Type Species. Birgeria mougeoti (Agassiz).

Distribution. Lower Triassic of Madagascar, East Greenland, Spitzbergen, Siberia, Idaho, and British Columbia; Triassic of Spitzbergen, Europe, and California.

Diagnosis. See Nielsen, 1949, pages 281-284; Schwarz, 1970, pages 78-79.

Birgeria sp.
Figure 7

Referred Specimen. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: NMC 9981, incomplete skull.

Description and Discussion. Birgeria is represented at Wapiti Lake by a single, incomplete weathered skull (NMC 9981; fig. 7A). A smooth-on peel, prepared after the removal of bone fragments from the specimen, reveals both an obliquely-angled suspensorium and a boomerang-shaped hyomandibular (fig. 7B). The latter is particularly characteristic of *Birgeria* (Nielsen, 1949, pl. 19). The delicate neural arches and the fine rays of the right pectoral fin can also be seen. The cheek area, with its specialized suborbital series (a unique derived character of *Birgeria*) is not preserved in this specimen.

FAMILY BOREOSOMIDAE

BOREOSOMUS STENSIÖ, 1921

Acrolepis (in part): Woodward, 1912, pp. 292-293.
Acrolepis (in part): Stensiö, 1918, p. 77.
Boreosomus Stensiö, 1921, pp. 210-211.
?Gyrolepis (in part): Priem, 1924, pp. 113-114.
Diaphorognathus Brough, 1933, p. 77.

Type Species. Boreosomus arcticus (Woodward).

Distribution. Lower Triassic of East Green-land, Spitzbergen, Madagascar, British Columbia, Alberta, Alaska, Ellesmere Island, and China.

Diagnosis. See Stensiö, 1921, pages 210-211.

Boreosomus sp.
Figure 8

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6258, section of trunk; AMNH 6259, skull and anterior trunk; AMNH 6260, skull and anterior trunk; AMNH 6261, skull and anterior trunk; AMNH 6262, nearly complete fish; AMNH 6263, opercular region and anterior trunk; NMC 9961, dissociated skull elements and scales; NMC 9978, partial skull and anterior trunk; NMC 12320, skull and anterior trunk; NMC 12321 A and B, nearly complete fish, part and counterpart.

From the Lower Triassic of Banff-Massive, Alberta: NMC 12322, skull.

From the Blind Fiord Formation, Blind Fiord, Ellesmere Island: NMC 26214 A and B, portion of trunk, part and counterpart.

Description and Discussion. The presence of *Boreosomus* in the Wapiti Lake fish assemblage has been noted previously by Gardiner (1966, p. 64). A dissociated skull, NMC 9961 (fig. 8A), includes a hyomandibular similar to that of *Boreosomus piveteaui* Nielsen, 1942 (Nielsen, 1942, fig. 70), from East Greenland, and to that of *B. gillioti* (Priem), 1924 (see Lehman, 1952, fig. 59), from Madagascar. A smooth-on peel of AMNH 6260 (fig. 8B) shows the cheek and gular regions with maxilla, preopercular, suborbitals, and gular plates typical of the Greenland and Madagascar species. The ornamentation of the opercular and subopercular, consisting of inter-rupted ridges, resembles that of *B. gillioti* (Lehman, 1952, pl. 22) more closely than that of *B. piveteaui*, which has continuous ridges.

Scales with typical *Boreosomus* striae and tubercles can be seen in a number of specimens. Unfortunately, the fins are missing in most of the specimens, but NMC 12321 shows the dorsal and pelvic fins situated nearly opposite each other in the middle of the body, as they are in *B. piveteaui.*

Body length of each of the two nearly com-
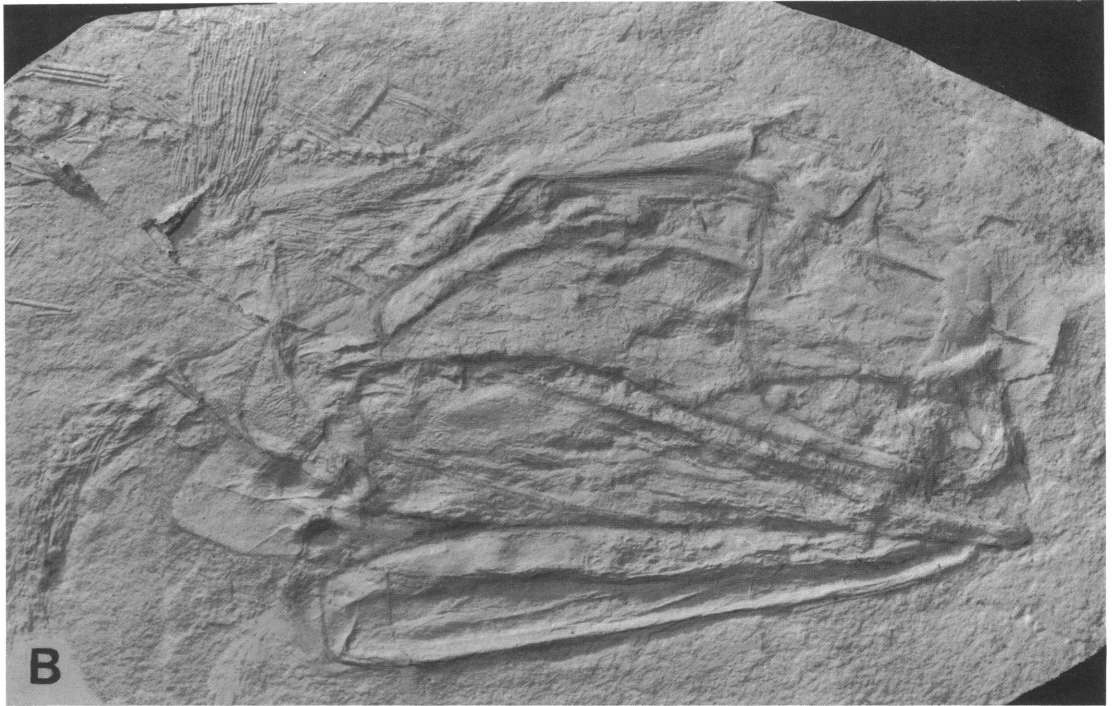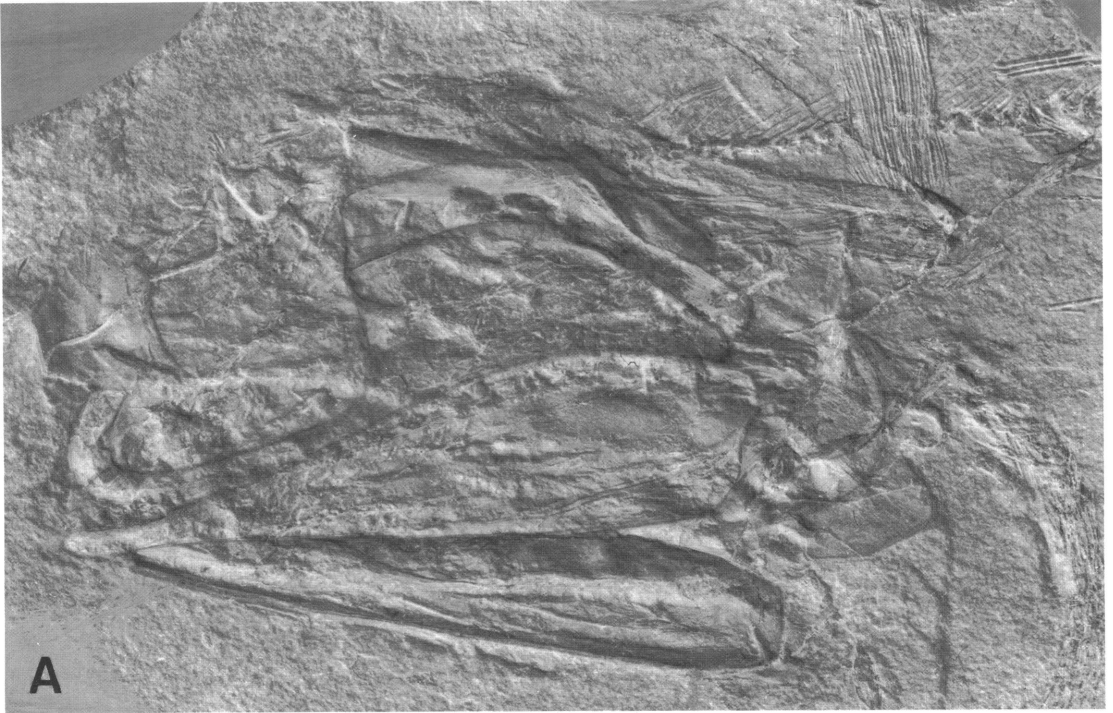
FIG. 7. *Birgeria* sp., NMC 9981, from Wapiti Lake. A. Skull. B. Smooth-on peel of skull. Both *ca.* ×0.92.

plete specimens (AMNH 6262, NMC 12321) is approximately 21 cm. This measurement falls within the range of *B. reuterskiöldi* Stensiö, 1921, and *Boreosomus* sp., both from Spitzbergen, on the basis of estimates made from drawings and photographs (Stensiö, 1921).

ORDER BOBASATRANIIFORMES

FAMILY BOBASATRANIIDAE

BOBASATRANIA WHITE, 1932

Platysomus (in part): Lambe, 1914, p. 17.
Platysomus (in part): Lambe, 1916b, p. 195.
Platysomus (in part): Burling, 1916, p. 98.
Platysomus (in part): Warren, 1936, p. 55.
Bobasatrania White, 1932, p. 80.
Bobasatrania: Russell, 1951, p. 218.
Lambeichthys Lehman, 1956, p. 80.
?*Haywardia* Tanner, 1936, p. 82.

Type Species. Bobasatrania mahavavica White.

Distribution. Lower Triassic of Madagascar, Greenland, Spitzbergen, British Columbia, Alberta, and possibly Idaho.

Diagnosis. See White, 1932, page 80.

Bobasatrania canadensis (Lambe, 1914)
Figures 9-11

Platysomus canadensis Lambe, 1914, p. 17.
Platysomus albertensis Lambe, 1916b, p. 195 (in error).
Platysomus brewsteri Warren, 1936, p. 55.
Bobasatrania ?*canadensis*: Russell, 1951, p. 218.
Lambeichthys canadensis: Lehman, 1956, p. 80.
Bobasatrania canadensis: Gardiner, 1966, p. 66.
?*Haywardia jordani* Tanner, 1936, p. 82.

Holotype. NMC 342, a nearly complete specimen from the Lower Triassic Spray River Group, Sulphur Mountain Formation at Johnson Creek, near Castle Mountain Railway Station, 12 miles northwest of Banff, Alberta. (The counterpart of the holotype is in the Banff Park Museum.)

Distribution. Lower Triassic of Alberta, British Columbia, and possibly Idaho.

Amended Diagnosis. Differs from other species of *Bobasatrania* in the following characters: the anterior four to six rays of the dorsal and anal fins are elongated (they are three to four times as long as the posterior rays); there are 98

to 110 dorsal fin rays and 80 to 95 anal fin rays; the pectoral fin rays extend posteriorly as far as the caudal peduncle.

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6200 A and B, fish lacking ventral margin and caudal fin, part and counterpart; AMNH 6201, complete fish; AMNH 6202 A and B, skull and anterior two-thirds of trunk, part and counterpart; AMNH 6203, complete fish; AMNH 6204, complete fish; AMNH 6205, fish lacking ventral border and caudal fin; AMNH 6206, fish lacking skull and dorsal margin of body; AMNH 6207, dorsal half of fish with caudal fin; AMNH 6208 A and B, fish lacking dorsal border and caudal fin, part and counterpart; AMNH 6209 A and B, complete fish, part and counterpart; AMNH 6210 A and B, posterior body with caudal fin, part and counterpart; AMNH 6211 A and B, nearly complete fish, lacking most of caudal fin, part and counterpart; AMNH 6212 A and B, fish lacking anterior dorsal margin, part and counterpart; AMNH 6213 A and B, complete fish, part and counterpart; AMNH 6214 A and B, partial skull and body, part and counterpart; AMNH 6215, fish lacking caudal fin, anterior ventral margin and part of skull; AMNH 6216, fish lacking most of skull and dorsal margin of body; AMNH 6217, dorsal half of fish; AMNH 6218, nearly complete fish, poorly preserved; AMNH 6219, nearly complete fish, poorly preserved; AMNH 6220, nearly complete fish, poorly preserved; AMNH 6274 A and B, partial skull and anterior of body, part and counterpart; AMNH 6275, caudal fin; NMC 9958, fish lacking anterior ventral margin; NMC 10110, scale patch; NMC 10111, disarticulated skeletal elements; possibly NMC 10112 A and B, concretionary remains, part and counterpart; NMC 12250, fish lacking anterior half of body and most of caudal fin; NMC 12251, fish lacking skull; NMC 12252, dorsal part of body with caudal fin; NMC 12253, mid-section of body; NMC 12254, fish lacking skull and dorsal border of body; NMC 12255, fish lacking posterior dorsal border, caudal fin and most of skull; NMC 12256, posterior half of fish; NMC 12257, skull and anterior part of fish; NMC 12258, skull and anterior ventral section of

FIG. 8. *Boreosomus* sp., from Wapiti Lake. A. NMC 9961, dissociated skull. *Ca.* ×1.06. B. Smooth-on peel of AMNH 6260, skull. *Ca.* ×1.47.

body; NMC 12259, fish lacking part of skull and anterior dorsal margin of body; NMC 12260, fish lacking most of skull; NMC 12261, skull and anterior ventral part of body; NMC 12262 A a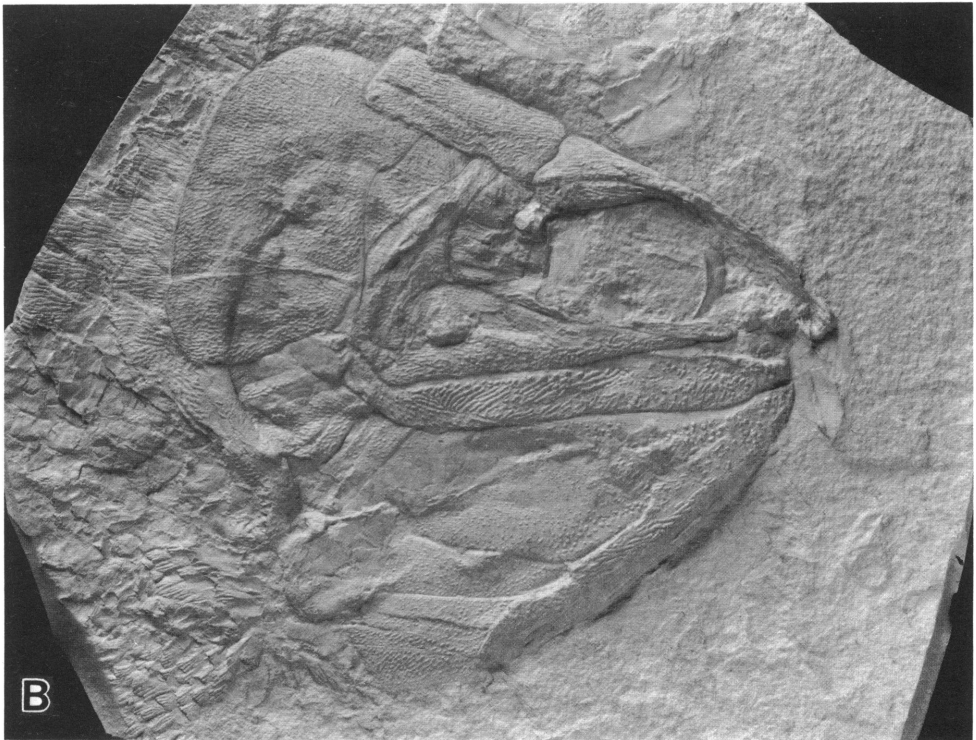nd B, skull and anterior body, partial caudal fin, part and counterpart; NMC 12263 A and B, posterior body, part and counterpart; NMC 12264, fish lacking skull; NMC 12265, nearly complete fish; NMC 12266 A and B, complete fish, part and counterpart; NMC 12267, partial skull and body; NMC 12268, fish lacking part of skull and caudal fin; NMC 12269, fish lacking ventral border; NMC 12270, fish lacking ventral margin; NMC 12271, complete fish, disarticulated; NMC 12272 A and B, fish lacking caudal fin, part and counterpart; NMC 12273 A and B, complete fish, part and counterpart; NMC 12274 A and B, nearly complete fish, lacking caudal fin, part and counterpart; NMC 12275 A and B, partial skull and body, part and counterpart; NMC 12276 A and B, skull and anterior body, part and counterpart; NMC 12277, fish lacking anterior skull; NMC 12278 A and B, caudal fin, part and counterpart; NMC 12279, skull; NMC 12280, portion of body including ventral angle; NMC 12281 A and B, partial skull and anterior body, part and counterpart.

From the Lower Triassic of southern Alberta and British Columbia: NMC 342 (type), nearly complete fish (from vicinity of Banff, Alberta); NMC 2385, nearly complete fish (from vicinity of Banff, Alberta); NMC 8865, posterior third of fish (from vicinity of Fernie, British Columbia); UAM 376, fish lacking anterior skull (from vicinity of Jasper, Alberta).

Description. Neurocranium: Because of extreme compression and masking by the dermal elements, it is not possible to make meaningful observations on the neurocranium. The parasphenoid extends the full length of the basicranium and has a well-developed ascending process. Its anteroventral surface is covered by an elliptical patch of closely spaced conical teeth. Nielsen (1952b) called a similar patch in the Greenland species, *B. groenlandica* Stensiö, 1932, a vomerine plate, perhaps because it seems to be partly attached to the ethmoid ossification. Although the anterior extent of the parasphenoid cannot be seen in *B. canadensis*, the tooth patch appears to be unpaired (Nielsen implied that it is

paired in *B. groenlandica*) and we prefer to regard it as the parasphenoid dentition.

Visceral Skeleton: The hyomandibular is characteristically rectangular, with a distinct anterodorsal process that articulates with the neurocranium. Bow-shaped ceratohyal ossifications are commonly present behind the mandible. Four elongate ceratobranchials can be seen in NMC 12274; they are in approximately the same relative position as are these elements in *B. groenlandica* (Nielsen, 1952b, fig. 2). The elements identified by Nielsen as the entopterygoid and the dermopalatine in *B. groenlandica* are also evident in NMC 12274.

Dermal Skull: The skull of *B. canadensis* (fig. 9B) closely resembles that of *B. groenlandica* (Stensiö, 1932; Nielsen, 1952b), as well as that of *B. mahavavica* White, 1932 (see Lehman, 1956), from Madagascar.

Appendicular Skeleton: The dermal shoulder girdle of *B. canadensis*, like the dermal skull, shows no obvious differences from that of *B. groenlandica* or *B. mahavavica*. The prominent radiating ridges seen on the median lamina of the cleithrum of *B. canadensis* have also been noted on a well-preserved specimen of *B. mahavavica* in the Muséum National d'Histoire Naturelle. Stensiö (1932) found no evidence of a median lamina in *B. groenlandica*, but this element must have been developed in this species to about the same degree that it is in *B. canadensis* and *B. mahavavica*.

The pectoral fin (fig. 10A) is composed of about 20 segmented rays, all of which are bifurcated distally. The longest rays extend posteriorly as far as the caudal peduncle. The origin of the pectoral fin is in approximately the same relative position as in *B. groenlandica* and *B. mahavavica*; it is not more elevated in *B. canadensis* than in the other two species, as claimed by Lehman (1956, p. 80). The pelvic fins are absent in all three species. There is no evidence in *B. canadensis* of pelvic bones such as Nielsen (1952b) described for *B. groenlandica*.

The dorsal fin includes 98 to 110 rays and the anal about 80 to 95 rays; in both fins the rays are segmented and bifurcated and are equal in number to the radials. A few anterior rays of both unpaired fins are elongated. Generally they are three or four times as long as the posterior
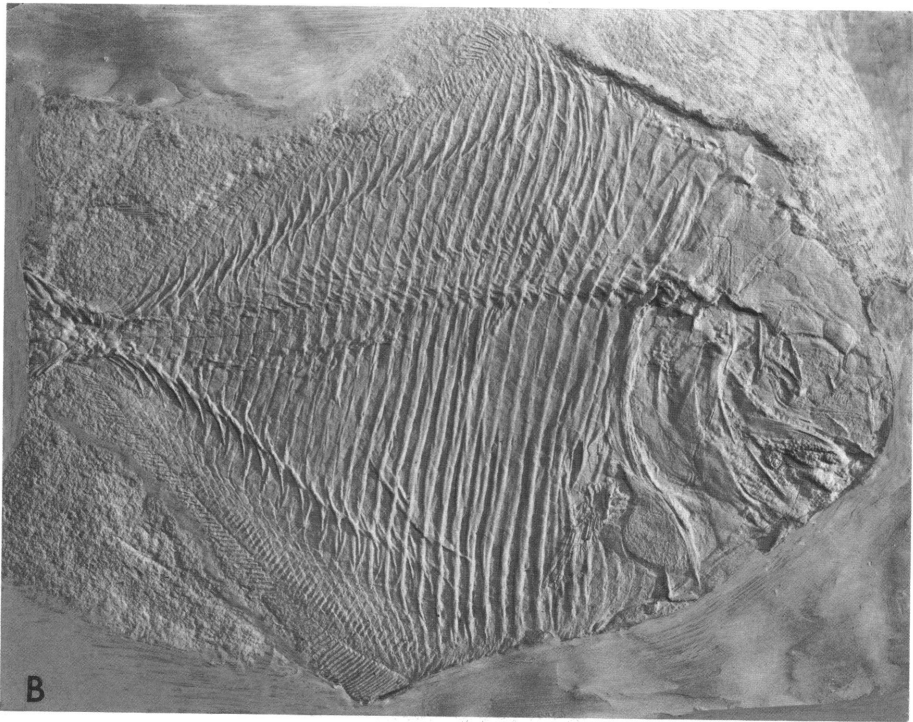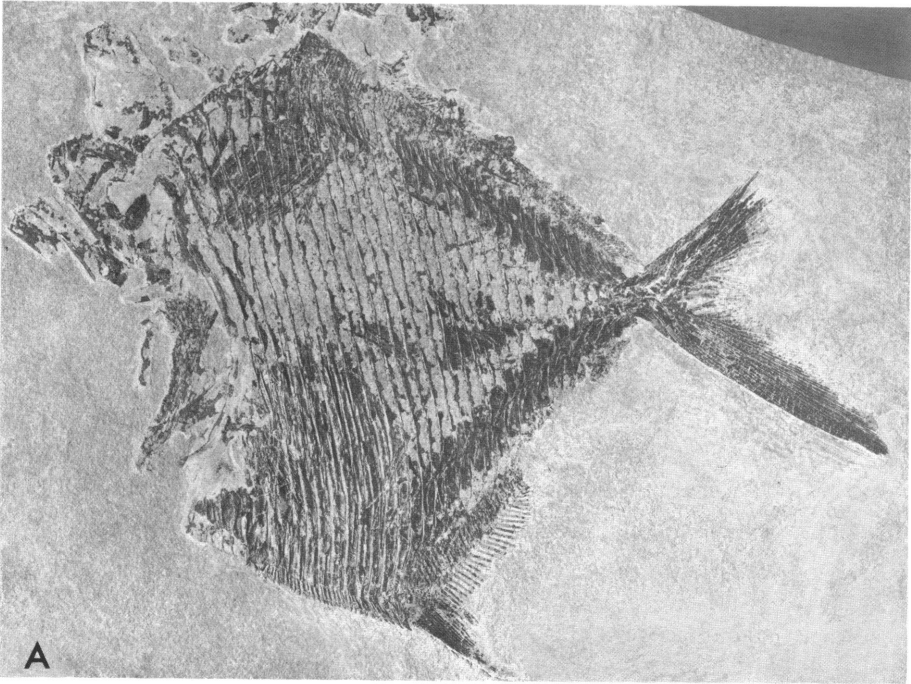
FIG. 9. *Bobasatrania canadensis*, from Wapiti Lake. A. NMC 12260, specimen lacking skull. B. Smooth-on peel of AMNH 6211 B, specimen lacking caudal fin. Both *ca.* ×0.58.
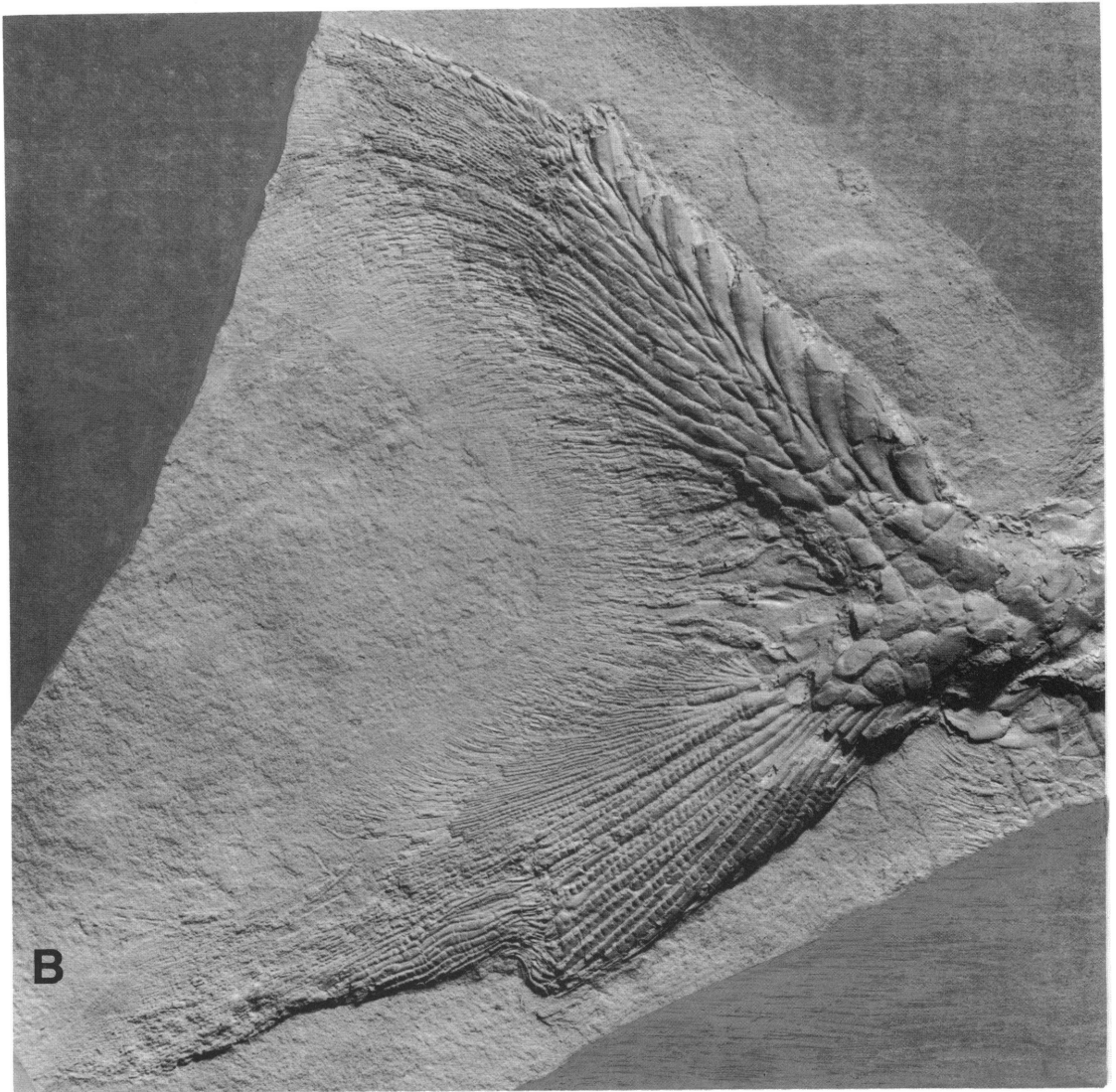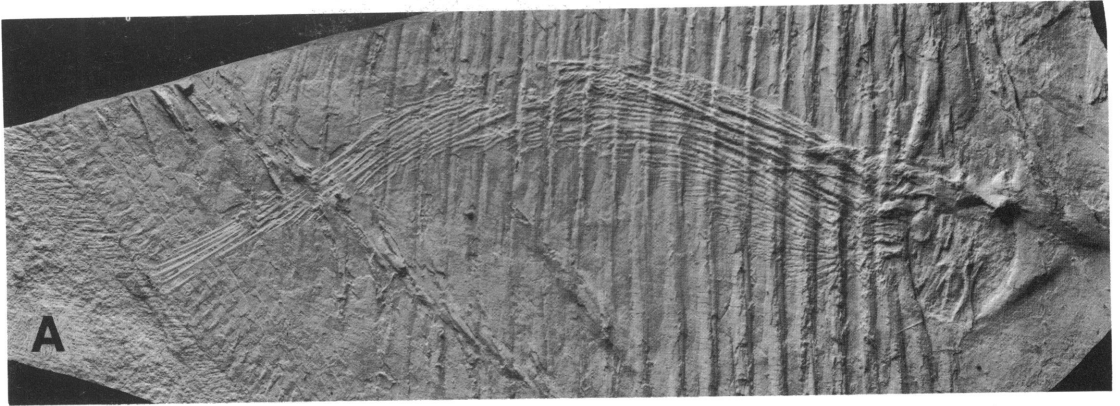
FIG. 10. Smooth-on peels of *Bobasatrania canadensis*, from Wapiti Lake. A. AMNH 6200 B, detail of pectoral fin. *Ca.* ×0.64. B. AMNH 6210 B, caudal fin. *Ca.* ×0.49.

rays, but in some specimens they are more than five times as long. A characteristic aspect of actinopterygian fin ray growth can be observed in the sample of *B. canadensis* from Wapiti Lake, which undoubtedly represents a growth series. The ray segments are relatively long and narrow in small individuals, while in the larger ones they are relatively broad and short.

Several specimens show a deeply forked caudal fin (fig. 10B) that is practically identical with that of *B. groenlandica* and *B. mahavavica*. The rays are closely spaced in both lobes; there are 18 to 21 rays in the dorsal lobe and 12 to 14 in the ventral one.

Squamation: The scale pattern in the restoration of *B. canadensis* (fig. 11) was traced directly from AMNH 6211 B and was checked against numerous other specimens. There are 30 vertical scale rows between the posterior border of the cleithrum and the posterior borders of the dorsal and anal fins in AMNH 6211 B, but the number varies from 29 to 32 for the entire Wapiti Lake sample. A marked reduction in scale size in the vicinity of both the dorsal and anal fins is characteristic of *Bobasatrania* and its closest relative, *Ecrinesomus* Woodward, 1910. The platysomids, which have a similar body form, also have smaller scales at the bases of the unpaired fins.

Body Proportions (fig. 9): The sample of *B. canadensis* from Wapiti Lake consists of the remains of 59 individuals. Of these, 22 have provided fairly accurate snout-to-caudal peduncle (standard length) measurements, which range from 7.75 cm. to 33.0 cm. As the small and large individuals occur at random within the fish zone, it may be assumed that all inhabited the same general environment and that the sample represents different stages of growth. The ratio of skull length to snout-to-caudal peduncle length varies from about 32 to 38 percent. The distance from the postcleithrum to the middle of the caudal peduncle was estimated for some 20 additional specimens; the range for this measurement, based on a total of 42 specimens, is 3.8 cm. to 50.0 cm.

The angles subtended by the anterior and posterior slopes of the body profile were measured on 24 specimens for the dorsal border and 21 specimens for the ventral border. These

angles range from 100 to 132 degrees for the former and from 103 to 129 degrees for the latter (measurements on the type specimen are 125 and 120 degrees, respectively). As there is no correlation between body length and size of angle, the apparently haphazard variation may be the result of postmortem compression.

Discussion. The distinct dermal skull patterns of *Bobasatrania* and *Ecrinesomus* (Lehman, 1956) make identification of these genera relatively easy, but they complicate any attempt to work out relationships with other chondrosteans. If we assume, as does Gardiner (1967), that *Bobasatrania* and *Ecrinesomus* had a palaeonisciform-like ancestor, it is evident that most of their dermal upper jaw and cheek elements are highly modified in terms of the primitive condition. Identification of the large ovoid bone situated behind the maxilla and below the infraorbitals is particularly difficult. In *Ecrinesomus* this element lacks a sensory canal and seems to articulate with the posterior border of the maxilla; in *Bobasatrania* it is separated from the maxilla and has a longitudinal sensory canal that is ventrally forked. Nielsen (1952b) and Lehman (1956) both called this element the supramaxillo-quadratojugal, but the homologies are far from evident. Identification of the dermal elements between the opercular and the infraorbitals is also uncertain. In *Ecrinesomus* there are three bones that Lehman (1956) called preoperculars 1-3; however, they all lack a sensory canal, and on the basis of topography they might be regarded as suborbitals. In the same position in *Bobasatrania* there are two elements carrying a well-developed preopercular canal. Both Nielsen and Lehman regarded the upper element as the preopercular and the lower one, which extends under the ventral border of the opercular, as the preoperculo-subopercular. If we admit that the sensory canals are not infallible guides to dermal bone homology—that they cross bones with which they are not typically associated and that they may have a superficial position or disappear entirely—then it is possible that both *Bobasatrania* and *Ecrinesomus* possess preoperculars.

The morphological uniformity among the several species of *Bobasatrania* makes it difficult to separate or relate these taxa on the basis of
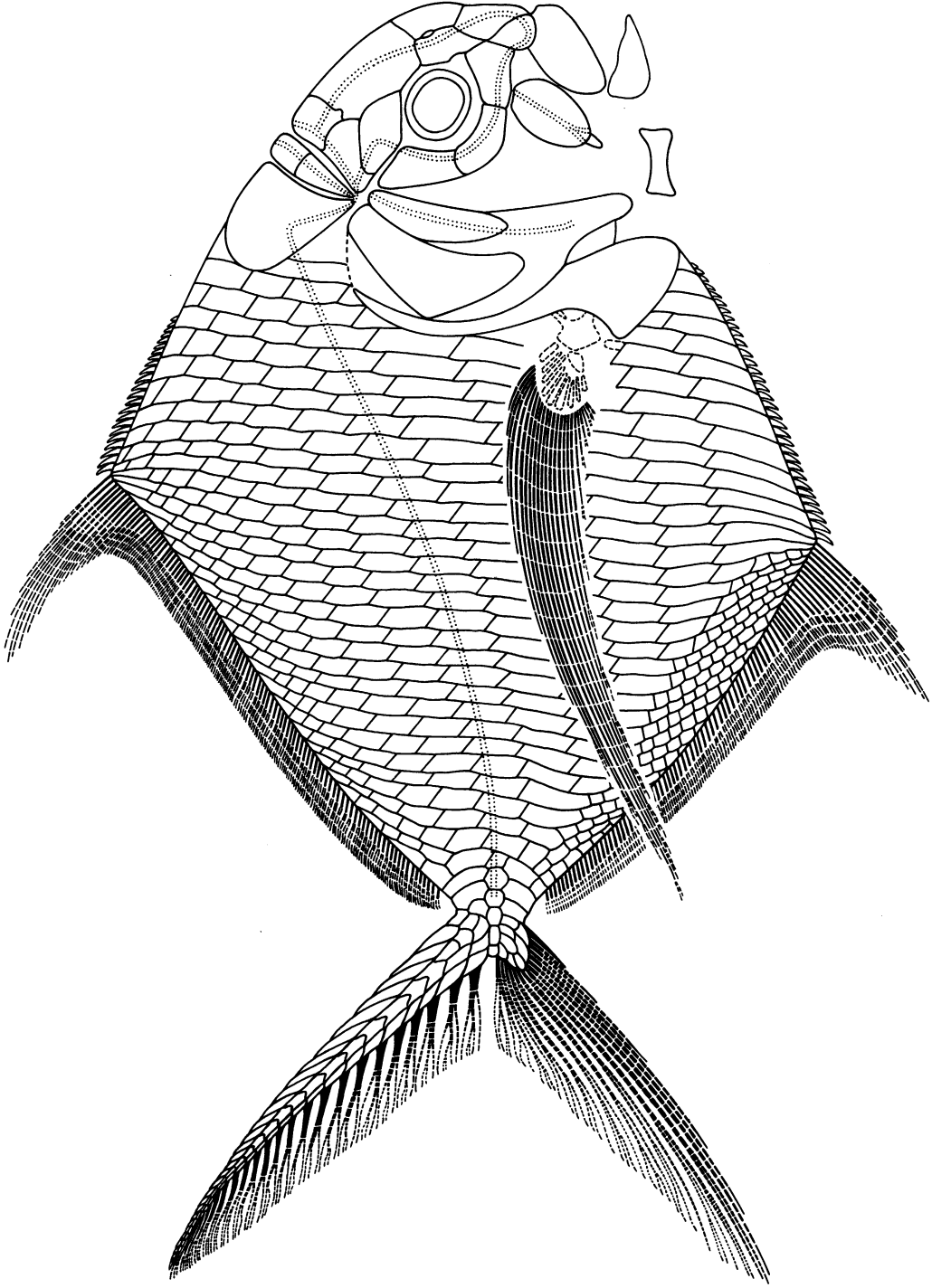
FIG. 11. Restoration of *Bobasatrania canadensis* in lateral aspect. (Based on AMNH 6200 B, AMNH 6210 B, AMNH 6211 B, and NMC 12260.)

derived characters. Lehman (1956, p. 16) noted the close resemblance between *B. groenlandica* and *B. mahavavica*. A third species, *B. nathorsti* Stensiö, 1921, from Spitzbergen is known only from a few fragments. Present evidence indicates that *B. canadensis* can be distinguished from the Greenland, Spitzbergen, and Madagascar species of *Bobasatrania* on the basis of its elongated pectoral fin. It is not possible to evaluate the apparent minor differences in the shape of the dermal cheek and the roofing elements.

ORDER PERLEIDIFORMES

FAMILY PERLEIDIDAE

PERLEIDUS DE ALESSANDRI, 1910

Semionotus (in part): Deecke, 1889, p. 120.
Perleidus de Alessandri, 1910, p. 49.
Colobodus (in part): Woodward, 1912, p. 296.

Type Species. Perleidus altolepis (Deecke).
Distribution. Lower Triassic of Madagascar, Siberia, China, East Greenland, Spitzbergen, and possibly British Columbia; Triassic of Italy.
Diagnosis. See Stensiö, 1932, pages 186-187.

Cf. *Perleidus*
Figure 12

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6265 A and B, anterior half of fish, part and counterpart; AMNH 6266, nearly complete fish with poor skull; AMNH 6267 A and B, anterior half of fish, part and counterpart; AMNH 6268 A and B, nearly complete fish, part and counterpart; AMNH 6269, nearly complete fish; AMNH 6270, nearly complete fish; AMNH 6271 A and B, nearly complete fish, part and counterpart; AMNH 6272, three incomplete fish; AMNH 6273, skull and anterior body; NMC 9960, skull; NMC 9982, anterior half of fish; NMC 10104, fish lacking caudal region; NMC 10105, fish lacking caudal fin; NMC 10106, skull and anterior body; NMC 10107, three nearly complete fish; NMC 10108, complete fish; NMC 10109, two nearly complete fish; NMC 12323, skull and anterior body; NMC 12333, nearly complete fish;

NMC 12334, fish lacking caudal fin; NMC 12335 A and B, fish lacking skull and caudal fin, part and counterpart; NMC 12336 A and B, complete fish, part and counterpart; NMC 12337 A and B, two fish, part and counterpart; NMC 26215, partial skull and anterior body.

Description and Discussion. About 30 specimens in two widely separated size ranges and with different body forms have been referred to the Perleididae mainly on the basis of the dermal cheek pattern. The postorbital expansion of the maxilla, the small number of branchiostegals, the relatively small opercular and the general skull profile favor comparison with the genus *Perleidus*.

Comparison of the dermal skulls among the perleidids, particularly among the better known taxa, reveals a fairly consistent pattern (Lehman, 1952, figs. 85, 86; Schaeffer, 1955, figs. 7, 8; Hutchinson, 1973, figs. 32, 36, 50) in spite of certain obvious differences among the included genera, such as the shape of the maxilla and preopercular, the number of branchiostegal rays and the loss of the postrostral (Hutchinson, 1973). The skull profile varies somewhat according to restoration, but the snout is blunt in all genera.

The smaller specimens (fig. 12), ranging from 5 cm. to 7 cm., have about 40 vertical scale rows, which are fewer than the number in *Perleidus madagascariensis* Piveteau, 1934 (see Lehman, 1952, fig. 92), but about equal to the number in *Meridensia* Andersson, 1916 (see Brough, 1939, p. 10). The origin of the dorsal fin is well in front of the origin of the anal fin, again as in *Meridensia*. However, the Wapiti Lake material is definitely more *Perleidus*-like in the dermal skull pattern and squamation (the scales have serrated posterior borders). Fin ray counts are not possible, but delicate fringing fulcra seem to be present on all fins.

The largest specimens (AMNH 6265, NMC 12323) consist only of the anterior half of the body. Their estimated total lengths range from 24 cm. to 30 cm. Because of the similarity of their body form to that of *Albertonia*, they were at first confused with this genus, but there is clearly an ovoid postorbital expansion of the maxilla that is fixed to the preopercular, and there is no evidence of an ethmoid process, which is found in the parasemionotids.
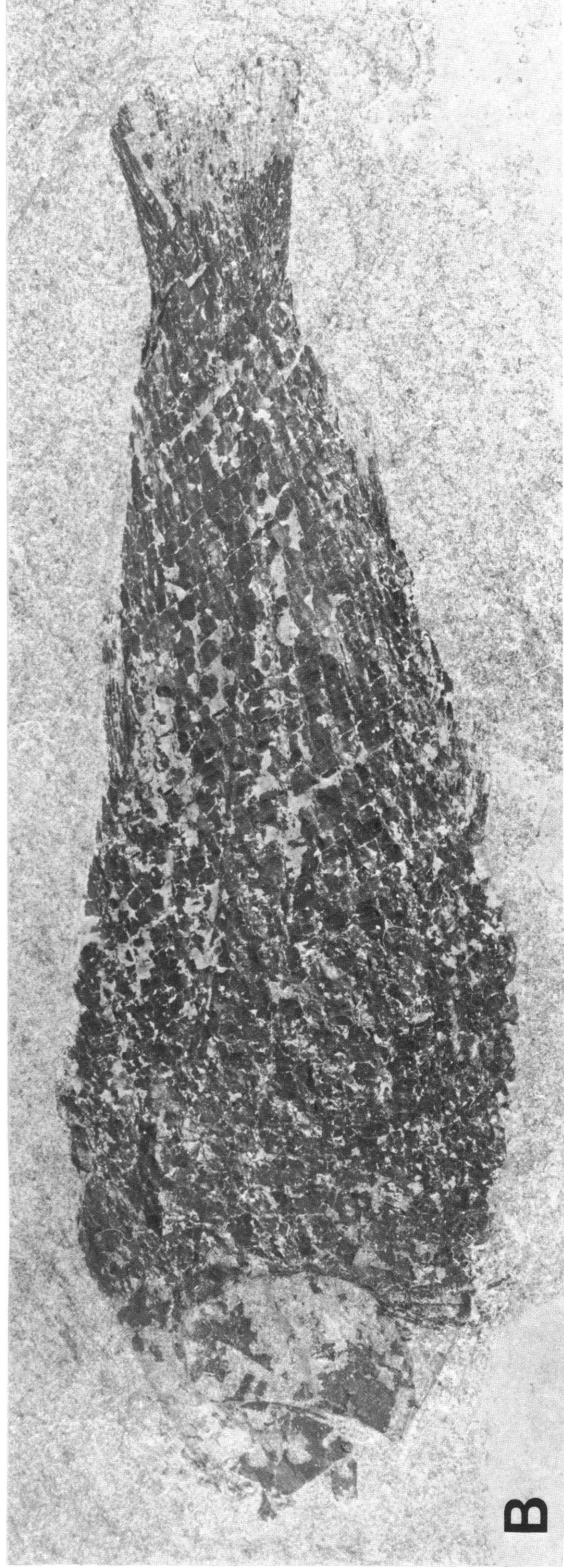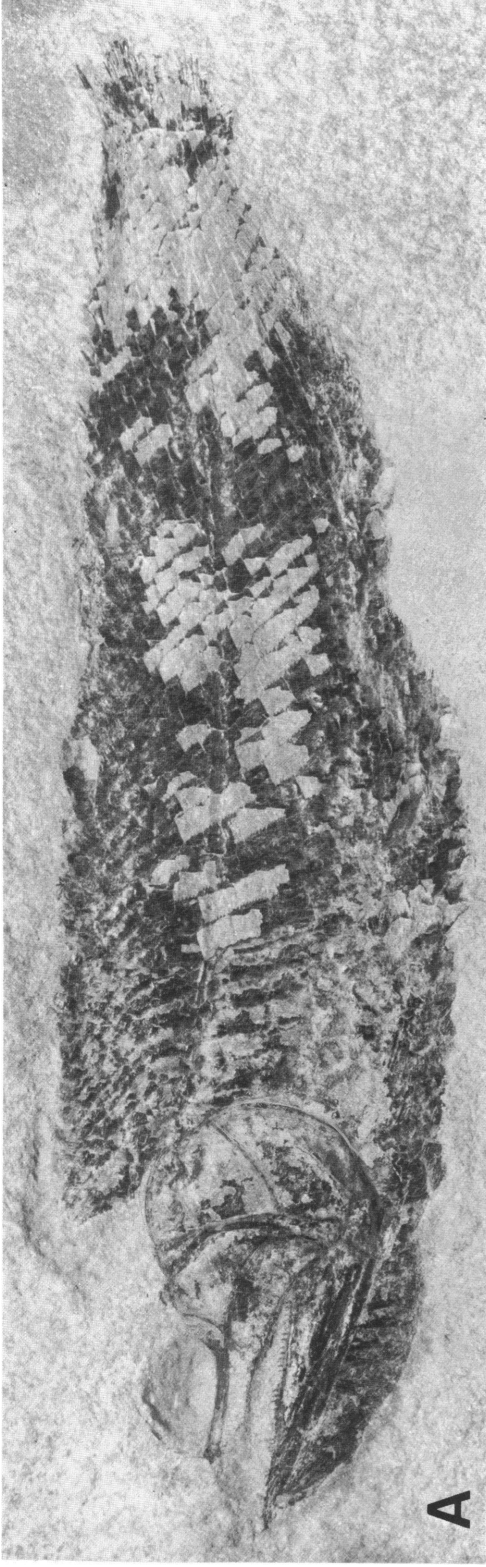
FIG. 12. Cf. *Perleidus*, from Wapiti Lake. A. NMC 10107, specimen lacking skull roof and caudal fin (one of three bearing this number). *Ca.* ×2.80. B. AMNH 6266, complete specimen. *Ca.* ×3.03.

ORDER PHOLIDOPLEURIFORMES

FAMILY PHOLIDOPLEURIDAE

AUSTRALOSOMUS PIVETEAU, 1930

Pristiosomus (in part): Priem, 1924, pp. 115-116.
Australosomus Piveteau, 1930, pp. 456-458.
Pholidopleurus (in part): Stensiö, 1931, pp. 88-89.

Type Species. *Australosomus merlei* (Priem).
Distribution. Lower Triassic of East Greenland, Madagascar, Tanzania, and British Columbia.
Diagnosis. See Nielsen, 1949, pages 173-176.

Australosomus sp.
Figure 13

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: NMC 12283, fish with poorly preserved skull; NMC 12284, fish with poorly preserved skull, lacking caudal region.
Description and Discussion. The two specimens of *Australosomus* (fig. 13) from Wapiti Lake provide only approximate fin ray and scale counts. The dorsal fin is composed of 27 to 30 rays and the anal of 35 to 40. The number of vertical scale rows is approximately 40. The estimated total length of the larger specimen (NMC 12284) is 15 cm.

Comparison of this material with the species of *Australosomus* described from Greenland (*A. kochi* Stensiö, 1932, *A. simplex* Nielsen, 1949, *A. pholidopleuroides* Nielsen, 1949), Madagascar [*A. merlei* (Priem), 1924], and Tanzania (*A. stockleyi* Haughton, 1936) is difficult because of poor preservation. The squamation of the Wapiti Lake specimens most closely resembles that of *A. kochi* in having at least one horizontal row of flank scales that are nearly three times as deep as the ones in the row immediately below. The other species from Greenland and Madagascar, and perhaps the one from Tanganyika as well, also have deepened flank scales, but the deepening is most pronounced in *A. kochi* and the Wapiti Lake *Australosomus*. The number of vertical scale rows in the Wapiti Lake specimens (40 to 42) is close to the number in *A. merlei* (40 to 44). *A. kochi*, *A. simplex*, and *A. pholidopleuroides* all have 50 or more.

It is impossible to refer NMC 12283 and NMC 12284 to any described species of *Australosomus*.

ORDER SAURICHTHYIFORMES

FAMILY SAURICHTHYIDAE

SAURICHTHYS AGASSIZ, 1834

Saurichthys Agassiz, 1834, p. 84.
Saurorhynchus Münster, 1840, p. 74 (*nomen nudum*).
Ichthyorhynchus Bellotti, 1857, p. 436.
Belonorhynchus Bronn, 1858, p. 12.
Giffonus Costa, 1862, p. 26.
Stylorhynchus Martin, 1873, p. 725.

Type Species. *Saurichthys apicalis* Agassiz.
Distribution. Lower Triassic of East Greenland, Spitzbergen, Russia, China, Madagascar, Australia, British Columbia, Alberta, and Ellesmere Island; Triassic of Europe and Australia.
Diagnosis. See Stensiö, 1925, pages 12-13.

Saurichthys sp.
Figures 14, 15

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6239, posterior skull and anterior body; AMNH 6240, skull and anterior body; AMNH 6241, skull; AMNH 6242, snout; AMNH 6243, skull and jaws; AMNH 6244, posterior skull and jaws; AMNH 6245 A and B, skull, part and counterpart; AMNH 6246, posterior part of fish; AMNH 6247, skull and most of body; NMC 9965, skull and jaws; NMC 12285, skull and jaws; NMC 12286 A and B, skull, part and counterpart; NMC 12287, skull and most of body; NMC 12288, three-dimensional skull and jaws; NMC 12289 A and B, skull and jaws, part and counterpart; NMC 12290, scale; NMC 12291, snout and part of nasal area; NMC 12292, scales; NMC 12294 A and B, skull and partial body, part and counterpart; NMC 26208, section of trunk with fins.
From the Lower Triassic of Banff-Massive, Alberta: NMC 12293, partial skull and jaws.
From the Blind Fiord Formation, Blind Fiord, Ellesmere Island: NMC 26209, palate.
Description. The genus *Saurichthys* is represented in western Canada by 20 specimens from
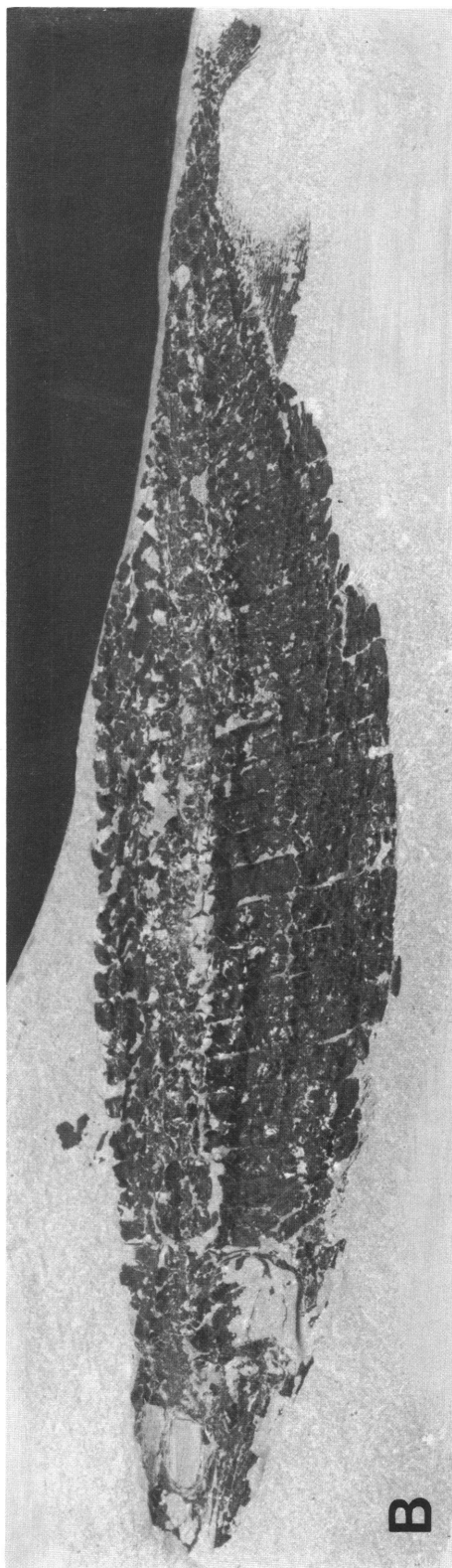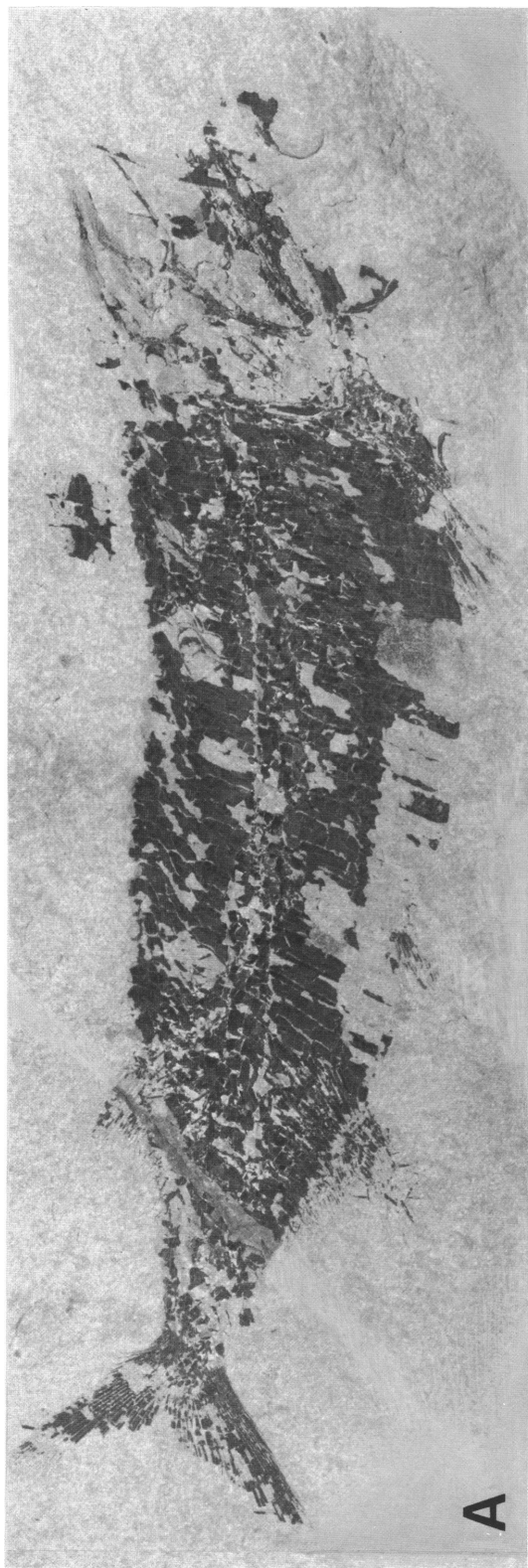
FIG. 13. *Australosomus* sp., from Wapiti Lake. A. NMC 12283, specimen with poor skull. *Ca.* ×1.59. B. NMC 12284, specimen lacking caudal region. *Ca.* ×1.38.
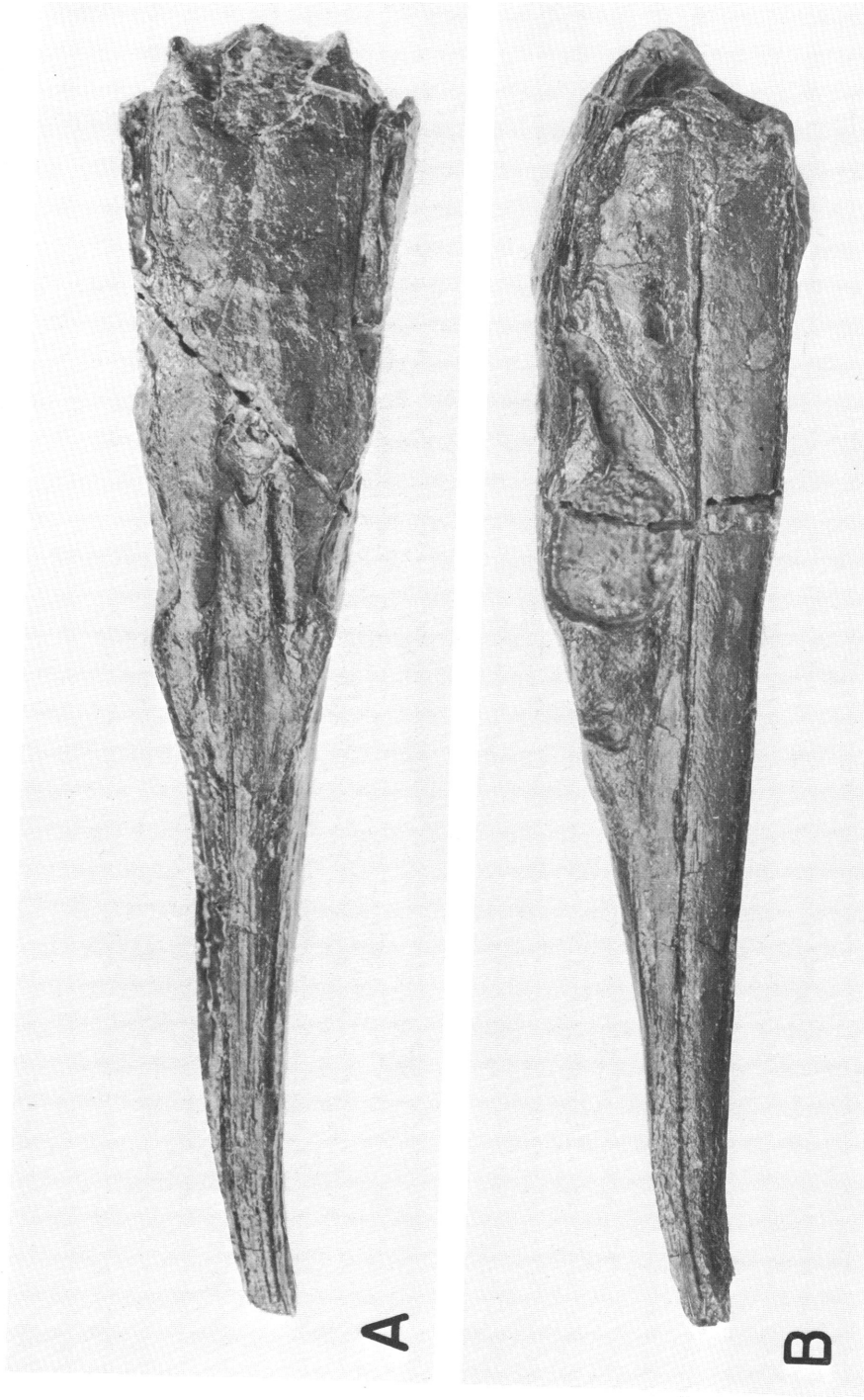
FIG. 14. *Saurichthys* sp., NMC 12288, skull, from Wapiti Lake. A. Dorsal view. B. Lateral view. Both *ca.* ×1.42.

Wapiti Lake and one from Banff-Massive, Alberta. A specimen from Ellesmere Island has also been referred to this taxon. The estimated total length for the sample ranges from 44.0 cm. to 120.0 cm. The skull elements can be seen rather well in NMC 12288 (fig. 14). The Wapiti Lake *Saurichthys* resembles *S. ornatus* Stensiö,

1925, from Spitzbergen in having two pairs of parietals. It also resembles most of the Late Triassic species in having an L-shaped preopercular. The body (fig. 15) is covered with minute tuberculated scales, as it is in most of the species from the Lower Triassic of Spitzbergen and Madagascar (Griffith, 1962, p. 354). There are a
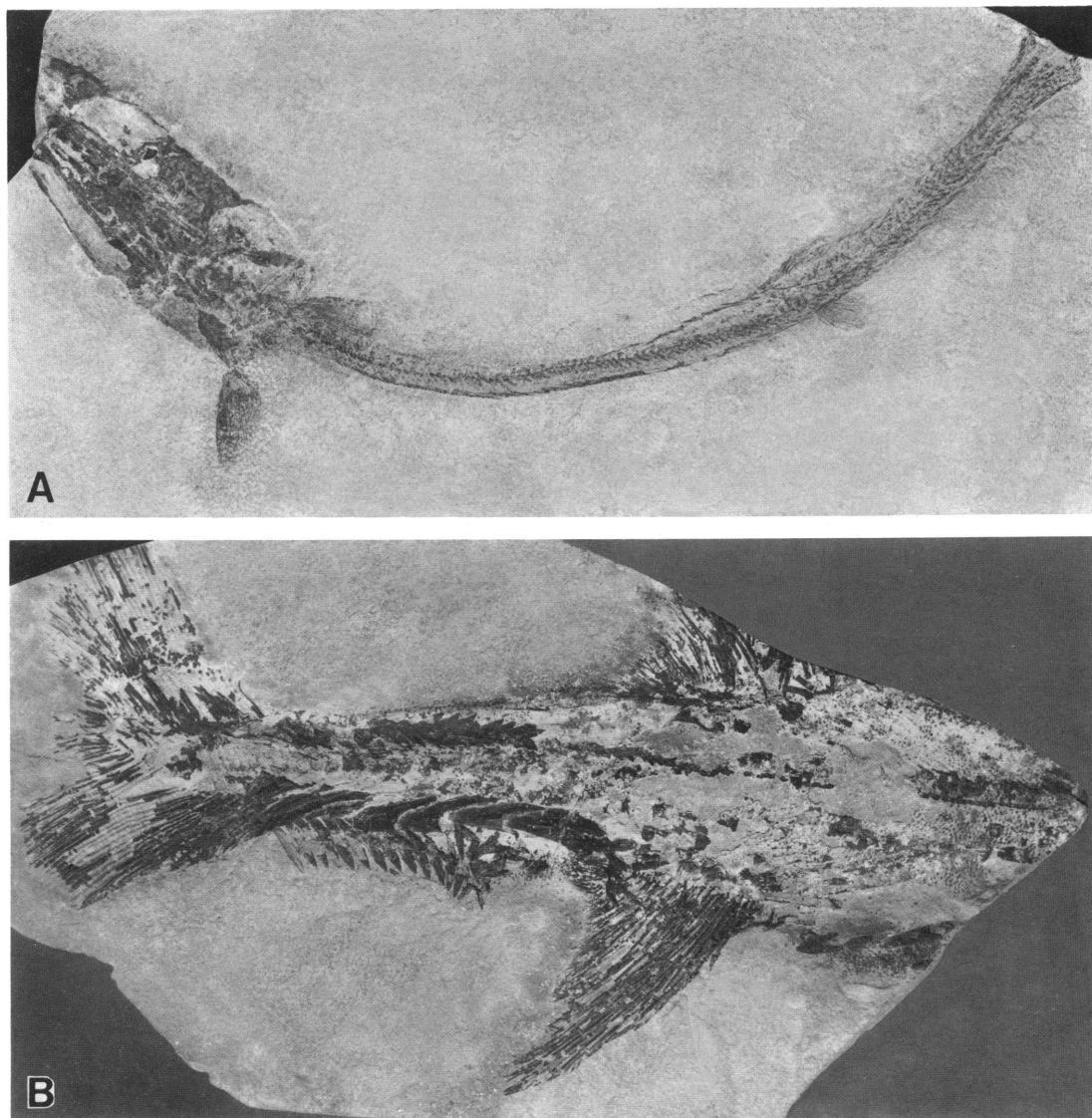
FIG. 15. *Saurichthys* sp., from Wapiti Lake. A. NMC 12287, partial skull and body with pectoral and pelvic fins. *Ca.* ×0.50. B. AMNH 6246, posterior portion of body with dorsal, anal, and caudal fins. *Ca.* ×0.58.

mid-dorsal row and a mid-ventral row of enlarged scales, or scutes, and a single row of smaller scales along the lateral line, a condition found in most described species. The mid-dorsal scutes anterior to the dorsal fin are ovate (NMC 12287); behind the dorsal fin they exhibit anterolaterally projecting wings. Anterior to the anal fin the mid-ventral scutes are ovoid and have well-developed median crests. In AMNH 6246 several scutes immediately anterior to the anal fin have anteriorly directed forks; behind the anal fin the scutes are elongated and oblanceolate. Both the dorsal and ventral scutes are ornamented with tubercles and ridges that radiate obliquely from the midline.

The pectoral fins (fig. 15), which are in-completely preserved in AMNH 6246 and NMC 12287, consist of 23 to 25 unsegmented and distally bifurcated rays. The smaller and more delicate pelvic fins have 23 to 26 rays and are also unsegmented. The opposing dorsal and anal fins are preserved in AMNH 6246 and NMC 12287. It is not possible to make an accurate ray count for the dorsal fin, but 25 to 30 unseg-mented rays can be counted in the anal fin of AMNH 6246.

The marginal dentition in both the upper and lower jaws consists of large laniaries with smaller teeth between them. An incomplete palate (NMC 26209) from Ellesmere Island shows laniaries that are more closely spaced along the posterior half of the rostropremaxilla.

Discussion. The first saurichthyid reported from the Triassic Spray River "Formation" was found near Massive, Alberta; it was described by Raymond (1925) as a new species of *Belono-rhynchus—B. dayi. Belonorhynchus* is now con-sidered a synonym of *Saurichthys.* The type specimen (MCZ 1564) consists of a trunk seg-ment with one fin (probably a displaced pectoral or pelvic rather than an anal, as suggested by Raymond) and poorly preserved displaced skull fragments, all in part and counterpart. There is reason to believe that this specimen represents part of the trunk anterior to the dorsal and anal fins. The mid-dorsal and mid-ventral scales have an ovate to chordate shape. The dorsal scales are more elongated than the ventral ones. The outer surfaces of the scales in both series are covered with a fine rugose ornamentation that parallels a low median ridge.

Reference of the Wapiti Lake *Saurichthys* material to *S. dayi* is not possible because of poor preservation. One specimen (NMC 12292) seems to include both mid-dorsal and mid-ventral scutes, all with the under (median) surfaces exposed. These scutes are much smaller than those described and figured for *S. dayi,* and an adequate comparison is not possible.

Lack of consistent data for the many (about two dozen) recognized species of *Saurichthys* makes it impossible to deal with the problem of interrelationships. According to Griffith (1962) tooth characters are not reliable, and differences in dermal skull pattern have not been sufficiently investigated. Although a single pair of parietals (as in *S. wimani* Stensiö, 1925) probably repre-sents the primitive saurichthyid condition, some species (e.g., *S. curioni* Bellotti, 1857; see Griffith, 1959) have a single median parietal, while others (e.g., *S. piveteaui* Beltan, 1958) have multiple parietal elements. The number in *S. madagascariensis* Piveteau, 1944 (see Beltan, 1968) varies from two to four. Thus the occur-rence of two pairs of parietals in both a Wapiti Lake specimen (NMC 12288) and in *S. ornatus* may have no significance in regard to relation-ship.

Vestigial scales are present on most of the body in the Wapiti Lake specimens, as they are in several Lower Triassic species (Stensiö, 1925, pp. 206-207; Griffith, 1962, p. 354), but the systematic value of this condition remains obscure.

In view of these considerations, the specific status of the Wapiti Lake *Saurichthys,* and in fact, the validity of the species *S. dayi,* cannot be determined without a systematic revision of the entire genus. For this reason a specimen (NMC 12293) of *Saurichthys* from Massive, Alberta (the locality for the type of *S. dayi*), is referred simply to *Saurichthys* sp., along with the mate-rial from Wapiti Lake and the single specimen from Ellesmere Island.

ORDER PARASEMIONOTIFORMES

FAMILY PARASEMIONOTIDAE STENSIÖ, 1932

Ospiidae Stensiö, 1932, pp. 225-226.
Tungusichthyidae Berg, 1941, p. 461.
Promecosominidae Wade, 1941, pp. 380-383.
Paracentrophoridae Gardiner, 1960, p. 347.

Distribution. Lower Triassic of Madagascar, East Greenland, Siberia, British Columbia, and Alberta; Middle and Upper Triassic of Australia.

Diagnosis. See Patterson, 1973, pages 283-287.

PARASEMIONOTIDAE, *INCERTAE SEDIS*

Figures 16, 17

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 6281, complete fish; AMNH 6291, fish with poor skull; NMC 9959, nearly complete fish; NMC 10113, complete fish; NMC 10114, fish lacking skull; NMC 10115, fish lacking anterior skull; NMC 10116, posterior portion of fish; NMC 10117, posterior portion of fish; NMC 10118, partial trunks of two fish; NMC 10119, poorly preserved complete fish; NMC 10122, complete fish; NMC 10123, fish lacking skull; UC 1151, nearly complete fish; UC 1152, skull and anterior body; UC 1153, portion of body with dorsal and anal fins; UC 1156, nearly complete fish; UC 1157, nearly complete fish; UC 1158, skull; UC 1189, portions of two bodies; UC 1191, skull and anterior body.

From the Lower Triassic of Banff-Massive, Alberta: NMC 10120, poorly preserved fish lacking posterior region; NMC 10121, poorly preserved fish; NMC 26213, skull and partial body.

Description. The 23 specimens listed above are small fusiform fishes (fig. 16), ranging in total length from 10 cm. to 19 cm. There are differences in skull form (fig. 17) that suggest they represent more than one taxon, but distortion and poor preservation prevent evaluation. The suspensorium is vertical and the maxilla is mobile. Both a supramaxilla and an inter-opercular are present. The preopercular is kidney-shaped and has a thickened posterior border for the sensory canal, and there is a well-developed coronoid process on the mandible (fig. 17A). UC 1158 shows a relatively long, shallow dentigerous ramus and an articular process on the maxilla (fig. 17C). Both conditions are suggestive of *Watsonulus* Brough, 1939 (see Lehman, 1952, pl. 37).

The number of fin rays seems to be about the same in all specimens: pectoral, 14 to 16; pelvic, nine or 10; dorsal, about 20; and anal, about 19.

The number of vertical scale rows between the cleithrum and the origin of the hypocaudal lobe is approximately 40. The scales are rhombic and thin; they tend to be ornamented with nearly horizontal parallel ridges in the anterior part of the body. More posteriorly they are nearly devoid of surface ornamentation, but they have denticulate posterior margins. UC 1151, one of the smallest specimens, has scales only in the vicinity of the lateral line; another small specimen, NMC 10122 (fig. 16A), is entirely devoid of squamation—probably due to preburial maceration. The same specimen also shows ossified neural spines and pleural ribs, but it lacks centra.

The skull-body proportion is the same in both the small and large specimens—about 1:4. It is possible that the small specimens represent young individuals.

Discussion. The specimens under consideration are referred to the Parasemionotidae in the sense of Patterson (1973, pp. 283-287). This family is difficult to define on the basis of unique shared derived characters. Patterson (1973, pp. 262, 287) considered it to be a paraphyletic, or "grade," group related to his subdivision Halecomorphi on the basis of the mobile maxilla and the presence of a supramaxilla, an interopercular and a small posttemporal fossa. All but the last character can be seen in the Wapiti Lake referred material. The participation of both the quadrate and the symplectic in the articulation of the jaw, which relates at least some parasemionotids to the amiids and caturids (both also Halecomorphi), has not been observed.

ALBERTONIA GARDINER, 1966

Elonichthys (in part): Lambe, 1916a, p. 39.
Dollopterus (in part): Berg, 1936, p. 166.
Dollopterus (in part): Aldinger, 1937, p. 206.
Albertonia Gardiner, 1966, p. 65.

Type Species. Albertonia cupidinia (Lambe).

Distribution. Lower Triassic of western Canada.

Diagnosis. A parasemionotid (as defined by Patterson, 1973, pp. 262, 287) specialized in having deeply fusiform body and greatly elongated pectoral fins. Small acuminate marginal teeth present on mobile maxilla and dentary. Suspensorium nearly vertical. Preopercular
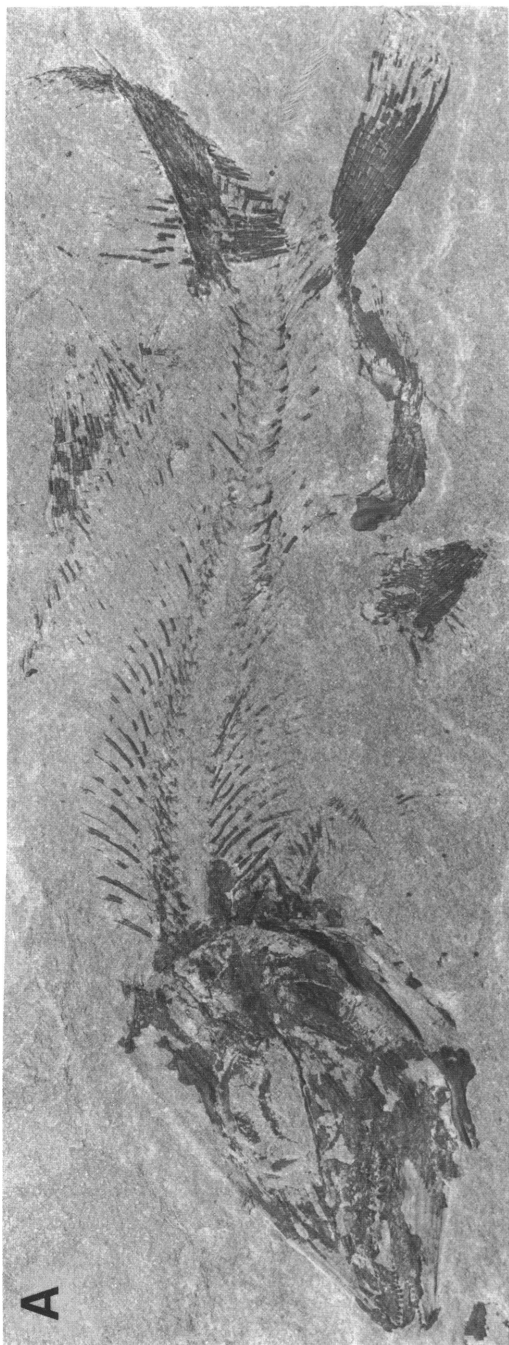
FIG. 16. Parasemionotidae, *incertae sedis*, from Wapiti Lake. A. NMC 10122, specimen lacking squamation. *Ca.* ×1.60 B. Smooth-on peel of UC 1156, specimen with complete squamation. *Ca.* ×1.74.

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FIG. 17. Smooth-on peels of skulls of Parasemionotidae, *incertae sedis*, from Wapiti Lake. A. UC 1191. *Ca.* × 2.40. C. UC 1158. *Ca.* × 2.21. D. NMC 10113. *Ca.* × 1.53.

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present; opercular and subopercular subequal. Longest pectoral fin rays about one-half length of body. All fins bordered by fringing fulcra; fin rays distally segmented. Caudal fin hemiheterocercal, weakly cleft, and probably equilobate. Scales rhomboidal, deeper than wide in anterior flank region; posterior border of all scales pectinate.

Albertonia cupidinia (Lambe, 1916)
Figure 18

Elonichthys cupidineus Lambe, 1916a, p. 39.
Dollopterus cupidineus: Berg, 1936, p. 166.
Dollopterus cupidineus: Aldinger, 1937, p. 206.
Albertonia cupidinia: Gardiner, 1966, p. 65.

Holotype. NMC 757, 757a, fragment of trunk with nearly complete pectoral fin, part and counterpart, from the Lower Triassic of Massive, Alberta.

Distribution. Lower Triassic of Alberta and British Columbia.

Specific Diagnosis. Same as for genus.

Referred Specimens: From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: NMC 9979, posterior portion of fish; NMC 12325, fish lacking skull; NMC 12326, pectoral fin with portion of trunk; NMC 12327, caudal fin; NMC 12328, nearly complete fish; NMC 12329, section of body with pectoral fin.

From the Lower Triassic of Banff-Massive, Alberta: NMC 757, 757a (type), section of trunk with pectoral fin, part and counterpart; NMC 9963, posterior body with caudal and anal fins; NMC 9964, fish lacking caudal region, NMC 12330, nearly complete fish; NMC 12331, nearly complete fish; NMC 12332, badly weathered anterior part of fish.

From the Toad-Grayling Formation, Needham Creek-Graham River-Horn Creek, British Columbia: NMC 26202, portion of pectoral fin rays; NMC 26204 A and B, posterior body with dorsal, anal, and caudal fins, part and counterpart; NMC 26205 A and B, fish lacking caudal region, part and counterpart; NMC 26206, section of fin with scale patch; NMC 26207, section of trunk including caudal peduncle.

Description and Discussion. The species Elonichthys cupidineus was erected by Lambe (1916a) for a single specimen (NMC 757, 757a) collected from Lower Triassic rocks near Massive, Alberta. The species was later referred to Dollopterus Abel, 1906 (Berg, 1936; Aldinger, 1937). Recently Gardiner (1966, p. 65) erected the new genus Albertonia to contain it (he also noted that Albertonia is probably a perleidid). Sixteen additional specimens from the Lower Triassic of western Canada (six of them from Wapiti Lake) are here considered conspecific with NMC 757, 757a, and are referred along with it to Albertonia cupidinia.

Albertonia cupidinia (fig. 18A) is a deeply fusiform fish: the maximum body depth is about one-third of the overall length. The impressively elongated pectoral fins, composed of approximately 21 rays, are equal to about one-half of the total body length. The pelvic fins, which are very much smaller and include nine or 10 rays, are situated at the deepest part of the ventral contour. The dorsal fin, composed of about 17 rays, arises in front of the anal, which has approximately 18 rays. The short-lobed hemiheterocercal caudal fin is composed of about 30 principal rays and is externally homocercal. The scales are rhombic with serrated posterior borders. There are about 40 scale rows between the cleithrum and the origin of the hypochordal lobe of the caudal fin.

Although skull remains are poorly preserved, the mobile maxilla, the interopercular, and the outline of the preopercular are evident in several acid prepared specimens (fig. 18B); they suggest that Albertonia is a parasemionotid.

Albertonia resembles Dollopterus, Thoracopterus Bronn, 1858, and Gigantopterus Abel, 1906, all of which also have hypsisomatic bodies and greatly elongated pectoral fins. These genera have been assigned to the family Perleididae, but as Lehman (1966, p. 116) pointed out, they are too poorly known for their affinities to be determined.

The inclusion of Albertonia in the Parasemionotidae increases the diversity in body and fin form previously known for this group. Unfortunately, parasemionotid interrelationships remain enigmatic.

CLASS CROSSOPTERYGII

SUBCLASS ACTINISTIA

ORDER COELACANTHIDA

FAMILY COELACANTHIDAE

WHITEIA MOY-THOMAS, 1935

Coelacanthus (in part): Priem, 1924, p. 111.
Whiteia Moy-Thomas, 1935, p. 215.

Type Species. Whiteia woodwardi Moy-Thomas.

Distribution. Lower Triassic of East Greenland, Madagascar, Alberta, and British Columbia.
Diagnosis. See Moy-Thomas, 1935, pp. 215-216.

Whiteia sp.
Figures 19, 20

Referred Specimens. From the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia: AMNH 5701 A and B, nearly complete fish, part
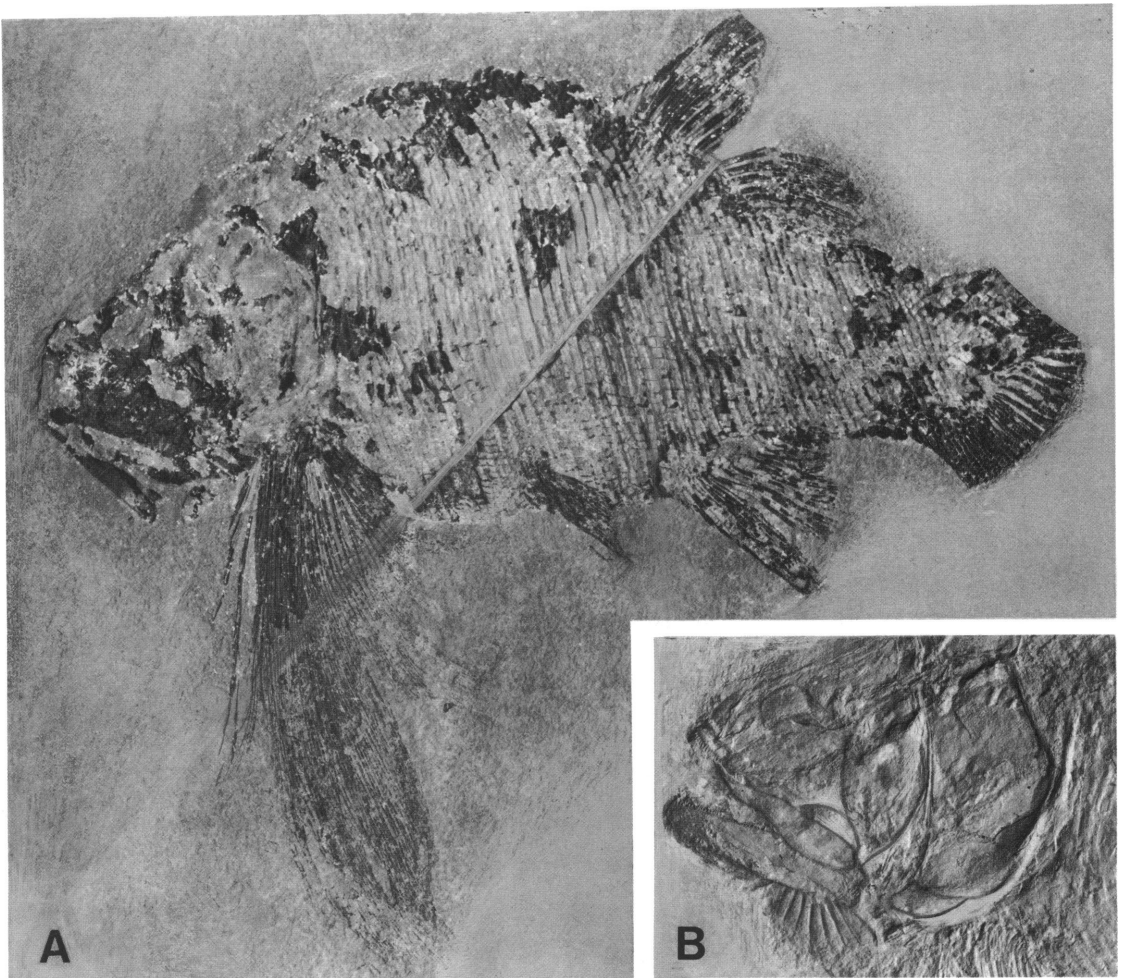

FIG. 18. *Albertonia cupidinia*, from Banff-Massive, Alberta. A. NMC 12330, specimen lacking caudal fin. *Ca.* ×0.84. B. Smooth-on peel of skull of NMC 9964. *Ca.* ×0.91.

and counterpart; AMNH 6248, weathered three-dimensional skull; AMNH 6249, partly dissociated fish; AMNH 6250, posterior portion of fish; AMNH 6251, basisphenoid; AMNH 6252, caudal region; AMNH 6253, disarticulated skull elements; AMNH 6254, cleithrum; AMNH 6255, skull elements; AMNH 6256, partial three-dimensional skull showing visceral skeleton in cross section; AMNH 6257 A and B, posterior part of trunk with caudal fin, part and counterpart; AMNH 6279, ceratohyal; AMNH 6290, disarticulated skull elements and scales; AMNH 6292 A and B, portion of skull and fin fragments, part and counterpart; NMC 9983, fins and gular plate; NMC 9984 A and B, fish lacking anterior of skull, part and counterpart; NMC 12295, section of trunk with second dorsal and anal fins; NMC 12296, skull and anterior of body; NMC 12297, caudal region; NMC 12298 A and B, disarticulated skull elements, part and counterpart; NMC 12299, anal and partial caudal fins; NMC 12300, caudal and anal fins; NMC 12301, complete fish; NMC 12302, portion of trunk with pelvic plate and fin, basal plates of dorsal fins; NMC 12303, skull and anterior part of body; NMC 12304, caudal region; NMC 12305, caudal region; NMC 12306, fin rays; NMC 12307, skull elements; NMC 12310 A and B, skull, part and counterpart; NMC 12311 A and B, skull in concretion, part and counterpart; NMC 12312 A and B, skull in concretion, part and counterpart; NMC 12313, three-dimensional skull in concretion; NMC 12314, skull in slab; NMC 12315 A and B, skull in concretion, part and counterpart; NMC 12316, partial three-dimensional skull; NMC 12317, partial three-dimensional skull showing basisphenoid in cross section; NMC 12318, partial three-dimensional skull; NMC 12319, three-dimensional skull.

From the Lower Triassic of Banff-Massive, Alberta: NMC 12308, skull elements; NMC 12309, palate.

From the Toad-Grayling Formation, Needham Creek-Graham River-Horn Creek, British Columbia: possibly NMC 26203 A and B, fin fragment, part and counterpart; NMC 26210, urohyal.

Description and Discussion. Of the 39 coelacanth specimens from Wapiti Lake, only four are relatively complete individuals (fig. 19A). Their estimated total lengths range from 17 cm. to 100 cm. Although none of the specimens has a well-preserved dermal skull (fig. 19B), it is reasonable to assign the sample to the genus *Whiteia* on the basis of the form of the basisphenoid, the shape and position of the pelvic fin supports and the ornamentation of the scales.

The basisphenoid (fig. 20B, C) is similar to that (fig. 20A) of *Whiteia woodwardi* Moy-Thomas, 1935, from Madagascar[1] (comparisons were made with specimens in the American Museum of Natural History and casts of specimens in the Muséum National d'Histoire Naturelle). It also resembles the basisphenoid of the Spitzbergen coelacanth *Wimania* Stensiö, 1921 (see Stensiö, 1921, pl. 5, fig. 1; Schaeffer and Gregory, 1961, fig. 3), but the antotic processes in *Wimania* are relatively wider than they are in *Whiteia*, particularly where they are in contact with the pleurosphenoid. The basisphenoid in NMC 12317 is roughly twice as large as that of *Latimeria* Smith, 1939, as figured by Millot and Anthony (1958, pl. 24). On the basis of the basisphenoid width-body length ratio in *Latimeria*, it is estimated that the Wapiti Lake *Whiteia* attained an overall length of about 300 cm.

The circumorbital series, the parasphenoid, the palatoquadrate and the urohyal are similar to their counterparts in *Whiteia woodwardi* (Lehman, 1952).

The pelvic plates resemble those of several species of *Whiteia* in their general proportions and in having well-developed medial processes (these processes are lacking in *Wimania*; see Stensiö, 1921, pl. 8, fig. 7). The pelvic elements of *Whiteia* differ considerably from those of another Greenland coelacanth, *Laugia* Stensiö, 1932 (see Stensiö, 1932, fig. 24). Other fin supports in the Wapiti Lake *Whiteia* are too poorly preserved to make detailed comparisons.

Fin ray counts are approximate: pectoral, 15 to 17; first dorsal, eight or nine; second dorsal, approximately 29; anal, 29 to 34. The number of

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[1] *Whiteia* is also known from the Triassic of East Greenland (Nielsen, 1936), but it has not been described in detail.

rays in the caudal fin cannot be counted and the supplementary caudal fin is not preserved.

Scale ornamentation consists of well-spaced parallel ridges. In the smaller specimens the scales have three or four ridges, in the larger ones there may be as many as 20 or more.

Coelacanthus banffensis Lambe

Remarks. Lambe (1916a, p. 38) erected the species *Coelacanthus banffensis* on the basis of a single specimen (NMC 756, 756a, type) consist-

ing of a pectoral fin and numerous scales from the Lower Triassic of Banff, Alberta. In our opinion the specimen is too fragmentary and too poorly preserved to make any meaningful observations. However, Gardiner (1966, p. 93) noted that "this species looks very much as if it belongs in the genus *Whiteia*." Peter A. Forey (personal commun., 1975) examined some additional coelacanth specimens from the Lower Triassic of Wapiti Lake and Banff in the University of Alberta collections. He concluded that these specimens could also be included in the genus *Whiteia*.
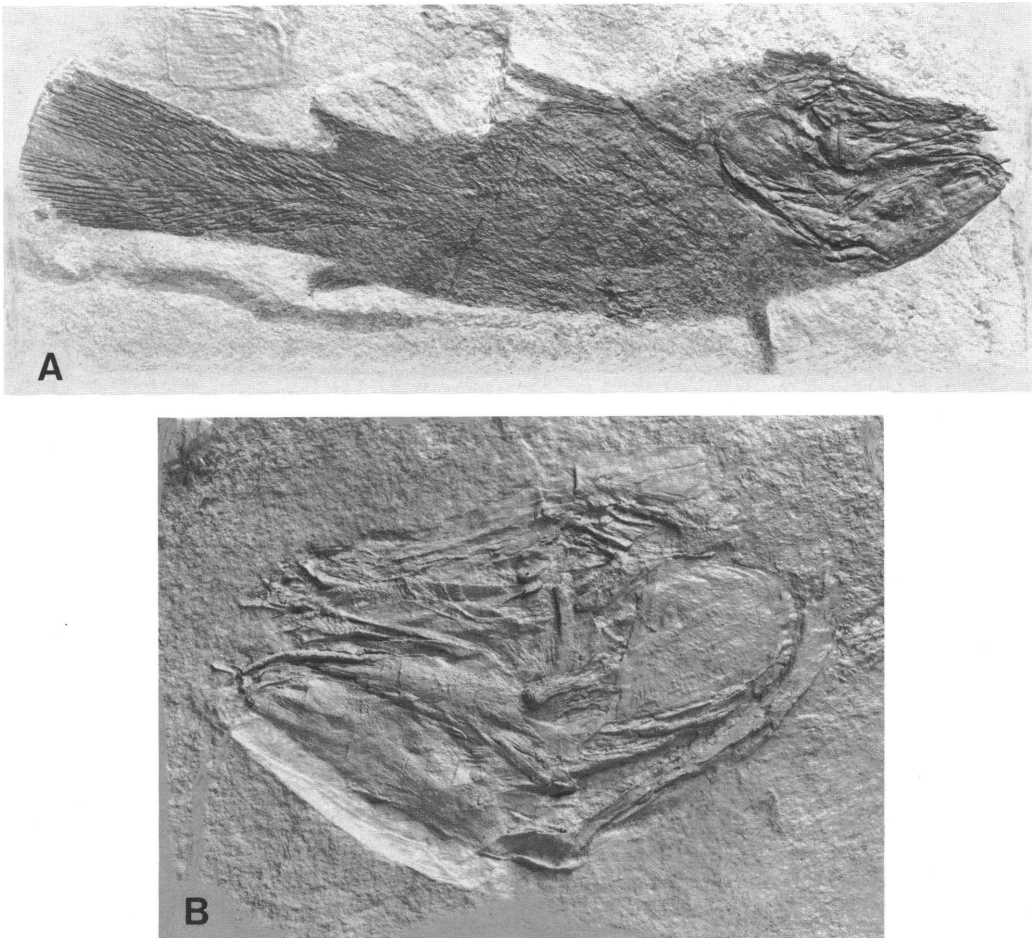

FIG. 19. *Whiteia* sp., NMC 12301, from Wapiti Lake. A. Entire specimen. *Ca.* ×0.75. B. Smooth-on peel of skull. *Ca.* ×1.50.

DISCUSSION
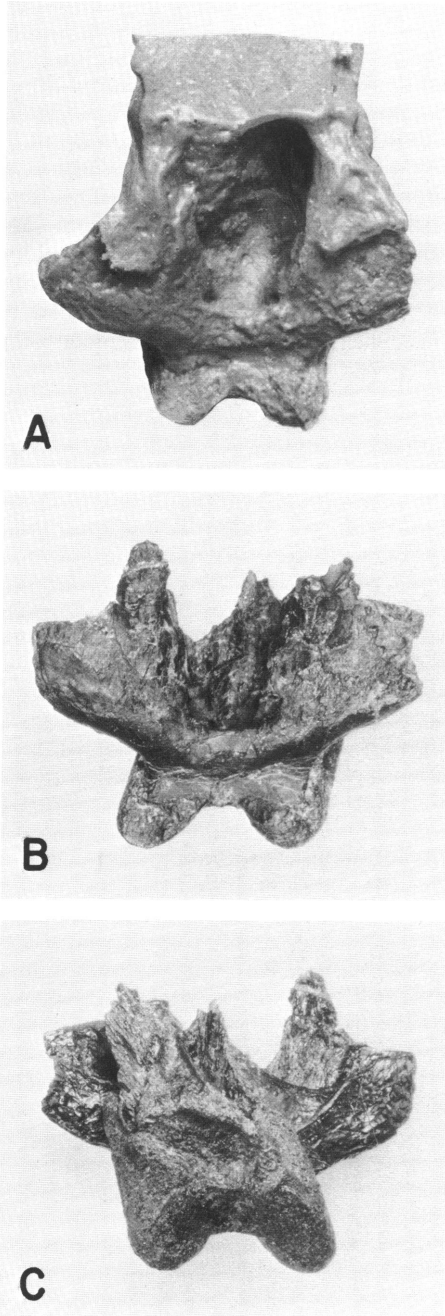

FIG. 20. A. *Whiteia woodwardi*, IP 213, from Madagascar. Basisphenoid in posterodorsal view. *Ca.* ×2.74. B., C. *Whiteia* sp., AMNH 6251, basisphenoid, from Wapiti Lake. B. Posterodorsal view. C. Ventral view. B and C *ca.* ×1.79.

Early Triassic (Scythian) marine fishes are known from more than a score of localities throughout the world. Although many of these have yielded only one or a few genera, the overall taxonomic resemblance is striking enough to suggest common ecological and zoogeographical factors. Before examining this matter further, it will be helpful to review the assemblages from each area and the age of the rocks in which each occurs (fig. 3 is a correlation chart for the more important localities). First we shall consider the areas that have yielded rather restricted assemblages.

In the United States, Lower Triassic marine fishes occur in the Bear Lake region of southeastern Idaho. A spine described by Evans (1904) as "*Cosmacanthus elegans*" (which is probably a hybodontid instead), was found "below typical *Meekoceras* beds." Since *Meekoceras* characterizes the base of the Thaynes Formation (Smithian-Spathian; see Kummel, 1954), the spine presumably comes from either the underlying Woodside Formation (Dienerian) or Dinwoody Formation (Griesbachian). Dunkle (personal commun., 1974) has recognized *Bobasatrania*, *Laugia*, and a perleidid from beds that belong to one or the other of these formations. He has also identified *Birgeria* and *Bobasatrania* from the *Columbites* zone of the Thaynes Formation. Tanner (1936) erected the genus *Haywardia* (which is probably a synonym of *Bobasatrania*) on the basis of material from the Woodside.

Fishes reported from the Lower Triassic (Sulphur Mountain Formation) in southern Alberta and British Columbia include: *Pteronisculus* (Lambe, 1916a); *Boreosomus* (this paper); *Bobasatrania* (Lambe, 1914; Warren, 1936; Russell, 1951; Gardiner, 1966; this paper); *Saurichthys* (Raymond, 1925; this paper); a parasemionotid (this paper); *Albertonia* (Lambe, 1916a; Berg, 1936; this paper); and *Whiteia* (Lambe, 1916a; Gardiner, 1966; this paper). Scattered occurrences of fossil fish material from the Toad-Grayling Formation to the north and northwest of Wapiti Lake in British Columbia (Pelletier, 1963) include a chondrichthyan (spines only), *Albertonia* and *Whiteia* (this paper).

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Boreosomus and a coelacanth have been reported from the Lower Triassic part of the Shublick Formation in the Killik-Itkillik area of Alaska (Patton and Tailleur, 1964).

Two specimens from the Blind Fiord Formation (Smithian) of Blind Fiord, Ellesmere Island, have been identified as *Saurichthys* and *Boreosomus* (this paper).

There are several scattered occurrences of Lower Triassic marine fishes in Siberia. The pholidopleurid *Arctosomus*, the palaeoniscid *Evenkia* and the parasemionotid *Tungusichthys* have been described from the Lower Tunguska River area (Berg, 1941; Obruchev, 1967). From the Olenek River region to the northeast, Obruchev (personal commun., 1959) lists *Acrodus, Birgeria,* and *Perleidus.* The genus *Tompoichthys* (Obruchev, 1967) comes from the Verkhoyansk area. Obruchev assigned it to the family Platysomidae, but on the basis of his illustration, we think it may be a bobasatranid. Finally, *Hybodus* has been recovered in the Magadan region (Obruchev, personal commun., 1959).

From the northern Shensi Basin in China, Chow and Liu (1957) reported *Gyrolepis, Palaeoniscus, Boreosomus, Perleidus,* and *Saurichthys.* The specimens are said to come from the possibly Lower Triassic Yan-an Formation. To the south, in Keichou (Kweichow) Province, there is an occurrence of *Boreosomus* (Patte, 1935), and in Kwangsi Province the Lower Triassic Lolou Series has yielded the coelacanth *Sinocoelacanthus* (Liu, 1964).

Saurichthys (Obruchev, 1967) and *Ceratodus* (Chabakov, 1931; Obruchev, 1967) have been found in the Lower Triassic sedimentary rocks of Mt. Bogdo, Sinkiang Province; however, it is uncertain whether or not the beds are marine in origin.

Waagen (1895) reported three species of *Acrodus,* along with the palaeonisciforms *Gyrolepis* and *Saurichthys,* from the Ceratite beds of the Salt Range in Pakistan. He also listed *Colobodus* from the underlying Permian *Productus* limestone of the same region. This identification is questionable, but if we are dealing with *Colobodus,* it is quite likely that Waagen made an error and that the *Colobodus* specimens occur in the same beds, the Kathwai Member (lowermost Scythian) of the Mianwali Formation (Kummel, 1966), as the three genera listed above.

A single edestid, possibly *Helicampodus,* is reported by Obruchev (personal commun., 1959) from supposedly Lower Triassic marine beds near Djulfa, Iran.

In addition to Wapiti Lake, four other localities have yielded Lower Triassic marine fish assemblages comprising rather large numbers of genera. These are in East Greenland, Spitzbergen, north Madagascar, and south Madagascar.

The well-known Early Triassic fishes from East Greenland (Stensiö, 1932; Nielsen, 1935, 1936, 1942, 1949, 1952a, 1952b, 1961) come from the Wordie Creek Formation (Griesbachian-Dienerian) of the Nordenskiöld Sub-Group. They occur in six successive zones ranging from the lower Griesbachian into perhaps the lower Dienerian (Perch-Nielsen et al., 1974). Most of them have been found in the Cape Stosch area. In all, 19 genera are represented: *Polyacrodus, Nemacanthus, Parahelicampodus, Boreosomus, Pteronisculus, Birgeria, Acrorhabdus, Perleidus, Bobasatrania, Australosomus, Saurichthys, Helmolepis, Ospia, Broughia, Parasemionotus, Watsonulus, Whiteia, Sassenia,* and *Laugia.*

The number of genera and the number of specimens in each zone vary considerably, but they are both highest for zones II, III, and V. Nielsen (1961) suggested that the variation in faunal composition is the result of alterations in the environment. The fish-bearing sediments were deposited in a shallow basin whose connection with the open ocean shifted. Conditions at times were fully marine and at other times brackish or freshwater. Although the sequence reflects an alternation of freshwater and marine conditions throughout its thickness, there is an overall transition from marine to nonmarine. The ammonites decrease in number rapidly from zone II to zone V, and, with a single exception, no elasmobranchs are found above zone II. *Boreosomus, Pteronisculus, Australosomus* and the coelacanths seem to be the most persistent members of the assemblage. Zone I has yielded a shark, along with *Bobasatrania* and *Laugia,* while *Pteronisculus* and a coelacanth are the only fishes represented in zone VI.

A second major Lower Triassic marine fish assemblage comes from West Spitzbergen and was originally described by Stensiö (1918, 1921, 1925). The fishes occur in the Sticky Keep Formation (Smithian-Spathian) of the Sassen-

dalen Group. The main concentration is in what was formerly called the "*Posidonomya* beds," or "fish level," of the Smithian Iskletten Member (Buchan et al., 1965). This member is characterized by the invertebrates *Arctoceras, Xenoceltites, Prosphingites spathi, Posidonia mimer,* and "*Pseudomonotis*" *occidentalis* (Tozer and Parker, 1968). Fishes also occur in the succeeding Kaosfjellet Member at the "*Grippia* level" and "lower saurian level." The Kaosfjellet Member is characterized by *Svalbardiceras spitzbergense, Keyserlingites subrobustus,* and *Posidonia aranea* and is considered Spathian in age (Buchan et al., 1965; Tozer and Parker, 1968). Lithologically the Sticky Keep Formation consists of dark gray siltstones and shaly siltstones with limestone concretions. Eighteen genera of fossil fish have been reported (Cox and Smith, 1973): *Acrodus, Hybodus, Palaeobates, Polyacrodus, Pteronisculus, Pygopterus, Acrorhabdus, Birgeria, Boreosomus, Bobasatrania, Perleidus, Saurichthys, Axelia, Sassenia, Wimania, Mylacanthus, Scleracanthus,* and *Ceratodus.* Except for *Acrodus, Hybodus,* and *Ceratodus* (and possibly *Polyacrodus*—it cannot be determined from which horizon it comes), the genera listed above occur in the "fish level." Only *Pteronisculus* and *Boreosomus* are common to all three fish-bearing horizons. In addition, *Acrodus, Hybodus, Palaeobates,* and *Birgeria* are known from the "*Grippia* level," and *Acrodus, Saurichthys,* and *Ceratodus,* from the "lower saurian level." The distribution of these fishes in the three levels suggests the presence of both freshwater and marine layers.

The two Lower Triassic marine fish assemblages from Madagascar come from regions that are approximately 600 miles apart. The more northerly locality, the Ankitokazo Basin, is richer in variety and number of fishes. The fish-bearing beds are marine shales of the Middle Sakamena Group that can be dated as Dienerian. They are characterized by an invertebrate fauna that includes *Glyptophyceras besairiei, G. gracile, Meekoceras ambilobense, M.* aff. *radiosum, Prionolobus spathi, Clypeoceras* cf. *crassum, C.* cf. *magnumbilicatus, C. madagascariense,* and *Koninckites.* The fishes have been studied in detail by Piveteau (1930, 1934, 1944-1945), Lehman (1952, 1953, 1956), Lehman et al.

(1959), and Beltan (1968). The assemblage includes: *Pteronisculus, Ambodipia, Birgeria, Boreosomus, Bobasatrania, Ecrinesomus, Perleidus, Australosomus, Saurichthys, Errolichthys, Broughia, Jacobulus, Ospia, Paracentrophorus, Parasemionotus, Thomasinotus, Stensionotus, Watsonulus, Lehmanotus, Devillersia, Piveteaunotus, Whiteia, Coelacanthus, Piveteauia, Paraceratodus,* and possibly *Ceratodus.* No elasmobranchs have been reported to date.

The region between Beroroha and Mandronarivo in the southwest has produced another Madagascar Lower Triassic marine fish assemblage. Here the fishes come from Bed 5 (Dienerian) of the Middle Sakamena Group. The rock is shale with intercalations of sand and limestone nodules. The most recent comprehensive study of the fishes was made by Lehman et al. (1959). The number of genera represented is not so large as it is in the northern basin. Especially notable is the absence of coelacanths and the presence (assumed on the basis of prismatic calcified cartilage) of elasmobranchs. Four chondrostean genera have been identified: *Bobasatrania, Sakamenichthys, Australosomus,* and *Saurichthys;* three parasemionotids: *Parasemionotus, Thomasinotus,* and *Watsonulus;* and one ceratodontid: *Paraceratodus.*

Tortochaux (1950) thought that the Middle Sakamena was lagoonal with marine intercalations. Lehman et al. (1959) believed that the presence of *Estheria* indicated a lagoonal environment. Ceratodontids suggest a freshwater milieu; elasmobranchs are in general marine, although they can invade rivers and lakes. The presence of *Estheria* and *Paraceratodus* suggest that we may be dealing with a fresh to brackish lagoonal environment into which marine fishes migrated.

Of the 12 fish taxa described from the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation at Wapiti Lake, six genera (*Pteronisculus, Birgeria, Boreosomus, Perleidus, Bobasatrania,* and *Saurichthys*) also occur in Scythian deposits in East Greenland, Spitzbergen, and Madagascar. *Palaeobates,* which is recorded from Spitzbergen, may also occur at Wapiti Lake; it is not known from either East Greenland or Madagascar, but other elasmobranchs are. *Australosomus* has been found at Wapiti Lake, in East Greenland, and in Madagascar, but it is unknown

in Spitzbergen. At least two parasemionotid taxa are present at Wapiti Lake, five in East Greenland, three in south Madagascar and 11 in north Madagascar (three are common to the two last localities and four are common to East Greenland and north Madagascar); none is known from Spitzbergen. The coelacanth *Whiteia* occurs at Wapiti Lake, in East Greenland and in north Madagascar. In addition, another coelacanth is known from East Greenland, two others from north Madagascar and five others from Spitzbergen. A single ceratodotid occurs in Spitzbergen and one (or possibly two) in Madagascar; none has been found either at Wapiti Lake or in East Greenland.

On the basis of the invertebrate faunas, the East Greenland Wordie Creek Formation (Griesbachian-lower Dienerian) is the oldest of the Lower Triassic marine fish-bearing units discussed. The fishes from Madagascar occur in slightly younger beds (Dienerian). Both the Iskletten Member (Smithian) and the Kaosfjellet Member (Spathian) of the Spitzbergen Sticky Keep Formation have yielded fish. The section of the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation in which the fish occur at Wapiti Lake is dated as Smithian. Because many of the genera reported from the different localities have a time range equivalent to at least the entire Scythian, the differences in the ages of the fish-bearing beds are probably of little significance.

Perhaps the most remarkable aspect of the Lower Triassic marine fish assemblages is the abrupt appearance of most of the included taxa at the beginning of the Triassic (Schaeffer, 1973). Although not so obvious as the change from the Permian to the Triassic, there was a marked modification in the composition of marine fish assemblages from the Scythian to the Anisian (it should be noted, however, that some genera—e.g., *Pteronisculus*, *Birgeria*, *Perleidus*, and *Saurichthys*—persisted into the Middle and Late Triassic). The assemblages from the Alpine Tessin (Anisian and Ladinian) are notable examples in that they include a large number of new actinopterygian taxa of unknown affinities.

The marine Scythian fish localities have been plotted on a world Mercator projection (fig. 21) that shows the seaways as reconstructed by Kummel (1973). The localities all fall within areas of marine deposition, which are known to have existed on all the continents except Antarctica and South America during this interval. A second map (fig. 22) shows the world distribution of ammonoids during the Lower Triassic.

When transferred to a map of Pangaea (Dietz and Holden, 1970), the fish localities can be seen to have had an essentially circumpangaeal distribution (fig. 23). As all the fishes (with the exception of the ceratodontids) are regarded as marine, two explanations could account for their distributional pattern: (1) they were mostly epipelagic forms that occasionally entered shelf seas; (2) they were shelf and epicontinental sea inhabitants that rarely invaded the open ocean. These two explanations are, of course, not mutually exclusive.

Fishes by themselves generally do not offer reliable clues regarding habitat or way of life. As noted above, the distribution of the fish localities simply agrees with the areas of Scythian marine sedimentation (on the basis of included ammonoids). The variation in numbers of genera and numbers of individuals from the different localities is probably fortuitous, particularly in view of the large number of identical and closely related genera and the relative abundance of specimens in the assemblages from British Columbia, East Greenland, Spitzbergen, and Madagascar. Since the fish are preserved in areas of shelf sedimentation, they must have been swimming in the shallow seas around Pangaea shortly before death and burial, regardless of whether or not they also lived in the deeper ocean away from the shelf. The distributional pattern for the ammonoids (and for the clam *Claraia*; Kummel, 1973) is similar to that for the fishes and is subject to the same restricted interpretation. It seems rather meaningless to consider the significance of faunal resemblances for either the fishes or the ammonoids in terms of low provinciality. The problems of provinciality, particularly in relation to Pangaea and its breakup, can be considered more convincingly in relation to benthic organisms (Valentine, 1971).

The sharks, mostly hybodontids, are represented generally by isolated teeth. Except for those of *Hybodus*, the teeth have low rounded crowns. The hybodont feeding mechanism is
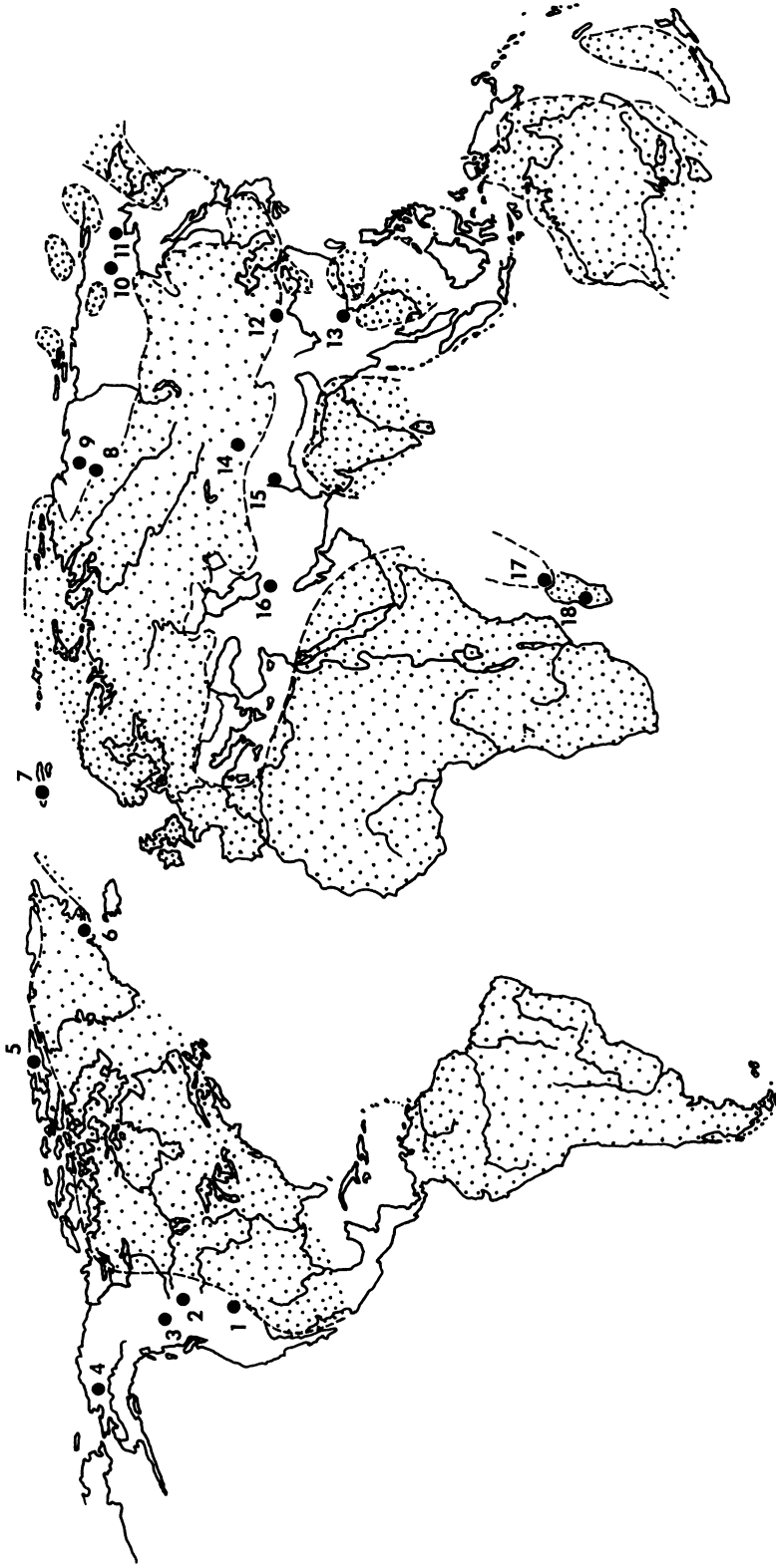
FIG. 21. Lower Triassic marine fossil fish localities shown on world Mercator projection. 1, southeastern Idaho; 2, southern Alberta and British Columbia; 3, Wapiti Lake, British Columbia; 4, Killik-Itkilik region, Alaska; 5, Ellesmere Island; 6, East Greenland; 7, West Spitzbergen; 8, Tunguska region, Siberia; 9, Olenek River region, Siberia; 10, Verkhoyansk region, Siberia; 11, Madagan region, Siberia; 12, north Shenshi Basin, China; 13, west Kwangsi-Kweichow, China; 14, Mt. Bogdo, Sinkiang, China; 15, Salt Range, Pakistan; 16, Djulfa, Iran; 17, north Madagascar; 18, south Madagascar. Clear areas represent seaways, stippled areas represent land. (Map after Kummel, 1973.)

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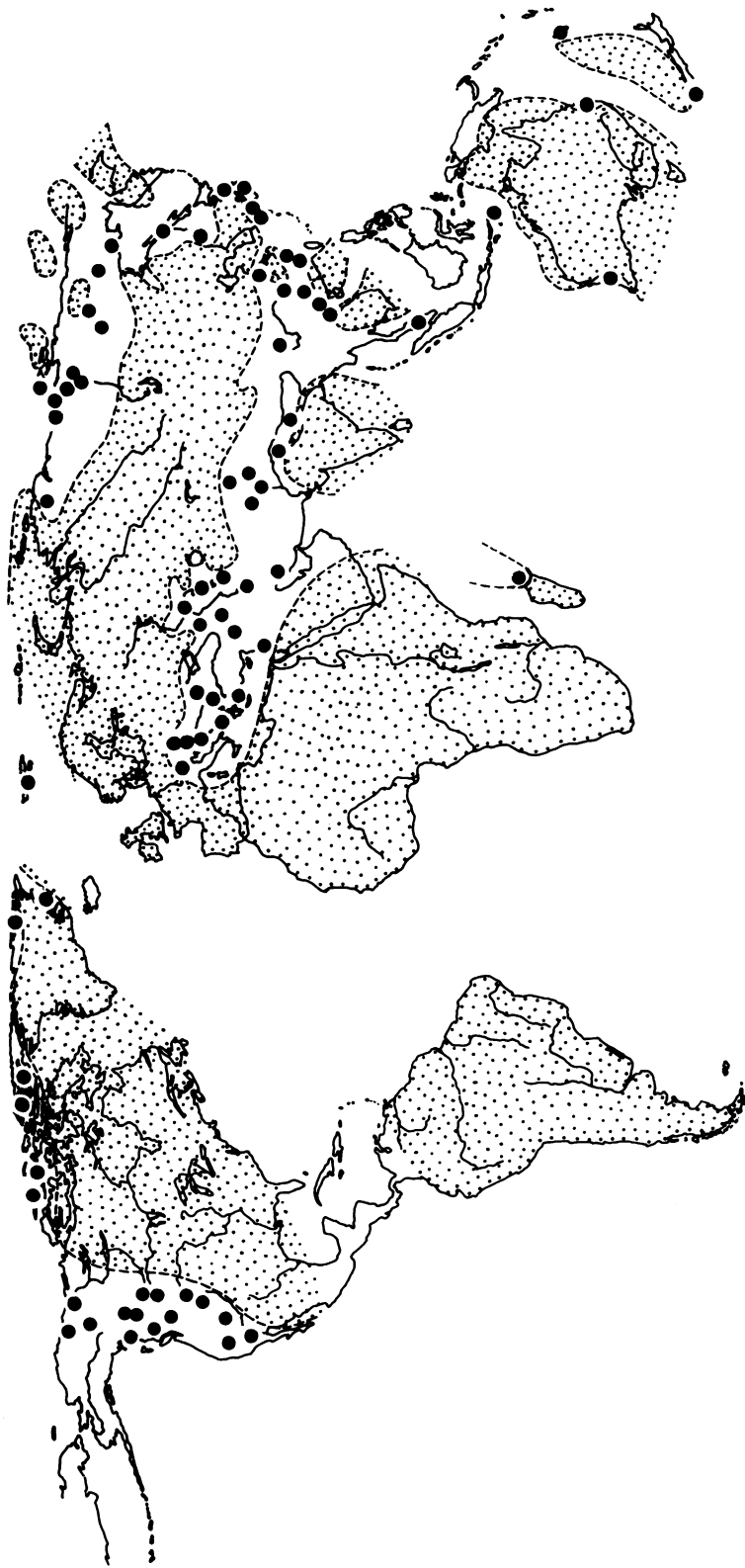FIG. 22. Distribution of Lower Triassic ammonoids shown on world Mercator projection. Stippled areas represent land, clear areas represent seaways. (After Kummel, 1973.)
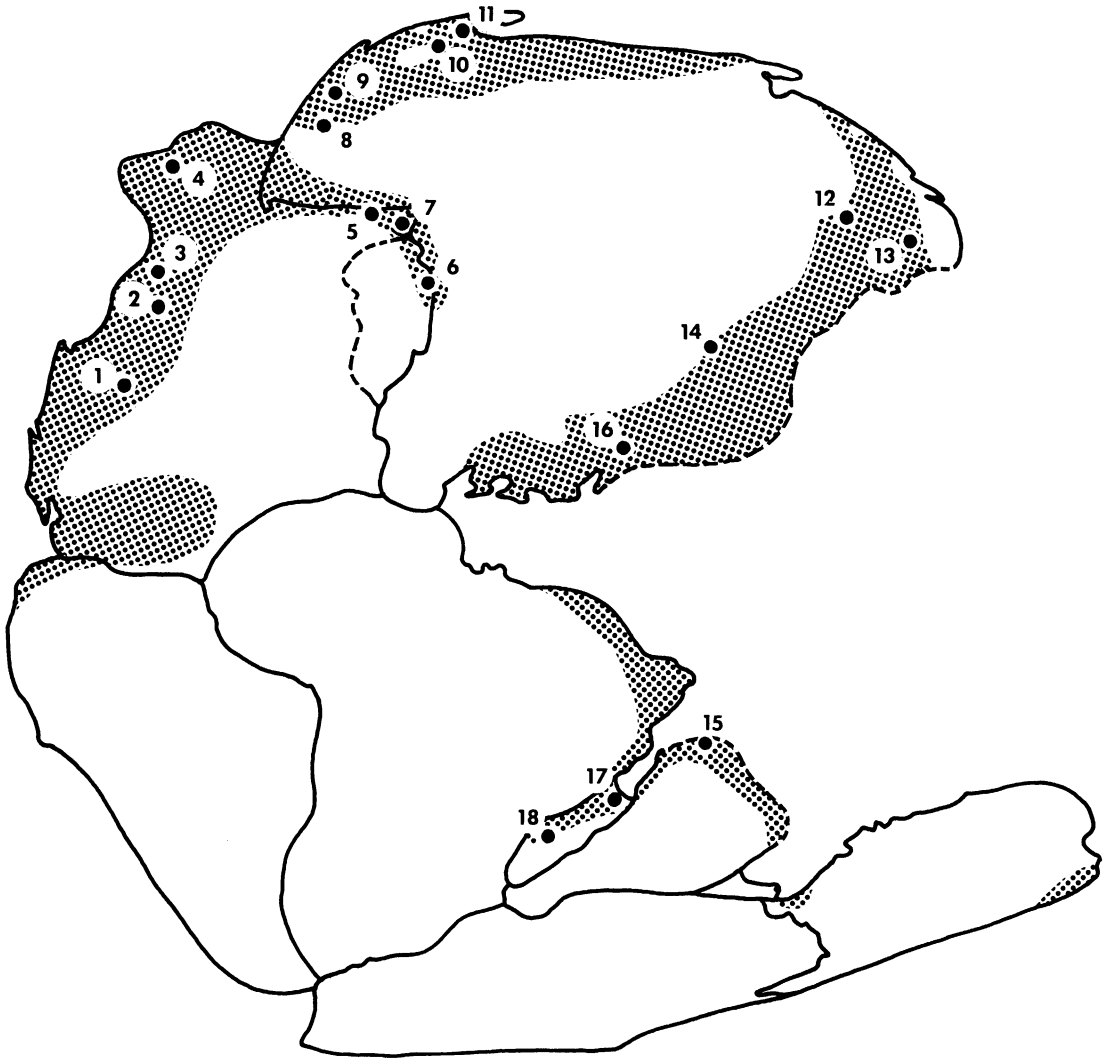
FIG. 23. Distribution of Lower Triassic marine fossil fish localities on predrift map of Pangaea. Locality numbers as in figure 21. Clear areas represent land, stippled areas represent seaways. (Map after Dietz and Holden, 1970.)

primitive compared with the derived condition in the galeoids, squaloids, and batoids (Schaeffer, 1967). The diet of these Triassic sharks remains problematical, but feeding apparently did not involve cutting and shearing, as it does in many galeoids and squaloids.

There are numerous taxa of Lower Triassic marine actinopterygians (including *Pteronisculus*, *Boreosomus*, *Perleidus*, *Australosomus*, and the parasemionotids) that are unrelated, or only distantly related. They are all relatively small (under 20 cm.) and have essentially fusiform bodies. Their weak dentition and small to moderate gape suggest a diet of plankton, detritus, larval fishes, algae, etc. The general picture is that of "small food" feeders or "grazers."

Saurichthys, with its elongated jaws and well-developed pointed teeth, may have been a

predator. Its elongated body with remote dorsal and anal fins resembles that of the long-nosed gar and the needlefishes among living teleosts. However, the feeding mechanism, inferred from the structure of the palatal complex and jaws, was of the conservative palaeonisciform type (Stensiö, 1925, fig. 40; Schaeffer and Rosen, 1961).

Another possible predator, *Birgeria*, also had a wide gape, mainly postorbital, and a powerful dentition. Its body is relatively shorter and more massive than that of *Saurichthys*, but the dorsal and anal fins are in the same remote positions (Nielsen, 1949, fig. 77). The jaw mechanism, again as in *Saurichthys*, was of the palaeonisciform type. It is possible that both genera fed by grasping their prey and engulfing it, using the jaws only for seizing and holding.

Bobasatrania may have had an ecological role resembling that of the pycnodonts. Like them, it has a hypsisomatic body, a small gape and weak marginal, but strong pharyngeal, dentition. The open cheek, free maxilla, and vertical suspensorium (Nielsen, 1952b) indicate a holostean-halecostome arrangement of the adductor jaw musculature. The combination of toothless jaws and pavement-like parasphenoid and pharyngeal teeth suggests that food was crushed before it passed into the esophagus.

The elongated pectoral fins, deep body, broad peduncle, and well-developed caudal fin of *Albertonia* suggest a slow, strong swimmer. In view of its weak marginal dentition and the apparent absence of a pharyngeal dentition, it may have been a nibbler or grazer.

The nine Lower Triassic marine coelacanth genera demonstrate a modest adaptive radiation in their dentition and in their dermal cheek elements. Their diet is even more speculative than that of the extinct actinopterygians. *Whiteia*, *Wimania*, and *Sassenia* have small, acutely pointed marginal teeth and, apparently, weak pharyngeal dentitions. *Axelia*, *Scleracanthus*, and *Mylacanthus* have relatively strong pterygoid and parasphenoid dentitions, which may be a shared derived condition. The dentition, along with other characters, suggests a close relationship among these genera (Stensiö, 1921).

Laugia appears to have fairly conventional coelacanth feeding equipment, including small conical teeth. As is well known, however, it is distinctive in the acanthopterygian-like positions of the pectoral and pelvic fins and in the unique shape of the scapulocoracoid, pelvic plate, and basal plate (Stensiö, 1932). In the poorly known *Piveteauia* (Lehman, 1952) the pelvics are in a thoracic position, but there is no evidence of close relationship to *Laugia*.

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