A New Genus and Species of Amiidae (Holostei: Osteichthyes) from the Late Cretaceous of North America, with Comments on the Phylogeny of the Amiidae

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A NEW GENUS AND SPECIES OF AMIIDAE (HOLOSTEI; OSTEOECHTHYSES)
FROM THE LATE CRETACEOUS OF NORTH AMERICA, WITH
COMMENTS ON THE PHYLOGENY OF THE AMIIDAE

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ABSTRACT—Melvius thomasi, new genus and new species, from the Late Cretaceous Hell Creek Formation of northeastern Montana and Wyoming, is one of the largest known amiiids (standard length 160 cm or more). It is based on disarticulated elements of the skull and axial skeleton. Additional isolated elements probably referable to this species are known from North and South Dakota, Utah, Texas and New Mexico. All known specimens occur below the Cretaceous–Tertiary boundary. Specimens of large amiiids from the Early Cretaceous Trinity Formation, Texas, may also be referable to this or a related taxon. Detailed comparison with other amiiids, described from more complete material, is not yet possible, but some features of the new taxon appear to relate it to Enneiles and Pachyamia. Melvius lived in estuaries and large rivers along the western margin of the Western Interior Sea.

INTRODUCTION


The largest species of Amia is A. uintaensis, known from the Paleocene and Eocene of the Rocky Mountains. Fragmentary remains of large Cretaceous amiiids, from Wyoming, Montana, South Dakota, Texas, and New Mexico (see map, Fig. 1) until recently have been relegated to this species, sometimes referred to as A. cf. A. uintaensis (Boreske, 1974). Associated material from the Hell Creek Formation of northeastern Montana is complete enough to show that these specimens are not referable to any named taxon.

Abbreviations—AMNH = American Museum of Natural History, New York; CM = Carnegie Museum, Pittsburgh; MNA = Museum of Northern Arizona, Flagstaff; SDSM = South Dakota School of Mines Museum of Geology, Rapid City; SMUSMP = Southern Methodist University, Schuler Museum of Paleontology, Dallas, Texas; UCM = University of Colorado Museum, Boulder; UCMP = University of California, Museum of Paleontology, Berkeley; UNM = University of New Mexico Paleontological Collections; UW = University of Wyoming, Museum of Geology, Laramie; YPM = Yale Peabody Museum, New Haven.

SYSTEMATIC PALEONTOLOGY

Family AMIIDAE Bonaparte, 1841
Genus MELVUS, new genus
MELVUS THOMASI, new species

Papichthys sp. indet., Brown, 1907:842
Papichthys sp. indet., Gilmore, 1924:27
Papichthys sp. indet., C. M. Sternberg, 1924:68
Amia sp., Greenwald, 1971:18
Amia cf. A. uintaensis, Boreske, 1974:64
Amia sp. cf. A. uintaensis, Breithaupt, 1982:132

Holotype—UCMP 129600, right maxilla and operculum, left angular. Fragments of right cleithrum, anterior right and left dentary, left ?premaxilla, left angular, post-temporal, and infraorbital; tooth crowns; 4 trunk and 6 caudal vertebrae, neural spines, lepidotrichia, and associated fragments of dermal bone. Collected by Mr. Harley J. Garbani in 1982.

Horizon and Locality—UCMP V83117, Garfield County, Montana. Detailed locality information is on file at the University of California Museum of Paleontology, Berkeley. Upper Hell Creek Formation, latest Cretaceous (Maastrichtian).

Etymology—For Mr. Melvin Thomas, Garfield County, Montana, in gratitude for his generous assistance to UCMP field crews.

Diagnosis—Very large amiid (standard length [tip of snout to base of caudal fin] may exceed 160 cm). Differs from all other known amiiids in having central trunk vertebrae ventrolaterally concave, anterior maxilla circular in cross section. Deep pit for articulation of premaxilla overlapping the most anterior maxilla alveo-
FIGURE 1. Index map showing collecting areas for *Melvius thomasi.*

ulus. Dentary with 14 teeth; horizontal ramus wider than deep. Cleithrum lacking sculpture, forming a 90 degree angle between dorsal and ventral arms. Basioccipital width more than twice its height. Differs from *Enneles* in having fused infraorbitals 4 and 5, and lacking the supramaxilla. Differs from all other amiids except *Pachyamia* and *Enneles* in having carinate teeth and alveoli with crenulated borders.

**Hypodigm**—Hell Creek Formation, Montana; UCMP 129904, right frontal fragment from V70208. UCMP 120226, tooth crowns from V73077. UCMP 129673, trunk vertebra; UCMP 120323, tooth crowns from V73085. UCMP 123289, 150+ tooth crowns; UCMP 130386, dentary fragment from V73087. UCMP 123381, trunk vertebra from V73090. UCMP 128813, tooth crown from V73103. UCMP 128852, tooth crowns from V74116. UCMP 128894, tooth crown from V74117. UCMP 129677, 2 trunk vertebrae, 1 caudal vertebra; UCMP 129675, right maxilla fragments; UCMP 129674, tooth crown and operculum fragment; UCMP 129676, tooth crown, from V76138. UCMP 129912, maxillary fragment and tooth crown from V76162. UCMP 130655, vertebra, from V77121. UCMP 130287, tooth crowns from V77130. UCMP 130286, tooth crown from V77119. UCMP 129905, dural bone fragments, from V78143. UCMP 129678, 2 tooth crowns from V80088. UCMP 129679, trunk vertebra from V80091. UCMP 129906, vertebra fragment; UCMP 129907, tooth crown, and UCMP 129908, post-temporal fragment from V80092. UCMP 130288, tooth crown from V80119. UCMP 129680, 3 caudal vertebrae; UCMP 129681, fragments of operculum, post-temporals, ?parietal, other fragments of dermal bone, and fin rays; UCMP 130387, vertebra, post-temporal, and other fragments from V81159. UCMP 129909, dural bone fragment; and UCMP 129910, vertebra, from V81257. UCMP 129911, vertebra, from V81258. UCMP 130088, tooth crown from V82210. UCMP 129682, 7 tooth crowns from V82013. UCMP 129683, anterior left maxilla, 2 trunk vertebrae and 1 fragment, lepidotrichia and dermal bone fragments; UCMP 129912, dural bone fragments; UCMP 129914, caudal vertebra; UCMP 129913, ?parietal fragment; UCMP 130089, maxillary fragment from V82060. UCMP 129915, vertebra, from V83024. UCMP 129916, dural bone fragments, from V83064. UCMP 129684, trunk vertebra fragment; UCMP 129917, tooth crown, from V83077. UCMP 129601, nearly complete left cleithrum and infraorbital, fragments of ceratohyal, from V83100. UCMP 129602, trunk vertebra from V83104. UCMP 129877, caudal vertebra from V83130. UCMP 129918, trunk vertebra from V83198. UCMP 129685, trunk vertebra from V83254. UCMP 129686, trunk vertebra from V84002. UCMP 129687, caudal vertebra from V84003. UCMP 130388, caudal vertebra from V84016. UCMP 129692, left frontal, fragments of post-temporal, ?parietal, and other skull bones, and trunk vertebra from V84050. UCMP 129876, trunk vertebrae, premaxilla, ?parietal, preopercular, other skull fragments, and lepidotrichia from V84128. UCMP 129878, posterior trunk vertebra, from V84130. UCMP 130147, vertebra and tooth crown from V84171. UCMP 130289, anterior trunk vertebra from V84182. UCMP 130144, 3 vertebrae, vertebra fragments and fin support; UCMP 130145, basioccipital and 3 vertebrae from V84225. UCMP 130146, 2 vertebrae, fin support, and skull fragment from V84227. AMNH 6385, anterior trunk vertebra. AMNH 11600, tooth crowns. AMNH 11604, opercular fragment. LACM 37887, 30783, 30412, 126131, vertebrae. LACM 30412, right dentary, 5 vertebrae, tooth crowns, basicranium and angular fragments. LACM 37218, opercular fragment.

Bug Creek Anthills, Montana; UCMP 129671, trunk vertebra from V65127.

Lance Formation, Wyoming; UCMP 72700, post-temporal from V5618. UCMP 54156 and 56277, trunk vertebrae; UCMP 72467, tooth crown from V5620. UCMP 56276, vertebra fragment; UCMP 72470, vertebra fragment; UCMP 72688, tooth crowns from V5711. UCMP 72647, vertebra from V5815. UCMP 62936, vertebra from V5817. UCMP 72469, anterior left maxilla fragment from V5921. UCMP 129951, 129952, vertebrae from V84216. UW 14276, right maxilla; 14621, right maxilla fragment; 14619, left maxilla fragment; 14618, anterior right maxilla frag-
ment; 14623, trunk vertebrae; 14622, 4 caudal vertebrae; 14620, left maxilla fragment from UW V79032. CM 256, trunk vertebra. YPM 6311, trunk vertebra.

Specimens tentatively referred to *Melvius thomasi*:
Hell Creek Formation, North Dakota; UCMP 131681, right dentary fragment, UCMP 131707, right ?parietal, UCMP 131708, skull fragments from V86075.
Hell Creek Formation, South Dakota; SDSM 64210, anterior trunk vertebra. SDSM 64289, 64314, 64333, 64344, 64362, tooth crowns.
Fruitland Formation, New Mexico; MNA P1.1809, 24 associated vertebrae and neural spines.
Fruitland or Kirtland Formation, New Mexico; UNM B466, B-691, B-406A, B-415, B-437, B-699, B-704, B-094, B-165a, B-165, B-443, vertebrae. UNM B-5406, ?parietal.
Kirtland Formation, New Mexico; LACM 55081, 55083, 55084, 55085, vertebra fragments.
Judith River Formation, Montana; UCMP 130632, anterior trunk vertebra.
Masuk Shale Member, Mancos Shale, Utah; vertebrae and tooth crowns, uncataloged UCM specimens.

**Description**

**Premaxilla**—The type specimen (UCMP 129600) includes a toothed fragment, which may be from the left premaxilla. It is wide, shallow, slightly roughened and convex dorsally, and has two alveoli. A second fragment, UCMP 129876, probably from the most anterior part of the premaxilla, has three large alveoli on the ventral surface, a deep pit on the dorsal surface, and part of a suture medial to the tooth row.

**Maxilla**—The type specimen, UCMP 129600, includes the best preserved maxilla (Fig. 2). It is essentially round in cross section, with a wide shelf medial to the tooth row. There are 18 preserved alveoli, the largest at the front. All are round and have deeply crenulated borders. The anterior end, from about the fourth alveolus forward, is angled strongly dorso-medially. A large, deep pit for articulation with the premaxilla overlaps the first alveolus medially. On the dorsal surface opposite this pit is a protruding knob of bone, approximately where infraorbital 1 would have made contact. The maxilla lacks sculpture but is pitted by many small foramina on the lateral surface above the tooth row. Posteriorly the maxilla deepens and narrows, although the medial shelf extends the length of the tooth row. The posterior end of the tooth row is broken away; behind the last alveolus the maxilla tapers dorsally to a thin, laterally convex blade. Although most of the postero-ventral portion is broken away, what remains suggests that there was a deep notch between two posterior arms of the maxilla. There is no evidence of a supramaxilla.
FIGURE 3. *Melvius thomasi*, n. gen., n. sp. Left frontal, UCMP 129692. A, dorsal; B, ventral; C, medial; D, lateral view. Anterior to right, except D. Scale bar = 1 cm.

Estes (1964:43) reported a fragment of a much larger maxilla, UCMP 72469, from the Lance Formation of Wyoming.

**Frontal**—A left frontal (Fig. 3), UCMP 129692, lacks only the postero-medial and antero-lateral tips. Length is approximately three times width. It is very thick near the anterior end. The sculpture consists of coarse ridges that radiate from a point near the midline opposite the orbit. The posterior dorsal surface of the bone is essentially planar, and the anterior dorsal surface is slightly concave upward.

The anterior part of the midline suture, where the bone thickens greatly, becomes correspondingly deep, almost 1 cm. The frontal apparently was sutured to the neurocranium along a wide band on the ventral surface, paralleling the midline suture. A second ventral suture extends from the midline opposite the front of the orbit to the lateral margin near the postero-lateral corner.

**?Parietal**—Three thick fragments of dermal bone, from UCMP 129680, 129692, and 129876 (Fig. 4A), may be fragments of parietals. There are deep sutures on the two edges. Coarse sculpture radiates from an area perhaps near the missing postero-medial corner.

**Post-temporal**—Several post-temporal fragments are known. This element (Fig. 4B) was evidently broadly triangular in dorsal view, only slightly wider than long, with a stout, forward-directed ventral spine. The sculp-

ture consists of coarse, often anastomosing ridges that radiate from a thickened area near the lateral margin. The most anterior portion, which would have lain beneath the extrascapular(s), is smooth; sculpture on the medial arm consists of ridges that do not anastomose.

**Gular**—The type specimen (UCMP 129600) includes the posterior portion of what is probably a gular (Fig. 5A). It is thinner than the skull roof bones, tapered toward the margins, and very delicately sculptured with radiating striae. Its outline is somewhat irregular.

**Opercular**—A partial right opercular (Fig. 5B) is included in the type specimen, UCMP 129600. UCMP 129600 is relatively thin (much thinner than bones of the skull roof) and the external surface is completely covered with fine ridges that radiate from the articular socket toward the margins. The anterior margin and most of the dorsal and posterior margins of UCMP 129600 are missing. AMNH 11604 and LACM 37218 preserve the thicker dorsal margin with its coarse sculpture; probably these specimens are from larger individuals than that of the holotype.

**Infraorbital**—The right infraorbital element (Fig. 6), UCMP 129601, may represent the fused infraorbitals 4 and 5 (terminology after Boreske, 1974, fig. 15). The ventral margin is broken away; the dorsal margin is broadly convex posteriorly and concave anteriorly where the element tapers to a blunt point. Fine sculpture radiates from near the anterior tip toward the margins, but the tip itself is smooth. Pores of the infraorbital canal open on the dorsal and ventral margins of the tip. Part of the posterior margin is broken away, but a deep notch suggests that this may be a compound element. The anterior tip probably contributed to the postero-ventral rim of the orbit. The holotype specimen, UCMP 129600, includes the anterior tip of the right infraorbital.

Jain (1985) documented several variations in the shape and number of infraorbitals of *Amia calva*; additional specimens of *Melvius* are needed to determine whether infraorbitals 4 and 5 are indeed fused, and if this is the usual condition.

**Preopercular**—UCMP 129876 includes a fragment that is probably the medial portion of the right preopercular (Fig. 7A). The lateral surface is coarsely pitted and has a thin flange extending from the postero-medial margin where it would contact the anterior border of the opercular. The antero-medial portion and the dorsal and ventral tips are broken away.

**Basioccipital**—The posterior part of a basioccipital (Fig. 7B), UCMP 130145, is wide and low; its posterior face is more than twice as wide as it is high. The element tapers anteriorly. The ventral surface is poorly preserved and there is no sign of aortal facets, but there is a wide midline groove that forms a notch on the ventral midline (but slightly offset to the left) of the posterior face. The parapophyseal articulation appears not to reach the posterior border. The lateral surface bears three narrow grooves. On the dorsal surface the bone is deeply excavated laterally, almost to the posterior border, perhaps for articulation with the exoccipital. The brain cavity is cone-shaped and does not reach the posterior border. The posterior tip of the cavity is flanked by a pair of neural facets that do not reach the posterior border, suggesting that there may have been two vertebral centra fused to the basioccipital.

**Cleithrum**—Although incomplete, the left cleithrum (Fig. 8), UCMP 129601, shows that the angle between antero-ventral and antero-dorsal limbs was about 90°.
FIGURE 7. Melvius thomasi, n. gen., n. sp. A, preopercular fragment, UCMP 129876; B, basioccipital fragment, UCMP 130145, ventral view. Scale bar = 1 cm.

degrees. The postero-ventral border curves gently down and forward. There is only a faint trace of sculpture along the ventral margin. The antero-ventral limb is thick and lies nearly in the vertical plane. It is perforated by a large foramen and crossed on its medial surface by a prominent ridge that descends from near the dorsal border posteriorly toward the ventral border. The dorsal tip is sharply grooved and tapers to a blunt point.

Dentary — The holotype specimen (UCMP 129600) includes the anterior left dentary (Fig. 9) and fragments of the right dentary. LACM 30412 includes a nearly complete right dentary (Fig. 10). The toothed portion is shallow and broad, and smoothly convex laterally. There are 14 alveoli of subequal size, although the most posterior is somewhat smaller than the others. The alveoli have crenulated margins, some with thin-walled tooth root fragments in place. A shelf medial to the tooth row exceeds the tooth row in width. The most medial one-third of this shelf is roughened, probably for the articulation of coronoids and the prearticular.

The medial surface of the dentary lies in the vertical plane and has a prominent Meckelian groove that extends forward to the symphysis. A large foramen within the groove lies at the level of the ninth alveolus. Posterior to the tenth alveolus the medial surface is open in a large Meckelian fossa, the ventral margin of which is broken away.

On the lateral surface the dentary is marked by numerous foramina. Posterior to the last alveolus the dorsal border turns sharply up into a coronoid process. At the base of the coronoid process is a prominent scar on the lateral surface, presumably for the insertion of part of M. adductor mandibulae (terminology of Allis, 1897).

A fragment of a particularly large dentary (UCMP 131681, Fig. 11A) was collected in 1986 from the Hell Creek Formation in southwestern North Dakota (see Fig. 1). Although the Hell Creek Formation there may be slightly younger than in northeastern Montana, this fragment is indistinguishable from LACM 30412 except for its larger size. I estimate from the proportions of LACM 30412 that UCMP 131681, if complete, would be at least 270 mm long.

Angular — The left angular of the type specimen (UCMP 129600) is convex laterally and thickened on the dorsal and ventral margins. It is externally somewhat rugose but not sculptured. The antero-ventral border is thick and tapers to a blunt point. The dorsal border has a wide longitudinal groove. The area of overlap with the dentary is indicated by an anteriorly convex ridge on the lateral surface (Fig. 11B). Pores on the postero-dorsal and postero-ventral edges indicate the course of the preopercular-mandibular canal.

Teeth — Two lanceolate tooth crowns are associated with the type specimen, UCMP 129600. Their oval bases suggest association with the coronoids or one of the palatal elements rather than the maxilla or dentary. They are enamelled, sharply pointed, and translucent. A strong carina extends from tip to base along each side of the crown.

A number of other tooth crowns from the Hell Creek Formation closely resemble those of the type specimen. Most are from localities where other elements of Melvius have been found. With them are a number of larger tooth crowns (Fig. 12) that are blunter and have round or oval bases. A few, including some from the Lance Formation, have remains of hollow dentine shafts that probably were longer than the enamelled crowns.

Fin Supports — A number of fragmentary lepidotrichia, epurals, and hypurals are associated with specimens of Melvius in the UCMP collections. None is articulated with vertebrae or limb girdles, so it is impossible to determine their position or total number.

Vertebrae — All the vertebrae are completely ossified; the notochordal pit is occupied by bone that forms a plug or spike. The anterior trunk vertebrae are as described and figured by Estes (1964) and Boreske (1974), being short antero-posteriorly and with broadly oval articular surfaces. Central trunk vertebrae (Fig. 13) have deeply excavated ventro-lateral surfaces between the basapophyses and aortal facets. The most posterior trunk vertebrae are nearly circular in outline where the basapophyses are most steeply inclined and may be twice the length of anterior vertebrae.

Caudal vertebrae decrease in width toward the tail until they are almost perfectly rectangular in cross section and a little higher than wide. At least some caudals are longer antero-posteriorly than some anterior trunk vertebrae. The two known urals are virtually square. Each has a small, rounded spur of bone on the postero-dorsal surface, but no other evidence of a fused neural arch.

Specimens Tentatively Referred to Melvius
A number of specimens that may be referable to Melvius thomasi or perhaps a related species come from older sediments or areas far removed from eastern Montana. Their identification should be possible when articulated material becomes available.
FIGURE 8. Melvius thomasi, n. gen., n. sp. Left cleithrum, UCMP 129601. A, lateral; B, medial view. Scale bar = 1 cm.

FIGURE 9. Melvius thomasi, n. gen., n. sp. Holotype left anterior dentary, UCMP 129600. A, dorsal; B, medial; C, lateral view. Anterior to right, except C. Scale bar = 1 cm.

?Parietal — A well preserved parietal from the Hell Creek Formation of North Dakota (UCMP 131707) is rectangular in outline (Fig. 14). Sculpture radiates from the postero-medial border. There is a prominent gliding surface along the posterior margin. Deep sutures on the medial and anterior borders indicate that this element was strongly connected to the skull roof. A tapered lateral margin suggests more tenuous contact.

A similar specimen, UNM B-5406, comes from the Fruitland or Kirtland Formation of New Mexico. It is slightly larger than UCMP 131707 (maximum length about 7.2 cm, maximum width about 4.3 cm). Surface sculpture is much coarser, and the bone is thicker, especially along the medial margin.

These specimens are somewhat enigmatic in the absence of articulated skull material of Melvius. The nearly rectangular shape is appropriate for parietals, but the broad gliding surface on the posterior margin is more suggestive of dermopterotics. However, there are no pores to indicate the presence or position of the lateral line canals, and sutures on the ventral surface are not comparable with either the parietal or dermopterotic in Amia (unknown in all other amoids).

The only articulated specimen perhaps referable to Melvius (MNA P1.1809) is from the Fruitland For-
mation of New Mexico. It includes two segments of the vertebral column, found lying approximately in a circle. The longer segment has 17 vertebrae from the anterior and mid-trunk region. The shorter segment has six posterior trunk vertebrae and an isolated caudal. This specimen demonstrates (Table 1) that there are at least 23 trunk vertebrae and that the vertebrae become wider, longer, and more excavated ventro-laterally near the mid-trunk. The neural arch bases are stout, and the neural spines are paired. Unfortunately, there is no neural spine associated with the caudal vertebra.

The basapophyseal angles of all the vertebrae in this specimen remained remarkably constant. Those of the anterior group vary between 110 and 100 degrees; those of the posterior group between 105 and 95 degrees. The wide basapophyseal angles suggest that Melvius had a wide, rounded body even near the caudal fin.

Size—Boreske (1974) analyzed growth in Amia using several different ratios involving measurements of external elements such as the parietal or head length. He determined that for all fossil and Recent species growth was essentially isometric, but recognized that internal elements were those most likely to grow allometrically. It is then with caution that I attempt to estimate body size from vertebral size.

Vertebral length in Amia calva apparently increases in almost direct proportion to standard length (SL, snout to base of caudal fin). I measured the sixth trunk vertebra and the standard length of several Amia specimens at the AMNH and plotted them in Figure 15. The regression line was derived from the ratios of vertebral length/standard length. Two central trunk vertebrae of Melvius, one from the type specimen and one a particularly large isolated vertebra (AMNH 6385), were measured and fitted to the regression line to achieve an estimate of the standard length of the two individuals. Although neither specimen may be the sixth vertebra, vertebral length increases gradually along the column (see Table 1) and this would affect the ratio only slightly.

The type of Melvius thomasi represents a relatively

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FIGURE 10. Melvius thomasi, n. gen., n. sp. Right dentary, LACM 30412, A, medial; B, dorsal view, anterior to left. Scale bar = 1 cm.

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FIGURE 11. Melvius thomasi, n. gen., n. sp. A, right dentary fragment, UCMP 131681, anterior to left. B, holotype left angular, UCMP 129600, lateral view, anterior to left. Scale bar = 1 cm.
small individual. Most known specimens are of much larger fish. Four vertebrae, AMNH 6385, UCMP 129602, 129878, and 129877 (Fig. 16), are particularly large. AMNH 6385, a central trunk vertebra, is 55 mm in width and 17 mm in length. The fish from which this vertebra came, if the ratio calculated in Figure 15 is correct, had a standard length of 161 cm. UCMP 129877 and 129878 are a posterior trunk vertebra and a caudal; both exceed AMNH 6385 in height. The posterior trunk and caudal vertebrae are among the smaller vertebrae in *Amia*. I have not attempted to estimate the length of the individuals these two vertebrae represent, but it may be in excess of 2 m.

Janot (1967) reported some very large specimens of *Amia robusta* from the Eocene of France, estimating that the largest of these represented individuals 2.6 m in length. It is impossible to know how she arrived at this estimate because no methodology was described, but none of the specimens is larger than the largest known specimens of *Melvius thomasi*, and most are considerably smaller.

**Biostratigraphy**—Since 1972 field crews from the UCMP have collected extensively in the upper 50 m of the Hell Creek Formation in Garfield and McCone counties, Montana. Specimens of *Melvius* have been found throughout at least the upper 30 m of the forma-

![Figure 12](image-url)

**FIGURE 12.** *Melvius thomasi*, n. gen., n. sp. Tooth crown, UCMP 72688. A, medial; B, crown view.

![Figure 14](image-url)

**FIGURE 14.** *?Melvius thomasi*. Right ?parietal, UCMP 131707, dorsal view. Anterior to left. Scale bar = 1 cm.

mation in both counties. While only about 50 individuals are known from this area, the fish should not be considered rare, especially in the sandy facies of large channel fillings where it almost always occurs. Neither is *Melvius* uncommon in the age-equivalent Lance Formation of Wyoming (Estes, 1964; Breithaupt, 1982).

The stratigraphically highest record of *Melvius* is at UCMP V73087 (Flat Creek 5), about 5 m below the top of the Hell Creek Formation (Archibald, 1982, fig. 8). A specimen from the Bug Creek Anthills (V65127, UCMP 129671) may be younger, but there is no definite stratigraphic evidence for the age of this locality (Fastovsky and Dott, 1986:279). Although the locality lies some 25 m topographically below the top of the Hell Creek Formation, the stream channel sediments in which the fossils are concentrated do not intertangle with the Hell Creek Formation and are uncapped. Similar deposits in the area that contain similar faunas are capped by one of the lowest coals of the overlying Tullock Formation (Puercan). The Bug Creek Anthills fauna may be a mixture of Puercan and reworked Cretaceous taxa (Bryant et al., 1986). No specimens of *Melvius* have been found in the Tullock Formation despite a collecting program as intense as that in the Hell Creek Formation. It thus appears that *Melvius* became extinct by the end of the Cretaceous. Specimens tentatively referred to *Melvius* from the Hell Creek Formation of South Dakota (Greenwald, 1971), the Aguja Formation of Texas (Boreske, 1974:64), and the Fruitland and Kirtland formations of New Mexico confirm that the range of the genus is limited to the Late Cretaceous.

The specimens below, tentatively referred to *Melvius*, may be more confidently identified as articulated specimens are found. I cannot certainly refer to *M. thomasi* any specimens found outside the Hell Creek and Lance formations of Montana and Wyoming, but...
their occurrence is of biogeographic and biostrati-
graphic interest.

A single vertebra (UCMP 130632) perhaps referable to *Melvius* from the Judith River Formation is prob-
ably Late Campanian in age. Two fragmentary verte-
brae collected by J. Eaton of the University of Colorado
Museum may be the stratigraphically lowest record of
*Melvius*. These come from the Masuk Shale Member
of the Mancos Shale in southern Utah, and are prob-
ably Early Campanian in age (J. Eaton, pers. comm.).
Large amiid vertebrae (UCMP 131260) with a sugges-
tion of ventrolateral excavation also occur in the
Trinity Formation of Texas (Aptian–Albian) and may
be referable to *Melvius*, but more material is needed
before more definite assignment can be made. A lancelo-
ate tooth crown (SMUSMP 62252) figured by Thur-
mond (1974, fig. 4) may also be referable to *Melv-
ius*.

**Comparison**—Comparison of *Melvius* with other
amiids is limited by the nature of the available ma-
terial. All other amiid genera except *Amia* are based
on articulated specimens preserved on slabs. The dis-
associated elements of *Melvius*, while providing worth-
while insights into anatomical details unknown for oth-
er fishes, do not yield the morphometric and meristic
data necessary for comparison to better-known genera.

In spite of these difficulties, some comparisons are
possible. Disarticulated skeletons of Recent *Amia* were
available for study in the UCMP and AMNH collec-
tions. An acid-prepared skull of *Enneles* from the Early
Cretaceous of Brazil (AMNH 11604) and detailed pho-
tographs of *Pachyamia* from the Late Cretaceous of
Israel were also available.

*Melvius* and *Amia* are quite dissimilar. *Melvius*
has a maxilla that is round in cross section anteriorly and
has a deep pit for articulation of the premaxilla, over-
lapping the anterior maxillary tooth. The posterior
margin of the maxilla is notched, and infraorbitals 4
and 5 appear to be fused. There are relatively few mar-
ginal teeth, and all of them are carinate, with enamelled
crowns. There is no supramaxilla, and the denta-
ry is wider than high. Length of the frontal is more than
three times width. On the medial surface of the op-
ercular, the articular socket extends dorso-posteriorly
from the anterior border, rather than being vertical.
The basioccipital tapers smoothly towards the anterior
deck, rather than narrowing and then broadening. The
limbs of the cleithrum meet in a gentle curve, not a
sharp angle, and the two limbs lie in the same plane;

![Figure 15](image-url)  
**FIGURE 15.** Estimation of standard length (tip of snout to base of caudal fin) in *Melvius thomasi*.
in *Amia* the antero-ventral limb is angled dorso-medially. The vertebrae are completely ossified, and the basiophyseal angles remain nearly constant along the length of the body.

*Pachyamia*, known from a single specimen in the Cenomanian of Israel, is similar to *Melvius* in a number of characters (see Character analysis and Fig. 17), and also in the presence of an elongate frontal (length more than three times width). There are insufficient data to determine whether this character is derived. The morphology of the cleithrum and angular are known to differ in *Pachyamia* and *Melvius*. The cleithrum in *Pachyamia* has a very narrow antero-ventral limb; that of *Melvius* was apparently broad, but in both genera the two limbs of the cleithrum lie in the same plane. The angular in *Pachyamia* rises to a blunt point at the postero-dorsal tip; that of *Melvius* apparently lacked this extension.

*Enneles*, like *Pachyamia*, shares several characters with *Melvius* (see Character analysis and Fig. 17). However, it lacks the elongate frontal, and has multiple supraorbitals and a supramaxilla.

Until comparable specimens of other amiid genera are available, it seems inadvisable to attempt fitting *Melvius* into a phylogeny such as that of Schultze and Wiley (1984, fig. 1). However, even with the present limitations, it is still possible to develop some hypotheses about the position of *Melvius* within the amiidae (Fig. 17).

**Polarity**—Schultze and Wiley (1984) cited several characters in support of considering the Parasemionotidae the sister-group of amiids + *Catus*, and *Amia* as the most derived amiid. I have accepted these polarity decisions. Olsen (pers. comm.) thinks that the parasemionotid *Watsonulus* in particular is an appropriate sister-group to the Amiidae + *Catus*. *Watsonulus* is the most primitive neopterygian (amiids, gars, teleosts, and their most recent common ancestor, sensu Patterson, 1973), having unreduced clavicles and a broad dorsal limb on the preoperculum (Olsen, 1984: 493). *Amia* may be considered the most derived amiid in having a very long dorsal fin (Schultze and Wiley, 1984: 153), and a premaxilla with much elongated nasal processes (Olsen, 1984, fig. 19). *Watsonulus*, *Catus*, and *Amia* share a uniquely derived jaw joint in which the symplectic takes part. Characters derived within the amiidae include the uniquely ossified vertebrae, fusion of the hypurals and neural centra, and a 1:1 hypural: fin ray ratio. For details on halecomorph and neopterygian relationships, see Olsen (1984:493).

**Character Analysis**—if *Watsonulus* is the sister group of amiids + *Catus*, and *Amia* is the most derived amiid, then it is possible to recognize some characters shared by *Melvius*, *Enneles* and *Pachyamia* (Fig. 17) that appear to be derived. All three genera share the posteriorly notched maxilla, crenulated alveoli, and

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**FIGURE 17.** Derived character states in *Melvius, Enneles,* and *Pachyamia*. 1, vomer differentiated. 2, maxilla with internally-directed articulatory head. 3, supramaxilla present. 4, interopercular present. 5, amiid scales. 6, 1:1 hypural: fin ray ratio. 7, 1:1 hypural: ural centrum ratio. 8, trunk vertebrae shorter than high. 9, carinate teeth with enamelled crowns and crenulated alveoli. 10, posteriorly notched maxilla. 11, loss of supramaxilla. 12, fusion of infraorbital 4 and 5. 13, frontal length: width ratio 3:1. 14, dermosphenotic excluded from orbit. 15, central trunk vertebrae ventrolaterally concave. 16, infraorbital 5 much reduced. 17, supernumerary supraorbitals. 18, loss of supraorbitals. 19, long dorsal fin. 20, long nasal process on premaxilla.
carinate teeth with enamelled crowns on long, hollow shafts. *Pachyamia* and *Melvius* also have in common a fused infraorbital 4–5, and loss of the supramaxilla. Although *Melvius* and *Enneles* share a wide medial shelf on the dentary, this part of the skull is unknown in *Pachyamia* and the character cannot be used to establish relationships. Because none of these characters is present in *Amia*, these genera cannot be included in its ancestry and must form another clade.

**CONCLUSIONS**

The large North American Late Cretaceous amiid formerly referred to *Protamia* or *Amia* cf. *A. uintaensis* is here referred to a new genus and species, *Melvius thomasi* (Fig. 18). Among the largest of known amiids (standard length estimated to be at least 160 cm), *Melvius* is most closely related to *Pachyamia* (Late Cretaceous of Israel) and *Enneles* (Early Cretaceous of Brazil). The paraseisonotid *Watsonulus* is the sister-group of *Amiidae* + *Caturus*, and *Amia* is the most derived amiid. Loss of the supramaxilla, presence of teeth with enamelled, carinate crowns and crenulated alveoli, a posteriorly notched maxilla, and fusion of infraorbitals 4 and 5 appear to be characters derived within the Amiidae. These characters define a clade including *Melvius*, *Pachyamia*, and *Enneles*. *Melvius* and other Mesozoic amiids probably were not restricted to fresh water. *Melvius* apparently became extinct by the end of the Cretaceous.

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**REFERENCES**


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