A NEW SPECIES OF THE FISH *AMIA* FROM THE MIDDLE EOCENE OF BRITISH COLUMBIA

by MARK V. H. WILSON

ABSTRACT. A new species of amiid fish is described from a semi-articulated skeleton found in Middle Eocene freshwater shales of the Allenby Formation, Princeton Group, south-central British Columbia. The new species is assigned to *Amia* because it lacks *Kindleia* specializations such as styliform teeth, and it shares skull specializations with *A. calva*, *A. scutata*, and *A. uintaensis*. The new species is reconstructed as a deep-bodied piscivore with large jaws and strong, sharp teeth. The holotype is the first identifiable skeleton to be found among many amiid scales recovered from numerous fossil-fish assemblages in southern British Columbia and northern Washington State.

THIS paper presents a description and partial reconstruction of a new species of amiid fish, based on a single partially articulated skeleton and several disarticulated skull bones from Middle Eocene freshwater shales in British Columbia. The significance of the discovery lies in the relatively complete information obtainable about the anatomy of this fish, and the resulting implications for the taxonomy of fossils of *Amia* elsewhere in North America.

Amia calva, the only living species of amiid, is confined to the fresh waters of south-eastern North America, but Late Cretaceous and Tertiary records of amiids are widespread in central and western parts of the continent (text-fig. 1), as well as in Europe and Asia. North American fossil amiids were reviewed by Boreske (1974), who recognized three valid fossil species in a single genus from the twenty-three species and seven genera previously described. Many of the rejected names were based on poorly preserved material or on single vertebrae, and were considered to be junior synonyms or *nomina dubia*. The three fossil species considered valid by Boreske are the Late Cretaceous to Middle Eocene *Kindleia fragosa*, the Palaeocene to Early Oligocene *A. uitaensis*, and the Oligocene *A. scutata*.

None of the previously known Eocene occurrences of *Amia* from British Columbia, Washington, and Oregon had been identified to species, because they consisted primarily of undiagnostic scales (Cavender 1968; Wilson 1977*a*, 1978*a*, 1979, 1980) which were nevertheless very common fossils. These westernmost records seemed to reflect habitats similar to those preferred by other *Amia* species including *A. calva* (Scott and Crossman 1973): warm, shallow, swampy conditions, as evidenced by lithology and the associated fishes, insects, and plants (Wilson 1980).

The discovery of the *Amia* specimens described here resulted from work by palaeobotanists on silicified plant fossils, preserved in an outcrop of alternating chert and coal layers in the Allenby Formation (Boneham 1968; Miller 1973; Robison and Person 1973; Basinger 1976; Basinger and Rothwell 1977). James Basinger discovered a trionychid turtle in shales immediately overlying the chert. When I revisited the site in 1977 and 1978, I obtained the fish specimens described here, along with coprolites containing fish bones, and disarticulated remains of small suckers (Catostomidae: *Amyzon* sp.), and trout-perches (Percopsidae: *Libotonius* sp.). The fish occur in the shales with carbonized plant fossils which include stems and twigs, dicotyledonous leaves, taxodiaceous leafy shoots, seeds, ferns, and amber (Wilson 1980).

GEOLOGY AND AGE

The specimens were found in a hard black siliceous shale immediately overlying a 10-m-thick outcrop of interbedded carbonaceous chert and coal which extends into the Similkameen River

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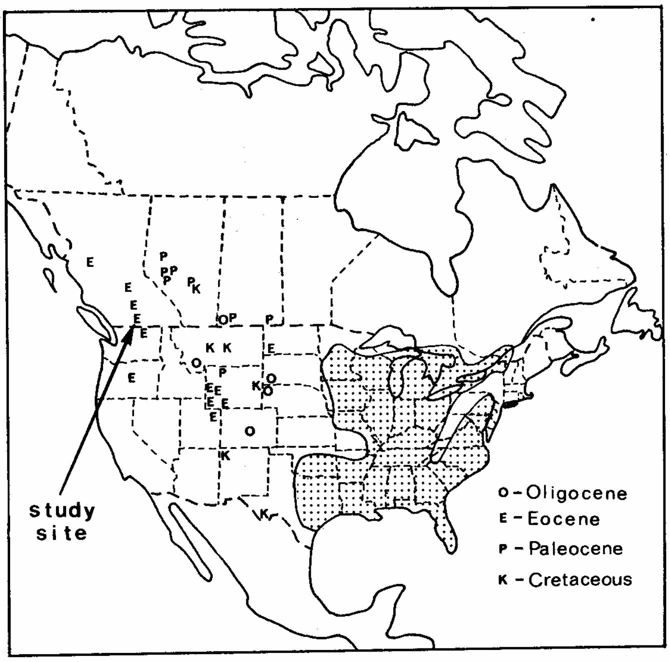


TEXT-FIG. 1. Map of North America showing the fossil locality. Also shown are Late Cretaceous through Oligocene sites from which remains of *Amia* and/or *Kindleia* have been reported (modified after Boreske 1974), together with the distribution of Recent *Amia calva* (stipple, after Scott and Crossman 1973).

from its east bank, 8·4 km south of Princeton, British Columbia (text-fig. 1). According to Boneham (1968) the fossiliferous layers are 550 m above the Princeton-Black Coal of the Allenby Formation, Princeton Group. The Allenby Formation consists of sedimentary rocks, deposited in fresh water, and yields an abundant assemblage of fishes and insects at several localities in the Princeton Basin (Wilson 1977*a*, 1977*b*, 1978*b*, 1980).

The age of the fossils is Middle Eocene, based on potassium-argon ages of approximately 47–50 million years for the Allenby Formation (Hills and Baadsgaard 1967), and on the occurrence of the mammalian genus *Trogosus* elsewhere in the formation (Russell 1935). Other occurrences of fossil amiid scales in British Columbia and in the Klondike Mountain Formation of Washington State are of a similar geologic age (Wilson 1977*a*, 1978*a*, 1979).

MATERIALS AND METHODS

The *Amia* fossils occur as fractured bone, spread parallel to bedding planes. The hard and tough matrix contains a faithful imprint of the original shape and ornamentation of the bones and, therefore, the specimens were prepared by removing the fossilized bone with mechanical tools and an ultrasonic probe. Casts of the resulting impressions were made in black latex. Measurements were taken from the original shale moulds. For photographic purposes the black-latex casts were coated with ammonium chloride. The reconstructions were made by drawing the outlines of the bones at uniform scale, using a camera lucida attached to a Wild M8 stereomicroscope, and then graphically assembling the bone outlines with regard to perspective distortions and suture outlines. For dermal roofing bones of the skull, the external surfaces of the bones correspond to their ornamented portions. Osteological terminology follows Boreske (1974) except that, following Janot (1967), the term 'posttemporal' is used in place of 'suprascapular' (Table 1). The abbreviation UAVP designates that specimens are deposited in the Vertebrate Paleontology Collections, Department of Geology, The University of Alberta.

TABLE 1. Abbreviations used in the figures

a	angular
ao	antorbital
br	branchiostegal
c	cleithrum
ch	ceratohyal
cot	coronoid teeth
d	dentary
ds	dermosphenotic
e	endopterygoid
es	extrascapular
fr	frontal
h	hyomandibular
io	infraorbital
la	lachrymal
m	maxilla
mc	metacleithrum
n	nasal
op	opercle
p	pectoral fin
pa	parietal
pop	preopercle
ps	parasphenoid
pst	parasphenoid teeth
pt	(dermo)pterotic
r	rostral
s	posttemporal
sa	surangular
sc	supracleithrum
sm	supramaxilla
so	subopercle
sy	symplectic
v	vomer
vt	vomerine teeth
vtb	vomerine tooth base

SYSTEMATIC DESCRIPTION

Class OSTEICHTHYES
Order AMIIFORMES
Family AMIIDAE Bonaparte, 1837
Genus AMIA Linnaeus, 1766

Type species. Amia calva Linnaeus, 1766.

Amia hesperia sp. nov.

Text-figs. 2–6

Diagnosis. Deep-bodied *Amia* having square parietals; long frontals with shallow orbital excavation; large nasals without anterior notch; large fourth infraorbital; deep maxilla, mandible, and opercle; dentary with large teeth; lachrymal with posterior notch; parasphenoid with long posterior ramus and short tooth patch; vomers with short tooth patch; vomers and coronoids with sharp, conical teeth; and cleithrum with arms at obtuse angle.

Holotype. UAVP 14758 (text-figs. 2–5 and 6A, B), an almost complete, partially articulated fish in part and counterpart with estimated total length about 55 cm, preserved as a mould in hard siliceous shale, and collected by the author's party in 1977.

Etymology. The specific epithet is from the Latin *hesperius* meaning 'western'.

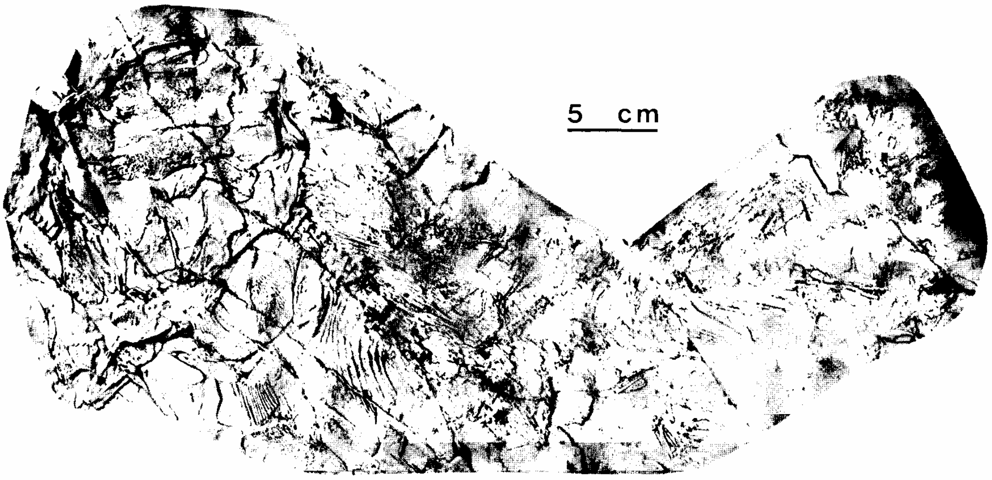
Locality and age. Ashnola chert site, 8·4 km S of Princeton, British Columbia (U.T.M. Grid Reference 1OUFK783724), from the Middle Eocene Allenby Formation, Princeton Group.

Non-type material. UAVP 13801, a patch of scales and two branchial tooth plates; UAVP 13804 (text-fig. 6C), a right dentary and maxilla; UAVP 13805, a right extrascapular (text-fig. 6F), right fourth infraorbital, and left fifth infraorbital; UAVP 13806 (text-fig. 6D), a branchial toothplate; and UAVP 13812 (text-fig. 6E), a right opercle. All of the above specimens were collected at the type locality in 1977, within a few centimetres of the holotype.

Description. Unless otherwise indicated, the following description is based on the holotype, which shows the dermal investing bones of the skull in the part (text-fig. 3) and many ventral and internal bones of the skull in the counterpart (text-fig. 4). The postcranial skeleton is present but not well preserved (text-fig. 2). Non-type material is limited, but corroborates conclusions based on the holotype.

Parietals are approximately square (text-fig. 3), and frontals are relatively long and narrow (width to length ratio 0·41), with shallow orbital excavations ('orbital concavity ratio' of Boreske 1974 is 0·117; 'dermosphenotic angle' is 136°). The 'parietal/frontal' ratio is 0·37. Extrascapulars are decidedly wider laterally than medially (text-figs. 3, 6F), dermopterotics substantially overlap the frontals laterally, and are tapered both anteriorly and posteriorly. Nasals are large, not notched anteriorly, and fit the anterior outline of the frontals posteriorly. The rostral is stout, and the ornamented area of the antorbitals is small.

Laterally, the lachrymal has a prominent posterior notch which fits the anterior end of the small second infraorbital (text-fig. 3). The large fourth infraorbital is deep posteriorly, where it has an angular margin. It tapers to the orbit, but forms less of the orbital rim than does the fifth infraorbital. The latter is about as deep anteriorly as posteriorly, and is considerably smaller than the fourth infraorbital.



TEXT-FIG. 2. *Amia hesperia* sp. nov., holotype, part, UAVP 14758a, latex peel of whole fish.

The premaxilla is not preserved. The maxilla is a stout, deep bone with a marginal row of numerous, very small teeth (text-figs. 3, 4). The posterodorsal margin of the maxilla has an elongate excavation which fits a long, deep supramaxilla.

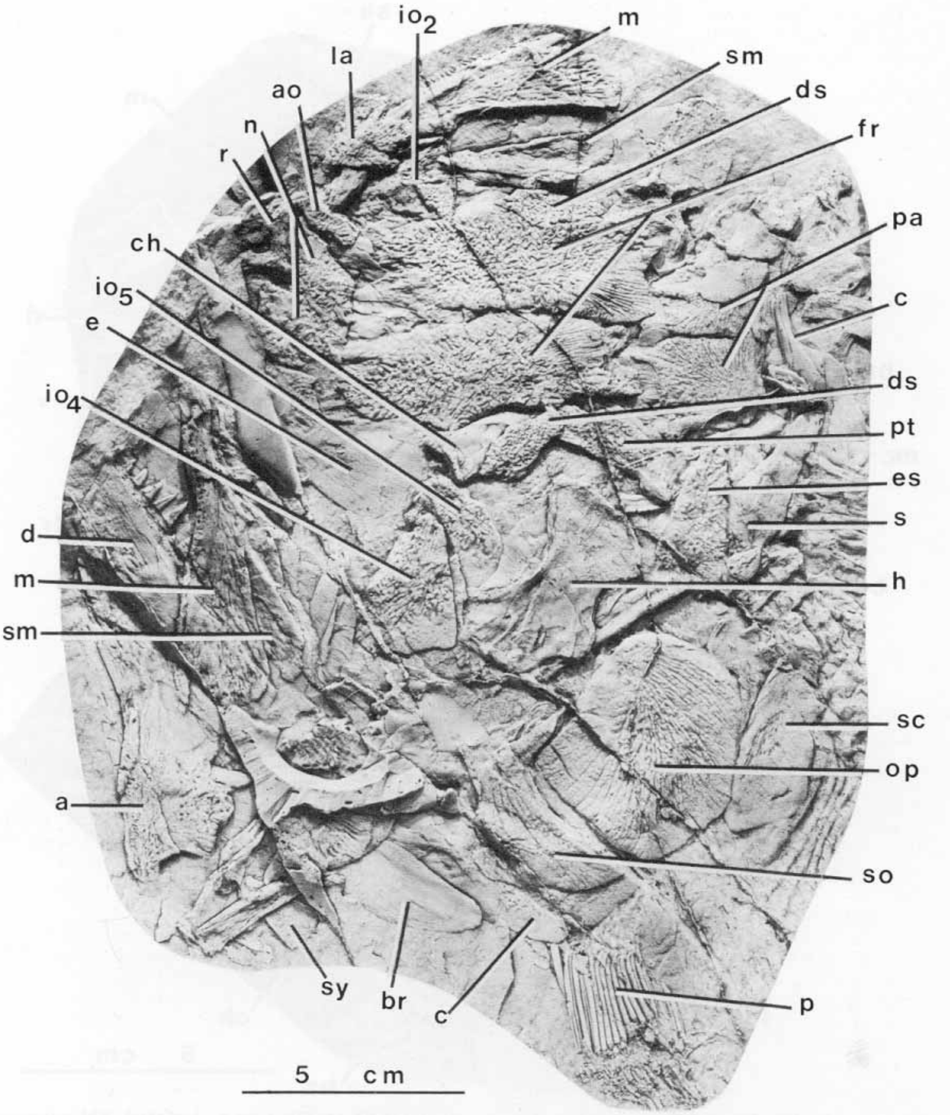
The mandible is deep and stout, with a steeply inclined posterior border formed by the angular and surangular (text-figs. 3, 4), a broad coronoid process, and a dentary with a long row of large, pointed teeth (text-figs. 3, 4, 6B). Proportions and shape of the dentary are more clearly shown in UAVP 13804 (text-fig. 6C), where, toward the front of the bone, the ventral margin is apparently angled ventrally. This is interpreted as a medial deflection of the mandibular ramus as seen most noticeably in *Kindleia fragosa* (Boreske 1974, figs. 16B, 18). The coronoids are not visible, but small, sharp teeth located internal to the dentary teeth, where coronoid teeth would be expected, are visible in the holotype (text-fig. 6B).

The parasphenoid (text-fig. 4) is partially obscured by a branchiostegal, a ceratohyal, an angular, and the vomers, but its proportions are evident. It has a relatively long posterior ramus, 0·84 times the length of its anterior ramus. The ascending process of the right side is partially covered in the holotype by an angular, but is approximately perpendicular to the long axis of the parasphenoid. The posterior portion of the parasphenoid tooth patch consists of many tiny denticles. Where it is not obscured by the ceratohyal (text-fig. 4), the anterior ramus of the parasphenoid appears devoid of denticles.

Vomers are elongate (text-fig. 4) but have short-toothed portions. Most teeth are broken, but unbroken teeth together with some broken tooth tips indicate that the vomerine teeth are conical and sharply pointed (text-fig. 6A). The endopterygoid (text-figs. 3, 4) is plate-like and bears numerous tiny denticles.

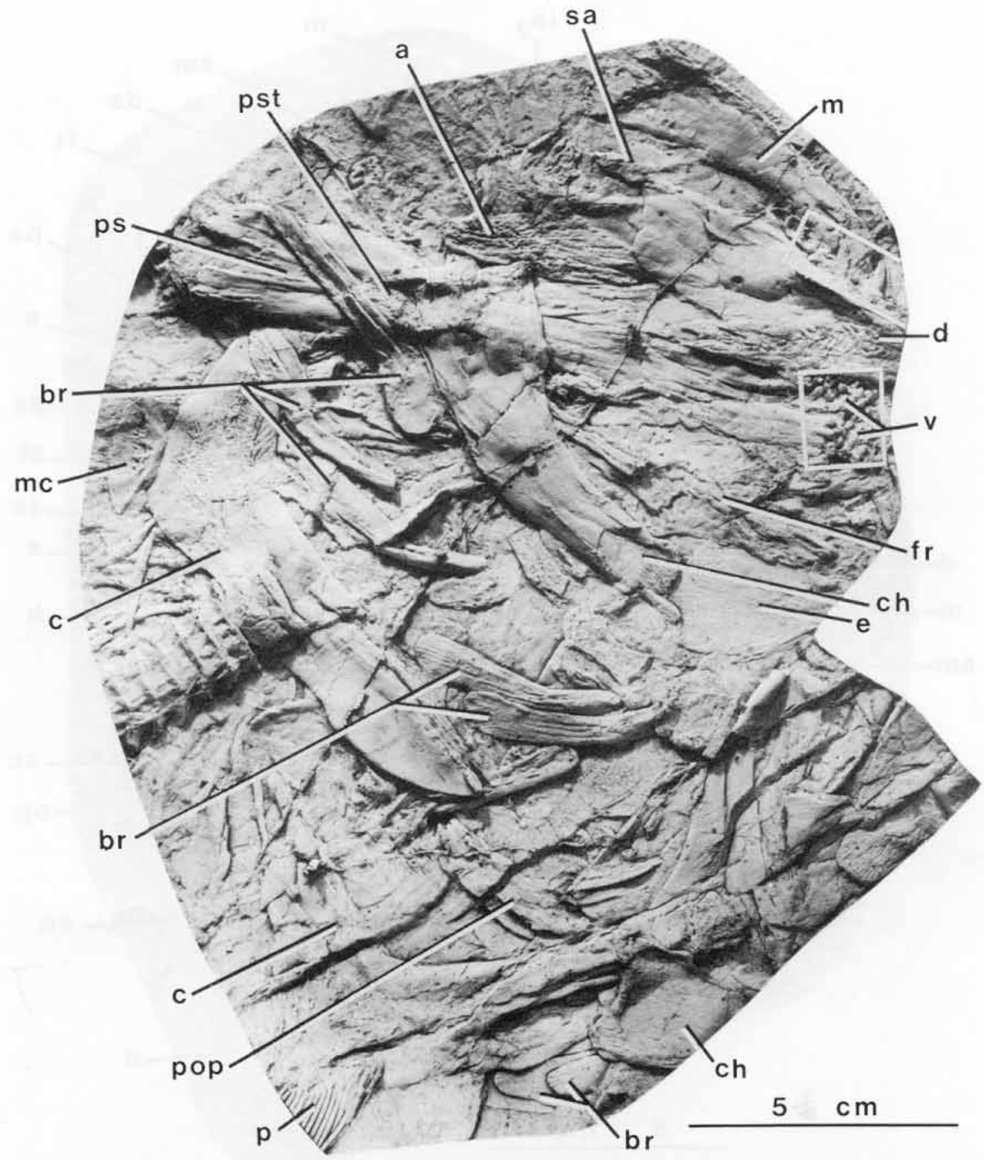
The opercular bones are deep relative to their length. The opercle in the holotype has a length to height ratio of 0·90, and these proportions are also seen in UAVP 13812 (text-fig. 6E). The subopercle has an elongate anterodorsal ramus. The preopercle is not well preserved (text-fig. 4), but seems similar to those of other species of *Amia*.

The hyomandibular, preserved in lateral view (text-fig. 3), has a posteroventrally directed opercular process and a moderately developed posterodorsal notch. The symplectic is partially visible in the holotype (text-fig.



TEXT-FIG. 3. *Amia hesperia* sp. nov., holotype, part, UAVP 14758a, latex peel of skull. Abbreviations Table 1.

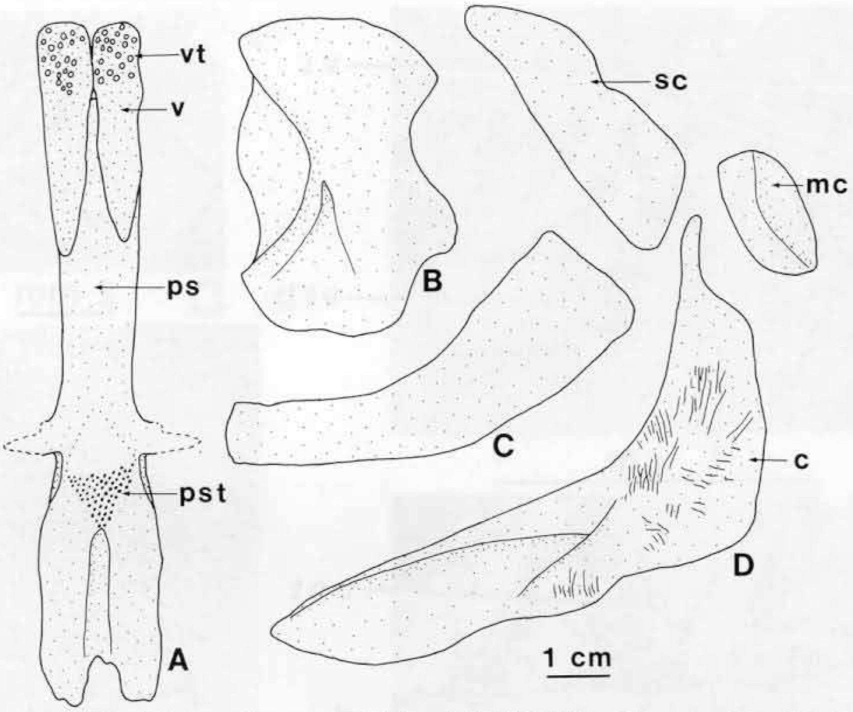
3). The ceratohyal (text-fig. 4) is typical of the genus, and bears branchiostegals which vary from narrow to broad. Branchiostegal ornamentation is extensive and posterior margins of preserved branchiostegals are rounded. Branchial arches are not preserved, but several tiny bones bearing numerous sharp, hollow, conical, and slightly curved teeth (text-fig. 6D) were found in the shales close to the holotype. In view of the similarity



TEXT-FIG. 4. *Amia hesperia* sp. nov., holotype, counterpart, UAVP 14758b, latex peel of skull. Abbreviations Table 1. The two areas outlined in white are enlarged in text-fig. 6A, B.

of teeth of these bones to teeth of the holotype, the bones are interpreted as branchial tooth plates of the same species.

The dermal pectoral girdle is well preserved in the holotype (text-figs. 3-5). The cleithrum is like that of other *Amia* species, but the ornamented area is more extensive than in *A. calva*. As well, the posterodorsal



TEXT-FIG. 5. *Amia hesperia* sp. nov., holotype UAVP 14758. A. Reconstruction of parasphenoid and vomers in central view. B. Left hyomandibular, lateral view. C. Left ceratohyal. D. Left dermal pectoral girdle in lateral view. Abbreviations Table 1.

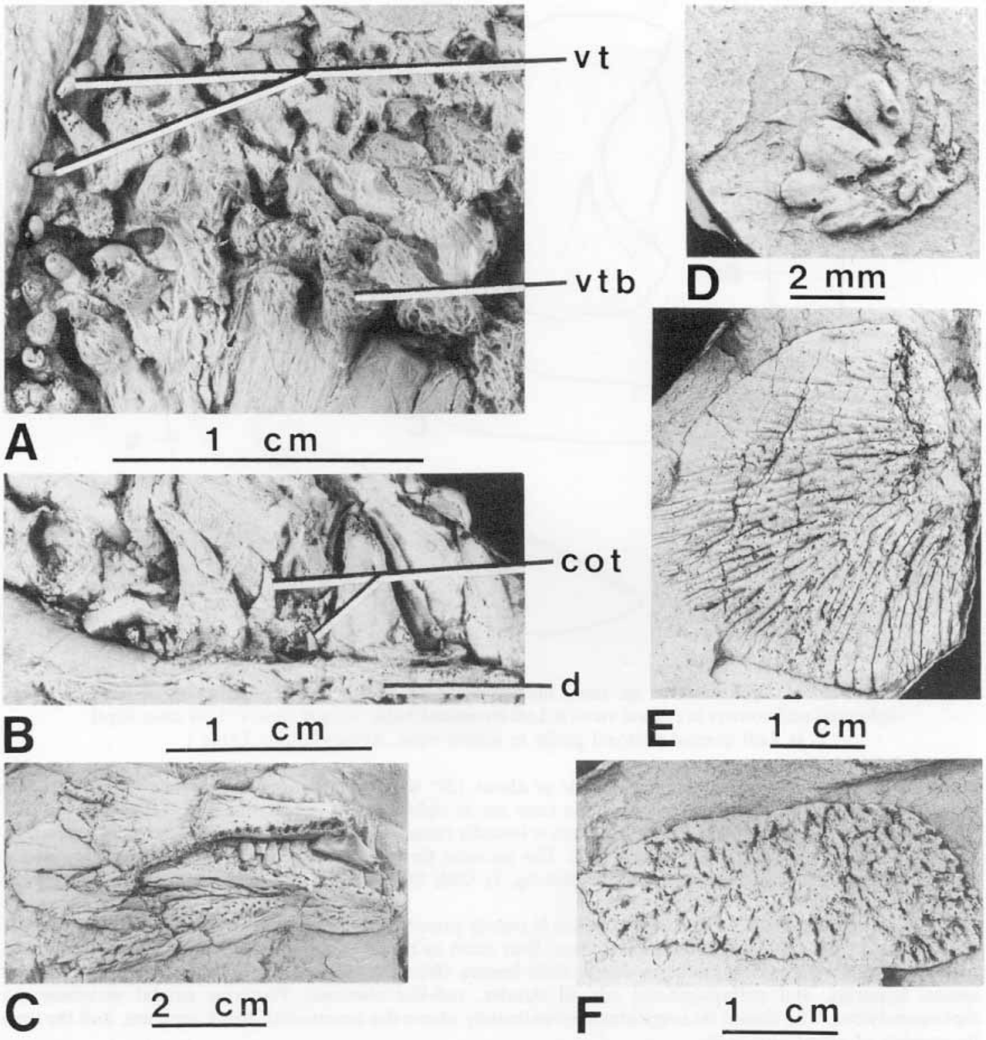
ramus of the cleithrum forms an obtuse angle of about 120° with the anteroventral ramus, as in *K. fragosa* but not in *A. calva* or *A. uintaensis* where the rami are at right angles to each other (Boreske 1974, fig. 21). The plate-like posterior portion of the cleithrum is broadly rounded. The posttemporal (text-fig. 3) is elongate, and the posterolateral portion is ornamented. The pectoral fin has about sixteen rays and originates medial to the posteroventral angle of the cleithrum (text-fig. 3). Only the general position of the pelvic fin is apparent in the holotype.

The postcranial portion of the axial skeleton is poorly preserved (text-fig. 2), but a few general statements are possible. Anterior trunk vertebrae are about four times as broad as they are long, and bear dorsal neural facets and ventral aortal facets as in other *Amia* species (Boreske 1974, fig. 11). Ribs, neural and haemal spines, hypurals, and pterygiophores are all slender, rod-like elements. Posterior caudal vertebrae are diplospondylous. The dorsal fin originates approximately above the seventeenth trunk centrum, and the anal fin consists of about nine rays.

Scales are thinner than those of Cretaceous and Palaeocene *K. fragosa* from Alberta (O'Brien 1969), thicker than scales of *A. calva*, but similar to other Eocene *Amia* scales from British Columbia (Wilson 1977*a*). They are mostly rounded apically and truncate basally, about two-thirds as wide as long, with an apical (posterior) focus, a thick, horseshoe-shaped rim of smooth lamellar bone around the lateral and apical margins, and a central area of somewhat thinner bone ornamented on the internal surface by small bumps. Externally the circuli or ridges radiate to the margins from the focus, which is approximately triangular and has its apex directed basally (anteriorly). In the focal area the circuli form a vermiculate pattern.

Reconstruction

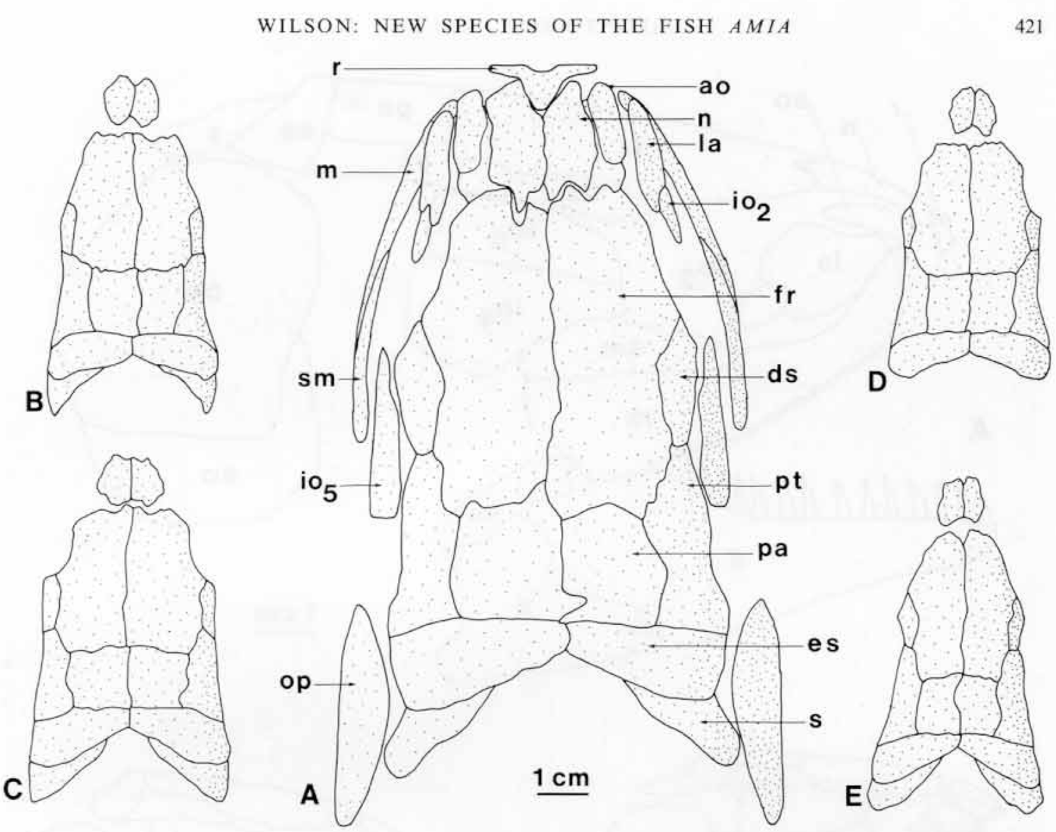
The parasphenoid and vomers of *A. hesperia* are reconstructed in text-fig. 5A. Notable features are the inferred short parasphenoid tooth patch, the ascending processes perpendicular to the



TEXT-FIG. 6. *Amia hesperia* sp. nov. A. Detail of anterior portion of vomers of holotype, UAVP 14758b, showing pointed vomerine teeth. B. Detail of dentary tooth row of holotype, UAVP 14758b, showing pointed coronoid teeth. C. Right dentary and maxilla, lateral view, UAVP 13804. D. Branchial tooth plate, UAVP 13806. E. Right opercle, lateral view, UAVP 13812b. F. Right extrascapular, dorsal view, UAVP 13805c. Abbreviations Table 1.

long axis of the parasphenoid, and the elongate vomers with their anterior one-third occupied by sharp teeth.

Text-fig. 7 shows the skull, reconstructed in dorsal view, compared with partial reconstructions of the skulls of *A. calva*, *K. fragosa*, *A. scutata*, and *A. uintaensis*. Notable are the elongate frontals with shallow orbital excavations, relatively short parietals, tapered extrascapulars, long



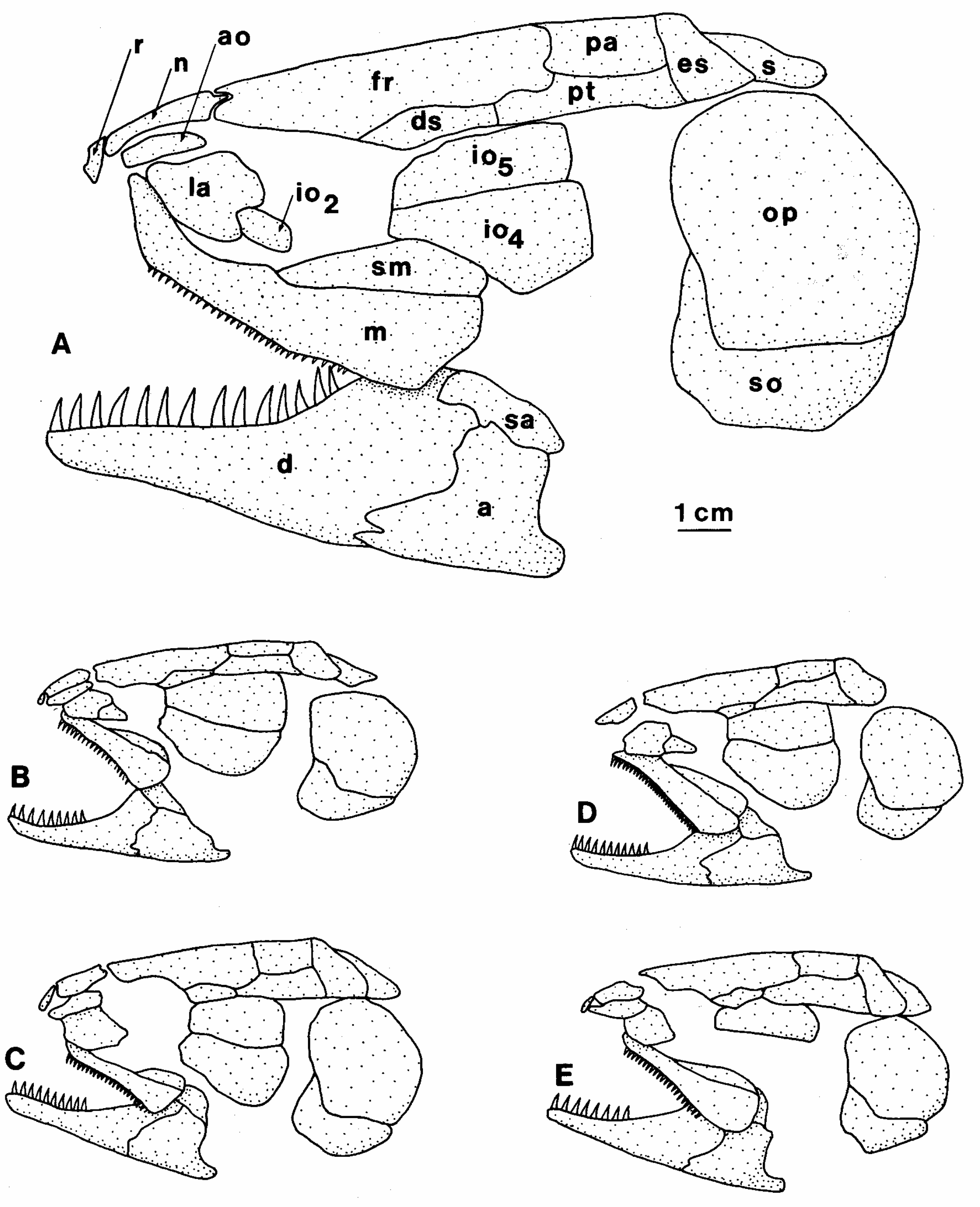
TEXT-FIG. 7. Comparison of dorsal skull reconstructions of North American amiids. A. *Amia hesperia*, sp. nov., based on the holotype, UAVP 14758. B. *A. calva*. C. *Kindleia fragosa*. D. *A. scutata*. E. *A. uintaensis*. B–E after Boreske (1974), not to uniform scale. Abbreviations Table 1.

dermopterotics, large nasals shown interdigitating with the frontals, and the over-all shape of the skull roof, which is elongate but only slightly narrower at the rear of the orbit than it is at the rear of the extrascapulars.

The skull of *A. hesperia* is reconstructed in lateral view in text-fig. 8. In this view the skull appears relatively deep and large-jawed. Features that contribute to the impression of skull depth are the large lachrymal, deep opercle and subopercle, deep maxilla and supramaxilla, deep mandible, and large teeth in the dentary. The obtusely angled cleithrum is additional evidence of a deep body. In view of the poor preservation of the postcranial skeleton, a reconstruction of the entire fish is not presented here. However, the evidence of the dorsal fin apparently originating over the seventeenth trunk centrum suggests that *A. hesperia* was long-bodied, rather than short and stout as was *K. fragosa* (Boreske 1974, fig. 21).

DISCUSSION

In addition to the one Recent and three fossil species of *Amia* from North America that were recognized by Boreske (1974), there are a number of nominal European and Asian fossil species (Boreske 1974; Janot 1967). Fairly complete information is available about several of these, including some which are most similar to the North American *K. fragosa* (*A. kehreri* Andreae, *A. valenciennesi* Agassiz, *A. munieri* Priem, and *A. russelli* Janot), and others which are similar to *A. uintaensis* (*A. robusta* Priem and possibly *A. mongoliensis* Hussakof). Janot (1967), Estes and Berberian (1969),



TEXT-FIG. 8. Comparison of lateral skull reconstructions of North American amiids. A. *Amia hesperia*, sp. nov., based on the holotype, UAVP 14758. B. *A. calva*. C. *Kindleia fragosa*. D. *A. scutata*. E. *A. uintaensis*. B–E after Boreske (1974), not to uniform scale. Abbreviations Table 1.

Boreske (1974), and Gaudant (1980) advocate synonymizing *Kindleia* Jordan with *Amia* Linnaeus. The main distinguishing features of *Kindleia* are the presence of styliform teeth on the coronoids, dermopalatines, and vomers; differences in proportions of some skull bones; and a shorter body with less separation between the skull and the origin of the dorsal fin and between the insertion of the dorsal fin and the caudal fin, and about twelve fewer trunk centra and eight fewer monospondylous caudal centra (Boreske 1974). These authors cited intra- and interspecific variability in *Amia*, and found the above differences insufficient grounds for separation into two genera, especially considering that Estes and Berberian (1969) believe most features of *Kindleia* to be primitive. Gaudant (1980), however, treats *Kindleia* as a subgenus of *Amia*, and cites several derived features shared by *K. fragosa* and *A. kehreri* in support of this view. Gaudant's list of shared derived characters is very similar to the list of features (above) that Estes and Berberian (1969) interpreted as mostly primitive. For example, Gaudant cites a relatively short, deep body; an enlarged fourth infraorbital; short parietals; and styliform coronoid, palatal, and vomerine teeth.

I agree with Gaudant that these characters are mostly derived, but go further in favouring the recognition of *Kindleia* as a genus distinct from *Amia*. To Gaudant's list of shared derived characters can probably be added the relatively short, wide frontal: the frontals of the geologically older but closely related genera *Urocles* (Lange 1968) and *Enneles* (Santos 1960) are long and narrow. An enlarged fourth infraorbital found also in *A. hesperia* and in *Enneles* (Santos 1960) should probably be removed from the list of derived features of *Kindleia*.

Retention of *Kindleia* as a separate genus is also useful because most species share a number of other similarities, some or all of which might be primitive. These include the deep orbital notch in the frontal; the short vomers; the small supramaxilla; the narrow maxilla and mandible; the short, truncated gular plate; and fewer than seventy-five vertebrae.

Boreske (1974) suggested that molluscs were a more important part of the diet for *Kindleia* than for *Amia*. At some localities in the Palaeocene Paskapoo Formation of Alberta, *Kindleia* remains are found with finely crushed mollusc shells concentrated in patches on bedding planes. To my knowledge gut contents have not been observed in *Kindleia* specimens, but the explanation of the styliform teeth as an adaptation to molluscivorous habits is a reasonable one. Perhaps the fish did not completely swallow the shells with their contents, or perhaps the patches of broken shells represent regurgitated gastric residues.

The new species described here clearly belongs with *Amia*. *A. hesperia* has none of the *Kindleia* specializations listed above. It shares with some or all of the other well-known species of *Amia* derived features such as a shallow orbital excavation in the frontal, a deep maxilla with elongate supramaxilla, the lack of an anterior notch in the nasal, the presence of a posterior notch in the lachrymal, and a tooth patch restricted to the front end of the vomer.

A. hesperia differs from valid North American species of *Amia* (Boreske 1974) in the following features. Compared with *A. uintaensis* it has slightly shorter frontals, shorter parietals, unnotched nasals, interdigitating nasals and frontals, posteriorly notched lachrymals, more angular fourth infraorbitals, a relatively longer posterior parasphenoid ramus, parasphenoid ascending processes more nearly at right angles to the long axis, shorter parasphenoid and vomerine tooth patches, and more obtusely angled cleithra. Compared with *A. scutata* and *A. calva* it has longer frontals, shorter parietals, interdigitating nasals and frontals, a shorter parasphenoid tooth patch, more rectangular opercles, and more obtusely angled cleithra. It differs further from *A. calva* in having longer pterotics, larger fourth infraorbitals, a relatively shorter posterior parasphenoid ramus, ascending processes more nearly at right angles to the long axis, and more extensive ornament on the cleithra.

A. robusta, a Palaeocene to Oligocene European species, is very similar to *A. uintaensis*. Compared with *A. hesperia* it has more elongate frontals, more rectangular parietals, a longer parasphenoid tooth patch, and more right-angled cleithra, judging by bones illustrated in Janot (1967).

Piscivorous habits for *A. hesperia* are implied by the large mouth and the large, sharp teeth. This supports previous conclusions (Wilson 1980) based on association of amiid scales with coprolites containing fish bones at many Eocene localities in British Columbia and Washington

State. I would predict that the amiid(s) occurring at these other localities will prove to be closely related to or conspecific with *A. hesperia*. The geographic distribution of Eocene amiid species in North America, with *A. hesperia* in the extreme west and *A. uintaensis* and *K. fragosa* in the mid-west, is suggestive of geographic ranges separated by a north–south barrier such as a continental divide similar to the one separating western and eastern species of fishes today.

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