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113

Middle Eocene Freshwater Fishes
from British Columbia

Mark V.H. Wilson



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Kayser, C.

1965 Hibernation. In Mayer, W.V. and R.G. Van Gelder, eds. Physiological Mammalogy. Vol. 2 — New York, Academic Press, pp. 180-278.

Ellerman, J.R., T.C.S. Morrison-Scott and R.W. Hayman.

1953 South African mammals, 1758-1951: a reclassification. — London, Printed by Order of the Trustees of the British Museum. 363 pp.

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Middle Eocene Freshwater Fishes from British Columbia

Abstract

The Middle Eocene freshwater fish fauna of British Columbia includes scales described as *Amiidae* gen. et sp. indet., and large samples of the hiodontid *Eohiodon rosei* from the Kamloops and Horsefly areas. The new salmonid *Eosalmo driftwoodensis* is morphologically intermediate between Recent Thymallinae and Salmoninae. The catostomid *Amyzon brevippine* from the Princeton area is redescribed, and *Amyzon aggregatum* sp. nov. is described from the Horsefly area. The percopsid *Libotoniuss blakeburnensis* gen. et sp. nov. is described from the Princeton area, and the priscacarid *Priscacara aquilonia* sp. nov. is described from the Horsefly area.

The fauna includes the most northerly Eocene percopsid and priscacarid, the oldest known hiodontid and salmonid, and some of the oldest known catostomids. The fauna is dominated by the genus *Amyzon* and shows similarities at the generic and family levels to the Green River Eocene fauna of Wyoming and to other Eocene and Oligocene faunas in North America.

Introduction

Knowledge of the North American Eocene freshwater fish fauna has been based almost entirely on the Green River fauna of Wyoming. The contemporaneous British Columbia fauna provides a new and different perspective because of its more northerly location, and because of the unusually large geographical area involved.

New specimens collected by the author during four field seasons form the basis for this study of the Eocene freshwater fishes of British Columbia. These new collections were obtained at 14 localities in six sedimentary basins, each representing the deposits of an ancient lake or river system, from which previously only three or four taxa in three families were known. Small parts of the fauna were described by Cope (1893), Lambe (1906), Hussakof (1916), and Cavender (1966). The fish-bearing sediments have also yielded other fossils including a prolific insect fauna which has been summarized by Wilson (1977b). Additional information on many of the taxa described here may be found in Wilson (1974).

Fossil fish are now known from about 20 localities in southcentral British Columbia, representing six areas of deposition referred to in this paper as the Princeton, Tulameen, Quilchena, Kamloops, Horsefly, and Driftwood Creek areas (Fig. 1). Precise locality information is unavailable for early collections, but the new Royal



Fig. 1 Map of the Eocene freshwater fish localities in British Columbia.

Ontario Museum and University of Alberta collections obtained by the author were probably recovered from many of the same localities. Exact information about Royal Ontario Museum localities (abbreviated by number as L86, L91, etc.) is on file in the Vertebrate Palaeontology Department of the museum. The localities and the numbers of specimens from each are summarized in Table 1.

Geology

Tertiary stratified rocks have been known in the interior of British Columbia since Bauerman (1885) reported shaly sandstones from the Kettle River Valley. Early attempts at dating the deposits by plants (Dawson, 1891) and insects (Scudder, 1895) suggested an Oligocene or Early Miocene age. However, Russell (1935) assigned fossil mammal teeth from Princeton sediments to the genus *Trogosus* Marsh, which is unknown from deposits younger than Middle Eocene. This date was confirmed by Gazin (1953) in his revision of the Tillodontia, and has since been corroborated by K-Ar dating of volcanics associated with the sediments (Rouse and Mathews, 1961; Mathews, 1964). The K-Ar dates are almost all Middle Eocene, ranging from 45 Ma to about 53 Ma B.P. Such dates have now been obtained from rocks in the Princeton, Tulameen, and Kamloops areas (Hills and Baadsgaard, 1967). Palynological correlation has extended the Middle Eocene determinations to include the sediments in the

Table 1. Summary of British Columbia Eocene fish specimens by locality and collection.

Localities	Fish	Scales	Fish Fragments and Bones
Princeton Area			
ROM L86, Whipsaw Creek	6		X
NMC Whipsaw Creek	10		X
UBC Mount Kennedy	1		
ROM L91, Blue Flame Mine		1	
ROM L92, Vermilion Bluffs		11	X
ROM L90, Opposite Vermilion Bluffs		3	X
ROM L93, Pleasant Valley #4 Mine		24	X
ROM L94, Tulameen Road			X
NMC Pleasant Valley	1	11	X
UBC Pleasant Valley			X
Tulameen Area			
ROM L95, Blakeburn Mine	9	47	X
NMC Collins Gulch			X
Quilchena Area			
NMC Diamond Vale Co. Mine	2	2	
Kamloops Area			
UBC Tranquille River			X
NMC Tranquille River			X
ROM L98, Red Point	5		X
NMC Red Point	4		
NMC South of Kamloops Lake			X
ROM L99, Split Rock	4		X
NMC Split Rock			X
UBC McAbee	9		
ROM McAbee			X
Horsefly Area			
ROM L88, Horsefly Mine upper beds	98	91	X
UA Horsefly Mine upper beds	1		
ROM L87, Horsefly Mine lower beds	42	19	X
NMC Horsefly Mine	26	7	X
UBC Horsefly Mine	11		X
ROM L89, Western Black Creek Road outcrop	4	47	X
ROM L97, Eastern Black Creek Road outcrop		7	X
Driftwood Creek Area			
ROM L96, Driftwood Creek	3	5	X
NMC Driftwood Creek	1		X
UBC Driftwood Creek	1		X
UA Driftwood Creek	2		
Totals	240	275	

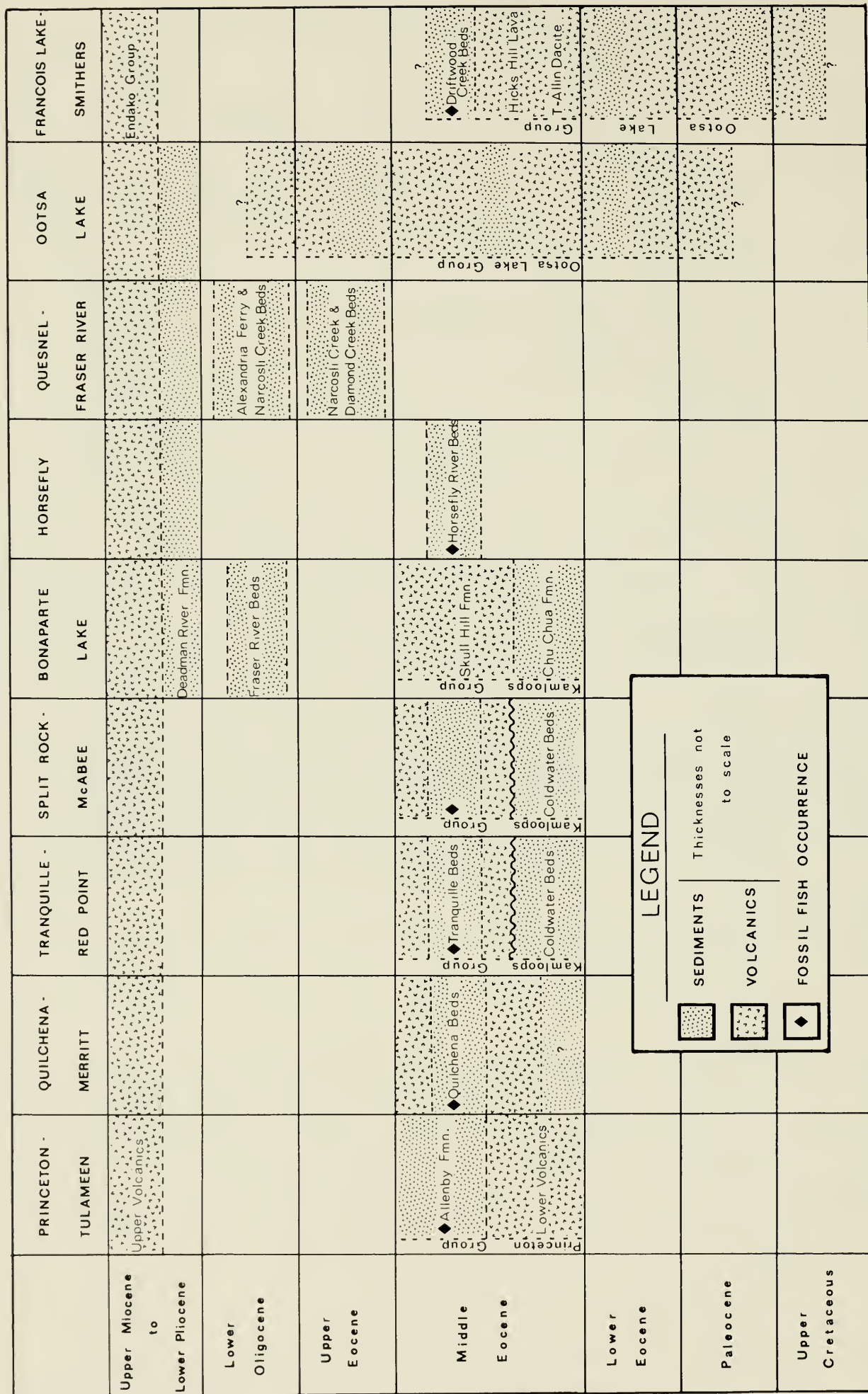


Fig. 2 Correlation chart of Tertiary volcanics and sediments in southcentral British Columbia, showing fish-bearing horizons.

Quilchena, Horsefly, and Driftwood Creek areas (Hills and Baadsgaard, 1967; Rouse, pers. comm.).

The fish-bearing sediments are interbedded in most areas with lavas of highly variable composition (Mathews and Rouse, 1963). The sediments include conglomerates, sandstones, siltstones, platy shales, and paper shales. Varved shales in the Horsefly area are inferred to have been deposited in the hypolimnion of a monomictic or meromictic lake, and the fish in the Horsefly sediments are preserved in the winter laminae (Wilson, 1977a).

The Eocene strata are slightly deformed, with local dips of less than 45°. Slumping is apparent at many outcrops and there are small folds in fish-bearing horizons in the Horsefly area and faults in the fish- and coal-bearing strata of the Tulameen area.

Although the sediments from the different basins are approximately contemporaneous, nomenclature varies greatly (Fig. 2). The Tertiary volcanics and sediments are known as the Princeton Group in the Princeton map-area (Rice, 1947), and the sedimentary member is called the Allenby Formation (Shaw, 1952). In the Nicola and Ashcroft map-areas the sequence is called the Kamloops Group, and the sediments are known as the Tranquille beds (Cockfield, 1948; Duffell and McTaggart, 1952). The sediments and volcanics in the Horsefly area are unnamed (Campbell, 1961), while the sediments at Driftwood Creek are included in the Ootsa Lake Group (Rice, 1949; Duffell, 1959).

Methods

The morphometric and meristic variables reported for the fish follow the conventions in Hubbs and Lagler (1947). Scale terminology follows Lagler (1947) and Chu (1935).

The following is a list of the museum abbreviations used in this paper: American Museum of Natural History, Department of Vertebrate Paleontology (AMNH); National Museums of Canada, Museum of Natural Sciences, Vertebrate Palaeontology Division (NMC); Royal Ontario Museum, Vertebrate Palaeontology Department (ROM); University of Alberta, Department of Geology, Vertebrate Paleontology Collections (UA); University of British Columbia (UBC); University of Michigan, Museum of Paleontology (UMMP); United States National Museum of Natural History, Department of Paleobiology (USNM).

Abbreviations Used in the Figures

Most bones have been named according to Norden (1961). Two exceptions are the caudal skeleton, where the terminology of Monod (1968) has been used, with the term uroneural instead of urodermal following the practice recommended by Patterson (1968a); and the infraorbital series, where the terminology of Nelson (1969) has been followed. The abbreviations are given in the following list:

a	angular (articular)	p	parasphenoid
ao	antorbital	pa	parietal
ap	anteriormost procurrent caudal rays	pal	palatine
br	branchiostegal ray	pcl	postcleithrum
ch	ceratohyal	pefr	pectoral fin ray
cl	cleithrum	pf	prefrontal (lateral ethmoid)
d	dentary	pfr	pelvic fin ray
ds	dermosphenotic	ph	parhypural
e	epural	pm	premaxilla
end	endopterygoid	pop	preopercular
f	frontal	pt	posttemporal
h	hypural	pu	preural centrum
hs	haemal spine	pv	pelvic bone
hy	hyomandibular	q	quadrate
io	infraorbital (suborbital)	scl	supracleithrum
iop	interopercular	soc	supraoccipital
la	lachrymal	sop	subopercular
m	maxilla	st	stegural
mc	midline of caudal fin	suo	supraorbital
met	metapterygoid	sy	symplectic
n	nasal	un	uroneural
ns	neural spine	ur	ural centrum
op	opercular	v	vomer

Systematic Section

Class Osteichthyes
Infraclass Holostei
Order Amiiformes

Family Amiidae **Fig. 3**

Material

NMC 2079, 2082, and 2085 from Horsefly Mine, collected by Lambe in 1906; ROM 11366 through 11378, 11381, 11388, 11391, 11399, 11400, 11404, 11410, and 11423 from Blakeburn Mine L95, collected by the author in 1970 and 1971; NMC 2043, 2051, and 2068 from Pleasant Valley, collected by Lambe in 1906; ROM 11425, 11427, 11436, 11439, 11444, and 11448 from Pleasant Valley L90 and L93, collected by the author in 1970 and 1971; ROM 11455, from Driftwood Creek L96, collected by the author in 1970; and other fragmentary specimens in NMC collections.

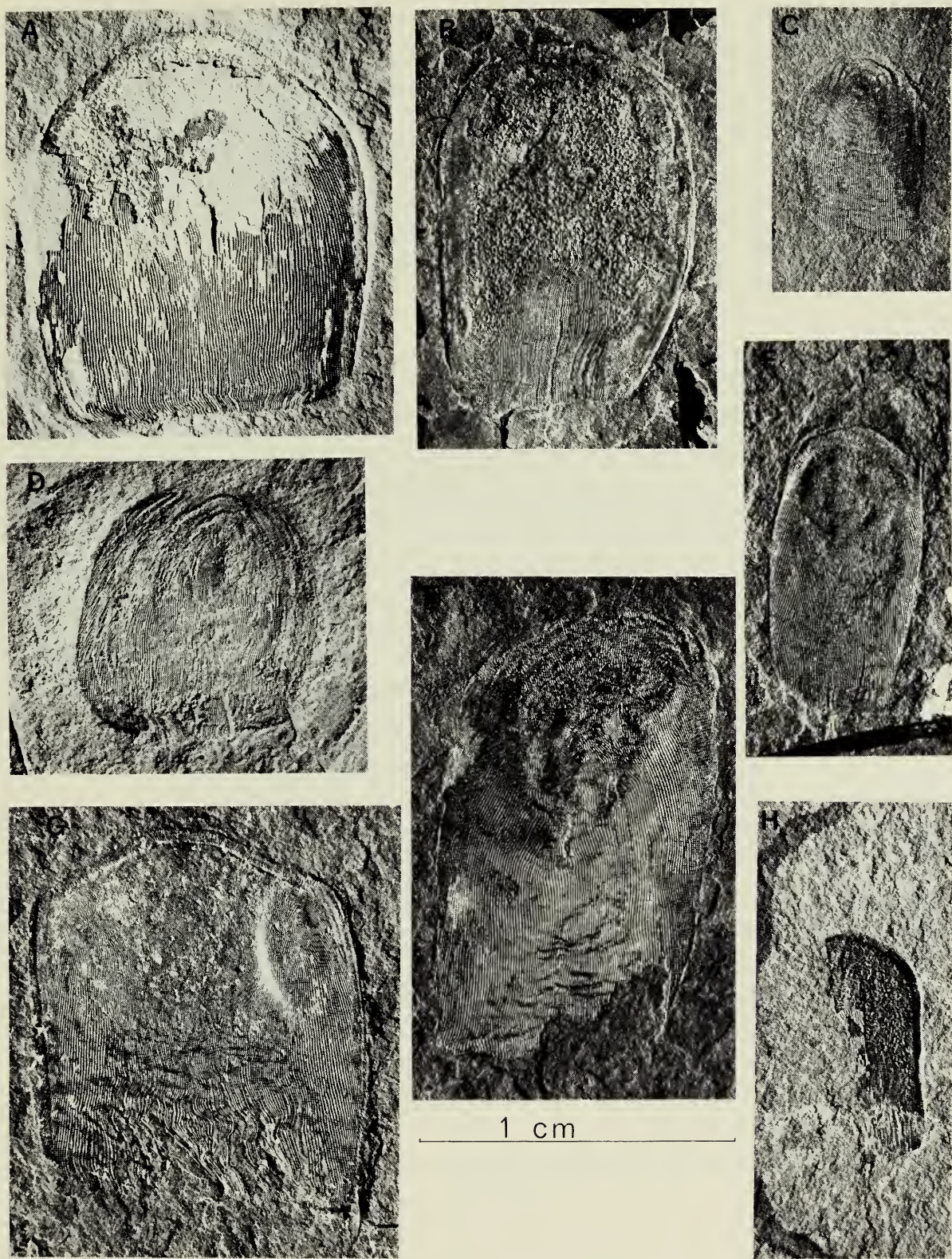


Fig. 3 Amiidae gen. et sp. indet., scales, apical end oriented toward top of page.

- A. ROM 11448 from Pleasant Valley L93.
- B. ROM 11436 from Pleasant Valley L93.
- C. NMC 2068 from Pleasant Valley.
- D. ROM 11427 from Pleasant Valley L93.
- E. ROM 11366 from Blakeburn Mine L95.
- F. ROM 11391 from Blakeburn Mine L95.
- G. ROM 11399 from Blakeburn Mine L95.
- H. ROM 11455 from Driftwood Creek L96.

Remarks

The British Columbia fossil amiid scales are similar to those of the Recent *Amia calva* and to amiid scales from the Clarno Formation of Oregon (Cavender, 1968). The scales lack radii, but strong ridges (circuli) radiate to the margins of the scale from the focus. The focus is a transverse area near the apical margin of the scale. Most specimens are longer than wide. The apicolateral corners are weak, and the apical margin is convex in every specimen. Laterobasal corners are strong and the basal margin is straight.

Infraclass Teleostei

Superorder Osteoglossomorpha

Family Hiodontidae

Eohiodon Cavender, 1966

Emended Diagnosis

Eocene Hiodontidae with body depth to standard length ratio 0.19 to 0.37, head length to standard length ratio 0.17 to 0.33, anal fin base length to standard length ratio 0.13 to 0.20; length of dorsal base into length of anal base about 1.3; dorsal origin in advance of anal origin by at least two vertebrae; vertebrae about 22 + 24 (total 44–49); D 11–13; A 14–18; P 10–13; V 6–10; C i,8,7–8,i.

Type Species

Leuciscus rosei Hussakof.

Remarks

The genus was originally defined on the basis of a few type specimens collected by Rose in 1912; Lambe had collected *Eohiodon* material from Kamloops Lake in 1906, but these specimens were catalogued in NMC collections as *Amyzon* sp. The above diagnosis is based on 56 specimens from the Kamloops Lake and Horsefly areas, including the types and Lambe's collection. Despite the increase in the known variation of the genus, essential differences noted by Cavender (1966) between *Eohiodon* and *Hiodon* are confirmed, especially in numbers of precaudal vertebrae and anal fin rays. *Hiodon* has a relatively longer trunk and anal fin than *Eohiodon*.

Eohiodon rosei (Hussakof)

Fig. 4

Leuciscus rosei Hussakof, 1916, pp. 18–20, fig. 1.

Eohiodon rosei (Hussakof), Cavender, 1966, pp. 311–320, figs. 1, 2, 4, 5A.

Diagnosis

Same as that for the genus.

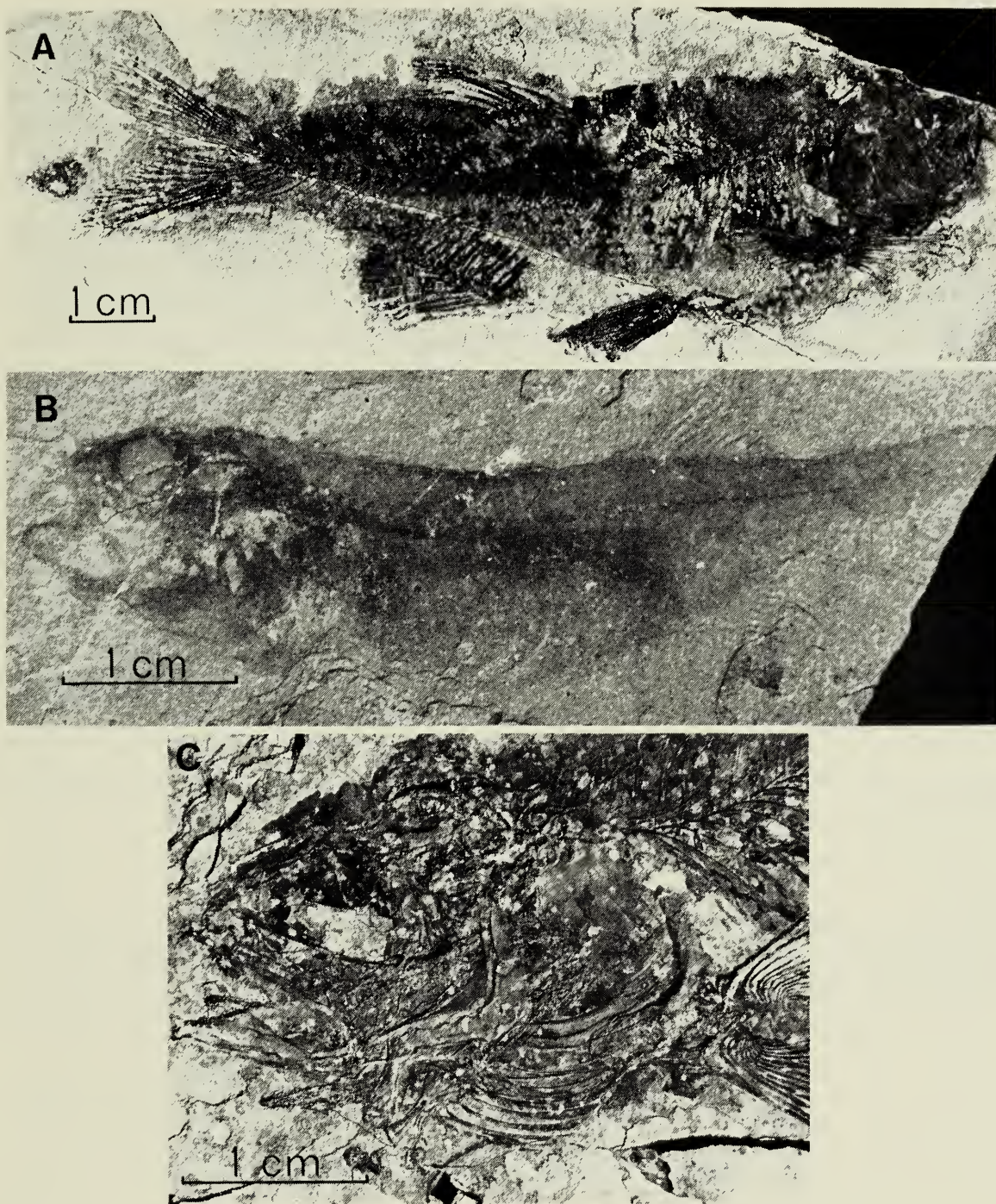


Fig. 4 *Eohiodon rosei* (Hussakof).

- A. ROM 11138, probable adult male, from Horsefly Mine L87.
- B. ROM 19412, probable juvenile, from McAbee.
- C. ROM 11141, skull, from Horsefly Mine L87.

Type Specimens

Holotype NMC 2156 A and B, a complete fish in part and counterpart; paratypes AMNH 8059 and 8059 A, a postcranial skeleton and a head not representing the same individual. The locality is Red Point, on the north shore of Kamloops Lake, British Columbia.

Material

NMC 2100, 2101, and 2102 from near Red Point; ROM 11151 through 11155 from Red

Point L98; ROM 11147 through 11150 from Split Rock L99; ROM 19404, 19405, 19408 through 19412, 19418, and 19419 from the McAbee locality; ROM 11099 through 11107, 11109, 11111 through 11119, 11121 through 11124, 11127, 11128, 11132, 11134, 11137 through 11141, and 11493 from Horsefly Mine L87.

Emended Description

The type specimens have previously been described (Cavender, 1966). Therefore, features not seen before and observations on variability made possible by the larger collections are emphasized here. Summary statistics for the species are presented in Table 2.

GENERAL FEATURES

All known specimens are preserved as articulated skeletons. The known standard lengths range from 38 to about 143 mm, and there is much variation in relative body depth. The fish is laterally compressed (all specimens are preserved in lateral view). Like the Recent genus *Hiodon*, the fish is relatively deep-bodied at the dorsal and anal fin origins, but tapers abruptly to a shallow caudal peduncle. Specimens over 50 mm standard length are divided almost equally between those with expanded anal rays (Fig. 4A) and those without, indicating approximately equal numbers of mature males and females respectively. Five specimens with standard lengths less than 50 mm (Fig. 4B) lack a modified anal fin. Recent *Hiodon* species mature at about 250 mm standard length (Cavender, 1966). No relationship between sex and relative body depth has been found.

SKULL

The posterior half of the skull roof is smooth because of the presence of expanded extrascapulars. The parietals appear to be separated at least posteriorly by the supraoccipital as in *Hiodon*; they are concave posterolaterally, indicating the presence of

Table 2. Summary univariate statistics for *Eohiodon rosei* from the Kamloops and Horsefly areas.

Variable	n	Mean ± S.E.
1. Number of dorsal fin principal rays	36	12.1 ± 0.133
2. Number of anal fin principal rays	31	15.8 ± 0.172
3. Number of pectoral fin rays	33	11.7 ± 0.159
4. Number of pelvic fin rays	18	8.22 ± 0.308
5. Number of vertebrae including ural vertebrae	16	45.3 ± 0.416
6. Ratio of body depth to standard length	13	0.255 ± 0.0114
7. Ratio of caudal peduncle depth to standard length	19	0.0864 ± 0.00284
8. Ratio of predorsal length to standard length	20	0.583 ± 0.00418
9. Ratio of preanal length to standard length	21	0.693 ± 0.00535
10. Ratio of head length to standard length	16	0.270 ± 0.00481
11. Ratio of upper jaw length to standard length	13	0.109 ± 0.00386
12. Ratio of mandible length to standard length	14	0.118 ± 0.00336
13. Ratio of dorsal fin base length to standard length	17	0.132 ± 0.00270
14. Ratio of anal fin base length to standard length	18	0.169 ± 0.00384

a lateral cranial fenestra ("tract of cartilage": Ridewood, 1904) in the position of a lateral temporal or preepiotic fossa (ROM 11141). The frontals resemble their counterparts in *Hiodon* in shape (notched anteriorly) and length, beginning in front of the orbit and ending near the posterior margin of the orbit. The pattern of sensory canal branches on the frontal is essentially the same as in the Recent genus. The pterotic forms a prominent horizontal ridge on the side of the skull as in *Hiodon*. The supraethmoid (mesethmoid), prefrontal (lateral ethmoid), and thin tubular nasals are present.

Narrow canal-bearing infraorbitals resembling those in *Hiodon* are visible in ROM 11152, but the exact number cannot be determined. Broad posterior infraorbitals are visible on many specimens, but the dermosphenotic has not been seen. The hyopalatine bones are very similar to their counterparts in *Hiodon*. In addition to the two hyomandibular processes articulating with the cranium, there is a broad anterior flange of bone and a long process posteriorly ending in the opercular condyle, as in *Hiodon*. Weak teeth are visible on the palatine, ectopterygoid, and endopterygoid of many specimens.

The premaxilla is apparently tapered both anteriorly and posteriorly. The maxilla (Fig. 4C) is toothed along the middle third of its concave ventral margin. The anterior third is pointed and curved; the posterior third is broad. Length of upper jaw into head length is about 2.4 (compared with an average of about 2.3 for *H. tergisus*). The dentaries are proportionally deeper than in *Hiodon*. Mandible length: head length ratio is about 2.3; mandible depth into mandible length is about 2.5.

Strong teeth fringe the glossohyal plate, with smaller teeth covering the rest of the surface of the glossohyal. Branchiostegals are difficult to count on all specimens but at least seven are present, the last one or two spathiform as in *Hiodon* (McAllister, 1968).

The horizontal arm of the preopercular is almost as long as the vertical arm (Fig. 4C). The preopercular sensory canal gives off four branches along the horizontal arm, and is one-third to half the width of the bone away from the anterior edge at the angle. The subopercular is similar in shape to that of *Hiodon*, but is not as deep.

APPENDICULAR SKELETON

The posttemporal, supracleithrum, cleithrum, and coracoid resemble those of *Hiodon*. The pectoral fin consists of 10 to 13 rays and extends beyond the anterior ends of the pelvic bones but not as far as the pelvic origin. The pelvic bones are thin and pointed anteriorly as in *Hiodon*. There are six to 10 pelvic rays which extend about three-quarters the distance to the anal origin.

VERTEBRAL COLUMN AND MEDIAN FINS

There are 44 to 49 vertebrae (including upturned vertebrae) of which about 22 are precaudal and 24 caudal. Of the former, about 18 are anterior to the dorsal fin origin, and about four are between the dorsal fin origin and the first caudal vertebra. The trunk vertebrae bear prominent ventrally directed parapophyses, and the ribs are sessile (inserted above and behind the parapophyses). The neural arches of the trunk vertebrae are expanded anteroposteriorly as in *Hiodon*, and bear paired neural spines. Epineurals and S-shaped supraneurals are present. All trunk vertebrae and most caudal vertebrae have a prominent midlateral ridge bounded above and below by a fossa. In the caudal series each centrum has two additional horizontal ridges above

and below the midlateral ridge. Prezygapophyses are apparent on the caudal vertebrae.

The dorsal fin originates between the pelvic and anal fin origins. It contains several rudimentary rays followed by one full-length unbranched ray and 10–12 branched rays, the last one double. The dorsal margin of the fin is straight, and the overall shape is triangular. The fin is supported by 13 to 16 long, narrow pterygiophores of which the second or third is usually the longest and the first is slightly expanded anteriorly.

The anal fin contains several rudimentary rays followed by one full-length unbranched and 13 to 17 branched rays, the last one double. The fin is supported by 16 to 19 pterygiophores, the first two of which support rudimentary rays and are apparently inserted anterior to the first haemal spine. In 20 of 37 specimens with estimated or measured standard lengths greater than 50 mm the first eight to 10 principal anal rays are longer and much thicker throughout their length than the rest, giving the fin a convex ventral margin. In specimens without a modified anal fin the ventral margin of the fin is slightly concave.

The usual condition of the caudal skeleton consists of three upturned vertebrae (two ural and one preural), seven hypurals, three uroneurals, one epural, and 16 branched rays. The neural spine of preural centrum 1 is short, that of preural centrum 2 full-length. The parhypural articulates but is not fused with preural centrum 1 (cf. Monod, 1968, figs. 108 *bis* and *ter*; Patterson, 1968a, text-fig. 11; Gosline, 1960, fig. 4: all figures of *Hiodon* showing the parhypural fused with preural centrum 1). The largest hypural is usually the first, and in several specimens it is pierced by a longitudinal foramen. The anteriormost vertebra articulating with procurent caudal rays varies from preural 3 to preural 5 both above and below.

A single specimen (ROM 11122) has the second hypural deeper than the first. ROM 11147 has a very short haemal spine on preural centrum 4; ROM 11141 on one side has double neural and haemal spines on preural centrum 4, while on the other side the centrum is divided by a transverse ridge, giving the impression of two short centra. The single epural varies in position, from close and parallel to the neural spine of preural centrum 2, where it resembles a continuation of the neural spine of preural centrum 1; to close to the upward curving uroneurals, where it resembles an additional uroneural. The seventh hypural is very small and appears to be absent in many specimens. The first two hypurals are apparently fused distally in at least two specimens, as in a ROM specimen of *H. tergisus* (ROM Ichthyology 30231). The observed variation in number of uroneurals is also paralleled in *Hiodon*. Specimens of *H. alosoides* have been reported with as many as four uroneurals (Patterson, 1968a), and the ROM *H. tergisus* specimen referred to above has two uroneurals on one side, and one on the other. The third uroneural is forked proximally in some *Hiodon* specimens (Patterson, 1968a; Monod, 1968, fig. 108 *ter*). Most *E. rosei* specimens have an unforked third uroneural. Two specimens have the third uroneural forked as in the *H. alosoides* figured by Patterson; a third has the extreme proximal tip of the third uroneural bifid. Most specimens have eight branched rays in the dorsal and ventral portions of the caudal fin, but about one-quarter have only seven branched rays in the ventral half, as in one of the two *H. tergisus* figured by Monod (1968).

LATERAL LINE AND PIGMENTATION

The lateral line is complete, extending onto the caudal peduncle as far as the posterior

margin of the hypural complex. Chromatophores are carried on the exposed portion of many scales, and are visible on many specimens along the dorsal body margin and on some dorsal skull bones. One small specimen (Fig. 4B) preserved as a dark film has chromatophores over most of the trunk and skull, as well as along the dorsal margin. A second longitudinal band of pigment follows the lateral line back to the caudal peduncle.

Eohiodon sp.

Fig. 5

Material

Fish ROM 11026 and 11062, scale ROM 11258, and a scale preserved near ROM 11080, all from Horsefly Mine L88; ROM 11452, two overlapping scales from Horsefly Mine L87; fish ROM 11494 from Pleasant Valley L94, and NMC IN-9 from Pleasant Valley.

Remarks

The two large fish specimens from L88 differ from the *E. rosei* samples in many ways, but most of the differences are exaggerated by severe distortion. ROM 11026 (Fig. 5B) appears considerably deepened and shortened during preservation, and significant differences are mostly associated with body depth. Counts for this specimen are: D 14; A 17; C i,8,8,i; dorsal pterygiophores 14; anal pterygiophores 17; caudal vertebrae about 24; hypurals seven; ural vertebrae two; uroneurals about three. Standard length is about 134 mm. Measurements as a proportion of standard length are body depth 0.51, anal fin base length 0.21. Anal base length is $1.31 \times$ the dorsal base length. Dorsal origin is in advance of anal origin. Anterior anal rays are not expanded. Mandible, maxilla, and premaxilla are typical of *Eohiodon*. This specimen can be included in *Eohiodon* on the basis of counts, but a final assignment to species requires study of additional undistorted specimens from the same locality.

ROM 11062 (Fig. 5A) is considerably elongated during preservation. The scales resemble those of *E. rosei*, including the presence of chromatophores along the dorsal body margin. The preopercular, opercular, glossohyal, dentary, maxillary, premaxillary, parasphenoid, and overlapping extrascapular are all visible, providing proof of the hiodontid relationships. There are seven hypurals, 17 branched caudal rays, and about 14 anal rays. Since the caudal ray formula (i,9,8,i) is unlike that of any specimen of *E. rosei*, and since the specimen is distorted, an assignment to species is premature.

Scales ROM 11258 and ROM 11080 from L88 are indistinguishable from scales described above as *E. rosei* and from hiodontid scales from Ochoco Pass Oregon (Cavender, 1968). Since there is little variability in the scales of the Hiodontidae, these specimens provide no clues to the relationships of the two L88 fish specimens discussed above. The exposed portion (apical field) of ROM 11080 is covered by a patch of chromatophores. The chromatophores also extend beyond the apical margin of the scale, where they are smaller and more closely spaced than on the scale itself. This indicates that the chromatophores are associated with a layer superficial to the scale proper, but firmly attached to it. Two large hiodontid scales (Fig. 5C) are also known from L87.

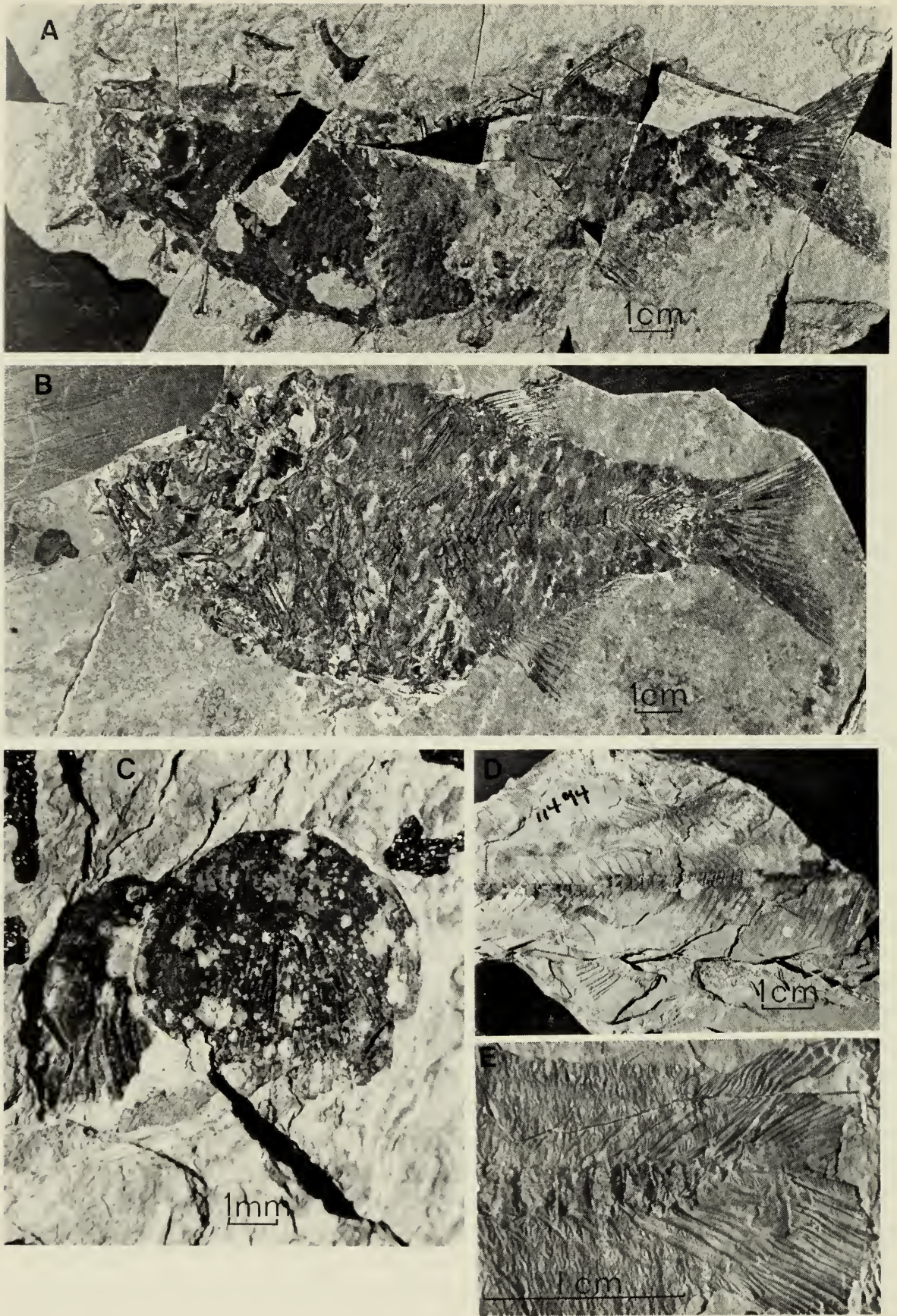


Fig. 5 *Eohiodon* sp.

- A. ROM 11062 from Horsefly Mine L88.
- B. ROM 11026 from Horsefly Mine L88.
- C. ROM 11452, two overlapping scales, from Horsefly Mine L87.
- D. ROM 11494, part of the trunk and caudal peduncle, from Pleasant Valley L94.
- E. NMC IN-9, caudal skeleton, from Pleasant Valley.

The two hiodontid specimens from the Pleasant Valley area near Princeton are fragmentary. ROM 11494 (Fig. 5D) is assigned to the Hiodontidae on the basis of the transversely ridged centra, knob-shaped neural arches in the trunk region, epineurals present in the trunk region, two displaced maxillae, and faint impressions of scales which show numerous basally directed radii. A tentative assignment to *Eohiodon* is based on the apparently short anal fin and the dorsal origin well in advance of the anal origin. NMC IN-9 (Fig. 5E) consists of a caudal peduncle, caudal skeleton, and fin. There are 16 branched rays, seven hypurals, two ural centra, and about three uroneurals, as in other hiodontids. A tentative assignment to *Eohiodon* is based on the length of the caudal peduncle (length of caudal peduncle to depth of caudal peduncle ratio greater than 1.8) which indicates that a short anal fin was present.

Discussion

The Eocene genus *Eohiodon* is remarkably similar to *Hiodon* in the details of its osteology, and can only be distinguished by anal fin and trunk vertebral counts, a few related body proportions, and size at maturity. The caudal skeleton of *E. rosei* is no more primitive than that of the Recent genus. Most of the observed variations are paralleled and even exceeded in the two Recent species of *Hiodon* (for example, number of uroneurals and branched caudal rays). There is no convincing evidence that *E. rosei* is not a direct ancestor of the Recent hiodontids.

Fossil hiodontids are now known from eight localities in three areas of British Columbia, all Middle Eocene. They are also known from the Eocene to Lower Oligocene Clarno Formation of Oregon and the Oligocene Grant shales of Montana (Cavender, 1968).

Superorder Protacanthopterygii

Family Salmonidae

Eosalmo, gen. nov.

Type and Only Species

Eosalmo driftwoodensis, gen. et sp. nov.

Diagnosis

Eocene Salmonidae with ascending process of premaxilla in middle of bone; large teeth on palatine, premaxilla, maxilla, and dentary; jaw articulation behind middle of orbit; postorbitals almost reaching preopercular; moderately low coronoid process on dentary; preopercular arms at right angles; posteroventral angle of interopercular very acute; frontals long, triangular, tapered anteriorly; parietals not separated by supraoccipital; large median extrascapular present; stegural with large fan-shaped process; caudal fin moderately forked; D 14–15 (total); A 13–15 (total); P 14–16; V 11; C i,9,8,i; vertebrae 52–57 (32–33 + 20–24); scales small, circuli very faint, radii absent, apicolateral corners well developed.

Eosalmo driftwoodensis, gen. et sp. nov.

Figs. 6A, 7

Diagnosis

Same as that for the genus.

Holotype

ROM 11178 A and B (Fig. 16A), an almost complete fish in part and counterpart with standard length of 307 mm, collected by the author in 1971.

Topotypes

ROM 11172 through 11176, collected by the author in 1970 and 1971; NMC 21100, a caudal peduncle, collected by E. J. Lees in 1936; and UA 12326 and 12327, collected by the author in 1975. The most complete specimens other than the holotype are ROM 11172 and 11174, and UA 12326 and 12327.

Type Locality

The Middle Eocene Driftwood Creek fossil beds (L96), a few miles east of Smithers, British Columbia.

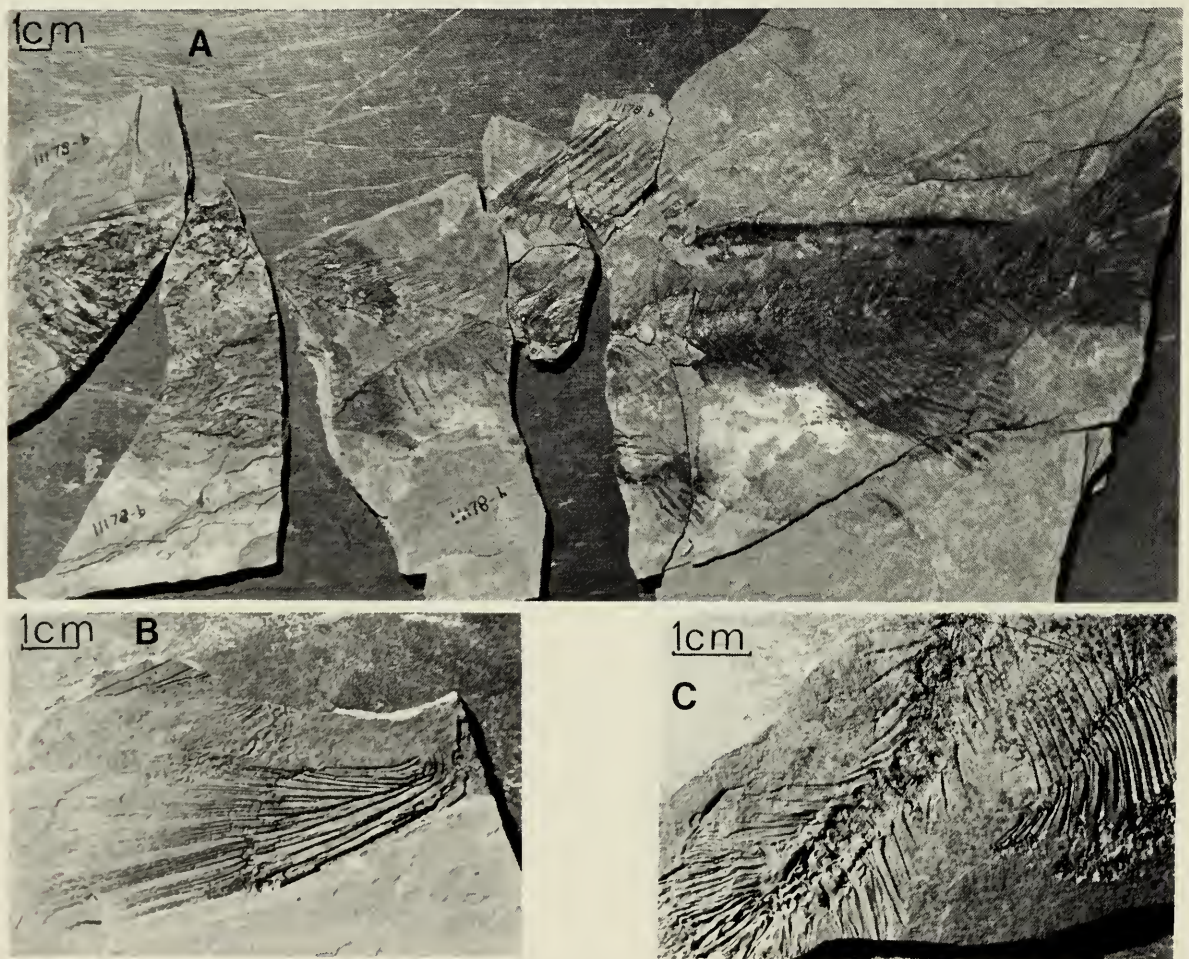


Fig. 6 *Eosalmo* gen. nov.

A *Eosalmo driftwoodensis* gen. et sp. nov., ROM 11178 (holotype), from Driftwood Creek L96.

B. *Eosalmo* cf. *E. driftwoodensis*, NMC 4571, pelvic fin, from Pleasant Valley.

C. *Eosalmo* cf. *E. driftwoodensis*, NMC J-45, caudal peduncle, from Pleasant Valley.

Description

GENERAL FEATURES

No specimen is completely preserved, although the holotype is almost so. Fragmentary specimens represent individuals of approximately the same size as the holotype, which is about 307 mm in standard length. The fish is similar in shape to Recent salmonids except that it appears shorter and stouter. Body depth and head length to standard length ratios are each 0.25 in the holotype. The mouth is of moderate size, and the fins are positioned as in recent genera. All specimens are preserved in lateral view, indicating that the fish was laterally compressed in life.

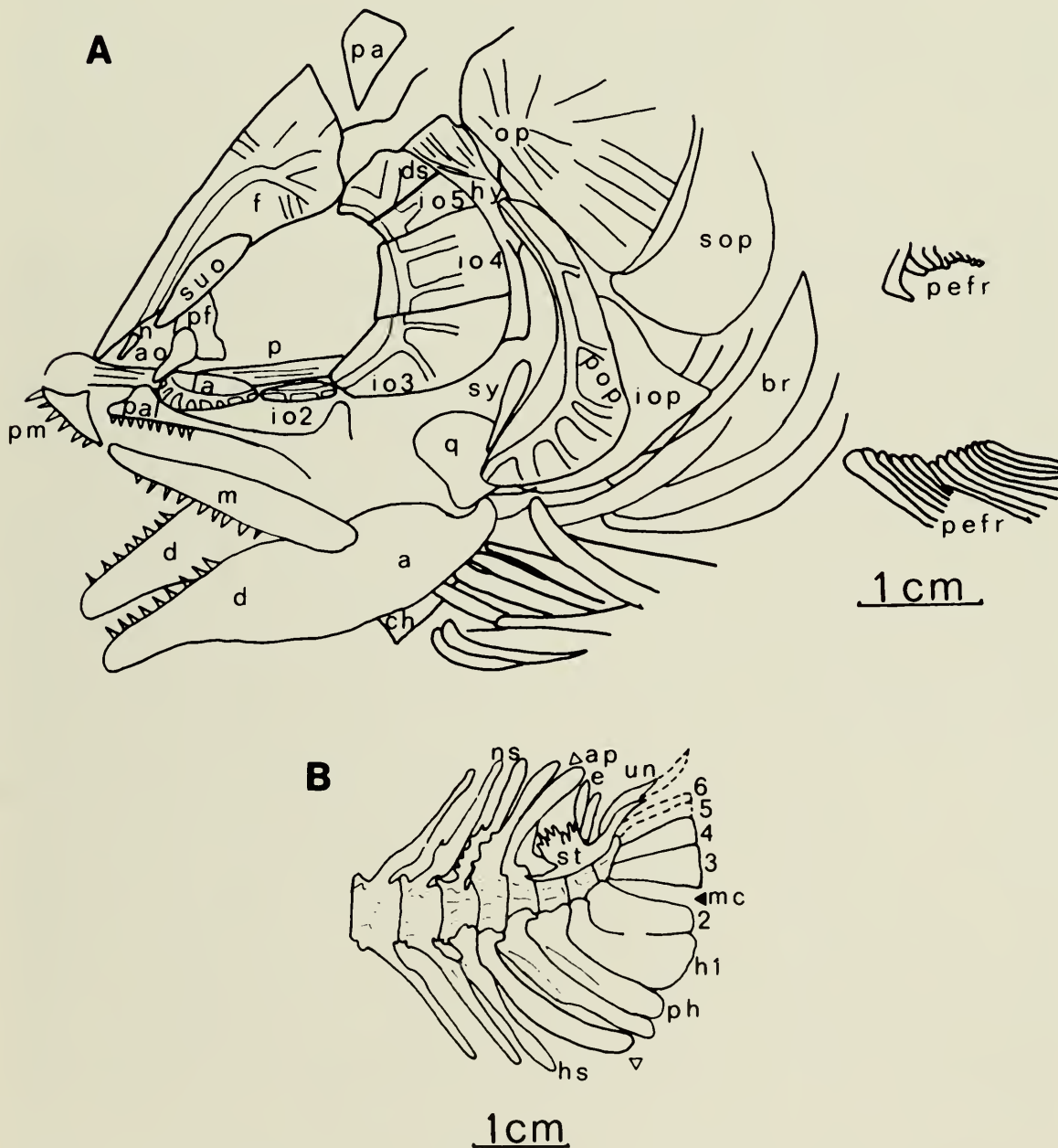


Fig. 7 *Eosalmo driftwoodensis* gen. et sp. nov., from Driftwood Creek L96. For abbreviations see p.6.
 A. Skull of a well-preserved but uncatalogued specimen in the Smithers, B. C. Tourist Bureau.
 B. ROM 11178 (holotype), caudal skeleton.

SKULL

The skull roof resembles that of *Thymallus* in general features. The supraoccipital is approximately rectangular in outline and convex dorsally, but apparently does not separate the parietals at the midline. The parietals (Fig. 7A) border a large lateral temporal fossa. On the holotype a large thin bone, apparently bilaterally symmetrical and over twice as wide as long, is situated at the rear of the skull roof. Along its anterior margin it bears a canal which appears to branch on either side of the midline. The bone resembles the large median extrascapular of *Thymallus* (Norden, 1961). In *Coregonus reighardi*, Cavendar (1970) does not show a median extrascapular but does show a single paired extrascapular with a branching canal.

The frontals (Fig. 7A) are triangular with internal angles of 30° anteriorly, 60° posteriorly, and 90° laterally. As with the parietals, there is no indication that they are separated posteriorly by the supraoccipital. Anteriorly they are not separated by cartilage, unlike the frontals of most other salmonids. The prominent supraorbital sensory canal runs in a bony tube from the lateral corner about halfway to the midline, then bends anteriorly and parallels the midline of the skull. A short posterior branch of the canal is visible in some specimens. About six pores can be counted along the anterior branch of the canal, which meets the margin of the frontal lateral to the pointed anterior end of the bone. Tubular nasals (Fig. 7A) lie lateral to the anterior ends of the frontals.

In the ethmoid region paired prefrontals and a median hypethmoid have not definitely been seen. The median supraethmoid is short, approximately triangular, and notched posteriorly, resembling the supraethmoids of *Thymallus*, and some species of *Coregonus* and *Salmo* (Norden, 1961; Valdykov, 1963).

There are several large and approximately circular endocranial ossifications in the region of the orbit. These probably represent well-ossified orbitosphenoid and pterosphenoid bones. The parasphenoid (Fig. 7A) is stout and longitudinally grooved.

The circumorbital series consists of eight bones, including a single supraorbital, an antorbital, a lachrymal, four suborbitals, and a dermosphenotic. The supraorbital is narrow and elongate, and is contained in a shallow emargination of the lateral edge of the frontal. The antorbital is shaped like a curved teardrop: broader and thicker posteriorly, pointed anteriorly, and with a concave dorsal margin. The lachrymal (Fig. 7A) resembles that of various salmonids such as *Brachymystax*, *Salmo* (Nelson, 1969), and *Thymallus* (Norden, 1961) in that the suborbital sensory canal curves around the bone near the anteroventral margin, giving off about six short branches. The lachrymal is tapered posteriorly where it receives the canal from a narrow second infraorbital. This infraorbital is slightly broader at its posterior end than at its anterior end, and bears two small ventrally directed canal branches in addition to the main canal running through the middle of the bone. Infraorbital 3 is distinctively shaped with a pointed anterior end, a squared posterior end, and a curved canal giving off two short branches posteroventrally; a single small branch anterodorsally between these two branches appear in one of the two specimens. The broad infraorbitals 4 and 5 reach almost to the preopercular, exposing only a small part of the hyomandibular beneath. The sensory canal runs close to the orbital margin of these bones, as in salmonines but not in coregonines and thymallines. Dorsal to the postorbitals the sensory canal branches within a bone interpreted as a dermosphenotic.

The hyomandibular (Fig. 7A) resembles that of *Thymallus* (Norden, 1961) in the presence of a large triangular anterodorsal thickened portion and a short opercular

arm, connected by a thin sheet of bone. The ventral ramus curves anteriorly and is connected to the anterodorsal condyle by a broad thin web of bone. The rod-like symplectic is pointed anteriorly and slightly thickened posteriorly. It apparently just fails to contact the ventral end of the hyomandibular. Anteriorly it fits into a notch in the triangular quadrate. The ectopterygoid is narrow and slightly concave ventrally. Anteriorly it joins the palatine which bears teeth along most of its length. Dorsally the palatine bears a rounded process as in Recent salmonids.

The premaxilla (Fig. 7A) is triangular with a well-developed ascending process located in the middle of the dorsal surface of the bone. The oral margin bears about eight long, slightly curved teeth. The maxilla also bears strong teeth along most of its ventral margin, and anteriorly it forms a knob-shaped process. The straight (not sickle-shaped) posterior portion is not as deep as in *Thymallus* (Norden, 1961) but is deeper than in most salmonines, and reaches to about the midline of the orbit. The length of the upper jaw is 0.098 of the standard length in the holotype.

The dentary and angular each forms about half of the mandible (Fig. 7A). The oral margin of the dentary bears strong teeth and rises gradually to a low coronoid process. The longer lower limb contains the mandibular canal in a bony tube. The mandible articulates with the quadrate ventral to the posterior quarter of the orbit, and the length of the mandible is about half that of the head.

The imperforate ceratohyal and epihyal are similarly shaped to those of *Thymallus arcticus* (Norden, 1961) and *Salmothymus ohridans* (Cavender, 1970). A toothed lingual plate (glossohyal) has not been seen, although it is probably present. There are about 10 pairs of branchiostegals, with three on the epihyal and seven on the ceratohyal. All branchiostegals are curved and spathiform, although the anterior ones are considerably narrower than the posterior ones. The posteriormost branchiostegals are broadened at their anterior ends and have clupeoid projections (McAllister, 1968) in that they are almost rectangular anteriorly.

The horizontal and vertical arms of the preopercular meet at approximately right angles, the horizontal arm being about half the length of the vertical, which is concave anteriorly (Fig. 7A). As in salmonines the preopercular is slightly rotated compared with *Thymallus* so that the vertical arm is inclined forward and the horizontal arm points anteroventrally. The preopercular sensory canal descends the anterior margin of the vertical arm, bends forward at the angle, and then curves ventrally to meet the ventral edge of the bone just behind the anterior tip. The canal gives off three to four branches along the horizontal arm and two branches near the ventral end of the vertical arm; all branches are markedly curved posterodorsally.

The opercular (Fig. 7A) is also rotated and situated higher on the skull compared with *Thymallus*, and the anteroventral corner of the bone forms an internal angle of about 60°. The subopercular is of typical salmonid shape with a prominent dorsally directed anterodorsal process and a deep main body. The interopercular has a convex ventral margin which meets a slightly concave posterior margin in an acute posteroventral corner (Fig. 7A), in marked contrast to the rounded margins of the other opercular bones. The dorsal margin of the interopercular is concave posteriorly and convex anteriorly where it meets the upward-curving ventral margin in a point.

APPENDICULAR SKELETON, VERTEBRAL COLUMN, AND MEDIAN FINS

What little can be seen of the pectoral girdle resembles the condition in Recent salmonids: supracleithrum long and broadened ventrally, cleithrum with long wide

anteroventral portion and short vertical portion, coracoid produced to a point posteriorly, and at least two postcleithra present. The pectoral fin contains about 14–16 rays, a condition similar to that in Recent salmonids. The pelvic fin contains a splint and 11 rays.

There are 52–57 vertebrae consisting of 20–24 caudals and 32–33 precaudals. Of the latter, about 19–20 are between the dorsal fin origin and the first caudal vertebra and about 13 are anterior to the dorsal fin origin. As in Recent salmonids there are supraneurals anterior to the dorsal fin, and the trunk vertebrae have paired neural spines. Epineurals are present on all but the last one or two trunk vertebrae, although the posteriormost epineurals are short and not articulated with any neural arch. Ribs are slender and except for the anteriormost ones do not reach close to the ventral body margin.

The centra are horizontally ridged and pitted as in Recent salmonids. Each caudal vertebra has small pre- and post-zygapophyses dorsally and ventrally. Neural and haemal spines are short and posteriorly directed; they do not approach the body margins and do not overlap the anal pterygiophores.

The dorsal fin (Fig. 7A) originates between the pectoral and pelvic origins. The dorsal margin is rounded, with the longest rays near the middle of the fin. There are 14–15 rays consisting of two or three short procurrent rays, two long unbranched rays, and 9–11 branched rays, the last one double. The fin is supported by about 12–14 slender proximal dorsal pterygiophores, which are expanded anteroposteriorly at their distal ends. A second series of short hourglass-shaped pterygiophores supports the fin ray bases, but the third series (Norden, 1961) could not be distinguished. The dorsal fin base length to standard length ratio is 0.16 in the holotype.

The anal fin, like the dorsal fin, has a slightly rounded margin (Fig. 6A). There are three or four unbranched rays followed by 10–11 branched rays, the last one double, for a total of 13–15 rays. They are supported by 12–13 pterygiophores in at least two series. The proximal pterygiophores are all long and slender, but do not overlap the short haemal spines. The first pterygiophore is not expanded anteriorly but lies very close to the second, and the first three pterygiophores are all inserted between the first and second caudal vertebrae in the holotype. The anal fin base to standard length ratio is 0.13 in the holotype.

In the caudal skeleton, the last few neural and haemal spines are markedly expanded anteroposteriorly (Fig. 7B). The peg-and-socket mechanism (Cavender, 1970) is visible on the haemal spines of preural centra 1 through 4. There are three upturned centra, including two ural centra and one preural centrum. The parhypural (haemal spine of the first preural centrum) is followed by two lower hypurals which appear to be fused to varying degrees. The number of upper hypurals cannot be accurately determined, since only the lower two (again apparently fused together) are not obscured by ray bases. The first uroneural is a large stegural with a fan-shaped anterodorsal process, as in most Salmoninae. The remaining uroneurals cannot be counted, although the second is visible in one specimen. Epurals vary from two (in two specimens) to three (in two specimens). The neural spine of the second preural centrum is broad and complete, and curves backward above the stegural. The epurals are short, reaching only to the dorsal margin of the expanded stegural. As in Recent salmonids, the posterior margin of the hypural complex forms a vertical line. Urodermals have not been seen.

There are 17 branched caudal rays, nine above and eight below the midline.

Procurrent rays reach as far anteriorly as the neural and haemal spines of the third preural vertebra. The caudal fin is emarginate, but the tips of the dorsal and ventral lobes and the apex of the fork are rounded in outline.

SCALES AND SOFT ANATOMY

Faint imprints of scales are present on several specimens, including the holotype, but isolated scale specimens are unknown. The scales are small and approximately square in outline. The apicolateral corners are well developed and the laterobasal corners less so but nevertheless evident. The apical and basal margins are broadly rounded. Circuli are faint and in the apical field they are widely spaced and follow wavy paths. There are apparently no radii. A row of lateral-line pores is visible in several specimens. The pores are superimposed on the haemal spines, with about two and one half pores per haemal spine (25 pores counted between 11 haemal spines). No scales have been seen on any skull bone.

An adipose fin is present in the holotype opposite the posterior end of the anal fin. Chromatophores are present scattered over the opercular, subopercular, and preopercular, but not the frontals, in one specimen.

Eosalmo cf. *E. driftwoodensis*

Fig. 6B, C

Material

NMC J-43 through J-45, probably representing one individual, consisting of the anal fin, caudal peduncle, and caudal skeleton; and NMC 4571, a pelvic fin. Both are from Pleasant Valley.

Remarks

The pelvic fin (Fig. 6B) is included in the Salmonidae because of faint imprints of scales resembling those of *Eosalmo driftwoodensis* described above. Although the pelvic ray count cannot be determined accurately, there are at least nine rays. This falls within the known range for Recent Salmonidae (Norden, 1961).

The caudal skeleton (Fig. 6C) confirms the presence of a salmonid during the Middle Eocene in British Columbia. However, there is not enough of the fish preserved to make a positive identification to species. The anal fin consists of 15 rays supported by about 12 pterygiophores. The ridged caudal vertebrae have short neural and haemal spines. There are about 20 caudal vertebrae, including the three upturned centra. The large fan-shaped stegural is present, along with three epurals, at least six hypurals, and eight branched rays in the ventral lobe of the fin. The neural spine of the second preural centrum is present but it is only about half the length of preceding neural spines.

Discussion

Apart from otolith and scale specimens, *Eosalmo driftwoodensis* represents the oldest known salmonid. The fossil genus *Thaumaturus* from the Eocene to Miocene of Europe (Laube, 1900; Voigt, 1934) is now generally agreed to be not closely related to the Salmonidae (Gosline, 1960; Nordon, 1961; Weitzman, 1960). The Miocene

has yielded *Protothymallus* Laube (1901) from Europe and *Salmo cyniclope* La Rivers (1964) from Nevada. Scales assigned to the Salmonidae have been described from deposits as old as Upper Cretaceous (David, 1946; Cockerell, 1919) but their relationship to *Eosalmo* is unknown.

Eosalmo is assigned to the Salmonidae on the basis of the presence of three upturned caudal centra, expanded neural and haemal spines in the caudal skeleton, and the large first uroneural (stegural). Other characteristics shared with the salmonids include the large elongate frontals, spathiform branchiostegals, highly ornamented vertebral centra, open lateral temporal fossa, supraneurals and epineurals in the trunk region, 19 principal caudal rays, and an adipose fin.

There are three subfamilies within the Salmonidae: the Coregoninae, including the recent genera *Coregonus*, *Prosopium*, and *Stenodus*; the Thymallinae, including the recent genus *Thymallus*; and the Salmoninae, including the recent genera *Oncorhynchus*, *Salmo* (including *Acantholingua*), *Salvelinus* (often including *Cristivomer*), *Hucho*, and *Brachymystax*. The recently described Pliocene salmonine *Smilodonichthys* from Oregon (Cavender and Miller, 1972) is apparently derived from an *Oncorhynchus*-like ancestor. *Eosalmo* appears to be structurally intermediate between Recent thymallines and salmonines. It resembles the salmonines in its fan-shaped stegural, ossified orbitosphenoid, infraorbital canal on the anterior edge of the postorbitals, postorbitals failing to reach the preopercular, fewer than 17 dorsal rays, and small scales lacking radii. It resembles the thymallines in its parietals not separated by the supraoccipital, small short supraethmoid, relatively short deep jaws, large extrascapulars, triangular frontals, and preopercular with arms at right angles (Behnke, 1968; Cavender, 1970; Monod, 1968; Nelson, 1969; Norden, 1961; Shaposhikova, 1967; Vladykov, 1954, 1962, 1963).

Superorder Ostariophysi

Family Catostomidae Genus *Amyzon* Cope, 1872

Emended Diagnosis

Eocene to Oligocene Catostomidae with terminal mouth; open frontoparietal fontanelle; elongate and slightly emarginate dorsal fin with 12 to at least 30 principal rays; emarginate caudal fin with 18–(19) principal rays and rounded tips; (3)–4–(5) upper hypurals; (7)–8–11 principal anal rays; body depth to standard length ratio 0.21 to 0.51; scales highly variable but primary radii in both apical and basal fields, focus generally basal, width about as great as length, laterobasal corners well developed, apicolateral corners absent, circuli becoming widely spaced in apical field.

Type Species

Amyzon mentale Cope.

Remarks

Cope described three species besides the type species from the *Amyzon* beds of Osino, Nevada and from the South Park (Florissant), Colorado: *A. commune*, *A. pandatum*,

and *A. fusiforme*. A fifth species, *A. brevipinne* Cope, was described from the Eocene sediments of Princeton, British Columbia. The above diagnosis is based on *A. mentale*, *A. commune*, *A. brevipinne*, and *A. aggregatum*, a new species from Horsefly, British Columbia. Very little is known about the other two species.

Amyzon brevipinne Cope

Fig. 8

Amyzon brevipinne Cope, 1893, p. 402.

Amyzon commune Cope, Lambe, 1906, p. 155, scale only from Pleasant Valley.

Diagnosis

Eocene *Amyzon* with body depth to standard length ratio 0.21 to 0.33, head length to standard length ratio 0.27 to 0.33, dorsal fin base length to standard length ratio 0.18 to 0.27; vertebrae 15–19 + 14–17; D 12–20; A 8–10; P 11–10; C i,8,8,i; scales maximum width to total length ratio 0.36 to 1.26, focus — basal margin to total length ratio 0.20 to 0.47, apical primary radii 0–9, apical secondary radii 0–18, basal primary radii 0–25, basal secondary radii 0–7, laterobasal corners moderately strong.

Holotype

NMC 6189, a fish lacking the tail (Fig. 8A); collected by G. M. Dawson in 1888, from the North Fork of the Similkameen River (Tulameen River), probably in Pleasant Valley.

Material

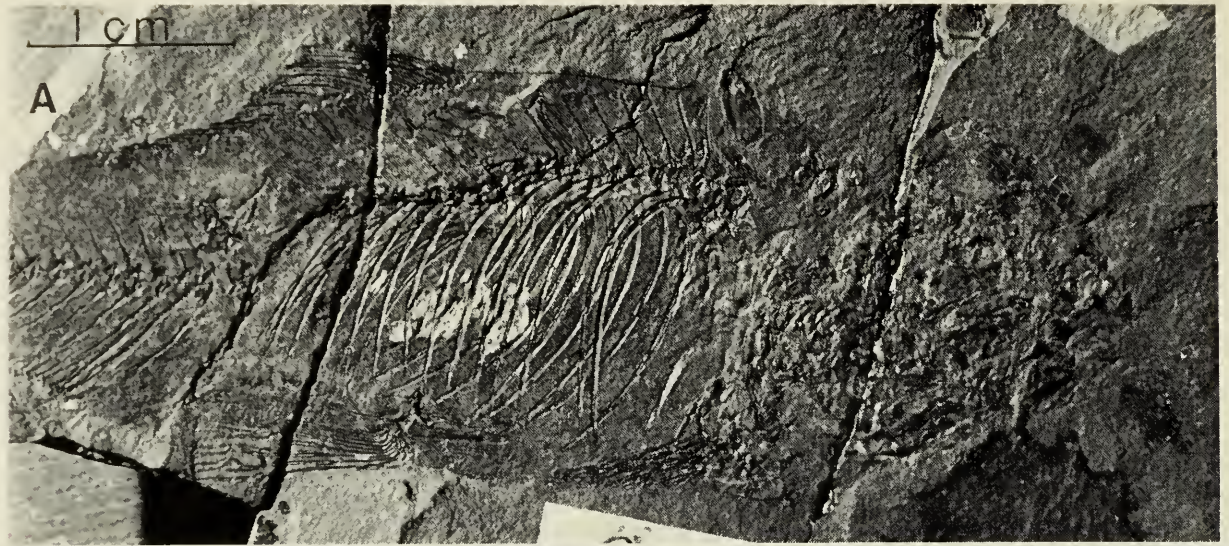
Fish: NMC 2092, 2104, 3132A through 3132J; ROM 11160 through 11164, 11166, 11167, 11169 through 11171, 19420; and numerous fragmentary specimens in NMC and ROM collections. Scales: specimens in NMC collections from Quilchena and Pleasant Valley and in ROM collections from Pleasant Valley L90, L92, L93, and L94, Whipsaw Creek L91, and Blakeburn Mine L95.

Emended Description

This description, emended from Cope (1893), is the first detailed account of a species of *Amyzon* and is intended to serve as a basis for comparison with other species. Summary statistics for the species are presented in Table 3.

GENERAL FEATURES

Specimens preserved as articulated skeletons (Fig. 8B) are almost all small, with standard lengths between 20 and 50 mm. The largest articulated specimen is the holotype which, if complete, would have a standard length of about 75 mm. Numerous isolated bones and fragmentary specimens from localities in Pleasant Valley (the type locality is probably also in Pleasant Valley) show that a large catostomid was present there, reaching estimated standard lengths of more than 200 mm. These large bones probably represent *A. brevipinne*, as no juveniles other than *A. brevipinne* are known from the same area. *A. brevipinne* is proportionately more shallow-bodied than other species of *Amyzon* with the possible exception of *A. mentale*; it may be



1 cm

distinguished from the latter by the number of dorsal rays. *A. brevipinne* also differs from *A. aggregatum* (below) and from *A. commune* in its proportionately shorter dorsal fin, shallower caudal peduncle, and other related characteristics. All known specimens of *A. brevipinne* are preserved in lateral view, indicating that the fish was laterally compressed in life. The mouth is terminal or only slightly subterminal.

SKULL

Several specimens including the holotype have incomplete impressions of the frontal, which has a prominent postorbital process and supraorbital notch similar to that figured by Cavender (1968, fig. 5) for various catostomids including specimens referred to *Amyzon*. The frontal also carries evidence for the presence of an open frontoparietal fontanelle, in the form of a posteromedian notch. A similar notch is present in several of the frontals figured by Cavender (1968), in *Carpiodes* (Gregory, 1933), and apparently in most other catostomids (Smith, 1966). The anterior margin of the frontal appears to be longitudinally striated anteriorly and rounded in small specimens including the holotype, rather than truncated as in the Clarno specimens figured by Cavender (1968). In a large specimen the frontal is broader and truncated anteriorly. The fontanelle extends back between the parietals which are approximately rectangular except for a posterolateral process, and a rounded lateral notch for the lateral temporal fossa. Dorsally the frontal bears a prominent longitudinal ridge on the posterior part of the bone, similar to that in Recent catostomids. Ventrally a ridge passes from the posterolateral corner of the frontal in a slight S-curve toward the anterolateral corner. Two ridges extend from the middle of the frontal to the frontal of the opposite side, just anterior to the frontoparietal fontanelle. Another small ridge proceeds from the middle of the frontal toward its anterior margin. A larger ridge extends laterally along the posterior edge of the postorbital process. The parasphenoid resembles the one from Ochoco Pass (Cavender, 1968) in that it extends straight back from the snout region to a point near the back of the orbit. There it expands dorsoventrally and bends dorsally about 30°, extending posterodorsally a distance almost two-thirds the length of its anterior ramus. It is likely that the Ochoco Pass parasphenoid is also referable to *Amyzon*.

The supraorbital is a small, rounded triangular bone with a pronounced convex curvature of its dorsal surface. A large infraorbital 3 forms the posteroventral margin of the orbit, but the other circumorbitals have not been seen.

The hyomandibular is similar to that of *Ictiobus* (Smith and Koehn, 1971), consisting of a vertical strut with a broad, thin flange anteriorly, but little expansion posteriorly. The strut is surmounted by a thickened portion consisting of an anterior condyle, an anterodorsal condyle, and a posterior opercular condyle. The dorsal and posterior corners of the plate-like dorsal portion of the quadrate are pointed (as in the

Fig. 8 *Amyzon brevipinne* Cope. Apical end of scales oriented toward top of page.

- A. NMC 6189 (holotype), from Pleasant Valley.
- B. NMC 3792, from Whipsaw Creek.
- C. ROM 11451, scale, from Whipsaw Creek L91 (Blue Flame Mine).
- D. NMC 2072, scale, from Pleasant Valley.
- E. ROM 11406, scale, from Blakeburn Mine L95.
- F. ROM 11375, scale, from Blakeburn Mine L95.
- G. ROM 11372, scale, from Blakeburn Mine L95.
- H. ROM 11395, scale, from Blakeburn Mine L95.

Table 3. Summary univariate statistics for *Amyzon brevipinne* Cope and *Amyzon aggregatum* sp. nov.

Variable	<i>Amyzon brevipinne</i>		<i>Amyzon aggregatum</i>	
	n	Mean \pm S.E.	n	Mean \pm S.E.
1. Number of dorsal fin principal rays	14	15.6 \pm 0.589	86	23.7 \pm 0.139
2. Number of anal fin principal rays	21	8.57 \pm 0.130	107	8.65 \pm 0.610
3. Number of pectoral fin rays	14	14.3 \pm 0.438	53	15.5 \pm 0.210
4. Number of pelvic fin rays	13	9.23 \pm 0.231	57	10.0 \pm 0.168
5. Number of vertebrae	15	31.5 \pm 0.506	64	33.5 \pm 0.135
6. Ratio of body depth to standard length	12	0.243 \pm 0.00948	58	0.414 \pm 0.00707
7. Ratio of caudal peduncle depth to standard length	12	0.0904 \pm 0.00355	62	0.147 \pm 0.00260
8. Ratio of predorsal length to standard length	12	0.548 \pm 0.00709	53	0.547 \pm 0.00452
9. Ratio of preanal length to standard length	12	0.766 \pm 0.00806	59	0.788 \pm 0.00365
10. Ratio of head length to standard length	11	0.301 \pm 0.00624	55	0.301 \pm 0.00314
11. Ratio of upper jaw length to standard length	5	0.0684 \pm 0.00331	28	0.0831 \pm 0.00276
12. Ratio of mandible length to standard length	9	0.109 \pm 0.00622	54	0.0908 \pm 0.00192
13. Ratio of dorsal fin base length to standard length	11	0.224 \pm 0.00878	54	0.351 \pm 0.00364
14. Ratio of anal fin base length to standard length	12	0.0951 \pm 0.00332	62	0.0924 \pm 0.00138

Ochoco Pass quadrate figured by Cavender, 1968), while the anterior corner is blunt. The rod-like ventral portion of the quadrate is pointed posteriorly, and bears a knob-shaped articular condyle on a short stalk anteriorly. The rod-like symplectic fits tightly into the notch in the quadrate and extends posteriorly beyond the tip of the quadrate.

The premaxilla attains its greatest width medially and tapers to a point dorsally where it forms a long ascending process. The alveolar process of the premaxilla is short and blunt, about the same length as the ascending process, and excludes the maxilla from only about half of the gape (cf. Cope, 1884, p. 748). The maxilla is greatly expanded, especially along its superior margin where it becomes almost angular, but tapers abruptly to a process which curves forward around the distal end of the premaxilla. Anteriorly the maxilla is tapered and curved slightly posteriorly where it forms two processes which encircle the rostral bone (not seen) at a point just beneath the tip of the ascending process of the premaxilla.

The mandible is robust and of a generalized type resembling that found in the carp and in *Ictiobus* (Smith and Koehn, 1971). The gnathic ramus is not ventrally deflected as it is in Recent bottom-feeding suckers (Smith, 1966). The angular is a roughly triangular bone bearing a stalked process with a socket on its posterior surface. Externally the mandible has three longitudinal ridges; the first extends backward from the lip along the oral margin onto the ascending process, the second and largest runs from near the symphysis posteroventrally to the articular process of the angular, and the third runs along the posterior third of the ventral margin of the mandible. On the internal surface a broad trough extends from the angular forward onto the dentary to a point beneath the lips. The dentary resembles the Ochoco Pass dentary (Cavender, 1968) except that the lips are less prominent (perhaps broken) in the latter.

There are probably three branchiostegals, although a precise count has not been made on any specimen. All are spathiform, with blunt clupeoid projections (McAllister, 1968), and distinct articular processes anteriorly. They are slightly curved and taper gradually from a wide anterior end to an almost pointed posterior end. The urohyal is twice as long as it is high, with its greatest depth at its fan-like posterior end. The anterior portion of the ventral edge is expanded laterally on the left side and the anterior end bears a stalked process. The stout, tapered pharyngeal bears a single row of about 30 curved, closely spaced, and slightly pointed teeth along its concave surface.

The vertical and horizontal arms of the broad preopercular are at right angles. The horizontal arm is over half as long as the vertical arm and the preopercular sensory canal runs down the middle of the bone. The interopercular resembles the one figured by Cavender (1968) from Ochoco Pass. It falls within Nelson's (1949) "IOP1" group because of the high angular posterior portion and broadly rounded posteroventral margin.

The opercular resembles Nelson's "OP1" group because of its straight anterior margin, angle of inferior border at least 30°, and height to width ratio. In 17 operculars from the Blakeburn, Pleasant Valley, and Whipsaw Creek areas, height to width ratios ranged from 1.33 to 1.59 (Mean 1.44, S.E. 0.0247). Small operculars had similar proportions to larger specimens. The subopercular has an almost straight dorsal margin and a broadly curved ventral margin. A small articular process extends from its anterodorsal corner.

The opercular series generally resembles Nelson's (1949) *Catostomus* group, but the branchiostegals do not. Neither of the operculars figured by Cavender (1968) resembles those of *A. brevipinne* because the opercular arm in this species is slender (as in Cavender's fig. 6) but oriented like the stout opercular arm in Cavender's fig. 2, and because the two Ochocho Pass specimens have height to width ratios of 1.81 and 1.97 (Student's t-value 17.4***, $df = 17$, compared with *A. brevipinne* operculars).

VERTEBRAL COLUMN AND MEDIAN FINS

Only three of the bones of the Weberian apparatus have been observed (for terminology see Nelson, 1948). The neural complex is a mid-sagittal plate with a vertical reinforcing ridge near its anterior margin. The anterior and dorsal margins are rounded whereas the posterodorsal corner is slightly angular and the posterior margin is almost straight. The ridge crosses to the posteroventral corner near the base of the bone, and in some specimens the bone is here produced into a point. The neural spine, which fits against the posterior margin of the neural complex, is pointed, concave anteriorly, and almost as high as the neural complex. The fourth pleural rib has a deep transverse plate, vertical ventral extensions of the pleural rib, small ventrally directed esophageal supports, and well-developed ossa suspensoria. The Weberian apparatus of *A. brevipinne* resembles that of the Ictiobinae (Nelson, 1948).

Exclusive of the Weberian apparatus there are 29 to 35 vertebrae, of which 15 to 19 are precaudal and 14 to 17 are caudal. Of the former, six to nine are anterior to the first dorsal pterygiophore, and six to 11 are between the first dorsal pterygiophore and the first caudal vertebra. Each centrum bears a prominent horizontal ridge on its lateral surface, bounded above and below by a fossa. The anterior trunk vertebrae bear prominent prezygapophyses and the neural spines arise from the posterior portion of the vertebrae. Proceeding posteriorly this condition gradually changes to one in which the neural spines arise from the anterior end of the vertebrae, the prezygapophyses are reduced, and postzygapophyses are more prominent. This condition is maintained through most of the caudal series.

Neural and haemal spines are long, slender, and posteriorly directed. Long slender intermuscular bones (epineurals) are preserved dorsally throughout the vertebral column and ventrally in the caudal series. Each epineural arises anteriorly from or near a neural or haemal arch and slants posterodorsally (dorsal series) or posteroventrally (ventral series) at a smaller angle with the vertebral column than the neural and haemal spines, ending near the tip of the spine of the second or third vertebra posterior to the vertebra of origin. Anteriorly each dorsal epineural is bifid, with one branch extending anteroventrally to insert on the neural arch, and the other branch curving anterodorsally. Each ventral epineural is similarly bifid anteriorly. The pleural ribs are long, slender, and tapered to a point near the ventral body margin. Anterior to the dorsal fin is a series of mid-dorsal supraneurals, each one occupying the space between two neural spines. Each supraneural is a triangular plate with its apex directed ventrally and slightly posteriorly between the two adjacent neural spines.

In general features the caudal skeleton is typical of the Catostomidae (Gosline, 1961; Monod, 1968). The neural and haemal spines of preural centra 2 and 3 are thickened, directed more posteriorly, and elongated so that they support procurrent caudal rays both above and below the fin. Prezygapophyses are more obvious on the

last few caudal vertebrae than on the rest of the caudal series, probably because of the change in orientation of the neural and haemal spines. On one specimen (ROM 11161) the neural spine of preural centrum 2 appears to be much shorter than usual. Another specimen (NMC 3132H) has a forked neural spine on preural centrum 3.

The parhypural and first hypural are apparently not fused proximally. The second hypural, first preural centrum, and pleurostyle are fused to form a V-shaped structure in the notch of which the third hypural is tightly articulated by a ball-and-socket mechanism. The rest of the hypurals, which decrease in size dorsally, are only loosely attached to the pleurostyle and are frequently found separated from the pleurostyle in the fossils. The total number of hypurals varies from five (three specimens) to six (10 specimens). The neural arch of the first preural centrum is slender, pointed, and concave anterodorsally. The single epural is long and slender, and is usually parallel to and close to the pleurostyle. The single urodermal on each side of the posterior end of the pleurostyle is relatively long and slender and is usually curved so that it is convex anterodorsally.

The caudal fin consists of one unbranched ray above and below the fin, eight branched rays in the ventral half (10 specimens), and eight branched rays in the dorsal half (seven specimens). The margin of the fin is forked, but the fork and extremities are rounded in outline.

The dorsal fin consists of 11 to 19 branched rays (the last one double), preceded by one unbranched ray and several rudimentary rays. It is supported by 13 to 20 pterygiophores which are pointed ventrally and expanded anteroposteriorly at their dorsal ends. The last (double) soft ray is supported by a small triangular pterygiophore. The first (anteriormost) pterygiophore consists of a vertical ramus and an anterior horizontal ramus connected by a thin sheet of bone. The dorsal margin of the fin is concave and the last dorsal ray is inserted at about the level of the twelfth preural centrum.

The anal fin consists of seven to nine branched rays (the last one double) preceded by one unbranched and several rudimentary rays. It is supported by eight to 10 pterygiophores of which the last is quite small and the first is reinforced anteriorly by a thin sheet of bone between the vertical strut of the pterygiophore and another shorter strut directed anterodorsally. The first two anal pterygiophores articulate with the anterior edge of the haemal spine of the first or second caudal vertebra. The fin is not noticeably emarginate and originates approximately opposite the posterior end of the dorsal fin base.

APPENDICULAR SKELETON

The posttemporal is a small thin bone, about three times as long as wide, with a slight longitudinal lateral ridge. The dorsal end is pointed, and the ventral end is rounded where it articulates with the supracleithrum. The supracleithrum is thin, elongate, and slender in lateral view. The bone is curved so that its anterior edge is concave. A ridge runs from the posterodorsal process diagonally across the upper third of the bone, and continues ventrally along the anterior edge.

The cleithrum resembles the cleithra of Recent catostomids in general shape with an elongate pointed vertical ramus and broad anterodorsal and ventral flanges. The anteroventral end is markedly curved ventrally, unlike the condition in *Catostomus* and *Moxostomus*, for example. The lateral ridge runs prominently down the middle of the vertical ramus, curves anteriorly at the angle of the bone, and then curves vent-

rally to end at the ventral edge posterior to the anteroventral process. Dorsal to the ridge on the lateral surface is a groove that runs in an arch from the angle of the bone to the tip of the anteroventral process. The anterodorsal edge of the cleithrum is produced into a broad point, reinforced by radial ridges. The postcleithrum consists of a sharply pointed dorsal ramus with a vertical anterior edge where it articulates with the cleithrum, and a curved ventral ramus which extends posteroventrally, terminating in a point near the ventral body margin. There is no thickening of the curved part of the ventral ramus similar to that found in *Catostomus*.

The coracoid is approximately triangular in shape and consists of a dorsal thickened rod and a ventral thin plate. The dorsal surface of the thickened portion is concave, as is the posterolateral edge of the plate-like portion, whereas the ventral edge of the plate is convex. The thickened rod terminates anteroventrally in two small pointed processes where it articulates with the coracoid of the opposite side, and posterodorsally in a complex of condyles where the coracoid articulates with the rest of the pelvic girdle. The plate-like portion bears a small pointed process at its ventrolateral corner, possibly for articulation with the postcleithrum. A large scapular foramen is located near the anterodorsal edge of the scapula. Two or three small processes along the posterior edge mark the points of attachment of pectoral radials.

Pectoral ray counts range from 11 to 18. The large observed range cannot be attributed to poor preservation, since very well-preserved specimens account for both the maximum and minimum observed values. The pectoral rays extend posteriorly about half the distance to the pelvic fin origin.

The pelvic bone consists of anterior and posterior portions joined by an expanded central ossification connected to the pelvic of the opposite side by a short blunt medial process. The posterior portion consists of a tapered rod extending posteriorly from the medial process. The anterior portion can be divided into a lateral strut separated from a median horizontal plate by a deep notch. The median plate terminates in a point at its anterolateral corner.

The pelvic fin consists of a lateral splint, one unbranched ray, and seven to nine branched rays, articulating with the posterior surface of the central ossification of the pelvic bone. The pelvic rays extend posteriorly about two-thirds the distance to the origin of the anal fin. The pelvic fin originates approximately beneath the origin of the dorsal fin.

SCALES

Summary statistics for the scales are presented in Table 4. Most of the characters recorded for the species show a high degree of variability (Fig. 8C—H). For instance, the ratio maximum width to total length for the 42 specimens measured ranges from 0.36 to 1.26 and the values are approximately normally distributed. It is therefore difficult to generalize about overall proportions except to comment that most specimens are longer than wide. The focus is basal to almost central and averages about one-third the length of the scale from the basal margin. Apicolateral corners are usually broadly rounded, but in five of 45 specimens examined they were judged to be approaching a more angular shape. Laterobasal corners vary from rounded to angular, with many of the smaller specimens approaching an almost circular outline. The apical margin is uniformly convex and the basal margin varies from almost straight to convex. In scales with angular laterobasal corners a single large central

Table 4. Summary univariate statistics for the scales of *Amyzon brevipinne* Cope and *Amyzon aggregatum* sp. nov., exclusive of regenerated scales.

Variable	<i>Amyzon brevipinne</i>		<i>Amyzon aggregatum</i>	
	n	Mean \pm S.E.	n	Mean \pm S.E.
1. Number of basal (anterior) primary radii	35	4.34 \pm 0.973	90	14.9 \pm 0.861
2. Number of basal (anterior) secondary radii	27	1.96 \pm 0.485	25	5.56 \pm 1.21
3. Number of apical (posterior) primary radii	44	3.59 \pm 0.329	130	6.69 \pm 0.196
4. Number of apical (posterior) secondary radii	39	4.64 \pm 0.665	121	5.39 \pm 0.312
5. Ratio of maximum width to total length	42	0.832 \pm 0.0318	129	0.867 \pm 0.0177
6. Ratio of focus - basal margin length to total length	42	0.339 \pm 0.0103	128	0.365 \pm 0.00413
7. Ratio of average diagonal length to total length	42	0.967 \pm 0.0167	129	1.00 \pm 0.0116

lobe usually projects basally beyond the laterobasal corners, giving an overall convex outline to the basal margin.

The number of primary and secondary radii in both apical and basal fields is highly variable. Generally speaking, the smaller scales have fewer radii of all types. Basal radii are fine and closely spaced, and number from none to 25 for primary radii and from none to seven for secondary radii. Apical radii are usually stronger, vary from none to nine for primary radii and from none to 18 for secondary radii, and are usually straight. Curved radii are occasionally encountered, especially near the corners of the scale and on asymmetrical specimens. Up to five lateral primary radii were counted, usually as continuations of the apical series around the apicolateral corners of the scale.

Circuli are very closely spaced in the basal and lateral fields, and generally parallel the margin of the scale there. In the apical field, they become heavier and more widely spaced, and often intersect the margin of the scale.

Regenerated scales from *A. brevipinne* localities are usually of large size, with numerous secondary radii in both apical and basal fields, and approach a square shape with slightly rounded corners. Both apical and basal margins are convex and laterobasal corners remain slightly stronger than apicolateral corners. The large unornamented area (focus) is usually in the centre of the scale.

Amyzon aggregatum, sp. nov.

Figs. 9, 10, 11A, E

Amyzon brevipinne Cope, Lambe, 1906, pp. 153–5, plate I, figs. 1, 2; NMC 6190 from Horsefly Mine.

Amyzon commune Cope, Lambe, 1906, p. 155, plate I, fig. 3; NMC 6191 from Horsefly Mine.

Amyzon brevipinne Cope and *Amyzon* sp., Cavender, 1968, p. 133, fig. 5D; specimens from Horsefly Mine including “NMC 1686” (probably NMC 9891).

Diagnosis

Eocene *Amyzon* with body depth to standard length ratio 0.26 to 0.51; head length to standard length ratio 0.24 to 0.34; dorsal fin base length to standard length ratio 0.28 to 0.43; vertebrae 16–19 + 14–18; D 21–27; A 7–11; P 12–20; V 7–15; C i, 8–(9), (7)–8–(9), i; scales maximum width to total length ratio 0.39 to 1.49, focus — basal margin to total length ratio 0.26 to 0.49, apical primary radii 2–14, apical secondary radii 0–22, basal primary radii 0–30, basal secondary radii 0–27, laterobasal corners mostly strong.

Holotype

ROM 11019 A and B, part and counterpart of an entire fish with standard length of 179 mm, collected by the author in 1970 (Fig. 9A).

Topotypes

ROM 11001 through 11018, 11020 through 11025, 11027 through 11038, 11040 through 11061, and 11063 through 11098, collected by the author in 1969 and 1970.

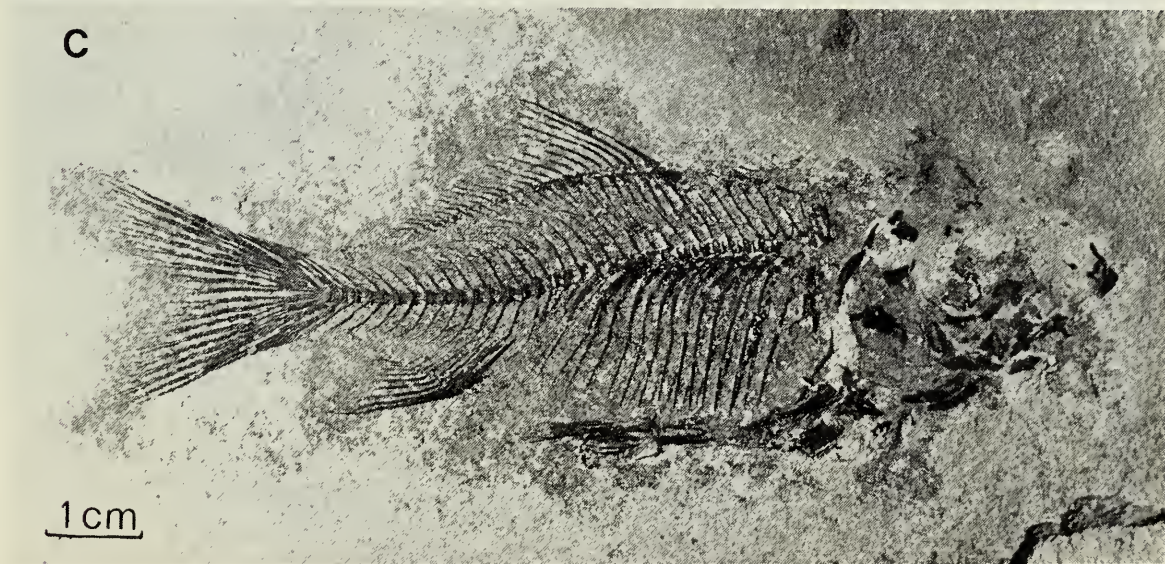
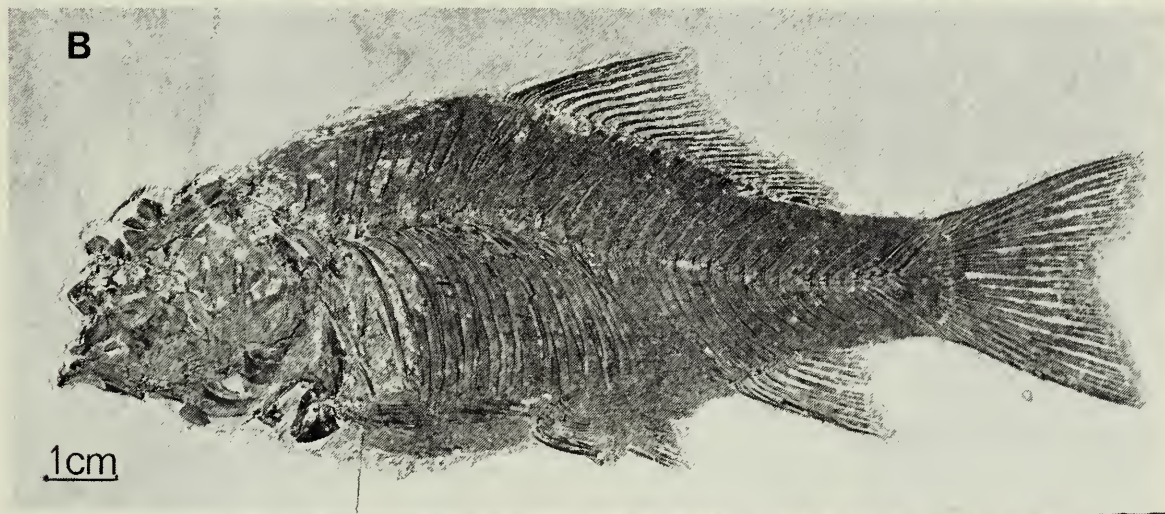
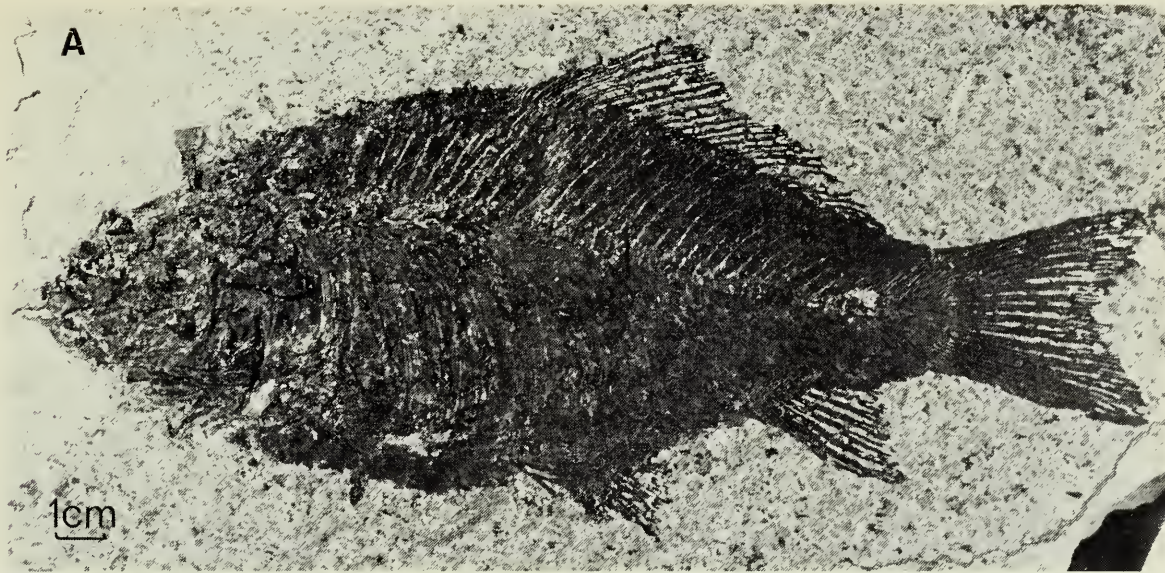


Fig. 9 *Amyzon aggregatum* sp. nov. from Horsefly Mine L88.

A. ROM 11019 (holotype).

B. ROM 11051.

C. ROM 11040.

Referred Material

NMC 6190, 6191 A, 6191 B, and 6191 C & D from Horsefly Mine, collected by J. B. Hobson in 1895; UBC B2301, ROM 19413 through 19416, 19421, 19424 through 19428, NMC 9891 A through 9891 I, and 9891 L through 9891 S from Horsefly Mine, probably mostly from the type locality, collected by R. B. Campbell, G. E. Rouse, and W. H. Mathews in 1959 and 1961; ROM 11108, 11110, 11125, 11126, 11129, 11131, and 11142 from L87; ROM 11143, 11145, and 11146 from L89; and various fragmentary specimens in ROM and NMC collections. Scales NMC 9891 O through 9891 R, ROM 11006 C, 11006 D, 11201 through 11226, 11228, 11229, 11231 through 11236, 11238, 11239, 11241, 11242, 11244, 11247 through 11249, 11251, 11252, 11254 through 11257, 11259 through 11264, 11266, 11269, 11270, 11272 through 11282, 11284 through 11288, 11291, and 11292, all from L88 (type locality); ROM 11139 C, 11293 through 11296, 11299, 11302 through 11304, 11307, 11308, 11310, 11312, and 11313 from L87; ROM 11314 through 11318, 11320 through 11322, 11325, 11327 A, 11327 C, 11329, 11332 through 11342, 11348, and 11351 through 11359 from L89; and 11360, 11362, 11363, and 11365 from L97.

Type Locality and Age

Horsefly Mine L88, probable age Middle Eocene.

Etymology

The specific name *aggregatum* is the neuter form of the Latin adjective *aggregatus*, -a, -um, which means collected, clustered, assembled.

Description

Summary statistics for the species are presented in Table 3. Those features of the skeleton that differ from the condition in *A. brevipinne* and those not visible in the specimens of *A. brevipinne* are emphasized below.

GENERAL FEATURES

Disarticulated bones are restricted to the skull, which is often crushed and distorted. The rest of the skeleton is invariably preserved intact (Figs. 9A-C, 10A). As with *A. brevipinne* the specimens are all preserved in lateral view, indicating that the fish was laterally compressed in life. Notable features distinguishing this species from *A. brevipinne* are its longer dorsal fin and its greater body depth to standard length ratio, which is reflected in various other ratios such as relative depth of caudal peduncle. Standard lengths of the known specimens range from 39 to 242 mm, with a modal standard length of about 175 mm (Fig. 12). All bones therefore appear considerably more robust than their counterparts in *A. brevipinne*, which is represented mostly by small specimens.

SKULL

The frontal resembles that of *A. brevipinne* except that it appears truncate anteriorly in all specimens and the dorsal ridge extends the entire length of the bone although it is highest just anterior to the frontoparietal fontanelle. Ventrally the same pattern of ridges exists as in *A. brevipinne*.

The parietal articulates across almost its entire width with the frontal. Laterally (where it borders the large lateral temporal fossa) the margin is concave and smooth

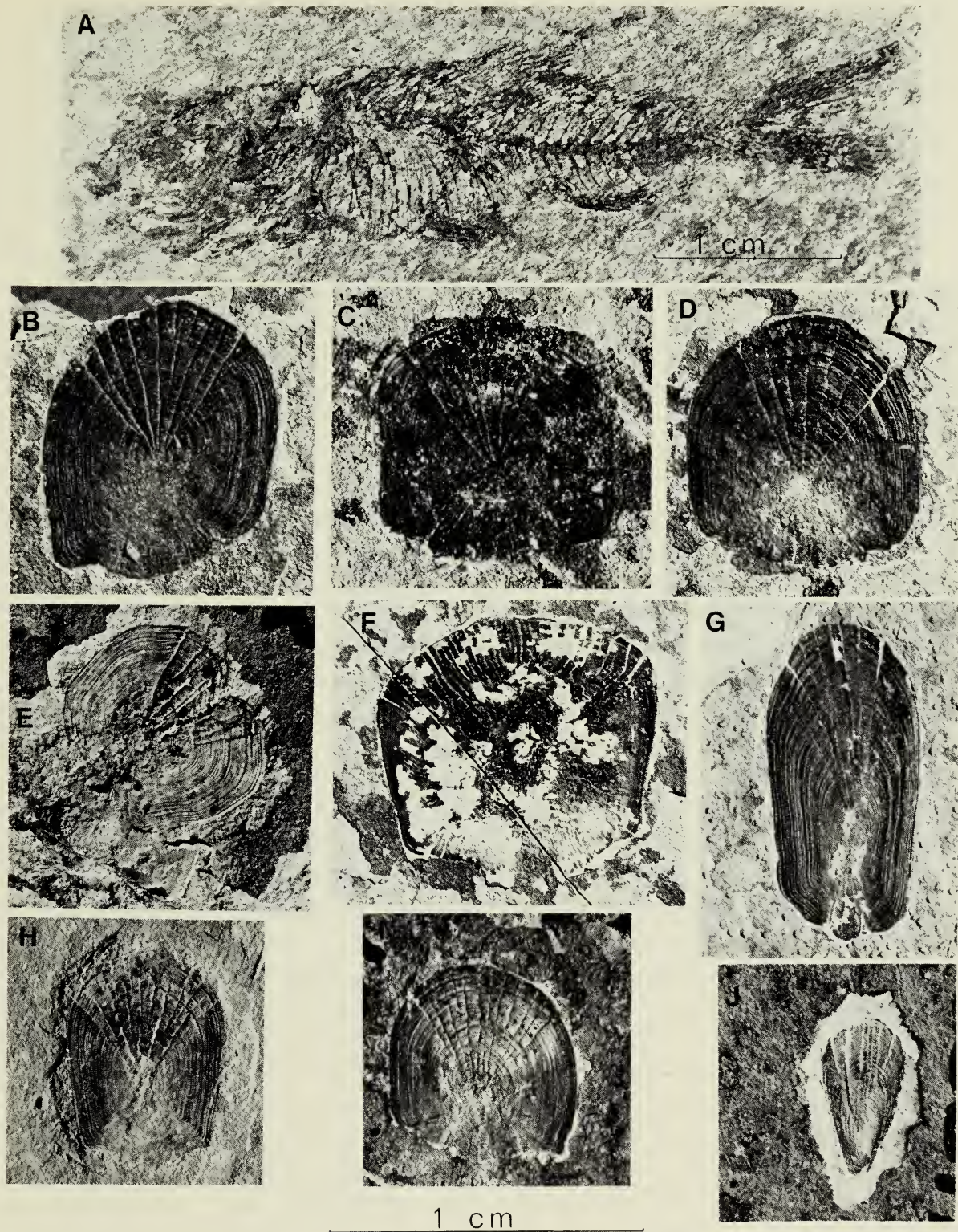


Fig. 10 *Amyzon aggregatum* sp. nov. Apical end of scales oriented toward top of page.

- A. ROM 11086 from Horsefly Mine L88.
- B. ROM 11279, scale, from Horsefly Mine L88.
- C. ROM 11228, scale, from Horsefly Mine L88.
- D. ROM 11285, scale, from Horsefly Mine L88.
- E. ROM 11242, scale, from Horsefly Mine L88.
- F. ROM 11271, regenerated scale, from Horsefly Mine L88.
- G. NMC 9891 R, scale, from Horsefly Mine.
- H. ROM 11307, scale with chromatophores, from Horsefly Mine L87.
- I. ROM 11317, scale with chromatophores, from Horsefly – Black Creek Road L89.
- J. ROM 11330, scale, possibly from the ventral midline of the body, from Horsefly – Black Creek Road L89.

leaving only a small anterolateral area for articulation with the pterotic, and a posterolateral process bearing two small dorsal ridges. The ventral surface of the parietal is smooth and slightly concave.

The parietals are separated medially by the supraoccipital which bears a pair of small ridges that form the posterior border of the frontoparietal fontanelle. The lateral margin of the sphenotic is distinctly notched when viewed from above, although the notch is shallower and narrower than that figured by Gregory (1933) for *Carpiodes*.

The robust supraethmoid has a convex dorsal surface with slightly rounded posterior margin, parallel sides, and slightly concave anterior margins on either side of the anteroventral process. The rostral bone is three or four times as long as it is wide and is narrower in the middle than at each end.

The supraorbital resembles that of *A. brevipinne*. The lachrymal is approximately elliptical with a short process extending from its dorsal margin. The large, broad infraorbital 3 forming the posteroventral border of the orbit is bent almost at right angles. The vertical arm is slightly longer than the horizontal arm and both are slightly tapered toward rounded tips. At least one infraorbital separates this bone from the lachrymal. Infraorbitals 4 and 5 are narrow and rod-like. The infraorbital sensory canal appears to follow the orbital margin along the large infraorbital 3, branching near the front of infraorbital 2. One branch curves dorsally to follow the orbital margin while the other proceeds anteriorly across the lachrymal.

The hyomandibular resembles that of *A. brevipinne*. The quadrate resembles the same bone in *A. brevipinne* except that the anterior corner of the dorsal plate is pointed like the Ochoco Pass quadrate (Cavender, 1968). The rod-like ventral portion is half again as long as the dorsal portion and appears to be pointed posteriorly. The ectopterygoid appears to extend ventrally as far as the anterior point of the quadrate.

The jaw bones resemble closely their counterparts in *A. brevipinne*. The ascending process of the premaxilla is slightly curved near its tip and the superior margin of the maxilla is produced to a broad point. The combined length of the upper jaw is relatively greater for this species than for *A. brevipinne*.

Mandible length as a ratio of standard length is smaller than for *A. brevipinne* although the observed ranges for the two species overlap considerably. The angular appears to vary from an elongate to a rather stubby extension of the mandible so that much of the variation in mandible length may be accounted for by the variation in the angular. The upper and lower jaw bones are usually preserved in an open-mouthed position. When fully protracted the lip of the dentary points downward and the margin of the upper jaw is almost vertical. The vertical diameter of the gape is approximately equal to the total length of the mandible, or about one-tenth of the standard length of the fish. In a closed position the lip of the dentary points approximately straight ahead, whereas the upper jaw margin slants upward at a 45° angle to the long axis of the fish.

The ventral margin of the urohyal bears lateral extensions. The vertically expanded portion is pierced by two foramina located one behind the other above the posterior end of the lateral extensions. Branchiostegals resemble those of *A. brevipinne*. The pharyngeals resemble those of *A. brevipinne* except that they appear relatively narrower. Twenty-eight teeth were counted on one specimen, and the teeth are slightly pointed in one specimen and blunt in another. The anteroventral limb is uniformly concave on its toothed side. The edentulous posterodorsal limb is short and pointed.

The preopercular, interopercular, opercular, and subopercular all resemble the

corresponding bones of *A. brevipinne*. A distinct longitudinal ridge on the lateral surface of the anterior half of the interopercular and a notch in the anterodorsal corner, not seen but probably present also in *A. brevipinne*, increase the resemblance to the interopercular from Ochoco Pass (Cavender, 1968). These features are also figured by Nelson (1949) as typical of the catostomid "IOP1". Opercular heights and widths were measured on eight specimens: height to width ratios ranged from 1.34 to 1.55 (Mean = 1.45, S.E. = 0.0246), very similar to the results for *A. brevipinne* operculars (Student's t-value 0.005ns, df = 23).

VERTEBRAL COLUMN AND MEDIAN FINS

The Weberian apparatus resembles that of *Carpiodes* (Nelson, 1948, fig. 5) in that the posterodorsal corner of the neural complex is higher than the anterodorsal corner and the neural spine reaches as high as the neural complex. The tripus (for terminology see Krumholz, 1943) resembles that of other catostomids in overall shape with a short blunt anterior ramus and a posterior ramus about half again as long as the anterior ramus. Both rami curve dorsally and the ventral margin of the bone is almost circular in outline. The articular process is long and directed anterodorsally. Little or no fenestration of the body of the tripus was seen in any of the four specimens found. A ridge extends along the posterodorsal margin from the articular process onto the posterior ramus. The transformator process appears as a continuation of the posterior ramus and is curved dorsally as in most other catostomids. The fourth pleural rib of the Weberian apparatus resembles that of *A. brevipinne* in its stout vertical pleural rib extensions, deep transverse plate, and ventrally directed esophageal supports.

Exclusive of the Weberian apparatus there are 32 to 37 vertebrae, 16 to 19 of which are precaudal and 14 to 18 caudal. From five to nine vertebrae are anterior to the first dorsal pterygiophore and seven to 13 are between the first dorsal pterygiophore and the first caudal vertebra. Vertebrae, neural and haemal spines, pre- and post-zygapophyses, and pleural ribs all resemble their counterparts in *A. brevipinne*. Prezygapophyses of the anteriormost vertebrae are very large and the prezygapophysis of the first normal vertebra lies up against the neural spine of the Weberian apparatus. Complete series of epineurals and supraneurals are present as in *A. brevipinne*.

The caudal skeleton is almost identical to that of *A. brevipinne* with the following exceptions. The total number of hypurals varies from five to seven, most specimens having six. The neural arch of the first preural centrum is slightly longer than in *A. brevipinne*, but reaches only as high as the ventral tip of the single epural. The paired urodermals are very slender, pointed at each end, and are usually bent in a shallow S-curve. A single specimen (ROM 11094) has a forked haemal spine on preural centrum 3 and a double neural crest on preural centrum 1.

The caudal fin consists of one full-length unbranched ray above and below the fin, eight or nine branched rays (usually eight) in the upper lobe, and seven to nine (usually eight) branched rays in the lower lobe. As with *A. brevipinne* the tips of the lobes and the apex of the fork are rounded in outline.

The dorsal fin consists of several rudimentary rays followed by one full-length unbranched ray and 20 to 26 branched rays, the last one double. It is supported by 20 to 27 pterygiophores. The shape of the fin and its pterygiophores resembles the condition in *A. brevipinne*. The last dorsal ray is inserted at about the level of the eighth preural centrum.

The anal fin consists of a few rudimentary rays followed by one full-length unbranched ray and six to 10 branched rays, the last one double. It is supported by six to 10 pterygiophores and originates anterior to the insertion of the dorsal fin.

APPENDICULAR SKELETON

The posttemporal, supracleithrum, cleithrum, and postcleithrum all resemble their counterparts in *A. brevipinne*. The coracoid appears considerably more robust, although preserving the overall outline seen in the other species. The division into rod-like and plate-like portions is less obvious. The bone has a distinct spherical curvature not seen in material of *A. brevipinne*. A prominent foramen pierces the coracoid near its posterodorsal corner.

Pectoral ray counts range from 12 to 20. The fin originates near the ventral body margin and the rays extend as far as the anterior end of the pelvic girdle, or about two-thirds the distance to the pelvic fin origin.

The pelvic bone resembles its counterpart in *A. brevipinne*. The fin consists of a lateral splint, one unbranched ray, and six to 14 branched rays. The fin extends posteriorly about two-thirds the distance to the anal fin origin, originating behind the origin of the dorsal fin.

SCALES

Summary statistics for the scales are given in Table 4. As in *A. brevipinne* the scales are highly variable (Figs. 10B-J, 11A,E). Circuli are arranged like those of *A. brevipinne*. Chromatophores are present on the exposed portion of many scales (Fig. 10H, I) and on one fish specimen they are concentrated in the anteroventral part of the trunk. They also form a margin around the opercular, which is devoid of scales, and can be seen on other skull bones.

Most scales are longer than wide, but the observed range of maximum width to total length ratios is 0.39 to 1.49. The focus is between one-quarter and one-half the total length from the basal margin. Apicolateral corners are usually broadly rounded whereas laterobasal corners are usually strong. The apical margin is convex, except in lateral line scales (Fig. 10E), while the basal margin is variable but usually convex.

Basal radii are fine, closely spaced, and number from zero to 30 for primary radii and from zero to 27 for secondary radii. Apical radii are stronger, usually straight, and vary from two to 14 for primary radii and from zero to 22 for secondary radii. Up to five primary and two secondary lateral radii were counted.

Regenerated scales from Horsefly localities (Figs. 10F, 11A) resemble those from *A. brevipinne* localities but are often of moderate size.

Discussion

The two British Columbia species are among the world's oldest undoubted catostomids. The Eocene Gobi "*Catostomus* sp." from China (Hussakof, 1932) is suspect because it is known only from broken operculars (Nelson, 1949). Recently a specimen of *Amyzon* has also been found in the Eocene Green River Formation (Cavender, pers. comm.).

The assignment of the genus *Amyzon* to the Catostomidae is not in doubt because the pharyngeal is known. Typical catostomid features include the caudal skeleton with 16 branched rays and four upper hypurals in most specimens. *Amyzon* resembles the Ictiobinae among Recent catostomids in its Weberian apparatus and certain fea-

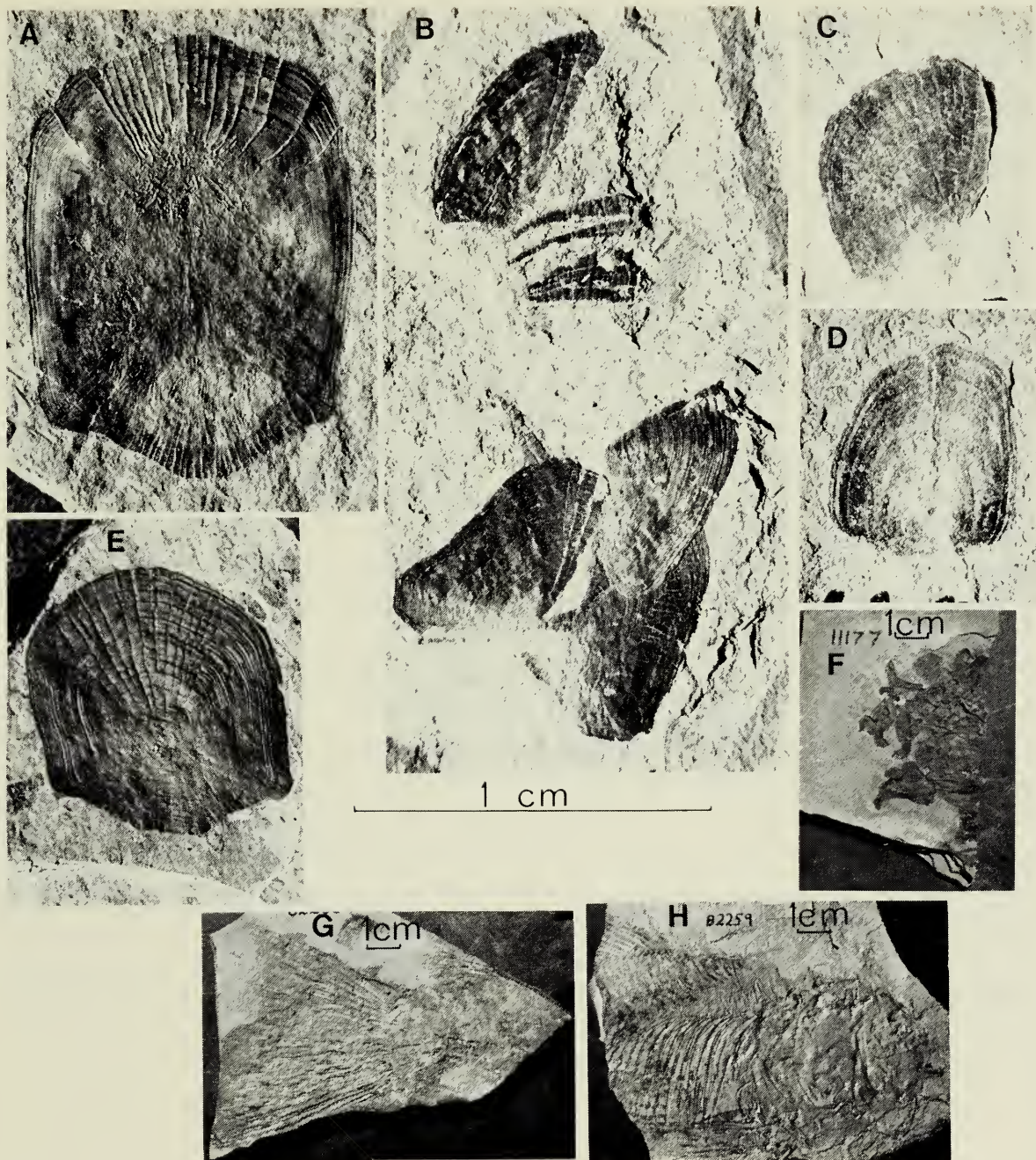


Fig. 11 *Amyzon aggregatum* sp. nov. and *Amyzon* sp. Apical end of scales oriented toward top of page.

A. *Amyzon aggregatum* sp. nov., ROM 11301, regenerated scale, from Horsefly Mine L87.

B. *Amyzon* sp., ROM 11453, scales, from Driftwood Creek L96.

C. *Amyzon* sp., ROM 19433, scale, from Driftwood Creek L96.

D. *Amyzon* sp., ROM 11454, scale, from Driftwood Creek L96.

E. *Amyzon aggregatum* sp. nov., ROM 11338, scale, from Horsefly – Black Creek Road L89.

F. *Amyzon* sp., ROM 11177, bones of snout, from Driftwood Creek L96.

G. *Amyzon* sp., ROM 19407, caudal peduncle and fin, from Tranquille River.

H. *Amyzon* sp., ROM 19400, head and part of trunk from Driftwood Creek L96.

tures of the skull roof such as the open frontoparietal fontanelle and the shape of the frontal (Cavender, 1968). Cope (1884) was correct in most of his observations on the skull, but the British Columbia species do not have the premaxilla extending beneath the whole length of the maxilla.

The two species described here differ markedly in certain meristic characters and in relative body depth. However, since there is remarkable similarity in the form of the skull bones and in the scales, there is little doubt that they should belong to the same genus. The same can be said for the species *A. mentale* and *A. commune* on which the genus was based. Thus, it appears that the genus *Amyzon* is well defined.

A great deal of variation is present within each species. Pectoral and dorsal ray counts vary widely from specimen to specimen. The variability in body depth within the Horsefly Mine sample led Lambe (1906) to conclude erroneously that two species were present. Nevertheless, it is possible to define and describe adequately both British Columbia species because of the large number of specimens available.

The availability of a large series of specimens from the combined Horsefly collections of *A. aggregatum* made possible a limited form of size-frequency analysis. A histogram of standard length frequencies (Fig. 12) appears to be negatively skewed. Strong peaks are apparent at about 175 and 220 mm, with weaker peaks at smaller sizes. The preponderance of large specimens indicates that preservation was selective according to size.

The peaks in the frequency histogram are reminiscent of year classes. ROM 11085, preserved with a cross section of one of its otoliths, was about five years old at death. The annulus-like growth rings on the operculars of ROM 11048 (three and one-half years) and ROM 11051 (five years), and the annuli on the scales of ROM 11043 (four years) and ROM 11492 (five years) provided additional evidence of age. The modal standard length of about 175 mm corresponds to an age of about five years. By extrapolation the smallest known specimens were about two years old and the largest about six years old when they died. Wilson (1977a) has explained the preservation of year classes as resulting from winter deaths in a small, stratified lake.

***Amyzon* sp.**
Fig. 11B-D, F-H

Material

ROM 11177 and 19400 from Driftwood Creek L96; NMC 6195 A, 6195 B, ROM 19402, 19403, and 19407 from near Tranquille on Kamloops Lake; scales ROM 11453, 11454, and 19433 from Driftwood Creek L96; and numerous scales from the Horsefly and Princeton areas not definitely assignable as *A. brevipinne* or *A. aggregatum* scales.

Remarks

The scales from Driftwood Creek (Fig. 11B-D) are too poorly preserved to be identified with certainty, but resemble the *Amyzon* scales described above in number of apical radii, basal focus, rounded apical margin, and moderately well-developed laterobasal corners. Skeletal material from Driftwood Creek consists of a well-preserved snout (Fig. 11F) and a less detailed anterior third of a skeleton (Fig. 11H).

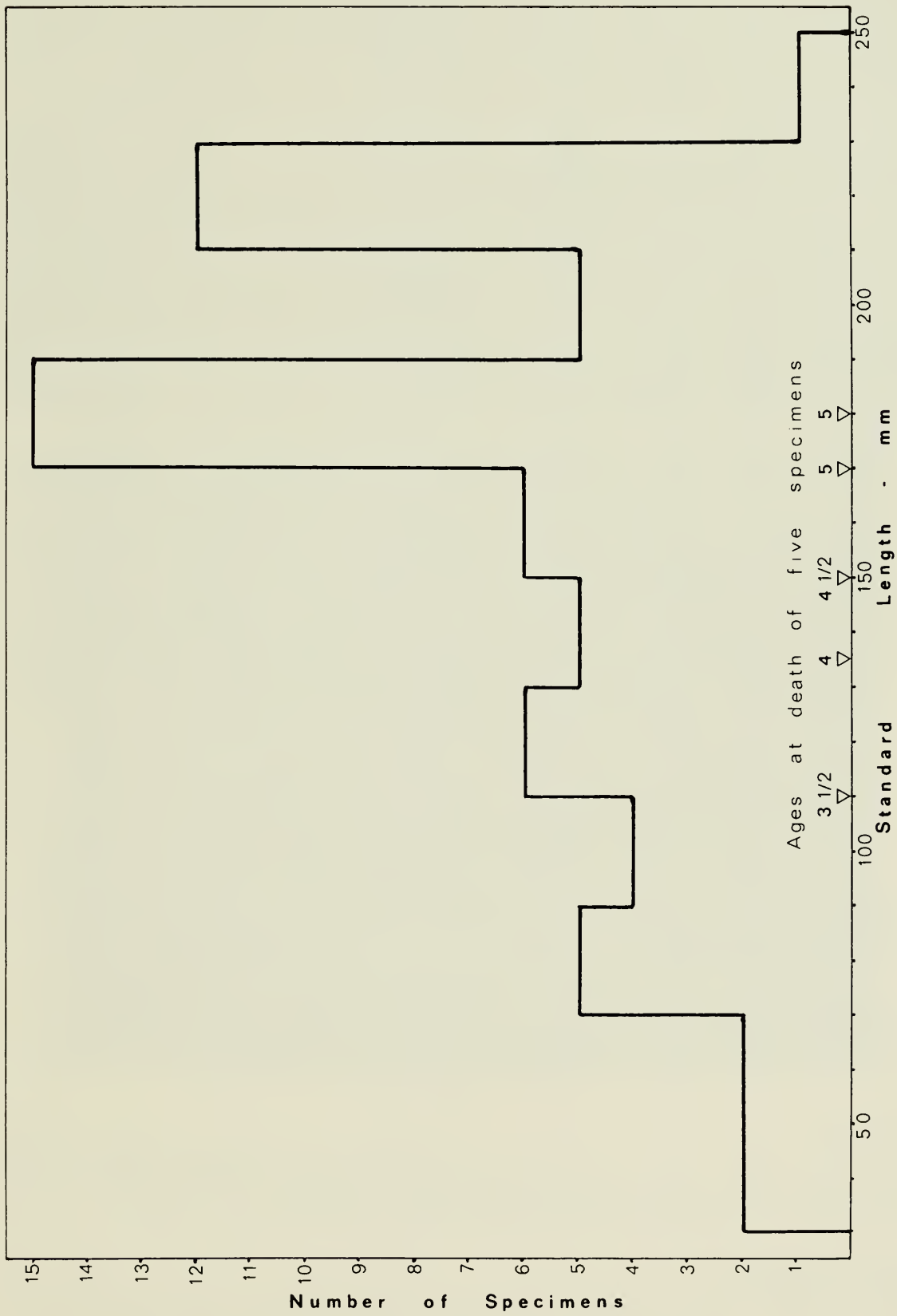


Fig. 12 Standard length - frequency histogram for specimens of *Amyzon aggregatum* from Horsefly area localities.

Fin ray counts are not available and the skull bones merely confirm observations common to both British Columbia species, especially with regard to the form of the maxillae, premaxillae, and mandibles.

Most of the Tranquille material is distorted by shearing of the sediments, making accurate measurements impossible. ROM 19407 appears to have a long dorsal fin ending over the eighth or ninth preural centrum. Of the two British Columbia species described to date it seems closer to *A. aggregatum*.

Superorder Paracanthopterygii

Family Percopsidae *Libotoni*, gen. nov.

Type and Only Species

Libotoni *blakeburnensis*, gen. et sp. nov.

Diagnosis

Eocene Percopsidae without postmaxillary process on premaxilla or levator maxillae superioris process on maxilla; premaxilla long and narrow; frontal tapered anteriorly; palatine toothed; endopterygoid, ectopterygoid, and vomer toothless; antorbital present; no spines on preopercular; opercular with some cycloid scales; percopsid projections on some branchiostegals; ceratohyal imperforate, without tooth plates; enlarged abdominal prezygapophyses; short, weak median fin spines; third, fourth, and fifth hypurals partly fused; caudal fin emarginate; vertebrae 15 + 18–19; D II–III, 8–9; A II, 8–9; P ii, 11–13; V i, 7; scales ctenoid with 7–9 long, slender ctenii each.

Libotoni *blakeburnensis*, gen. et sp. nov.

Figs. 13, 14

Diagnosis

Same as that for the genus.

Holotype

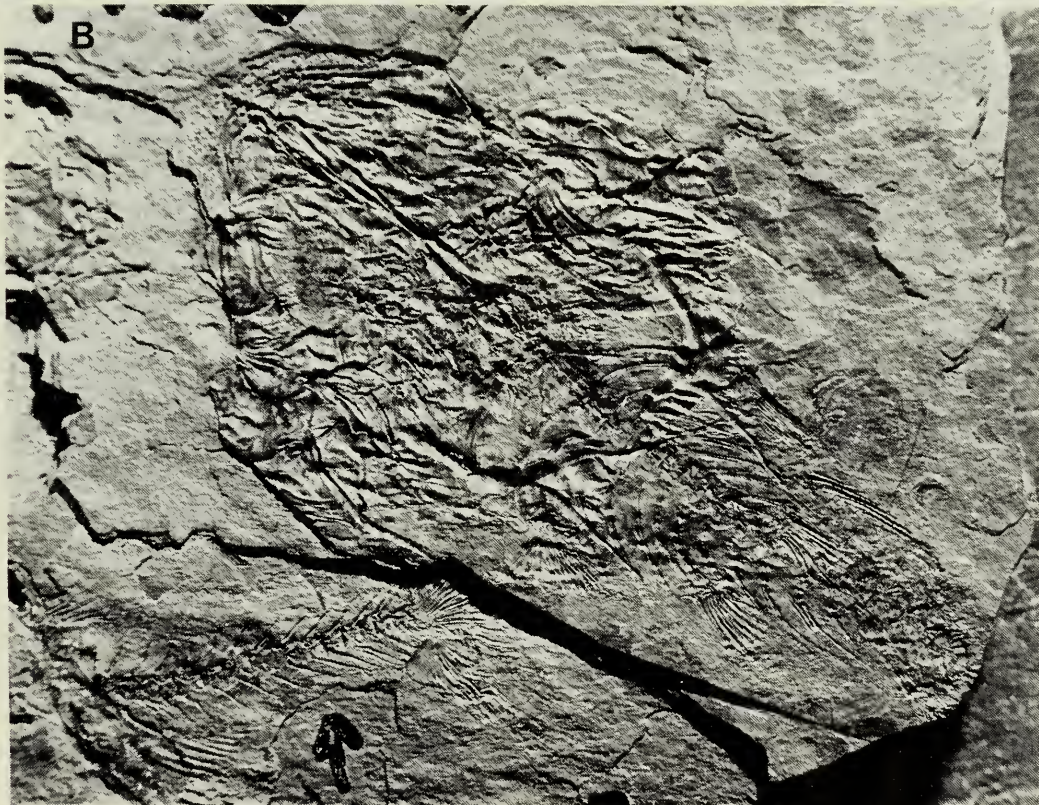
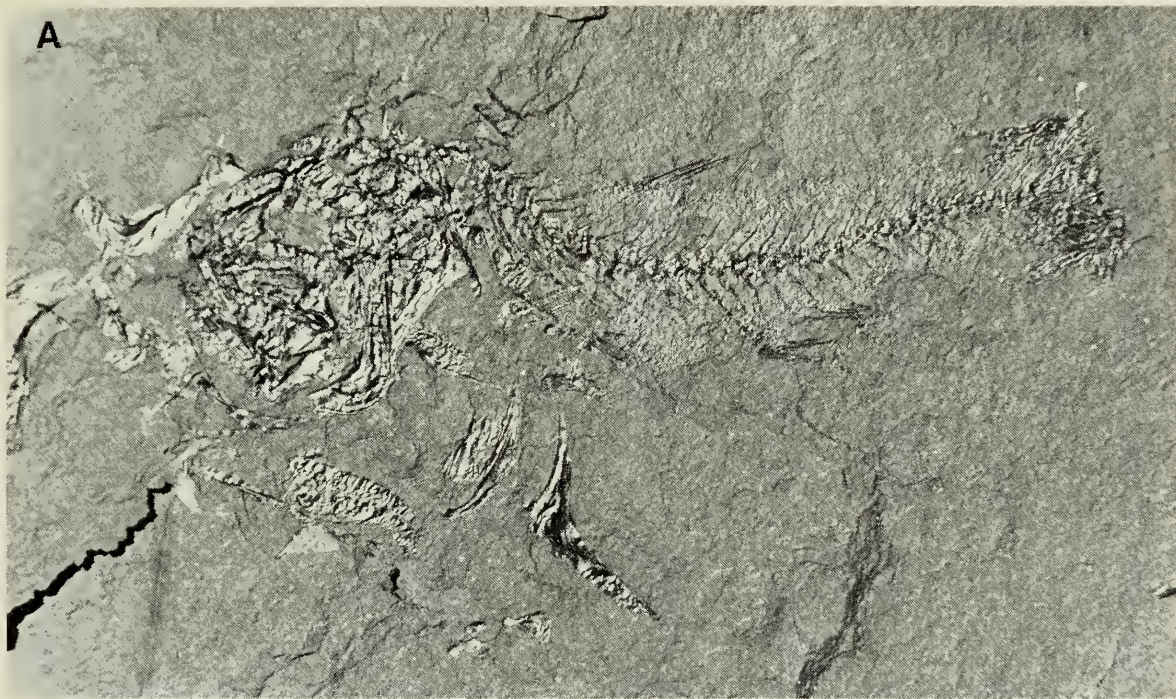
ROM 11157 A and B (Fig. 13A), an almost complete fish in part and counterpart, collected by the author in 1970, and preserved in black platy shale.

Topotypes

ROM 11156, 11158, 11165, and 11497 through 11500, all preserved in black or dark brown shale, and collected by the author in 1970 and 1971.

Referred Material

ROM 11168 and 11488 through 11490 from Whipsaw Creek L86, donated by R. Liboton in 1969; and an isolated pair of frontals, NMC 3132 K, collected by H.M.A. Rice in 1941, also from near Whipsaw Creek. All of these specimens are preserved as delicate impressions in brown paper shale rich in plant fossils.



1 cm

Fig. 13 *Libotonius blakeburnensis* gen. et sp. nov.

A. ROM 11157 (holotype) from Blakeburn Mine L95.

B. ROM 11168 (above, right), a dorsoventrally compressed specimen, and ROM 11488 (below, left), a laterally compressed caudal peduncle, both from Whipsaw Creek L86.

Type locality

Blakeburn Mine L95 (now an open-pit coal mine) south of Coalmont, British Columbia.

Etymology

Libotoni is named in honour of René Liboton, owner of a rock shop and fossil museum at Vaseaux Lake, British Columbia, and donor to the ROM of specimens of *Amyzon brevipinne* and *Libotoni* *blakeburnensis* from Whipsaw Creek L86.

Description

GENERAL FEATURES

Summary statistics for the species are given in Table 5. The known specimens (Fig. 13) represent only a small size range, from about 30 to possibly 40 mm in standard length. The head is relatively large compared with the body. About half of the specimens are preserved with the skull and anterior part of the body dorsoventrally flattened, indicating that the fish was approximately circular in cross section with a broad, flat skull. The body depth to standard length ratio is comparable to that of other Eocene and Oligocene fossil percopsiforms. Many of the bones are extremely thin and have a distinctly crenulated appearance, especially near their margins.

SKULL

The supraoccipital completely separates the parietals anteriorly. The parietals (Fig. 14C) are concave laterally where they border the posttemporal fossae, as in other percopsiforms. The frontals (Fig. 14A-C) are broadest at the rear of the orbit and taper gradually to their anterior tips, as in *Tricophanes* and *Aphredoderus*. A prominent ridge parallels the midline of the skull along the anterior two-thirds of each frontal. The frontals also appear to be raised at the midline, producing a broad trough running forward on each side. Another trough crosses the midline of the frontals at their

Table 5. Measurements as ratios of standard length for *Libotoni* *blakeburnensis* gen. et sp. nov.

Variable	n	Mean ± S.E.
1. Ratio of body depth to standard length	1	0.202 —
2. Ratio of caudal peduncle depth to standard length	2	0.104 ± 0.116
3. Ratio of predorsal length to standard length	2	0.468 ± 0.0266
4. Ratio of preanal length to standard length	2	0.663 ± 0.0152
5. Ratio of head length to standard length	1	0.305 —
6. Ratio of upper jaw length to standard length	2	0.158 ± 0.00144
7. Ratio of mandible length to standard length	2	0.164 ± 0.00176
8. Ratio of dorsal fin base length to standard length	1	0.136 —
9. Ratio of anal fin base length to standard length	1	0.112 —

broadest point. Posterolaterally the supraorbital sensory canal appears to be bone enclosed, as in the Percopsidae. Approximately triangular prefrontals and rounded triangular nasals are present (Fig. 14A-C). The vomer has an arrowhead-shaped body and a narrow elongate shaft, both apparently edentulous (Fig. 14A, C). The parasphenoid is similarly narrow (Fig. 14C), resembling the condition in *Percopsis*. The pterotics resemble those of other percopsiforms with a median shelf and a longitudinal groove along the lateral edge.

The circumorbital series includes an antorbital, a lachrymal, and an undertermined number of narrow infraorbitals. The lachrymal (Fig. 14A) is elongate, bluntly rounded at each end, and deepest in the middle. A prominent ascending process is located just anterior to the middle of the bone. In one specimen (Fig. 14A) a small thin bone is found anterior to the ascending process, corresponding in position to the antorbital of *Percopsis* and *Sphenocephalus*. The infraorbitals appear to have a ridge following the orbital margin. None of the circumorbitals is spiny.

The hyomandibular has a straight flattened shaft and a broadly expanded head on which ridges radiate from a posterior focus to the opercular condyle and to the anterodorsal articulations with the cranium (Fig. 14A, C). The posterior edge of the shaft is only slightly expanded, but the anterior edge supports a broad web of bone that is notched anteroventrally. The metapterygoid has a rectangular anterodorsal portion and a broad triangular anteroventral portion with a blunt process posterodorsally where it articulates with the hyomandibular. The quadrate is also triangular, with a deep notch for the narrow, pointed symplectic. The ectopterygoid and the endopterygoid are toothless, but the palatine has numerous teeth on a lateral flange (Fig. 14A, C).

The premaxilla is long and narrow, but apparently with an unsegmented alveolar process (Fig. 14A). Strong teeth are present along its entire length. The maxilla (Fig. 14A, C) is narrow except near its distal tip where it is expanded as in other percopsiforms. There is no sign of a postmaxillary process on the premaxilla, dorsal process on the shaft of the maxilla, or a supramaxilla. The upper jaw length to head length ratio is about 0.52.

The dentary is deep and rounded ventrally (Fig. 14C). The ventral arm extends beyond the level of the posterior tip of the narrow dorsal arm, which has teeth along slightly more than half of its oral margin. The angular has a prominent rounded coronoid process and a long pointed anterior process. The ventral portion is rounded, deep, and pointed anteriorly where it curves under the ventral arm of the dentary. A small retroarticular was probably present. The lower jaw length to head length ratio is about 0.55. The quadrate-angular joint lies below the middle of the orbit. In the closed position the mouth is oblique.

The ceratohyal is imperforate, and neither it nor the epihyal have been seen with tooth plates. Of the six acinaciform branchiostegals the heads of at least the fourth and fifth have percopsid projections (Fig. 14B; McAllister, 1968).

The arms of the preopercular (Fig. 14C) meet at right angles, and the horizontal arm is about half the length of the vertical. The bone is not greatly broadened at the angle and there are no spines on the preopercular margin in any specimen. The horizontal arm is deep and blunt anteriorly whereas the vertical arm tapers gradually to its tip. The ridge overhanging the sensory canal descends the anterior edge of the vertical arm, bends forward at the angle, and follows the dorsal margin of the horizontal arm. Only at the angle is the ridge located away from the anterodorsal

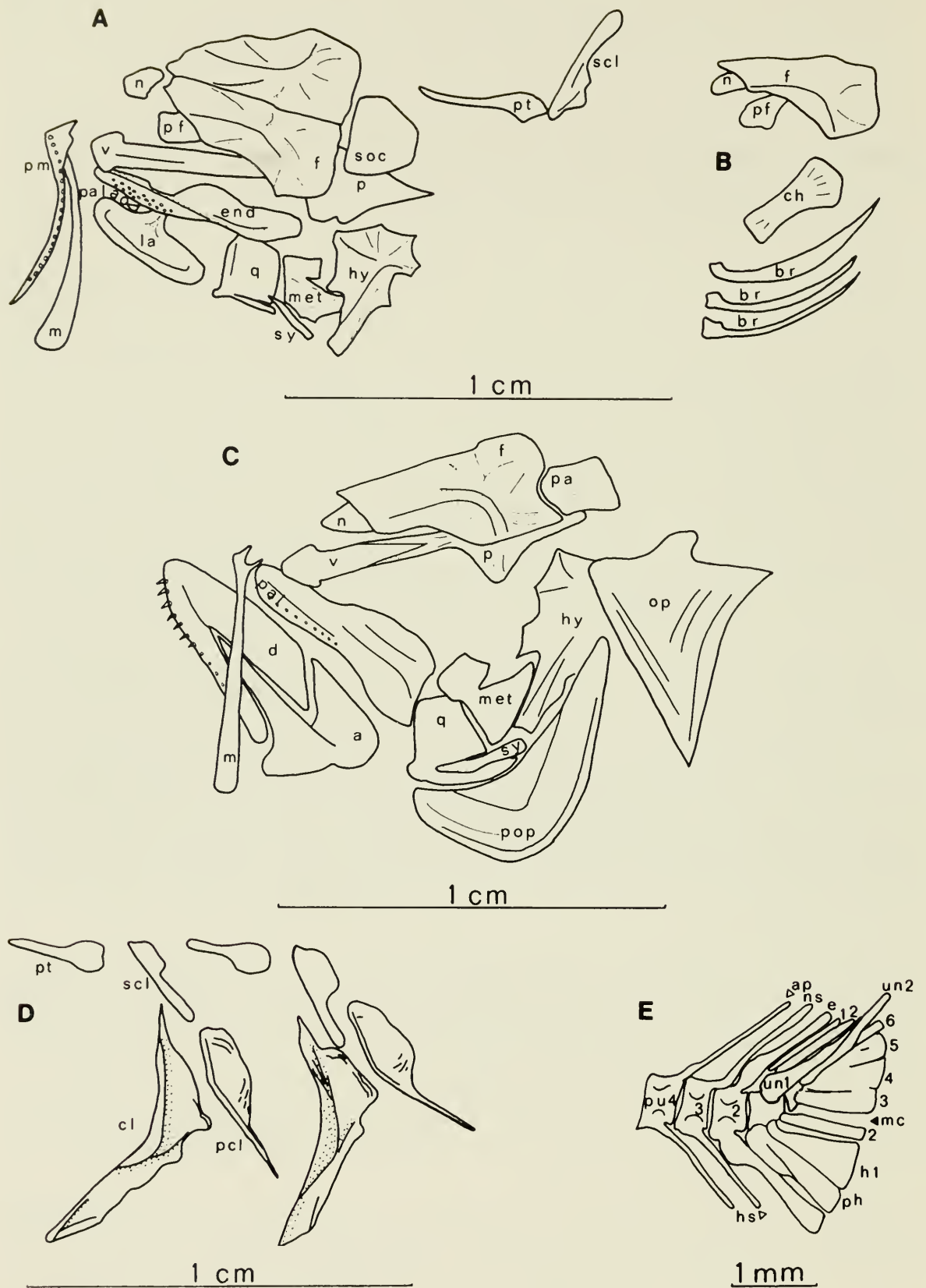


Fig. 14 *Libotonius blakeburnensis* gen. et sp. nov. from Blakeburn Mine L95. For abbreviations see p. 6.

- A. ROM 11165, dorsoventrally compressed skull.
- B. ROM 11157 (holotype), isolated skull bones.
- C. ROM 11156, partially disarticulated skull, right side.
- D. ROM 11157 (holotype), left pectoral girdle, anterolateral view (left), and right pectoral girdle, posteromedial view (right).
- E. ROM 11157 (holotype), caudal skeleton.

margin. The subopercular is blunt and recurved anteriorly, slightly curved and tapered posterodorsally. The opercular (Fig. 14C) resembles those of *Aphredoderus* and *Erismatopterus*, with a blunt posterodorsal process in addition to the large posterior spine. The anterodorsal margin is truncate, another resemblance to *Aphredoderus*. At least five cycloid scales are visible near the point of suspension in one specimen.

VERTEBRAL COLUMN AND MEDIAN FINS

There are 18–19 caudal vertebrae including the second ural centrum, and about 15 abdominals. Of the latter, eight are between the dorsal fin origin and the first caudal vertebra and about seven are anterior to the dorsal fin origin. Many of the hourglass-shaped centra in the caudal series have curved neural and haemal spines. Prezygapophyses are prominent on the posterior caudal vertebrae and on many of the abdominal vertebrae, a resemblance to *Amphiplaga* and *Sphenocephalus*.

The neural and haemal spines of the first few preural vertebrae have small midsagittal expansions. The rest of the caudal skeleton is identical with that of the Percopsidae and Aphredoderidae except for the degree of fusion of the hypurals (Fig. 14E). The parhypural articulates with the combined first preural and first ural centra. Hypural 2 is distinct from hypural 1. Hypurals 3 to 5 are apparently fused, although grooves mark most of the boundary between hypurals 3 and 4, and some of the boundary between hypurals 4 and 5. The sixth hypural is distinct. It is not known whether the second ural centrum is fused to hypurals 3 and 4. There are two uroneurals, the first expanded anteriorly, two epurals, and a complete neural spine on preural centrum 2, as in other percopsiforms. No doubling of neural and haemal spines has been seen. The fin is emarginate with rounded extremities and fork, as in *Tricophanes*.

There appear to be two to three spines and eight to nine soft rays in the dorsal fin. The anal fin originates just behind the end of the dorsal fin and contains two spines and eight or nine soft rays. The first two anal pterygiophores are inserted anterior to the haemal spine of the first caudal vertebra. Both dorsal and anal fins appear to have rounded margins. Median fin spines are weaker than in related species, with a longest dorsal spine length to body depth ratio of about 0.35.

APPENDICULAR SKELETON

The posttemporal and supracleithrum (Fig. 14D) lack serrations, but otherwise resemble the corresponding bones in other percopsiforms. The cleithrum resembles that of the Percopsidae in that it has a large posterodorsal plate. The expanded upper and spine-like lower postcleithra are fused. The pectoral fin contains about 13–15 rays, although the first two are short and unbranched.

The pelvic girdle is small and delicate, and is crossed by the postcleithra although no evidence of articulation has been seen. The anterior, median, and posterior limbs of the pelvic bones are all present. The pelvic fins originate behind the tips of the postcleithra but anterior to the level of the dorsal fin origin. Each fin contains a splint and eight rays, the first unbranched, as in *Amphiplaga* and *Percopsis*.

SCALES

The cycloid scales on the operculum of one specimen are approximately circular in outline, with fine concentric circuli, an apical focus, and strong primary and secondary basal radii. *Aphredoderus* has basal radii according to Lagler (1947) and Cock-

erell (1913). The ctenoid scales that cover the rest of the body have seven to nine long slender ctenii each.

Discussion

The Percopsiformes have recently been revised by Rosen and Patterson (1969) to include six genera other than *Libotoni*: *Sphenocephalus* Agassiz from the Cretaceous of West Germany, *Erismatopterus* Cope and *Amphiplaga* Cope from the Middle Eocene Green River Formation, *Tricophanes* Cope from the Oligocene Florissant Lake beds and from the *Amyzon* shales at Osino Nevada, and the Recent genera *Percopsis* and *Aphredoderus*. Like *Erismatopterus*, *Libotoni* is known only from black and brown shales, rich in carbon. *Amphiplaga* is found only in pale limestones and marls.

Libotoni may be distinguished from all other percopsiforms, as revised by Rosen and Patterson (1969), by the suite of characters given in the diagnosis above, as well as by the following: premaxilla unsegmented, no posterolateral crest on frontals, palatine toothed, lachrymal margin not spiny, parasphenoid narrow, opercular not excavated dorsally, large suprapostcleithrum, first pelvic ray unbranched, body depth to standard length ratio about 0.20, parhypural touching centrum, first two hypurals unfused, caudal fin moderately forked.

Libotoni can be assigned to the Percopsidae (including *Percopsis*, *Aphredoderus*, and *Erismatopterus*) because it shares certain percopsid specializations assumed to be derived states (Rosen and Patterson, 1969): reduction of teeth on the endopterygoid, ectopterygoid, vomer, and ceratohyal; reduction of spines on the lachrymal and preopercular; reduction of scales on the skull bones (although not as reduced as in *Erismatopterus* and *Percopsis*); enlargement of the suprapostcleithrum; increase in vertebral counts, especially abdominals; reduction in dorsal and anal spine counts and size; and reduced caudal peduncle depth. In addition, *Libotoni* lacks the following aphredoderid specializations: segmented premaxilla; posterolateral frontal crest; complete exposure of the supraorbital sensory canal; fusion of the first two hypurals, and the branched first pelvic ray.

Superorder Acanthopterygii

Family Priscacaridae Jordan, 1923

Genus *Priscacara* Cope, 1877

Type Species

Priscacara serrata Cope.

Priscacara aquilonia, sp. nov.

Figs. 15, 16

Diagnosis

Eocene *Priscacara* with body depth to standard length ratio 0.44; head length to standard length ratio 0.38; fine teeth on premaxilla and dentary; preopercular finely serrate at angle; opercular with three or four strong spines; slender pelvic spine; last

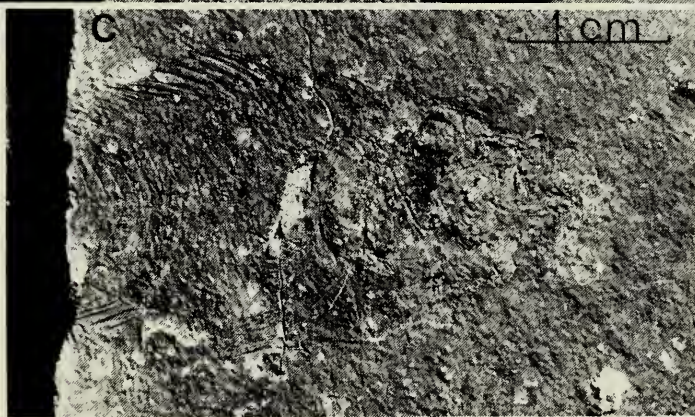
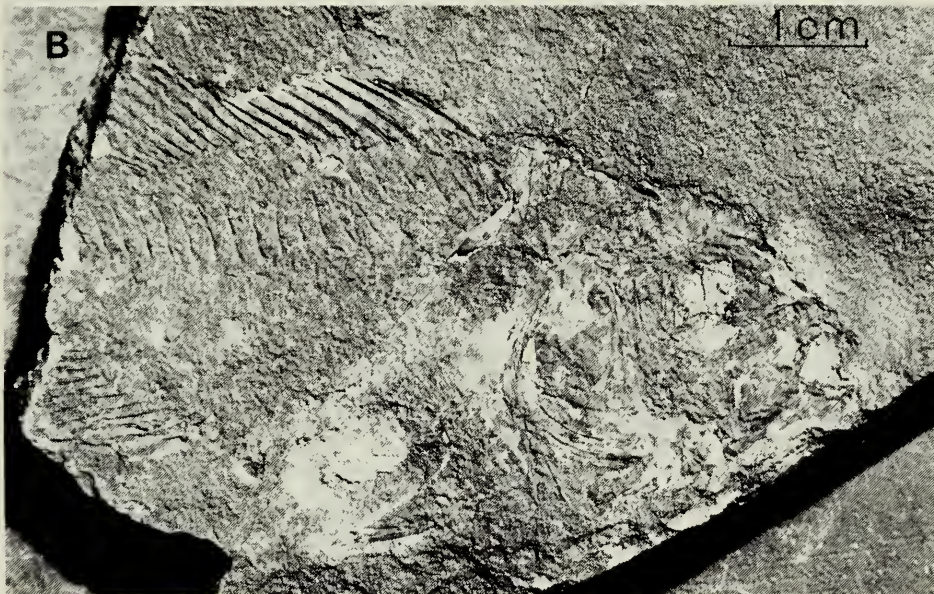
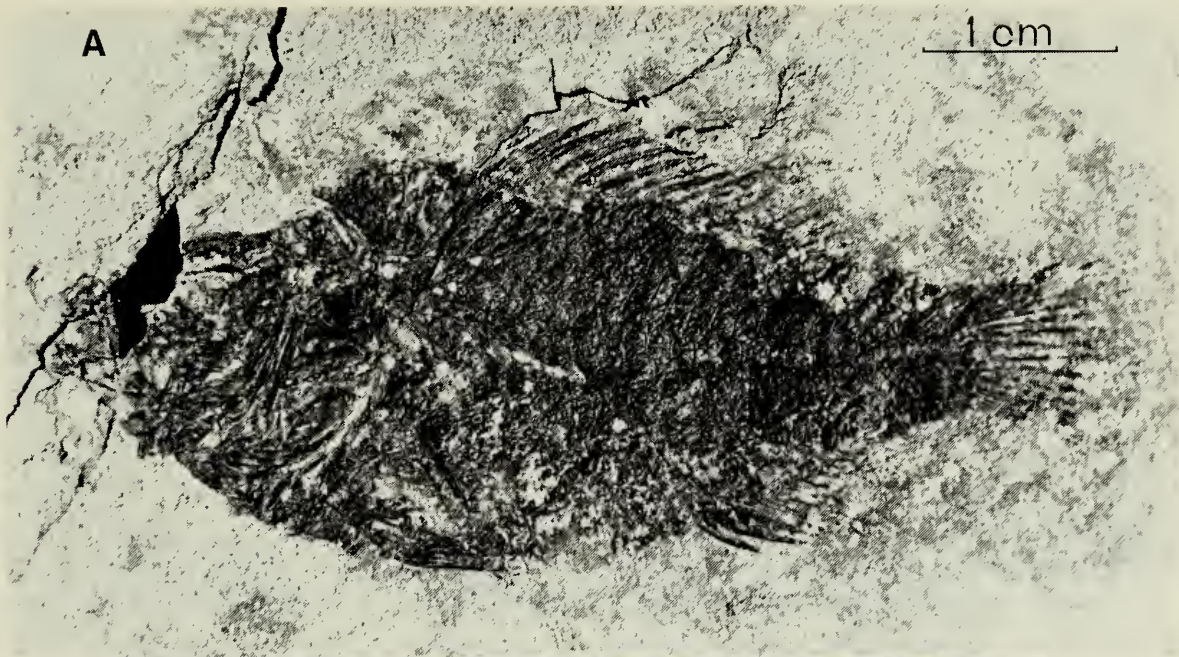


Fig. 15 *Priscacara aquilonia* sp. nov.
A. ROM 11139 (holotype) from Horsefly Mine L88.
B. ROM 11120 from Horsefly Mine L87.
C. ROM 11133 from Horsefly Mine L87.

dorsal spine longer than preceding spine; pelvic origin slightly in advance of dorsal; D X-(XI),11; A III,9-10; P 12-13; V I,5; C i,8,7,i; vertebrae 11-12 + 14; scales strongly ctenoid.

Holotype

ROM 11039 A and B (Fig. 15A), part and counterpart of a fish with standard length of 44.8 mm, collected by the author in 1970.

Type Locality

Horsefly Mine L88, north of Horsefly, British Columbia.

Material

UA 12239, lacking the head, from the type locality, collected by the author in 1975; ROM 11133 and 11120, both lacking the caudal region, collected by the author in 1971 from Horsefly Mine L87, about 10 m below the type locality in the same outcrop.

Etymology

The Latin adjective *aquilonius*, *-a*, *-um* means northern, northerly. *P. aquilonia* is the most northerly *Priscacara* discovered to date.

Description

GENERAL FEATURES

Priscacara aquilonia was apparently a small species, as all four specimens are less than about 55 mm in standard length (Fig. 15) even though large specimens of other fish species are known from the same deposits. The body depth to standard length ratio is slightly less than has been found in most other *Priscacara* species, although the head length to standard length ratio is among the highest. In the holotype especially, the snout is attenuated and the dorsal margin of the skull is less steep than in most *Priscacara* species. The greatest body depth immediately in front of the dorsal fin is about 0.44 of the standard length. The head length to standard length ratio is about 0.38. All four specimens are preserved in lateral view.

SKULL

The frontals (Fig. 16A,B) are thick bones bearing a series of prominent ridges; one parallels the orbital margin, another crosses the midline of the skull near the back of the frontal where it meets its counterpart on the other frontal, and the third extends posteriorly to meet the pterotic. The narrow parasphenoid slopes posteroventrally from the snout across the middle of the orbit. The postorbitals are narrow and the lachrymal is only moderately enlarged so that it does not conceal the upper jaw bones.

The hyomandibular is expanded anteriorly and its shaft is inclined so that the ventral tip is anterior to the middle of the head of the bone. Ridges radiate from the centre of the head but the exact outline of this portion is not preserved. The condyle on the quadrate (Fig. 16A) is located below the anterior third of the orbit. The narrow ectopterygoid and broad endopterygoid are apparently toothless.

The premaxilla (Fig. 16A) has a well-developed median ascending process, pointed and reaching about half the distance to the frontal. A broad, rounded process is

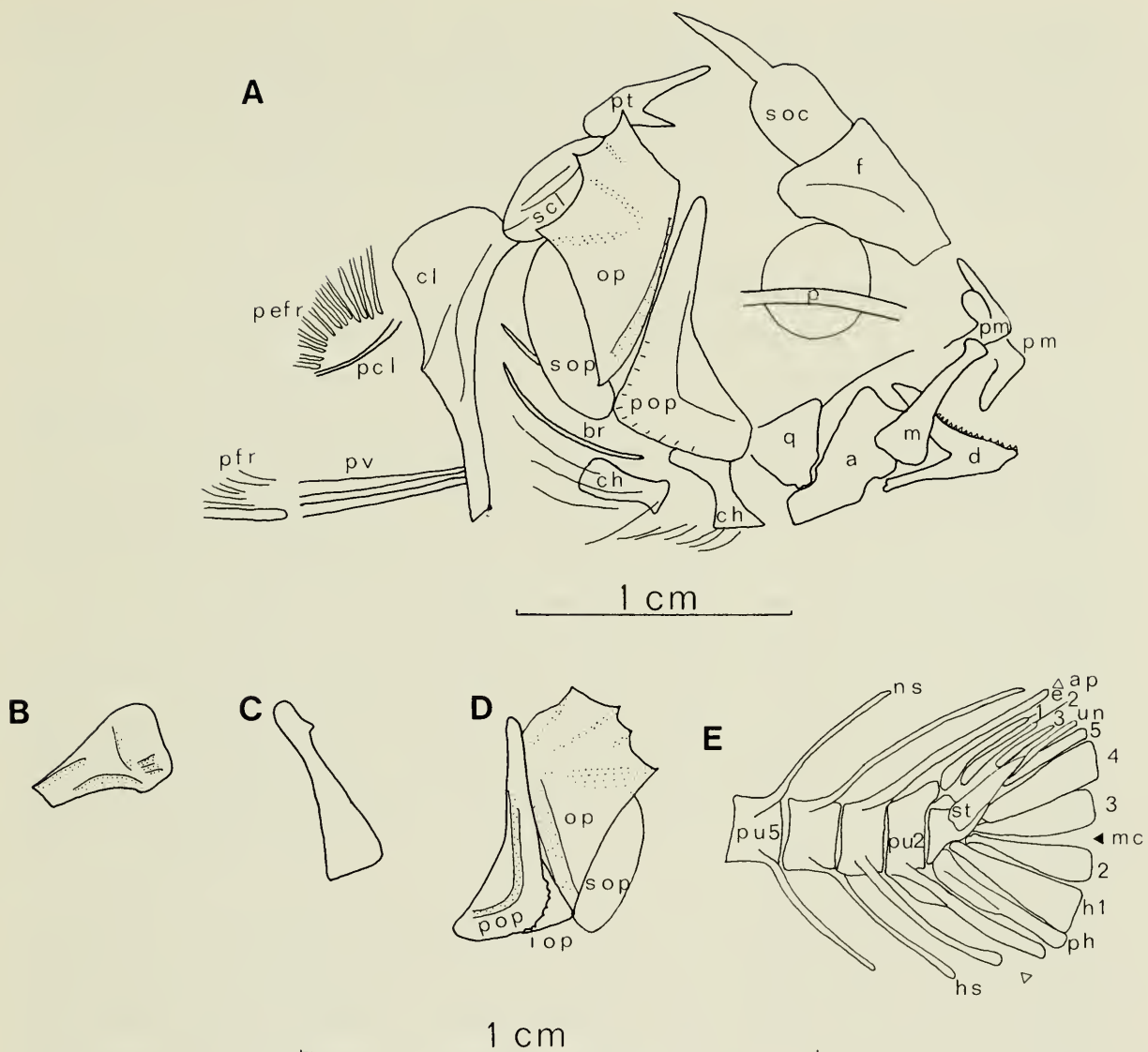


Fig. 16 *Priscacara aquilonia* sp. nov. For abbreviations see p. 6.
 A. ROM 11120, skull, from Horsefly Mine L87.
 B. ROM 11133, frontal, from Horsefly Mine L87.
 C. ROM 11133, maxilla, from Horsefly Mine L87.
 D. ROM 11039 (holotype), opercular bones, from Horsefly Mine L88.
 E. ROM 11039 (holotype), caudal skeleton, from Horsefly Mine L88.

adjacent to the ascending process and about half the length of the latter. The oral margin of the premaxilla is toothed. The maxilla, excluded from the gape by the premaxilla, is about twice as broad posteriorly as anteriorly (Fig. 16A, C). The posterodorsal margin is straight whereas the anteroventral margin is concave where it overlaps the coronoid process of the mandible. The upper jaw length is about 0.32 of the head length.

The mandible is short and stout, about twice as long as deep, and has a high coronoid process (Fig. 16A). Fine teeth fringe the steeply ascending oral margin of the dentary. The ventral arm of this bone is only slightly longer than the dorsal arm. The mandible length is about 0.44 of the head length.

There are about six acinaciform branchiostegals. The ceratohyal is hourglass-shaped and apparently imperforate (Fig. 16A).

The preopercular has well-developed horizontal and vertical arms, the former about half the length of the latter (Fig. 16A, D). The preopercular border is preserved

only in the holotype where it is armed by short, widely spaced serrations. The interopercular is visible only where its subrounded posteroventral corner is exposed. The opercular is pointed dorsally and ventrally and has three strong posteriorly directed spines, each connected by a ridge to the point of suspension (Fig. 16A, D). The subopercular is large.

VERTEBRAL COLUMN AND MEDIAN FINS

There are 25 or 26 vertebrae distributed as 14 caudals and 11 (two specimens) or 12 (two specimens) precaudals. Of the latter, about two are anterior to the first dorsal pterygiophore. Each centrum has a horizontal lateral ridge and bears stout neural and haemal spines which overlap the dorsal and anal pterygiophores. The spines in the caudal series are somewhat S-shaped. Pleural ribs are short and stout, reaching about half the distance to the ventral body margin. Three long supraneurals are present anterior to the dorsal fin, i.e., the first anterior to the first neural spine and the second and third between the first and second neural spines.

There may be two sets of intermuscular bones in the holotype. One set consists of stout bones which appear to insert on the centra as far back as the seventh vertebra and which lie parallel to the vertebral column. The second set is represented by faint impressions of posterodorsally directed long, slender bones. These insert progressively lower on the centra but it is not possible to tell whether they insert on the ribs as do the epipleurals of other perciforms (Merriman, 1940; Blair and Brown, 1961; Dineen and Stokely, 1956).

The caudal skeleton is preserved in the holotype (Fig. 16E) and in UA 12239. It is composed of five hypurals, two uroneurals including the stegural, and apparently three epurals of which the first lies partly over the neural crest of the second preural centrum. There are no free ural centra. The neural and haemal spines of the third preural centrum articulate with procurrent caudal rays. The caudal fin is rounded with 15 branched rays, eight above and seven below the midline.

The dorsal fin contains 10 spines, 11 or 12 soft rays, and 19 or 20 long pterygiophores. The last dorsal spine is slender and slightly longer than the one immediately anterior to it. UA 12239 has an additional small spine anterior to and close to the first well-developed spine.

The anal fin contains three stout spines and nine or 10 soft rays. It is supported by 12 pterygiophores of which the first three are close together and are inserted anterior to the first haemal spine.

APPENDICULAR SKELETON

The cleithrum is markedly expanded dorsally and its ventral ramus is almost vertical (Fig. 16A). The supracleithrum and posttemporal are long and stout. The infra-postcleithrum is long and directed posteroventrally where it ends above and behind the pelvic fin origin. The pectoral fin originates about one-third of the body depth from the ventral body margin and contains 12 to 13 rays.

The pelvic bones are long and slender and meet the cleithrum near the ventral tip of the coracoid (Fig. 16A). The pelvic origin is slightly behind the pectoral origin and the longest rays extend about half the distance to the anal fin. Each pelvic fin contains a long, slender spine and five rays.

SCALES

Cycloid scales have been seen on the opercular, subopercular, and interopercular, but not the preopercular. Dark spots interpreted as chromatophores have been seen on all four of these bones. The strongly ctenoid scales that cover the rest of the body except the head have about 10 strong primary basal radii. About 30 long slender ctenii fringe the apical margin, with about three rows of small ctenii anterior to them in the apical field. The ctenii are arranged in staggered concentric rows, with those of every other row in line with each other. Both apical and basal margins appear to be rounded and concentric circuli are developed in the lateral and basal fields.

Discussion

Priscacara aquilonia is the northernmost *Priscacara* yet discovered. With *P. campi* Hesse from the Roslyn Formation of Washington State it demonstrates that the genus is not restricted to the vicinity of the Green River Formation, and that members of the genus lived in truly fresh water.

Cope (1884, 1886) originally divided the genus into two sections based on dorsal soft-ray counts and size of the pelvic spine. Jordan (1923) erected the new genus *Cockerellites* for those species with 13 or 14 soft dorsal rays and a thin pelvic spine, but included only one of the three described species (*P. liops* Cope) fitting this description. If *Cockerellites* is used, it should also include *P. clivosa* Cope and *P. pealei* Cope because they also have the long soft dorsal of 13-14 rays and thin pelvic spine, and they share with *P. liops* an anal fin with 10-11 soft rays. *P. aquilonia* falls into the genus *Priscacara* (*sensu stricto*), with *P. serrata* Cope, *P. cypha* Cope, *P. oxyprion* Cope, *P. campi* Hesse (1936), and *P. dartonae* Eastman (1917), all of which have a soft dorsal of 10-11 rays, a soft anal of 8-10 rays, and a thick pelvic spine, except that *P. aquilonia* has a pelvic spine only half as thick as most of the dorsal and anal spines. Some additional data were presented for Green River *Priscacara* species by Thorpe (1938). Haseman (1912) found at least 24 and usually 25 vertebrae in the specimens of *Priscacara* that he examined, although Cope had counted only 22-24 vertebrae. Cope probably omitted predorsal vertebrae from his counts, as did Hesse (1936).

Other characters which can be used to distinguish the well-known species of *Priscacara* (*sensu stricto*) from *P. aquilonia* are as follows: *P. campi* D X,11, A III,8, vertebrae 8? + 13, relatively deep-bodied; *P. dartonae* D XI,11, A III,8, vertebrae 10 + 15; *P. serrata* D X,11, A III,10, vertebrae 9? + 14; *P. cypha* D XI,10-11, A III,9, P 15, vertebrae 8-9? + 14; *P. oxyprion* D X,11, A III,8, vertebrae 10? + 14. Relatively little is known about the two other species, *P. testudinaria* Cope (thick pelvic spine, D XI,12?, vertebrae 8? + 16) and *P. hypsacantha* Cope (thick pelvic spine, D X,9, A ?,9, vertebrae 10? + 14). The genus is currently being revised by Cavender (pers. comm., 1976) who believes that the number of valid species will have to be reduced.

Priscacara (*sensu lato*) has been referred to the Pomacentridae (Cope, 1884; Woodward, 1901), the Cichlidae (Haseman, 1912), the Centrarchidae (Regan, 1916), and the separate family Priscacaridae (Jordan, 1923). Most authors have placed it with the Cichlidae, although Romer (1966) continued to list it with the Pomacentridae. Haseman (1912) ruled out association with the Pomacentridae and Labridae, both of which are marine families. The fused lower pharyngeals retaining a suture resemble the condition found in the Cichlidae, while the pharyngeals in the

Centrarchidae are separate. However, unlike the Cichlidae, *Priscacara* has vomerine teeth in at least some species and lacks cichlid specializations such as the long ascending process of the premaxilla. McAllister (1968) said that the opercular is spineless in the Cichlidae and Pomacentridae, but the opercular of *P. aquilonia* and some Green River *Priscacara* species is distinctly spined.

The caudal skeleton is of little help because *Priscacara* has a generalized caudal skeleton similar to that figured for *Kuhlia* by Gosline (1961) and *Parakuhlia* by Monod (1968). Patterson (1968b) gave a long list of genera in different families with this type of caudal skeleton, regarded as the most primitive perciform type, which could give rise to those found in the other families under consideration by loss and fusion of the various elements. In view of the uncertainties which still surround any assignment of *Priscacara* to a Recent family it is here classified in the separate family Priscacaridae.

Summary and Conclusions

The Eocene freshwater fish fauna of British Columbia is described from more than 14 localities in six separate sedimentary basins. Included in this study are 240 fish and 275 fish scales collected during 1969, 1970, 1971, and 1975. Previous studies using mammal teeth, K-Ar determinations, and palynology have established Middle Eocene ages of about 50 Ma B.P. for all localities.

Scale specimens described as Amiidae gen. et sp. indet. are indistinguishable from amiid scales from the Ochoco Pass fauna of Oregon and from scales of the Recent *Amia calva*. Large collections of the hiodontid *Eohiodon rosei* from the Kamloops area (the type locality) and from the Horsefly area provide new information on the variability of the species. Two distorted hiodontid specimens from Horsefly Mine L88 may not be conspecific with *E. rosei*, and are therefore described as *Eohiodon* sp. Hiodontid scales from *E. rosei* localities are indistinguishable from Ochoco Pass hiodontid scales.

The salmonid *Eosalmo driftwoodensis* gen. et sp. nov. is morphologically intermediate between Recent Thymallinae and Salmoninae. Salmonid specimens resembling *Eosalmo* are also described from the Princeton area.

The catostomid *Amyzon brevipinne* Cope from the Princeton area is redescribed, and *A. aggregatum* sp. nov. is described from the Horsefly area. Peaks in the histogram of standard length frequencies of *A. aggregatum* probably represent year classes, with a modal standard length of 175 mm representing fish about five years old at death. Small samples of *Amyzon* from the Kamloops and Driftwood Creek areas are not assignable to species.

The percopsiform *Libotoniuss blakeburnensis* gen. et sp. nov. from the Princeton area is assigned to the Percopsidae because it shares presumably derived character states with the Percopsidae. The new species *Priscacara aquilonia* is described from four small specimens from the Horsefly area.

The British Columbia Eocene fauna includes the most northerly Eocene percopsid and priscacarid, the oldest known hiodontid and salmonid, and some of the oldest known catostomids. The fauna is dominated by the genus *Amyzon* which occurs in

each of the main areas sampled. *Eohiodon* was found in three of the four main areas, and was abundant in two of these. The faunas of the Horsefly and Kamloops areas seem most similar because of the presence of large numbers of *Eohiodon rosei* in both and the probable presence of *Amyzon aggregatum* in both. This is consistent with previous palynological correlations (Hills and Baadsgaard, 1967) which suggested a similarity in age between the Princeton area and Driftwood Creek localities, with the Horsefly and Kamloops area localities slightly older. *Priscacara* is known from the Green River Formation and from the Eocene Roslyn Formation of Washington State, providing additional evidence of the Eocene age of the British Columbia sediments.

Similarities at the family and genus levels exist between the British Columbia Eocene and other Eocene and Oligocene localities in North America (Table 6). The discovery of a percopsid and of a *Priscacara* in the British Columbia fauna (this report) and of a species of *Amyzon* in the Green River Formation (Cavender, pers. comm.) increases the known similarity between the two faunas. Future accurate determinations of the Florissant and Nevada *Amyzon* species and of the Clarno (Ochoco Pass) and Grant hiodontid and *Amyzon* species may permit more reliable comparisons of these deposits with the British Columbia Eocene. A faunal list by Dunkle (*in* Pearson, 1967) and University of Alberta collections obtained during 1976 show that the Republic Washington fauna includes amiid scales, *Eohiodon*, *Eosalmo*, *Amyzon*, and a percopsid. A description of the Republic fauna will be given elsewhere, but the fauna may best be considered as a southward extension of the British Columbia Eocene fauna.

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Table 6. Occurrence of British Columbia Eocene taxa in other North American Eocene and Oligocene freshwater localities.

	British Columbia		Washington		Wyoming	Oregon	Nevada	Colorado	Montana
	Princeton	Horsefly Kamloops	Republic	Roslyn	Green R.	Ochoco Pass	Elko Osino	Florissant	Grant L.
Amiidae	X	X	X		X	X		X	X
Hiodontidae	X	X	X			X			X
<i>Eosalmo</i>	X		X						
<i>Amyzon</i>	X	X	X		X	X	X	X	X
Percopsidae	X		X		X				
<i>Priscacara</i>		X		X	X				

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