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A new species of the paracanthopterygian *Xenyllion* (Sphenocephaliformes) from the Mowry Formation (Cenomanian) of Utah, USA

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Abstract

A new species of *Xenyllion* (Sphenocephalidae) is described from the Upper Cretaceous (earliest Cenomanian) Mowry Formation of Utah, USA. The nearly complete, mostly articulated specimen represents a one-year-old individual and is about 38 mm in standard length. The specimen is included in Sphenocephaliformes because of the presence of a recurved spine on the posterodorsal extension of the opercle, large, widely-spaced spines on the preopercle, mandibular sensory canal enclosed in a bony tube, fine parallel ridges on the lateral face of the angular, and short ventral limb on the preopercle. The Utah specimen is a member of the genus *Xenyllion* because it lacks scales on the opercle, lacks an arch on the frontal bone, and lacks foreshortened vertebral centra. The new species differs from *X. zonensis* in six ways, including an opercle that has prominent ridges and spines on the ventrolateral margin, a broad rectangular subopercle that does not taper posterodorsally, and a cleithrum that is uniformly wide along its length and lacks a large posterodorsal lobate expansion. The new species shows that the diversity of *Xenyllion* is greater than previously thought and is comparable to that of the European *Sphenocephalus* from the Campanian. *Xenyllion* inhabited the Mowry Sea, suggesting that the genus originated in the Boreal Ocean and in a cool climate at or before the Albian/Cenomanian boundary.

Introduction

The Sphenocephaliformes (Acanthomorpha) contain two marine genera, *Xenyllion* WILSON & MURRAY, 1996, and *Sphenocephalus* AGASSIZ, 1838, ranging in age from the earliest Cenomanian to the Campanian (ROSEN & PATTERSON 1969, WILSON & MURRAY 1996, STEWART 1996). The name of the order was first used by MURRAY & WILSON (1999), based on the suborder Sphenocephaloidei of ROSEN & PATTERSON (1969). The order consists of one family, the Sphenocephalidae, which was erected by PATTERSON (1964: 383) for *Sphenocephalus*. *Sphenocephalus* in turn consists of two taxa of Campanian age: *S. fissicaudus* AGASSIZ, 1839, from Baumberg, Westphalia, and *S. brachypterygius* ROSEN & PATTERSON, 1969, from Sendenhorst, Westphalia, Germany. *Xenyllion zonensis* WILSON & MURRAY, 1996, was initially described from the earliest Cenomanian marine Fish Scales Formation of Alberta, Canada. *Sphenocephalus* and *Xenyllion* are united by and distinguished from all other paracanthopterygians in having opercles with deep, rounded excavations in their dorsal margins and preopercles with large spines along their posteroventral margins (WILSON & MURRAY 1996, MURRAY & WILSON 1999).

The holotype of *Xenyllion zonensis* consists of a partial disarticulated head and some postcranial elements (WILSON & MURRAY 1996: fig. 2). In the same volume of Mesozoic Fishes in which *X. zonensis* was first described, STEWART (1996) described two skeletons from the Mowry Formation, Utah, USA, and conservatively attributed them to the Alberta taxon, *X. zonensis*. STEWART (1996) noted one major difference between northern and southern *Xenyllion* specimens: the specimens from Utah had opercles with robust ridges extending from the posteroventral margin. However, neither WILSON & MURRAY (1996) nor STEWART (1996) ever directly compared the fossils. We here compare the specimens from Alberta and Utah and show that there are several differences between *X. zonensis* from Alberta and the specimens from Utah, indicating that a new taxon should be erected. In the present work we have two main objectives: (1) to redescribe the Utah form as a new species and to compare it to *X. zonensis*, *Sphenocephalus fissicaudus*, and *S. brachypterygius*, and (2) to discuss the factors influencing acanthomorph diversification in the contexts of extinction, environments, and climate change.

Materials and methods

Institutional abbreviations

DINO, Dinosaur National Monument, Vernal, Utah, USA; **FHPR**, Utah Field House of Natural History State Park Museum [Field House Parks and Recreation], Vernal, Utah, USA; **NHM**, Natural History Museum, Palaeontology Department (**P.**, paleontology register; **OR.**, old register), London, United Kingdom; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, Canada; **USNM**, National Museum of Natural History, Smithsonian Institution, Department of Paleontology, Washington D.C., USA.

Fossil material examined

An initial assessment of the material of *Xenyllion* indicated characteristics of a variety of acanthomorphs including the percopsiforms. MURRAY & WILSON (1999), in their study of morphological traits, suggested a sister-group relationship between the sphenocephaliforms and the extant, North American, freshwater order Percopsiformes within the clade Paracanthopterygii originally named by ROSEN & PATTERSON (1969). However, more recent molecular phylogenies of extant fishes by MIYA et al. (2003) indicated that the percopsiforms belonged to a clade with the relationships (Polymixiiformes (Percopsiformes (Gadiformes, Zeiformes))), while MIYA et al. (2005) proposed the relationships ((Polymixiiformes, Percopsiformes) (Gadiformes, Zeiformes)). DILLMAN et al. (2010) also supported a sister-group relationship between Polymixiiformes and Percopsiformes. We focused our osteological comparisons of the new species to sphenocephaliforms, percopsiforms, and polymixiiforms in the Late Cretaceous and early Cenozoic fossil records.

Sphenocephaliformes: Sphenocephalidae: *Xenyllion zonensis* WILSON & MURRAY, 1996, UALVP 32093, 32095a,b, 32133a,b (holotype), 32073 (left opercle), 32131 (right opercle), 32227 (right preopercle), 32185 (right dentary), marine Mowry Sea, Fish Scales Formation (PLINT et al. 2009) formerly known as the Fish Scale Zone of the Shaftesbury Formation (WILSON & MURRAY 1996), with the base of the Zone approximating the latest Albian to earliest Cenomanian, 99.6 to 96.5 Ma, (PLINT et al. 2009), Alberta, Canada; *Xenyllion* sp. FHPR 701 (= UFH.V.85.2.1 in STEWART 1996: fig. 2a), early Cenomanian (PIERSON 2009), marine Mowry Sea, Mowry Formation, Utah, USA. *Sphenocephalus fissicaudus* AGASSIZ (1838), NHM P.3932, P.8772, P.8773, P.8774, P.9059, late Campanian in age, Baumberg, Westphalia. *Sphenocephalus brachyptergius* ROSEN & PATTERSON, 1969, NHM P.2100, late Campanian in age, Sendenhorst, Westphalia, Germany.

Polymixiiformes: Polymixiidae: *Homonotichthys dorsalis* DIXON (1850), WHITLEY, 1933, NHM P.1952, P.5701, P.36239, OR.41673, middle Cenomanian to lower Turonian (zones of *Holaster subglobosus* to *Inoceramus labiatus* or *Terebratulina lata*) of Kent and Sussex (PATTERSON 1964: 298; LEHMANN 1999), England; *H. pulchellus* DIXON (1850), WHITLEY, 1933, NHM OR.25886 (holotype), P.10639, middle Cenomanian of *Holaster subglobosus* zone of Kent and Sussex (PATTERSON 1964: 301; LEHMANN 1999), England.

Percopsiformes: Percopsidae: *Massamorichthys wilsoni* MURRAY, 1996, UALVP 21660, 23535, 30842a,b (holotype), 39094, freshwater Paskapoo Formation (Paleocene, age 60 Ma), Alberta, Canada; *Lateopisciculus turrifumosus*, MURRAY & WILSON, 1996, UALVP 22870, 34771 (holotype), 34772, freshwater Paskapoo Formation (Paleocene, age 60 Ma), Alberta, Canada. *Erismatopterus levatus* (COPE, 1870), TMP 1983.019.0015, 1983.019.0023; NHM P.61238, P.61239, from the Green River Formation (Eocene, 52 Ma), Kemmerer, Wyoming, USA. *Amphiplaga brachyptera* COPE, 1877, NHM P.61235, P.61236, P.61237 from the Green River Formation (Eocene, 52 Ma), Kemmerer, Wyoming, USA.

Aphredoderidae: *Trichophanes foliarum* COPE, 1878, NHM P.12506, UALVP 27059, from the Florissant Formation (late Eocene, 34 Ma [MEYER 2003]), Florissant, Colorado, USA.

Order incertae sedis, family Asineopidae: *Asineops squamifrons*, COPE, 1870, NHM P.61240; TMP 1986.224.0126; UALVP 14722, 17829; USNM 11111; from the Green River Formation (Eocene, 52 Ma), Kemmerer, Wyoming, USA.

Age and growth

Yearly growth was recognized by regions of raised circular ridges alternating with grooves in certain bones such as vertebral centra (NEWBREY et al. 2007, 2008). Each annular mark is defined as a narrow valley following a raised ridge. To measure growth, the center of the notochordal foramen was marked using an ocular grid and radial distance (RD mm) to each sequential annular mark (i.e., toward the distal margin) was determined to the nearest 0.01 mm using a digital micrometer under a binocular dissecting microscope (NEWBREY & WILSON 2005). No consistent orientation of the centra could be used for RD measurements due to the incomplete nature of some centra. NEWBREY & WILSON (2005) determined that the methodology has a mean measurement error of 0.06 ± 0.01 S.E. mm. The age and growth analysis includes eight taxa (n = 17 individuals); taxa include the sphenocephalids *Xenyllion* (n = 2 taxa) and *Sphenocephalus* (n = 2 taxa), a polymixiid *Homonotichthys* (n = 1 taxon), and the percopsiforms *Massamorichthys*, *Erismatopterus*, and *Amphiplaga* (n = 3 taxa).

Systematic paleontology

Class Actinopterygii COPE, 1887
Teleostei MÜLLER, 1845
Euteleostei GREENWOOD et al., 1966
Acanthomorpha ROSEN, 1973

Order Sphenocephaliformes ROSEN & PATTERSON, 1969

Diagnosis. Preopercle with large spines on posteroventral edge; opercle with posterodorsal edge recurved.

Family Sphenocephalidae PATTERSON, 1964

Emended diagnosis. Frontal bones with pair of large, anteriorly diverging crests; gape large, premaxilla long, with notched postmaxillary process; one supramaxilla; teeth present on entopterygoid; ceratohyal deep and with a beryciform foramen; preopercle, opercle, and infraorbitals with large spines; dorsal and anal fins with four or five spines each; adipose fin present; upper and lower postcleithra not fused; pelvic fins with seven rays; caudal fin with 16 branched rays; pelvic splint present; and lateral line uninterrupted.

Genus *Xenyllion* WILSON & MURRAY, 1996

Emended diagnosis. Differing from *Sphenocephalus* in frontal bone having no arch; mandibular sensory canal enclosed in bony tube for more than half length of dentary, vs mostly open sensory canal of *Sphenocephalus*; lateral surface of angular ornamented with fine, parallel ridges; supramaxilla long; preopercle with short ventral limb; opercle not scaled; branchiostegal rays eight or more; second centrum not greatly foreshortened compared to first; scales cycloid and crenate, taller than long.

Type species: *Xenyllion zonensis* WILSON & MURRAY, 1996.

Xenyllion stewarti, sp. nov.

(Figs. 1–4)

Diagnosis. Mandibular sensory canal with four pores anteriorly vs two in *X. zonensis*; maxilla rectangular posteriorly; opercle with prominent ridges and serrations on ventrolateral margin; subopercle broad, rectangular, not tapered posterodorsally; cleithrum uniformly wide along its length.

Etymology. Named for J. D. STEWART who first recognized and described *Xenyllion* from Utah.

Holotype: FHPR 701 (Fig. 1), a nearly complete skeleton originally described as having an articulated head, paired fins, and scales (STEWART 1996: fig. 2A). The caudal peduncle is disarticulated but the caudal fin remains in place (Fig. 2), although the caudal endoskeleton is missing. The standard length is about 38 mm.

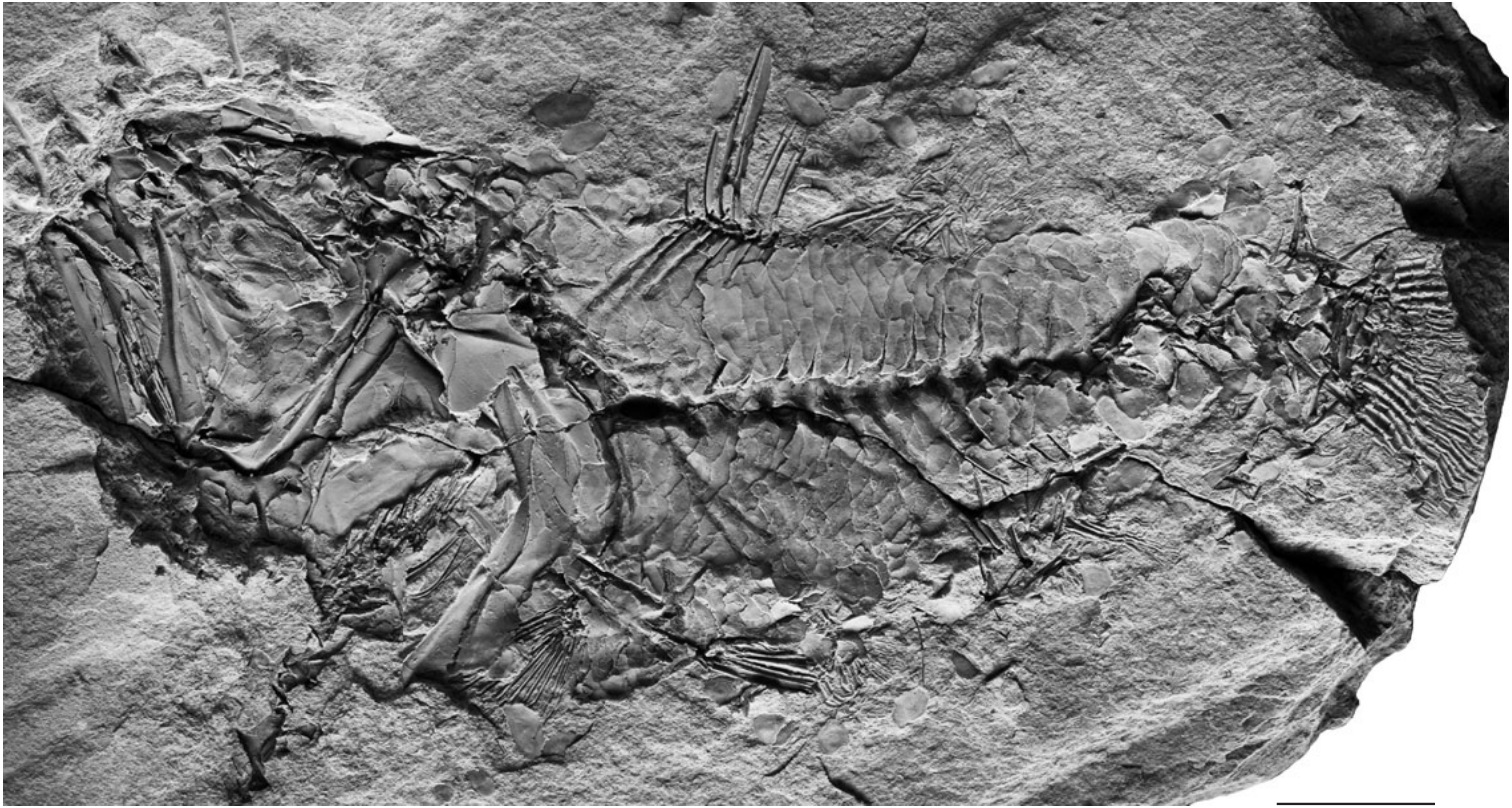


Fig. 1.
Xenyllion stewarti, sp. nov. (holotype FHPR 701) preserved in left lateral view. The fossil is coated with ammonium chloride. Scale bar = 5 mm.

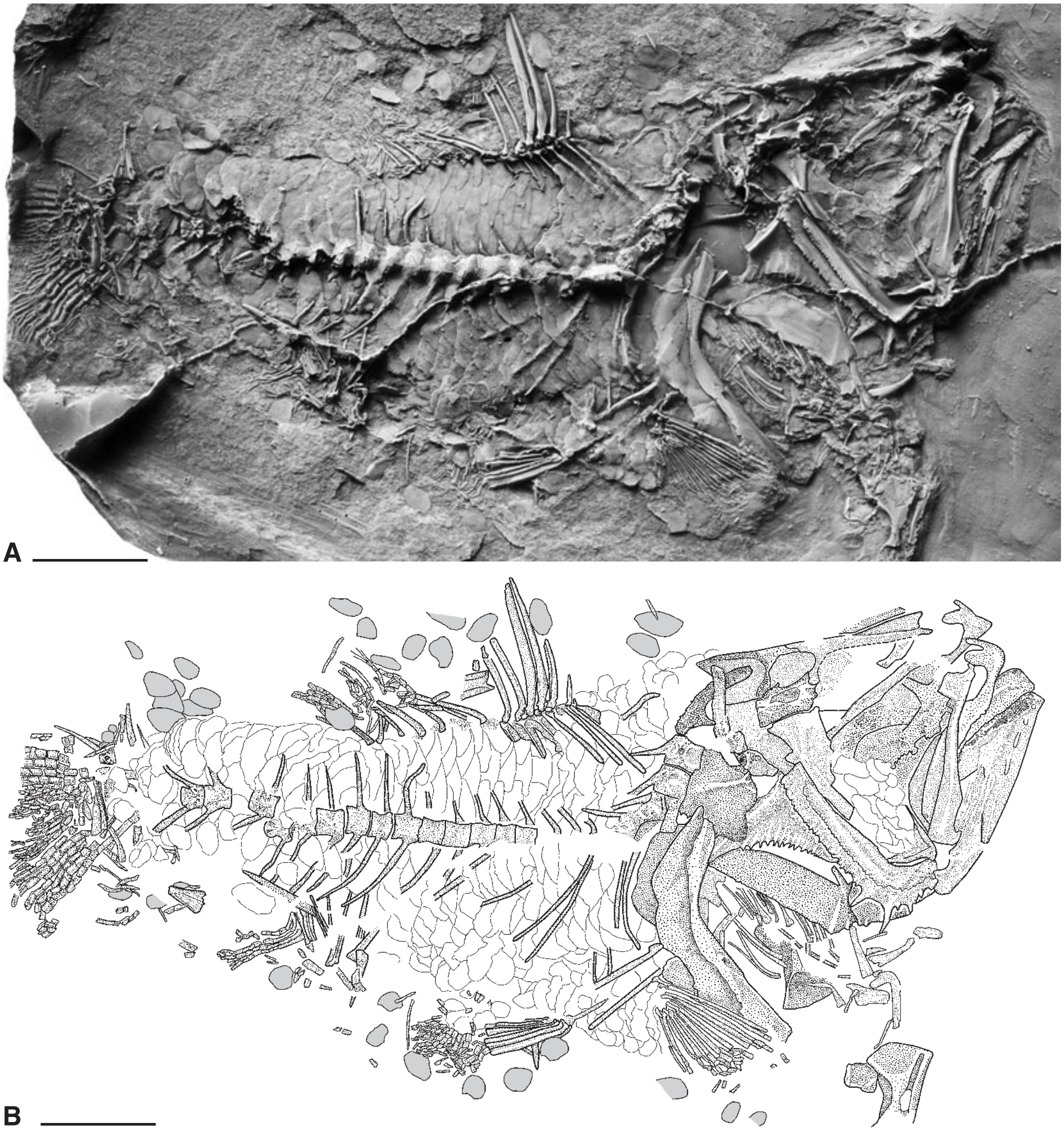


Fig. 2.
A reversed left lateral view of the holotype of *Xenyllion stewarti*, sp. nov. (FHPR 701); **A**, latex peel coated with ammonium chloride; **B,** tracing of the latex peel. Scale bars = 5 mm.

Type locality: Vernal, Utah, locality data on record with FHPR.

Age and horizon: Earliest Cenomanian, Mowry Formation.

Description

The illustrations show mainly medial views of head bones as most of the bones are missing and represented by impressions (Figs. 2, 3). A latex peel was made for illustration and interpretation (Fig. 2A, 3A). Three planes are represented in the head region: left lateral, midline, and right lateral as noted on the illustration (Fig. 3B). *Xenyllion stewarti*, sp. nov., is primarily compared to specimens of *X. zonensis* (see figures in WILSON & MURRAY 1996) and *Sphenocephalus* spp. (see figures in ROSEN & PATTERSON 1969 and Figs. 4H,I,L,M, 5, 6, 7A–C: *S. brachypterygius* Figs. 4I,L, 5A; *S. fissicaudus* Figs. 4H,M, 5B, 6A,B, 7A–C).

Skull roof. The frontal bone (the "frontal" of actinopterygians is homologous with the parietal bone of sarcopterygians including tetrapods; SCHULTZE 2008) extends much of the length of the head to the supraoccipital (Fig. 3A,B). The anterior portion of the frontal is trough-like and sharply truncated as in *Sphenocephalus* (NHM P.9059, ROSEN & PATTERSON 1969: fig. 28) but the bone is incomplete and poorly preserved along the midline at the anterior end. The anterior end of the frontal is similar to that of *Xenyllion zonensis* (WILSON & MURRAY 1996: fig. 4d). Little else can be determined about the frontal of FHPR 701. The parietal bones (the "parietal" of actinopterygians is homologous with the postparietal of sarcopterygians; SCHULTZE 2008) are small, subovate, and do not contact each other at the midline (Fig. 3A,B). The supraoccipital crest is relatively low as in *Sphenocephalus* (Fig. 5; NHM P.2100, P.9059; ROSEN & PATTERSON 1969: fig. 29).

Occipital region. The base of the exoccipital is wide and the visible exoccipital facet has a small, shallow, round cup, flush with the vertically oriented wall of the exoccipital, which is only visible on the original specimen. In contrast, *Percopsis* has exoccipital facets that face more posteroventrally (ROSEN & PATTERSON 1969: fig. 10a).

The basioccipital is wedge-shaped in lateral view (Fig. 3A,B). The basioccipital facet is relatively small in diameter but is about 30 % larger than the exoccipital facet of *Percopsis* (ROSEN & PATTERSON 1969: fig. 10a). Laterally, the basioccipital shows ornamentation with some fine ridges and two larger pits. The parasphenoid of FHPR 701 lacks teeth, as does that of *Xenyllion zonensis* (UALVP 32133).

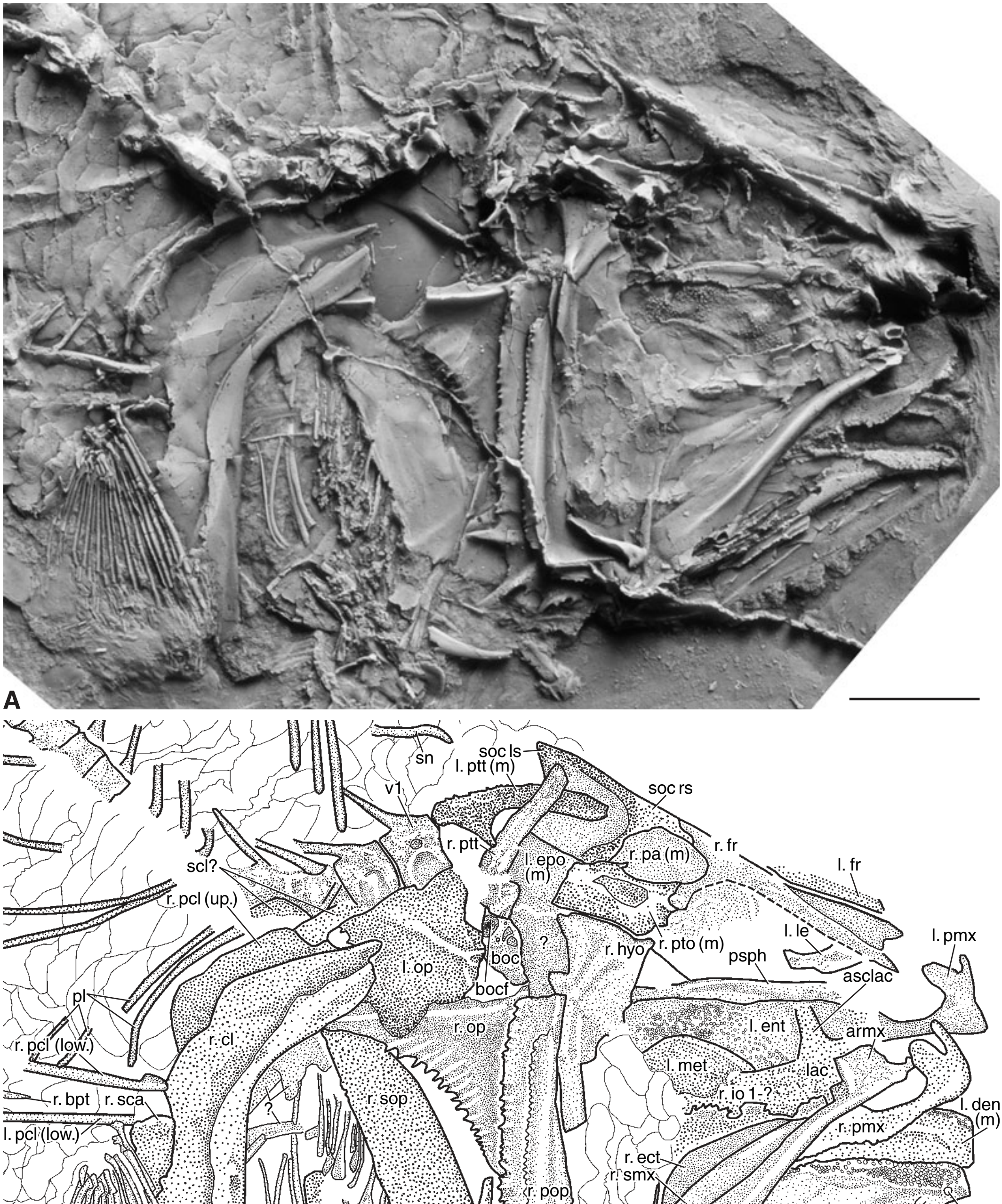
Jaws. The gape of FHPR 701 is large and the maxilla reaches past the orbit (Figs. 2, 3), unlike the condition in *Sphenocephalus* in which the maxilla only extends a distance of one third of the orbit (NHM P.2100, P.8772, P.9059) (Figs. 5A,B, 7). The pre-orbital region of FHPR 701 is short.

The ascending process of the premaxilla is narrow and about the same height as the articular process (Fig. 3A,B). The alveolar process of the premaxilla is not completely preserved in FHPR 701 but is depicted as long in STEWART's (1996: fig. 2b) second *Xenyllion* specimen from the Mowry Formation and in *Xenyllion zonensis* (UALVP 32133; WILSON & MURRAY 1996: figs. 2c, 4a). The postmaxillary process is present but its preservation is incomplete posteriorly such that no gadoid notch can be confirmed like that shown in *X. zonensis* (WILSON & MURRAY 1996: fig. 4a). A strong gadoid notch is visible in both species of *Sphenocephalus* (NHM P.2100, P.9059). The polymixiiform *Homonotichthys dorsalis* has a postmaxillary process that extends much of the length of the premaxilla and lacks a gadoid notch (NHM P.5701).

The long maxilla is toothless and rod-like anteriorly (Fig. 3A,B), like those of *Xenyllion zonensis* and *Sphenocephalus brachypterygius* (UALVP 32133, NHM P.2100), being reinforced by a strong mid-lateral ridge that disappears near the posterior end of the maxilla. However, posterior to the postmaxillary process, the maxilla widens steadily both dorsally and ventrally into a broad, subrectangular posterior end (Fig. 3A,B). In *X. zonensis* (UALVP 32133) the broad posterior end of the maxilla is distinctly triangular (WILSON & MURRAY 1996: fig. 2c), but in *Sphenocephalus* the process is straight dorsally and expanded ventrally (ROSEN & PATTERSON 1969: fig. 29).

One long and narrow supramaxilla is present (Fig. 3A,B). The supramaxilla has a straight dorsal margin; it tapers anteriorly and sharply posteriorly, and extends over half the length of the maxilla. The

Fig. 3. ▷
Photographs and interpretive tracings of the skull of the holotype of *Xenyllion stewarti*, sp. nov. (FHPR 701). **A,** latex peel coated with ammonium chloride; **B,** tracing of the latex peel. Scale bars = 3 mm. Abbreviations: **abr msc?**, probable accessory branches of the mandibular sensory canal?; **ang**, angular; **armx**, articular head of maxilla; **asclac**, ascending process of the lacrimal; **asph**, autosphenotic; **boc**, basioccipital; **bocf**, basioccipital facet of occipital condyle; **bpt,** basipterygium; **br**, branchiostegal; **cb**, ceratobranchial; **ch**, ceratohyal; **cl**, cleithrum; **den**, dentary; **ect**, ectopterygoid; **ent**, entopterygoid; **epo**, epiotic; **fr**, frontal bone; **hb**, hypobranchial; **hyo**, hyomandibula; **io**, infraorbital; **iop**, interopercle; **l.**, left; **lac**, lacrimal; **le**, lateral ethmoid; **low.**, lower; **ls.**, left side; **m.**, medial view; **mes**, mesethmoid; **met**, metapterygoid; **msc**, mandibular sensory canal; **mx**, maxilla; **na**, nasal; **op**, opercle; **orb**, orbitosphenoid; **pa**, parietal bone; **pb**, pharyngobranchial; **pcl**, postcleithrum; **pl**, pleural rib; **pmx**, premaxilla; **pop**, preopercle; **psph**, parasphenoid; **pto**, pterotic; **ptt**, posttemporal; **qu**, quadrate; **r.**, right; **rs.**, right side; **sca**, scapula; **scl**, supracleithrum; **smx**, supramaxilla; **sn**, supraneural; **soc,** supraoccipital; **sop**, subopercle; **uh**, urohyal; **up.**, upper; **v1**, first vertebral centrum.

A
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supramaxillae on *Sphenocephalus fissicaudus* and *S. brachypterygius* are relatively short, rectangular, and slender (ROSEN & PATTERSON 1969: fig. 29).

The right dentary of FHPR 701 has a bone-enclosed mandibular sensory canal below the dentigerous surface (Fig. 3A,B). In contrast, the mandibular sensory canal is open along most of the length of the canal in *Sphenocephalus* except for a narrow bridge on the anterior half of the dentary (ROSEN & PATTERSON 1969: 402). Furthermore, the posterior half of the mandibular sensory canal in *Homonotichthys dorsalis* is open in a groove and has one terminal pore and two lateral pores (NHM OR.41673, PATTERSON 1964: 293). The dentary of FHPR 701, preserved anteriorly in lateral view but posteriorly as a possible impression of the lateral side, shows a large, anterior terminal pore and three small antero-posteriorly elongate, lateral pores (Figs. 3A,B, 4A). The elongate lateral pores might be openings of accessory branches of the mandibular sensory canal and are interpreted as lateral pores because no pores are visible on the medial face of the left dentary (Figs. 1, 3). *Xenyllion zonensis* also has a bone-enclosed sensory canal (UALVP 32133, 32185, 32186) with a large terminal pore on the anterior end (Fig. 4B) as also seen in FHPR 701. No pores are visible on the medial face of the counterpart dentary of *X. zonensis* (UALVP 32185; Fig. 4B counterpart). The dentary figured in WILSON & MURRAY (1996: fig. 4c) shows the terminal pore on the anterior end of the dentary. The toothed surface of FHPR 701 forms a shelf that overhangs the ramus of the dentary laterally, like those of percopsiforms (*Massamorichthys wilsoni*, UALVP 30842-b; *Lateopisciculus turrifumosus*, UALVP 34771, 34772). The toothed margin of the dentary extends posteriorly as in that of *S. brachypterygius* (NHM P.2100) and as reported for that of *S. fissicaudus* (ROSEN & PATTERSON 1969: 402).

The angular is striated on the lateral surface and shows an open groove for the mandibular sensory canal (Fig. 3A,B) as in *Xenyllion zonensis* (UALVP 32133, WILSON & MURRAY 1996: fig. 3c). The angular of *Sphenocephalus fissicaudus* has an open groove for the mandibular sensory canal but lacks striations (NHM P.8772, P.8774).

Hyoid arch and palate. The hyomandibula of FHPR 701 has a single head oriented at about 70° from the long ventral shaft, unlike the hyomandibula of *Xenyllion zonensis*, which has a single head oriented nearly perpendicular to its ventral shaft. The ventral shaft in FHPR 701 is curved, unlike the straight shaft of *X. zonensis* (Fig. 3A,B; WILSON & MURRRAY 1996: figs. 3e,f) and *Sphenocephalus fissicaudus* (Fig. 5B, NHM P.9059). The posterior margin has a short, relatively robust opercular process (Fig. 3A,B).

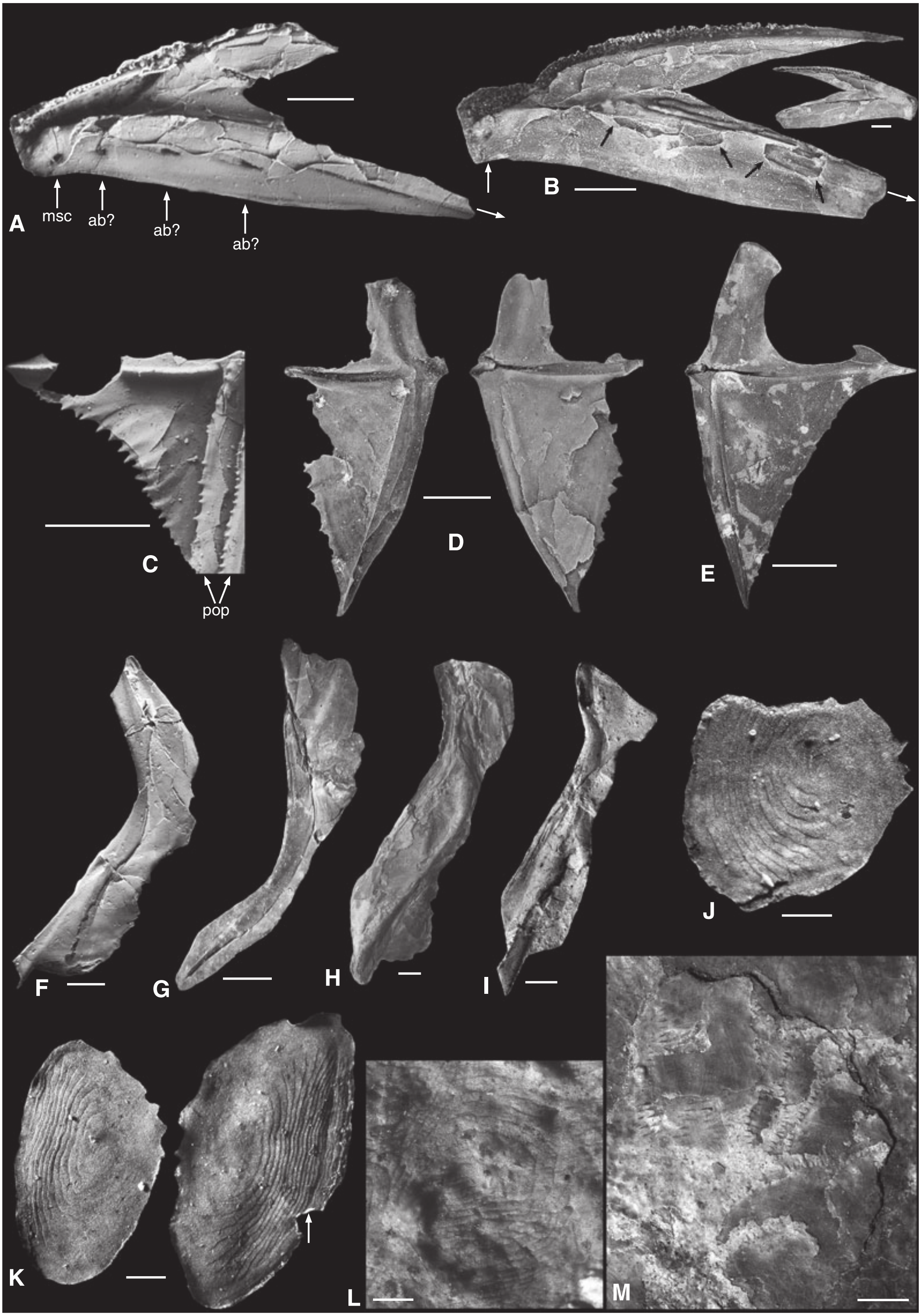
The entopterygoid of FHPR 701 is covered in small teeth, with tooth bases denser posteriorly, but the outlines of these bones cannot be discerned. Tooth density in FHPR 701 is not as great as that in *Sphenocephalus brachypterygius* (NHM P.2100).

The anterior ceratohyals are deep, with an elongate, oval beryciform foramen (MCALLISTER 1968), and are crossed by the groove for the hyoidean artery on the lateral face (Fig. 2B), a condition very similar to those of *Xenyllion zonensis* and *Sphenocephalus* (ROSEN & PATTERSON 1969: fig. 31; WILSON & MURRAY 1996: fig. 3h). The anterior ceratohyal in *Homonotichthys dorsalis* is very different, with no beryciform foramen but with distinct anterior "heads" for the articulation of the dorsal and ventral hypohyals (NHM P.5701, PATTERSON 1964: fig. 42). The anterior branchiostegal rays are narrow and long (Fig. 3B), but do not have percopsiform projections, similar to the condition in *Sphenocephalus fissicaudus* (NHM P.8772, P.9059, ROSEN & PATTERSON 1969: fig. 31) and *X. zonensis* (UALVP 32133, WILSON & MURRAY 1996: fig. 3h).

Fig. 4.

▷

Comparison of elements of the holotype of *Xenyllion stewarti*, sp. nov. (FHPR 701), Mowry Formation, Utah, USA, and *X. zonensis*, Fish Scales Formation, Alberta, Canada. **A,** left dentary of *X. stewarti*, arrows indicate openings for the mandibular sensory canal. **B,** part and counter part of right dentary of *X. zonensis* (UALVP 32185), black arrows indicate areas of broken and missing bone that expose the bone enclosed mandibular sensory canal; counterpart shows medial view but reduced in size by 68 %. **C,** latex peel of right opercle and preopercle of *X. stewarti*. **D,** molds of lateral and medial sides of left opercle of *X. zonensis* (UALVP 32073). **E,** mold of medial side of left opercle of *X. zonensis* (UALVP 32131). **F,** right cleithrum of *X. stewarti*. **G,** mold of lateral side of right cleithrum of *X. zonensis*, (UALVP 32133). **H,** right cleithrum of *Sphenocephalus fissicaudus* (NHM P.8772), dorsally incomplete, image inverted from right to left. **I,** mold of left cleithrum of *S. brachypterygius* (NHM P.2100), dorsally incomplete, medial view. **J,** isolated scale occurring near the pelvic fin of *X. stewarti*. **K,** isolated scales occurring near the region posterior to the supraoccipital of *X. stewarti*, arrow points to annulus in anterior field of scale. **L,** scale of *S. brachypterygius* (NHM P.2100). **M,** scales of *S. fissicaudus* (NHM P.8772). Specimens A–F are coated in ammonium chloride. Scale bars A–G, K, M = 1 mm; H, I = 2 mm; J–L = 0.25 mm. Abbreviations: **ab?,** probable accessory branches of the mandibular sensory canal; **msc**, mandibular sensory canal; **pop**, preopercle.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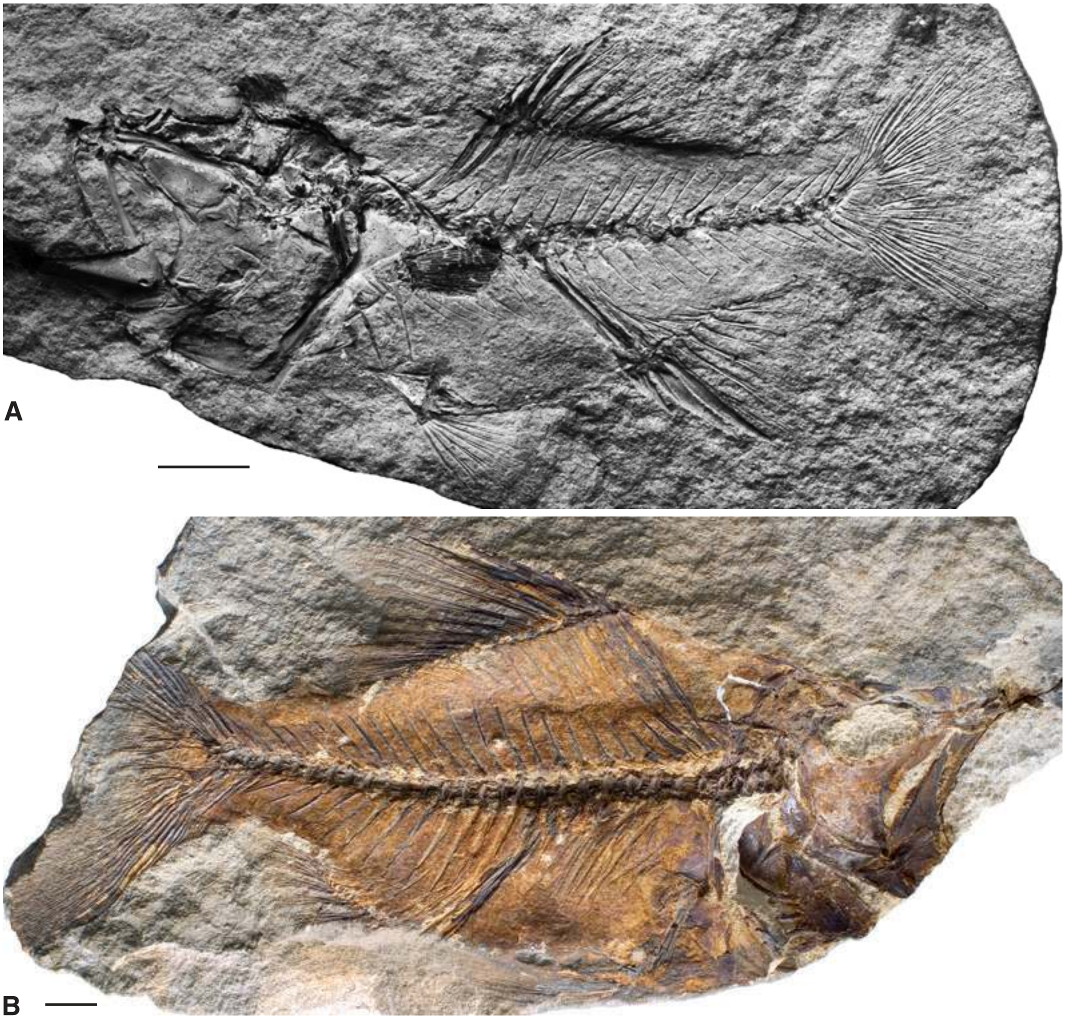

Fig 5.
Two specimens of Sphenocephalidae, *Sphenocephalus*. **A**, *S. brachypterygius* (NHM P.2100). **B,** *S. fissicaudus* (NHM P.9059). Scale bars = 1 cm.

Opercular region. The preopercle of *X. stewarti* is robust, and has a very short ventral arm with a blunt end (Fig. 3A,B). The ventral arm is about one-quarter as long as the vertical arm. The horizontal and vertical arms form an angle of about 90° as in *Xenyllion zonensis* (WILSON & MURRAY 1996: fig. 4e). In contrast, the angle between the horizontal and vertical arms in *Sphenocephalus fissicaudus* is about 120° and in that species the ventral arm is at least half the length of the vertical arm (Figs. 5B, 6A; ROSEN & PATTERSON 1969: fig. 29). The ventral arm of *Homonotichthys pulchellus* (NHM P.10639) is also very short as in *Xenyllion*. The sensory canal ran in an open groove but was covered laterally by a flange following the length of the sensory canal. The flange has fine serrae along its length, unlike the flange in *Sphenocephalus*, which had a single short spine at the angle of the limbs (Fig. 6A; ROSEN & PATTERSON 1969) and that of *H. dorsalis*, which lacks serrations (NHM P.1952). The posterior edge of the vertical limb of the preopercle of FHPR 701 is serrated but not continuously. The serrations are very fine and not longer than tall, also as in *X. zonensis* (UALVP 32095, 32133). Serrations on the posterior margin of the vertical limb of *Sphenocephalus* are relatively similar to each other in size but extend continuously along the limb (ROSEN & PATTERSON

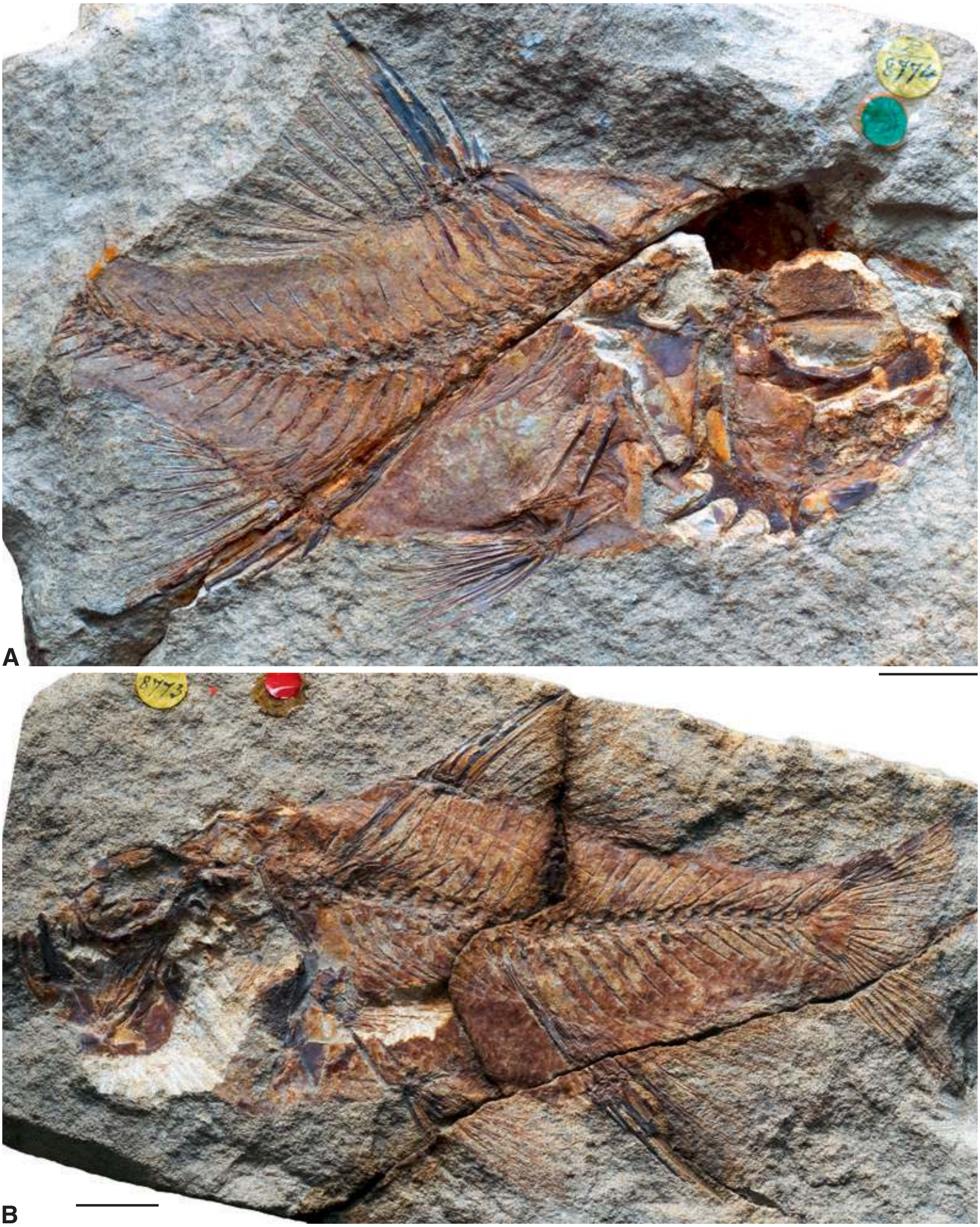

Fig. 6.
Two specimens of Sphenocephalidae, *Sphenocephalus*. **A**, *S. fissicaudus* (NHM P.8774). **B,** *S. fissicaudus* (NHM P.8773). Scale bars = 1 cm.

1969: 402) as do those of *H. dorsalis* (NHM P.1952). Two long and robust spines occur in FHPR 701, one ventrally on the vertical limb and one on the posteroventral corner. On the ventral limb, there is one spine that is larger than the others, along with much smaller serrae. The spines and serrae are very similar in *X. zonensis* (UALVP 32095, 32133). However, in *Sphenocephalus* the ventral and posteroventral spines are large (NHM P.8774, ROSEN & PATTERSON 1969: fig. 29). The margin of the ventral limb of *H. dorsalis* is covered in fine serrae (NHM P.1952).

As STEWART (1996) reported, the opercle of FHPR 701 has 15 prominent ridges and serrations on its ventrolateral margin (Figs. 1, 3, 4C). The ridges are 3–4 times as long as the serrations and significantly raised above the surrounding surface of the opercle. These serrations are largest dorsally and smallest ventrally. However, the ridges are only visible on the lateral face of FHPR 701 (Figs. 3, 4C). Some weak ridges (defined as low and not more than twice as long as their associated serrae) are present on the opercle of *Xenyllion zonensis* (UALVP 32073, 32131; Fig. 4D,E). WILSON & MURRAY (1996: fig. 4g) depicted 14 small, short serrations on a complete opercle preserved in medial view. *Xenyllion zonensis* shows both fine and weak or longer and robust serrae on the opercle (Fig. 4D,E). *Sphenocephalus fissicaudus* was illustrated with only three ridges associated with serrations by ROSEN & PATTERSON (1969: fig. 29).

The subopercle of FHPR 701 is a broad, rectangular bone that tapers only slightly compared to that of *X. zonensis* (WILSON & MURRAY 1996: 378) and *Sphenocephalus fissicaudus* (NHM P.8774). The subopercle of FHPR 701 shows at least one small projection on the ventral margin (Fig. 3A,B). STEWART (1996: 388) reported a single ridge perpendicular to the long axis of the subopercle ending in a prominence or blunt spine on the posteroventral margin. The “prominence” appears broken and rough as if a spine might have been present. No spines are present on the subopercle of *Sphenocephalus* (NHM P.8774, P.9059). The anterior projection of the subopercle turns sharply upward into a spike as in *S. fissicaudus* (NHM P.9059) and *Homonotichthys pulchellus* (NHM OR.25886). The interopercle is posteriorly deep, with two robust serrae and ridges on the posteroventral margin, unlike that reported for *S. fissicaudus* (ROSEN & PATTERSON 1969: 403).

Infraorbitals. The lacrimal and infraorbitals are incomplete on FHPR 701 but have short, fine serrae extending from the anteroventral and ventral margins. *Sphenocephalus fissicaudus* has large spines on the circumorbital bones (NHM P.8772, P.8774, PATTERSON & ROSEN 1969: fig. 29). The dorsal projection on the lacrimal is greater than two times longer than wide, making it more robust compared to that of *S. fissicaudus*, which is 4–8 times longer than wide (NHM P.8772, P.8773) (Figs. 6B, 7A). The infraorbitals of *Homonotichthys dorsalis* and *H. pulchellus* have a wide ascending process that is hooked posterodorsally, but they lack serrae and spines (NHM P.5701, P.36239, OR.25886).

Vertebral column. There appear to be 10 precaudal centra and 10 (probably 11) caudal centra in FHPR 701 (Figs. 1, 2A,B). The first centrum is not foreshortened, but it is very wide, robust, and appears to be modified in having a tripartite anterior surface, which is a synapomorphy for the Neoteleostei following WILEY & JOHNSON (2010). The exoccipital condyles are widely separated, extend anteriorly, are small in diameter, shallow, and not as well developed as are those of *Sphenocephalus fissicaudus* and the polymixiid *Homonotichthys dorsalis* (NHM P.8772, P.36239; Fig. 7C–E,G). The first centrum of FHPR 701 has two lateral pits (Fig. 3A,B). There is a large ventrolateral pit for a parapophysis, unlike the first centrum of the percopsiforms figured in ROSEN & PATTERSON (1969). *Sphenocephalus fissicaudus* (NHM P.9059) has a partial first centrum with a short, robust parapophysis extending from it (ROSEN & PATTERSON 1969: fig. 33). However, *S. fissicaudus* (NHM P.8772; Fig. 7C) also has a large pit that extends the length of the centrum; the pit is associated with the parapophysis. The pit of *X. stewarti* extends most of the length of the centrum and is deep. The first centrum of the polymixiid *H. dorsalis* is foreshortened and has a lateral depression variably subdivided by fine ridges that fill the lateral surface of the centrum, leaving small circular fossae; there is no evidence of a parapophysis (NHM P.36239; Fig. 7E,G). The dorsolateral pit in FHPR 701 is centrally located and extends about 30 % the length of the centrum, smaller than that in *S. fissicaudus*, which extends half the length of the centrum (NHM P.8772). There is a large, single, ventral fossa extending the length of the centrum and partially visible in FHPR 701, in contrast with the one in *S. fissicaudus* that extends 80 % the length of the centrum (NHM P.8772). The single ventral fossa in *H. dorsalis* extends the length of the centrum but is only deepened posteriorly (NHM P.36239; Fig. 7F). The first neural arches of *Xenyllion*, *Sphenocephalus* (FHPR 701; NHM P.8772, P.9059), and *H. dorsalis* (NHM P.5701) are not in close articulation with the exoccipital and supraoccipital, unlike the condition in *Mcconichthys longipinnis* (GRANDE 1988: fig. 3b).

The second centrum is not greatly foreshortened in FHPR 701, a condition similar to that of *Homonotichthys dorsalis* (NHM P.36239; Fig. 7E,G). In contrast, the second, third, and fourth centra in *Sphenocephalus* are foreshortened (NHM P.9059; ROSEN & PATTERSON 1969: fig. 33). There is a large lateral pit for a parapophysis, again unlike *Sphenocephalus* and percopsiforms. The pit extends most of the length of the centrum and is as deep as in the first centrum. There is a partial single ventral pit.

The single supraneural bone is long, narrow, and slightly S-shaped (Fig. 3A,B) as in *Sphenocephalus fissicaudus* (NHM P.8772). *Sphenocephalus fissicaudus* also has additional variation in supraneural morphology, such as the supraneural shaped like a curved wedge as figured in ROSEN & PATTERSON (1969: fig. 32, NHM P.8773).

Paired fin support. The left posttemporal is visible in medial view (Fig. 3A,B). It is ventrally incomplete, and has ornamentation like that of *X. zonensis* (WILSON & MURRAY 1996: fig. 4f). The posterior margin has serrae on its ventral half. The dorsal arm is long, of uniform width, and curved. The incomplete right posttemporal is also visible but shows only the dorsal arm.

STEWART (1996: 388) suggested that the cleithrum in WILSON & MURRAY (1996: fig. 3i) was figured upside down, based on his material in which the broader portion of the cleithrum was the ventral portion, rather than the dorsal portion as interpreted for *X. zonenesis* by MURRAY & WILSON (1996). An initial comparison of sphenocephalid cleithra was made to determine the correct orientation of isolated cleithrum UALVP 32133 (Figs. 4F,H). We agree with WILSON & MURRAY (1996) rather than STEWART (1996) for three reasons. One, the dorsal arm is shorter than the ventral arm on the posterior margin of the main shaft in FHPR 701 and specimens of *Sphenocephalus* (NHM P.2100, P.8872, P.8873) (Figs. 4F,I, 6B, 7B). The shorter of the two arms in *Xenyllion zonensis* (UALVP 32133) is the one figured as dorsal in WILSON & MURRAY (1996) suggesting it is in the correct orientation. Two, the dorsal shaft does not extend to the tip of the cleithrum in FHPR 701 as also seen in UALVP 32133, suggesting that it was figured in correct orientation (Fig. 4F,I). Three, the articulated cleithra in FHPR 701 and *Sphenocephalus* (NHM P.2100, P.8772, P.8773) have large posterodorsal expansions as seen in UALVP 32133 (Fig. 4F,I), again, suggesting that it was figured in correct orientation. Therefore, all comparisons among the specimens agree with the conclusion that the cleithrum of UALVP 32133 (WILSON & MURRAY 1996: fig. 3i) is correctly oriented.

The angle between the arms of the cleithrum of FHPR 701 is about 123°, which is similar to that for *Xenyllion zonensis* (120°) (UALVP 32133) and falls within the range (120–130°) for specimens of *Sphenocephalus* (NHM P.2100, P.8872, P.8873; Fig. 4F,H). The cleithrum of FHPR 701 has a broad ventral apron as in *Sphenocephalus* (Fig. 4F,I). It is relatively uniformly wide, unlike that of *Xenyllion zonensis* (UALVP 32133), which has a very narrow ventral arm. The dorsal arm in *X. zonensis* has a large, lobate, posterodorsal expansion (UALVP 32133; Fig. 4G). The dorsal arm in *S. fissicaudus* is well developed into a broad posteriorly rounded expansion (NHM P.3932, P.8772). However, the dorsal expansion in *S. brachypterygius* is much less broad and is triangular (NHM P.2100; Figs. 4I, 5A). The cleithrum of *Homonotichthys dorsalis* is also posteriorly expanded on its dorsal arm (NHM P.5701).

The upper postcleithrum on FHPR 701 is flat and extends over half the length of the cleithrum (Fig. 3A,B). *Sphenocephalus* has large, short (not tall), semicircular, posteriorly-expanded plates on the upper postcleithra, whereas the lower postcleithra are simple rods (NHM P.8772; Fig. 7A,B). The lower postcleithra in FHPR 701 are rod-like, with very small, semicircular, posterodorsal expansions. In *Homonotichthys*, lower postcleithra are simple rods but have very small posterior expansions (PATTERSON 1964: fig. 43).

The pectoral fins of FHPR 701 are relatively large and positioned low on the body compared to those of *Sphenocephalus* (Figs. 5, 6, 7A). Fourteen rays are visible in the left pectoral fin in the peel of FHPR 701 (Fig. 3A); *S. fissicaudus* has 15 pectoral rays (ROSEN & PATTERSON 1969).

The pelvic fin of FHPR 701 has seven rays as does that of *Sphenocephalus* (Figs. 3A,B, 5, 6, 7A; ROSEN & PATTERSON 1969). The splint in FHPR 701 is relatively larger than that in examined specimens of *Sphenocephalus*.

Dorsal and anal fins. The dorsal fin consists of four spines and nine branched rays (Fig. 2A,B). The fourth spine is the most robust, is less tapered than the more anterior spines, the pointed tips of which are preserved, and thus is likely the longest spine. The longest dorsal spine in *Sphenocephalus fissicaudus* is the fifth of five spines (Figs. 5B, 6; NHM P.8773, P.8774, P.9059; ROSEN & PATTERSON 1969). *Sphenocephalus brachypterygius* (Fig. 5A, NHM P.2100) has four spines, of which the fourth is the longest. The anal fin of *X. stewarti* is disarticulated; however, there are at least eight anal pterygiophores. There is evidence of at least two long anal spines in FHPR 701 (Figs. 1, 2); PATTERSON (1964) reports that sphenocephalids have five anal spines. The presence of an adipose fin cannot be confirmed.

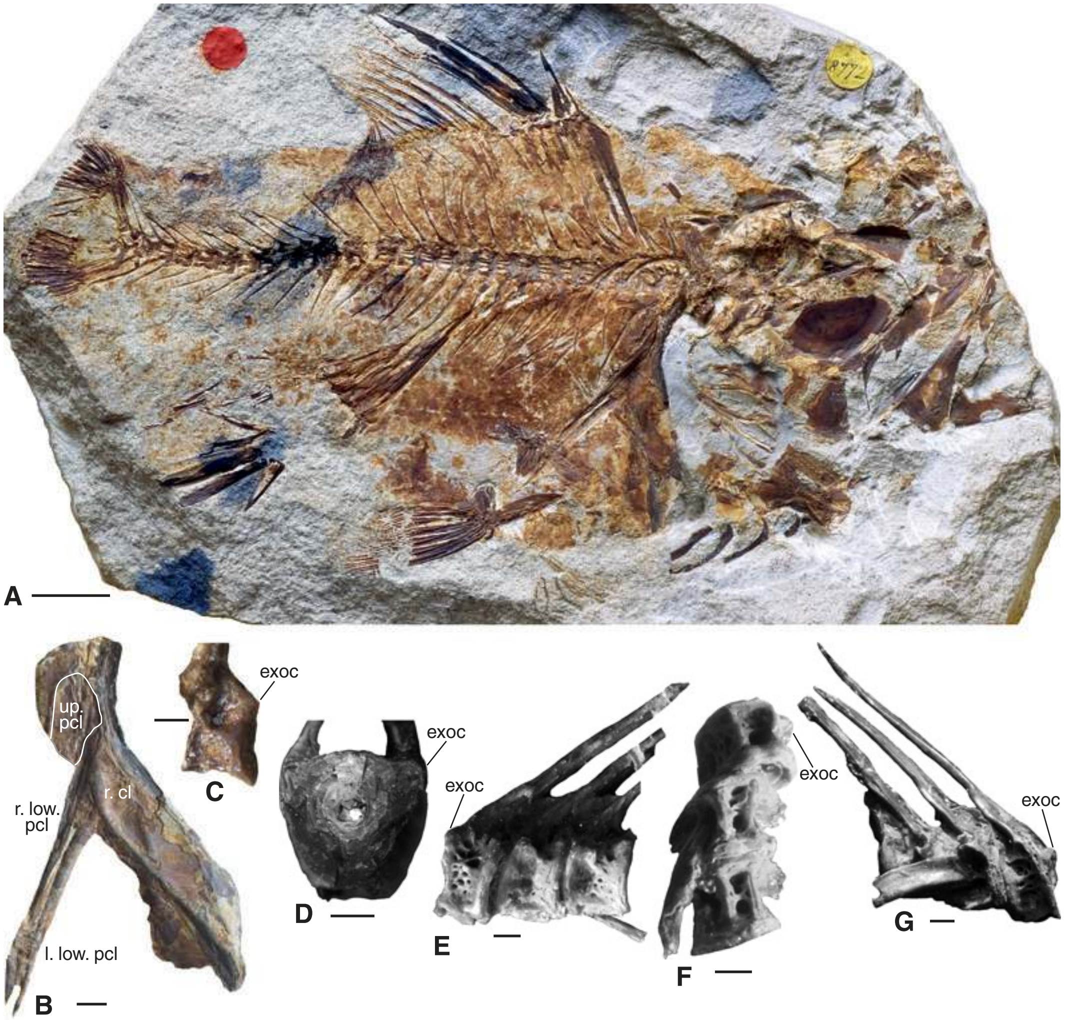

Fig 7.
Specimens of Sphenocephalidae and a polymixiform. **A–C**, *Sphenocephalus fissicaudus* (NHM P.8772); **A**, skeleton. **B,** right cleithrum and upper and lower post cliethra of *S. fissicaudus* (NHM P.8772), dorsally incomplete. **C,** first vertebral centrum in right lateral view. **D–G** vertebral centra of *Homonotichthys dorsalis* (NHM P.36239). **D,** anterior view, **E**, left lateral view; **F,** ventral view; **G,** right lateral view. Scale bars: A = 1 cm, B = 2 mm, C–G = 1 mm. Abbreviations: **cl**, cleithrum; **exoc**, exoccipital condyle; **l.**, left; **low.**, lower; **pcl**, postcleithrum; **r.**, right; **up.**, upper.

Caudal fin. The caudal fin is incomplete but it can be seen that it was forked. There are eight branched rays in the lower lobe; the number of branched rays in the upper lobe cannot be determined but is likely symmetrical with the lower lobe. The upper lobe shows evidence for segmented and unsegmented procurrent rays as also in both species of *Sphenocephalus* (NHM P.2100, P.9059).

Scales. STEWART (1996: 389) pointed out that there is no clear understanding of the morphology of scales of *Xenyllion* and *Sphenocephalus* because of the use of ambiguous definitions. STEWART (1996) described *Xenyllion* as having two types of scales, both cycloid and crenate scales. We follow the terminology of ROBERTS (1993) and DANIELS (1996) who describe three types of 'spined' scales: crenate, spinoid, and ctenoid. 'Crenate' scales have simple marginal indentations and projections giving the posterior margin a serrate appearance. ‘Spinoid’ scales have spines continuous with the main body of the scale and not forming on scalelets (subunits forming on the surface of the scale). Ctenoid scales have spines usually forming on scalelets (DANIELS 1996). ROSEN & PATTERSON (1969) described *Sphenocephalus fissicaudus* as having ctenoid scales, which is imprecise as the term ‘ctenoid’ at the time of the description would have included both spinoid and ctenoid type scales.

Small cycloid scales cover the cheek just anterior to the vertical arm of the preopercle and below the posterior infraorbitals of FHPR 701. Small, cycloid scales are also present on the cheek of *Sphenocephalus fissicaudus* (NHM P.8774; ROSEN & PATTERSON 1969). No scales can be seen on the opercle of FHPR 701, unlike the condition in *Sphenocephalus*, which has small cycloid scales on the opercula (NHM P.8774). However, small cycloid scales are on the subopercle of FHPR 701 and *Sphenocephalus* (NHM P.8774).

Body scales of FHPR 701 are taller than long, relatively large (2.3 mm height), subcircular to subovate, with strong circuli present in the anterior, dorsal, and ventral fields (Fig. 4J,K). The posterior margins of isolated body scales have 3–6 small, short, broad, triangular serrae (Fig. 4J,K). The figured isolated scales are located ventrally, posterior to the pelvic fins (Fig. 4J) and near the dorsal margin posterior to the head (Fig. 4K). Circuli are present in some of the posterior fields near the focus of the scales of FHPR 701 but are very faint. The focal areas of most scales of FHPR 701 are ovate and not well defined by circuli (Fig. 4J,K). In contrast, the scales of *S. brachypterygius* from the mid-abdominal area are cycloid, relatively small, and more circular compared to those of *S. fissicaudus* (NHM P.2100, P.8772) (Fig. 4L,M). The focal areas of *S. brachypterygius* are centrally located but they are irregular to circular in shape (NHM P.2100). In *S. fissicaudus*, scales are spinoid and subcircular with a single, broad, low lobe in the center of the anterior field (NHM P.8772, P.8774) (Fig. 4M). The focal areas of the scales of *S. fissicaudus* are round, centrally located, and surrounded with well-defined circuli (NHM P.8772, P.8774). Some of the circuli on scales of FHPR 701 have somewhat sinuous patterning (Fig. 4J,K). However, circuli of *S. brachypterygius* are deeply incised and often show small, triangular wave-form patterns in the anterior and posterior fields (NHM P.2100; Fig. 4L). Scales of the Eocene *Asineops squamifrons*, which is of uncertain phylogenetic position, also have centrally located foci and deeply incised circuli with triangular wave-form patterns (NHM P.61240, TMP 1986.224.0126, UALVP 17829, USNM 11111). The spinoid scales of *Homonotichthys dorsalis* are circular, with a posteriorly situated focus and featureless posterior fields (NHM OR.25886).

The posterior margins of scales on FHPR 701 have 3–6 ($\bar{x}=3.7$, $n=12$) small, triangular, short serrate projections that are about as long as they are tall along the posterior margins (Fig. 4J,K). In contrast, scales of *Sphenocephalus fissicaudus* each have 11–25 long, narrow spinoid projections ($\bar{x}=14$, $n=11$ scales from

Table 1.
Age and size of Late Cretaceous and Early Cenozoic acanthomorph fossils.

Taxon	Museum code	Catalog number	Stage/Epoch	Formation	Structure aged	Age (years)	SL (mm)
Xenyllion stewarti	FHPR	701	Cenomanian	Mowry	centrum/scale	1	~38
X. zonensis	UALVP	32133	Cenomanian	Fish Scales	centrum	1	?
Sphenocephalus fissicaudus	NHM	P.3932	Campanian	Baumberg	scale	1	?
S. fissicaudus	NHM	P.8772	Campanian	Baumberg	scale	3	127
S. fissicaudus	NHM	P.8773	Campanian	Baumberg	scale	2	107
S. fissicaudus	NHM	P.8774	Campanian	Baumberg	scale	1	?
S. fissicaudus	NHM	P.9059	Campanian	Baumberg	centrum	4	167
S. brachypterygius	NHM	P.2100	Campanian	Sendenhorst	centrum	1	94
Homonoticthys dorsalis	NHM	P.1952	Cen.–Turo.	?	centrum	5	?
H. dorsalis	NHM	P.5701	Cen.–Turo.	?	centrum	5	?
Massamorichthys wilsoni	UALVP	30842	Paleocene	Paskapoo	centrum	4	140
Erismatopterus levatus	TMP	1983.019.0023	Eocene	Green River	centrum	2	65
E. levatus	NHM	P.61238	Eocene	Green River	centrum	1	47
E. levatus	NHM	P.51362	Eocene	Green River	centrum	1	46
Amphiplaga brachyptera	NHM	P.61236	Eocene	Green River	centrum	3	88
A. brachyptera	NHM	P.61235	Eocene	Green River	centrum	3	90
A. brachyptera	NHM	P.61237	Eocene	Green River	centrum	3	84

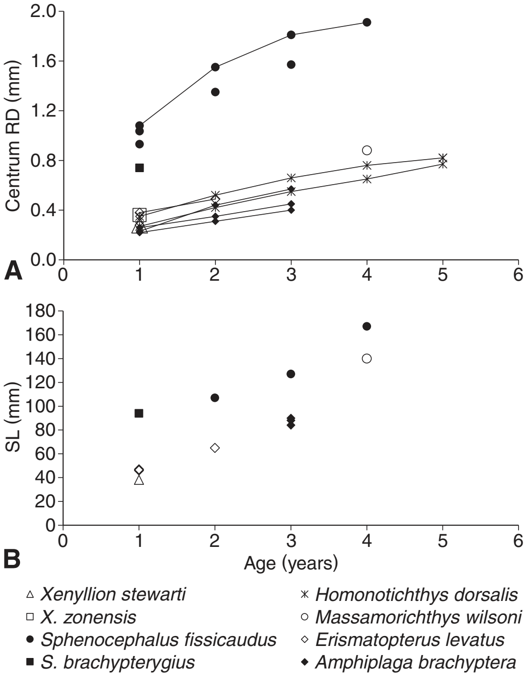

Fig. 8.
Age, size of centra, and standard length of eight taxa of acanthomorphs from the Cenomanian to the Eocene of North American and Europe. **A,** Age and growth profiles from centra of *Xenyllion* (*X. stewarti*, sp. nov., FHPR 701; *X. zonensis*, holotype, UALVP 32133) compared to two sphenocephalids *(Sphenocephalus)*, a polymixiiform *(Homonotichthys)* and three taxa of Percopsidae from the Paleocene and Eocene *(Massamorichthys, Erismatopterus,* and *Amphiplaga)*; growth is measured in radial distance (RD). **B,** Age and standard length (SL) of *X. stewarti* compared to *Sphenocephalus, Massamorichthys, Erismatopterus,* and *Amphiplaga*. Data and specimen numbers are listed in Table 1. Each line represents a growth profile from a single individual. Data points not connected by lines represent single individuals.

NHM P.8772; Fig. 4M) along the posterior margin of the scales as also seen in the scales of *Amphiplaga brachyptera* (NHM P.61235, P.61236, P.61237) with a range of 16 to 21 ($\bar{x}=19$, $n=10$ scales from NHM P.61236) and *Percopis omiscomaycus* (ROBERTS 1993: fig. 12c). The scales of *S. brachypterygius* lack serrate or spinoid projections (Fig. 4L) as do those of *A. squamifrons* (NHM P.2100, P.61240). Scales of *Homonotichthys dorsalis* lack triangular waveform circuli, but the spinoid projections range in number from 6 to 11 ($\bar{x}=7.6$, $n=11$ scales, NHM OR.25886).

Scales each show one annulus on FHPR 701 and annuli occur only in the anterior fields. Each annulus is indicated by an anastomosis of circuli near the anterior margin (Fig. 4K).

Age, growth and size. Age was determined from the cone of the occipital centrum of FHPR 701. A single annular mark can be identified as a groove. The radial distance of the first year of growth (0.28 mm) is very similar to that of a centrum from the holotype of *Xenyllion zonensis* (0.36 mm, UALVP 32133; Fig. 8A). *Sphenocephalus fissicaudus* and *S. brachypterygius* have much larger radial distances at age 1, their centra being at least twice the size (at 0.74–1.10 mm) of those of *Xenyllion* at the same age (Fig. 8A). Based on our sample, individuals of *Sphenocephalus* lived up to at least 4 years old. *Homonotichthys* and the Paleocene and Eocene percopsiforms examined have radial distances of 0.23–0.38 mm and thus bracket those of *Xenyllion* at age 1. The Campanian *Sphenocephalus* represents a group with a size and lifespan comparable to those of the percopsiforms and the Cenomanian/Turonian polymixiid *Homonotichthys dorsalis*, which lived up to at least age 5 (Fig. 8A, Table 1).

The standard length (SL) of the holotype of *Xenyllion stewarti* is about 38 mm, which is only 40 % of the SL of *Sphenocephalus brachypterygius* at age 1 (Fig. 8B, Table 1). However, *X. stewarti* is about the same SL as *Erismatopterus levatus* at age 1 (Fig. 8B). *Sphenocephalus fissicaudus* ranged in size from 107 mm SL at age 2 to 167 mm SL at age 4. *Massamorichthys wilsoni,* despite its small centrum diameters, had a SL similar to that of *S. fissicaudus* at ages 3–4 (Fig. 8B). *Massamorichthys wilsoni* has a centrum size at age 1 very similar to those of *Xenyllion*, *Homonotichthys*, *Erismatopterus*, and *Amphiplaga*. However, *M. wilsoni* attains lengths much greater than in those four genera and the greater length is due to higher vertebral count. Vertebral count is much greater for *M. wilsoni* (43–43) than it is for other taxa examined in this study: about 21 in *Xenyllion*, about 26 in *H. dorsalis*, about 30 in *Trichophanes foliarum*, about 29–31 in *A. brachyptera*, and about 29–30 vertebrae in *E. levatus* (PATTERSON 1964, ROSEN & PATTERSON 1969, GRANDE 1984, MURRAY 1996).

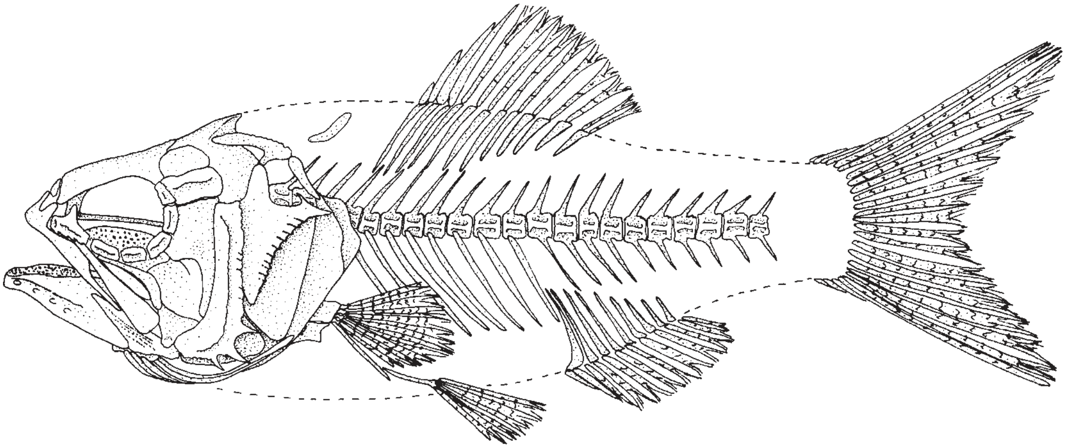

Fig. 9.
Reconstruction of the holotype of *Xenyllion stewarti*, sp. nov. (FHPR 701), Mowry Formation, Utah, USA.

Discussion

The new sphenocephalid species *Xenyllion stewarti* from the Mowry Formation, Utah (see reconstruction in Fig. 9), differs from *X. zonensis*, from the Fish Scales Formation, Alberta, in the morphology of three structures; the opercle, subopercle, and cleithrum. First, the opercle of *X. stewarti* has prominent ridges and serrations on the ventrolateral margin, unlike *X. zonensis*, which has serrations but no prominent ridges. The subopercle of *X. stewarti* is broad, rectangular, and does not taper posterodorsally, whereas that of *X. zonensis* is tapered. Third, the cleithrum of *X. stewarti* differs considerably in two ways from that of *X. zonensis*: the cleithrum tapers dorsally to the tip of the shaft in *X. stewarti* but in *X. zonensis* it has a posterodorsal, lobate-shaped expansion, and the cleithrum of *X. stewarti* is uniformly wide along its length whereas the cleithrum of *X. zonensis* has a narrow anteroventral arm.

Xenyllion stewarti and *X. zonensis* together differ from *Sphenocephalus* in nine major ways. Specimens of *Xenyllion* lack an arch on the frontal. The mandibular sensory canal on the dentary is enclosed in a bony tube for more than half the length of the dentary, unlike the open sensory canal of *Sphenocephalus* as reported by ROSEN & PATTERSON (1969). Species of *Xenyllion* have fine, parallel ridges ornamenting the lateral surface of the angular, whereas species of *Sphenocephalus* lack such ridges. The preopercle of *Xenyllion* has a short ventral limb that is about half the length of the ventral limb of *Sphenocephalus*. There are eight or more branchiostegal rays in *Xenyllion*, compared to six in *Sphenocephalus*. The second centrum in *Xenyllion* is not foreshortened. The scales of *X. stewarti* are taller than long, with relatively few, short projections, unlike the crenate serrate scales of *Sphenocephalus*, which are subcircular and have many long serrate projections. Lastly, individuals of *Xenyllion* were much smaller in size at a given age, as compared to individuals of *Sphenocephalus*.

Xenyllion stewarti is classified as a paracanthopterygian even though it does not have foreshortened centra. The lack of foreshortening in the first two centra posterior to the basioccipital of *Xenyllion* is different from the foreshortening of the second, third and fourth centra of *Sphenocephalus* (ROSEN & PATTERSON 1969). Foreshortened centra are also seen in *Mcconichthys*, *Massamorichthys*, and gadiforms (GRANDE 1988, MURRAY & WILSON 1999). However, not all percopsiforms have foreshortened centra; for example, they are not found in *Erismatopterus*, *Amphiplaga*, and *Aphredoderus* (MURRAY & WILSON 1999). The polymixiiform *Homonotichthys dorsalis* also lacks foreshortened centra in the second and third positions (PATTERSON 1964).

Factors influencing acanthomorph diversification

The two species of *Xenyllion* represent early acanthomorph fishes from North America, and are among some of the oldest known from anywhere. Acanthomorphs are diverse today and comprise about half of all living fishes (NELSON 2006). The apparently very rapid acanthomorph diversification that occurred during the Cenomanian to the Campanian and again in the late Paleocene (PATTERSON 1993) is likely related to a combination and timing of factors regarding their small sizes and changes in climate, environment, and extinction of associated ichthyofaunas in the Late Cretaceous.

Known specimens of *Xenyllion* are young and small in size. All fossils of *Xenyllion* examined from the Fish Scales Formation and the Mowry Formation represent very small fishes, the largest specimens being those described in this study. It is tempting to suggest that no large individuals existed in the populations of *Xenyllion*. However, habitat partitioning cannot be ruled out as the *Xenyllion* specimens could hypothetically represent young individuals with adults residing in other areas, although there is no evidence for this. Furthermore, age was determined for only two individuals of *Xenyllion* (both 1-year-olds) and, as a result, no population age structure could be inferred. Nevertheless, centrum size at age 1 for *Xenyllion* was very similar to that of the small Cenomanian/Turonian polymixiiform *Homonotichthys dorsalis*. These species and other early members of the clade have relatively small centrum sizes and small standard lengths. Both Campanian species of *Sphenocephalus* are considerably larger in centrum size and SL at the same age as *Xenyllion*, suggesting large size is a derived trait in sphenocephalids. SANTINI & TYLER (2003) and TYLER & SANTINI (2005) have also suggested that the acanthomorphs, tetraodontiforms, caproids, and zeiforms increased in size. Cretaceous esocoids and hiodontids are also small in size compared to those of their later (Paleogene, Neogene, and extant) relatives (NEWBREY et al. 2007, 2008). NEWBREY et al. (2008) showed that the esocid lineage shifted to larger sizes after globally cool events at the Cretaceous/Paleogene and Pliocene/Pleistocene boundaries.

We suggest that sphenocephalids might have attained larger sizes during the global cooling following the Cenomanian/Turonian Thermal Optimum. *Xenyllion* is first reported from the Mowry Sea in the earliest Cenomanian and during a globally cool climate (WILSON & MURRAY 1996, STEWART 1996, FORESTER et al. 2007). The Mowry Sea was connected to the Boreal Ocean in the North but had no outlet to the south (PLINT et al. 2009), suggesting that *Xenyllion* might have originated from a lineage found in cooler Arctic waters. The early Cenomanian is a relatively cooler time in both the tropics and temperate areas (FORSTER et al. 2007). *Sphenocephalus* also occurs in a globally cool climate but one that follows the Cenomanian/Turonian Thermal Optimum. Analysis of sea surface temperatures indicates that a number of global temperature changes occurred during the mid-Cretaceous, with temperatures gradually declining from the mid to late Albian before increasing again through the Cenomanian (FORSTER et al. 2007). In what is now Britain, temperature reached a high at the Cenomanian/Turonian Thermal Optimum, followed by a long, highly variable decline in temperature throughout the rest of the Cretaceous (JENKYNS et al. 2004). A second, smaller thermal spike occurred in the Turonian (JENKYNS et al. 2004). Temperatures remained very warm in the higher latitudes from the Cenomanian/Turonian boundary to the Coniacian, as evidenced by turtle assemblages from high latitude localities (TARDUNO et al. 1998, VANDERMARK et al. 2009).

The relatively small sizes of Cenomanian acanthomorphs and a warming climate in the middle Cenomanian (i. e., Cenomanian/Turonian Thermal Optimum) may have helped to promote rapid diversification leading to the great diversity seen in the group today. ESTABROOK et al. (2007) found that molecular substitution rates are faster in North American cyprinid fishes with small body mass, high temperature, and faster metabolic rate than they are in their larger relatives living in cooler habitats. However, that study considered only cytochrome B sequences and a small subset of cyprinids. Their conclusions may not have as much relevance for marine fishes. Nevertheless the hypothesis is valid; small acanthomorphs with short life spans likely also had faster metabolic and substitution rates in warmer water. For example, the Cenomanian/Turonian Thermal Optimum (JENKYNS et al. 2004) was a very warm time that might have fostered increased diversification of early acanthomorphs. In support of this idea, marine acanthomorphs are more diverse by the end of the Cenomanian (% composition of acanthomorphs in the sampled assemblage = 26 %) compared to that in the Albian/earliest Cenomanian. Acanthomorphs are uncommon in the faunas of the Albian/earliest Cenomanian deposits. Here we report on a second species of *Xenyllion* in the earliest Cenomanian deposits (WILSON & MURRAY 1996, STEWART 1996). GONZÁLEZ-RODRÍGUEZ & FIELITZ (2008) described one taxon, *Muhichthys cordobai*, from the Muhi Quarry (Albian or Cenomanian). In contrast to the Cenomanian/Turonian Thermal Optimum, acanthomorph diversity is lower (7 %) in the early Turonian when it is cool but the overall number of taxa sampled is low (PATTERSON 1993). Marine acanthomorph diversity increases only about 4 % during the relatively cool Coniacian to Maastrichtian interval, a much smaller increase than in the late Cenomanian (PATTERSON 1993). Furthermore, marine acanthomorph diversity more than doubles ($\bar{x} = 76$ %) in assemblages after the warming of the late Paleocene and Early Eocene Thermal Maximum (PATTERSON 1993, ZACHOS et al. 2001). In addition, CAVIN et al. (2007) report that diversity of marine acanthomorphs is positively correlated with sea temperature.

Changing environments and new habitats also likely promoted rapid diversification of early marine acanthomorphs by providing new habitats for niche diversification. The mid-Cretaceous was a time of marked change in oceanic patterns correlated with the final breakup of Pangea and the opening of the South Atlantic Ocean between Africa and South America. During this time, there were fluctuating, but high, sea levels (e. g., HAQ et al. 1988, SMITH et al. 1994, KULHANEK & WISE 2006), which would have created more shallow-water habitats for the early acanthomorphs on the continental shelves.

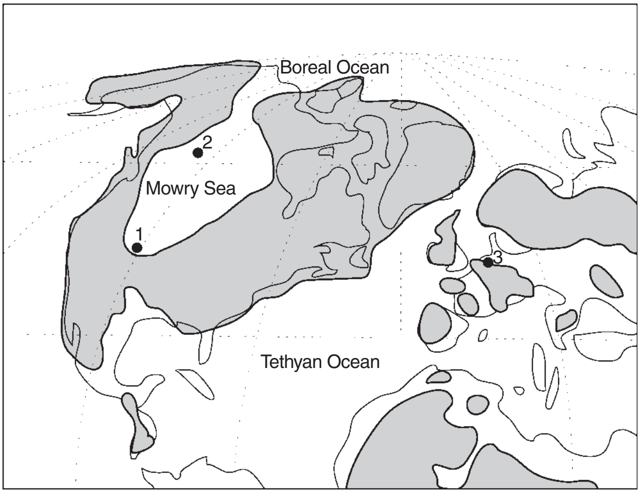

Fig. 10.
Paleocoastline map of North America during the Cenomanian before the connection of the northern Mowrey Sea and Boreal Ocean to the southern Tethyan Ocean; after SMITH et al. (1994) and PLINT et al. (2009). Filled circles are localities of sphenocephalids: **1**, *Xenyllion stewarti*, sp. nov. (Mowry Formation, earliest Cenomanian); **2**, *X. zonensis* (Fish Scales Formation, earliest Cenomanian); **3**, *Sphenocephalus fissicaudus* and *S. brachypterygius* (Baumberg and Sendenhorst localities, late Campanian).

Xenyllion shared the Mowry Sea with an ichthyofauna associated with the Boreal Ocean (Fig. 10). The southern opening of the Mowry Sea to the Tethys Ocean (i. e., Western Interior Seaway [WIS]) would have mixed northern and southern fish faunas and changed selection pressures due to new competition and predation. A number of faunas from this time period have been reported in the United States and Mexico (e. g., STEWART 1996), representing the southern part of the fauna. Fewer faunas are known from the northern waters of the WIS, although this is changing with recent studies (e. g., COOK et al. 2008, UNDERWOOD & CUMBAA 2010). CUMBAA et al. (2010) examined a number of faunas from the mid-Cenomanian throughout the seaway and indicated evidence of changing faunas with latitude. These changes might be correlated with cooler northern temperatures and warmer southern ones; however, CUMBAA et al. (2010) noted a complicating factor that the differing environments represented by their sites – nearshore versus deeper waters – might have influenced the faunas as much as latitude. Furthermore, the effects of new competition and predation might have been short-lived or not important. FRIEDMAN (2009, 2010) argued that the K-P extinction played a major role in the evolution and diversification of acanthomorphs through filling of vacant niches. FRIEDMAN's argument is plausible, but if many acanthomorphs are small in the Cretaceous and unlikely to preserve, we are less likely to document radiation patterns; future studies of microvertebrate material can function to test this hypothesis.

Acanthomorph diversification is likely a function of the response of fish evolution to climate change and extinction. Tests of these ideas will be made from new finds of Cretaceous acanthomorphs. The Mowry Sea and the Cretaceous Interior Seaway in North America may have played an important role in diversification of sphenocephalids and some other acanthomorphs. Given the climatic and environmental changes at the Albian/Cenomanian boundary, *Xenyllion* might represent a group that was much more diverse than is currently known. *Xenyllion* occurred in the Mowry Sea, which opened to the north, suggesting that Albian and Albian/Cenomanian boundary deposits in the Arctic might yield fishes closely related to *Xenyllion*. The Albian/Cenomanian *Muhichthys cordobai* from Mexico is very different from sphenocephalids and has affinities with western Tethyan acanthomorphs, suggesting attainment of some diversity by the end of the Albian (GONZÁLEZ-RODRÍGUEZ & FIELITZ 2008). We would expect acanthomorphs from the lower latitudes of Mexico, with their faster metabolic rates, to be more diverse than high latitude forms. Acanthomorphs from lower latitudes would be adapted for stable, warm environments. However, higher-latitude fishes are more adapted for seasonal thermal fluctuation, characteristic of colder periods. High-latitude acanthomorphs dispersing into lower latitudes, during cold periods, might find unoccupied habitats conducive for diversification.

Clearly more work is needed to document diversity and describe fishes from the Fish Scales Formation. A comprehensive study of early acanthomorphs and their phylogeny is also needed and would give us a better understanding of the diversification of marine and freshwater acanthomorphs lineages in North America (GONZÁLEZ-RODRÍGUEZ & FIELITZ 2008).

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