A NEW SPECIES OF *HOPLOPTERYX* FROM THE CARLILE FORMATION (CRETACEOUS) OF SOUTH DAKOTA

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ABSTRACT

A species of the beryciform fish genus *Hoplopteryx*, collected from rocks of Turonian Age in the Pool Creek Member of the Carlile Shale Formation, is described from the fossil record of South Dakota for the first time. The specimens are part of the Bishop Collection, now housed in the repository at the South Dakota School of Mines and Technology (SDSM). Despite their geographic distance from the core of *Hoplopteryx* distribution, the South Dakota specimens lie within the first half of the known geologic range of the genus. They are distinctive in that they occur at a very high paleolatitude compared to all other known specimens of *Hoplopteryx*. They differ anatomically from all previously described species, particularly the type species *Hoplopteryx antiquus*. They are consistently small. They are also distinct in the crests and depressions of the skull. The absence of a walled mucus cavity on the frontals and the ornamentation of cranial bones are particularly distinctive in the South Dakota hoplopterids. We herein describe them as a new species, *Hoplopteryx dakotaensis*.

Keywords

Hoplopteryx, beryciform, South Dakota, paleobiogeography

INTRODUCTION

During the latter decades of the 20th century, Dr. Gale Bishop collected fossil decapod crustaceans from the Pool Creek Member of the Carlile Shale Formation in Butte County, South Dakota (Bishop and Williams, 1991) and adjacent Meade County. Dr. Bishop also discovered and collected the remains of a number of fossil fish that were associated with the fossil crustaceans which were the object of his research. Beryciform fish had been reported previously by Cobban (1951a) from the upper part of the then-unnamed lower member of the Carlile Shale Formation north of Belle Fourche, South Dakota. Many of the South Dakota fish are also beryciforms, and belong to the genus *Hoplopteryx*.

Patterson (1993) considered the genus *Hoplopteryx* to be the best-known Cretaceous trachichthyid beryciform. The genus is widely distributed in Europe and Lebanon (Smith-Woodward 1901, 1902; Patterson 1964, 1993; Ekrt et al. 2008), and has previously been reported from Texas (Bardack and Teller-Marshall 1982) and tentatively from Alabama (Applegate 1970). *Hoplopteryx* has never yet been reported from South Dakota, however. Paleogeographic distribution of the best-known species, *Hoplopteryx lewesiensis*, is shown in Figure 1. Patterson (1964) considered eight of the described species of *Hoplopteryx* to be valid, although he later suggested that there were only six valid species (Patterson 1993: Table 2). We find that the specimens representing the new species are distinct from all eight of the species reported by Patterson (1964). We do not consider these differences from previously described *Hoplopteryx* species to justify creation of a new genus.

The Bishop Collection includes beryciform fish remains from the Olson and Kudlock ranches in Butte County, South Dakota. The fish are preserved in three dimensions and consist mainly of articulated skulls (including the opercular apparatus) which are infilled with carbonate matrix (Figure 2). Post-opercular elements, including parts of the pectoral girdle and some scales, are also represented in several of the specimens. Fish that include post-opercular elements generally preserve at least some vestige of the body contour. One specimen (Figure 3 – SDSM 110292) preserves approximately half of the anterior body in addition to

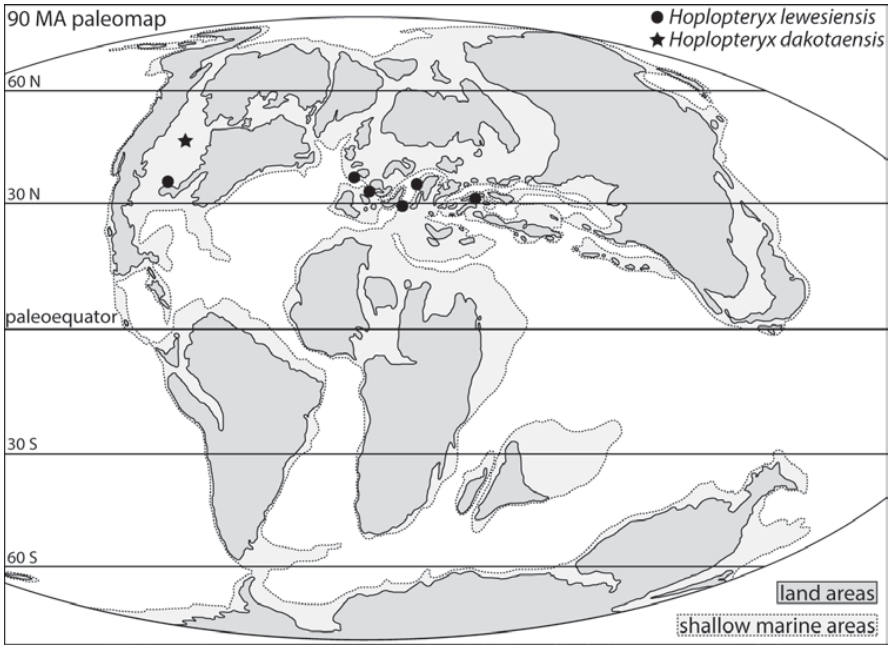

Figure 1. Paleogeographic map showing the global distribution of* Hoplopteryx lewesiensis *and* H. dakotaensis*. Map is based on a 90 MA Ron Blakey Mollwide Plate Tectonic Map. North is to the top.

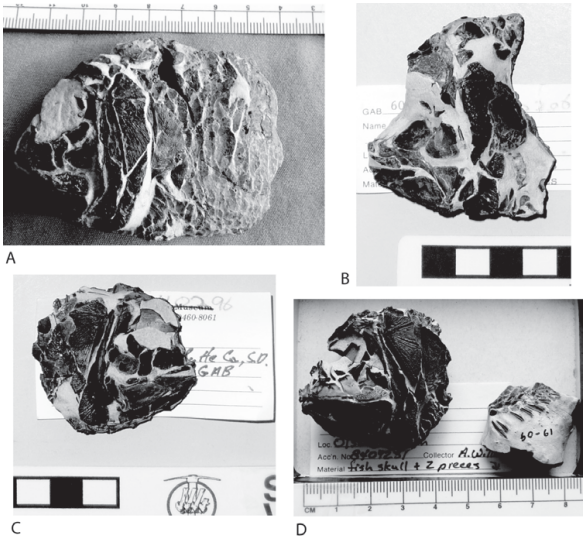

Figure 2. **Hoplopteryx dakotaensis** *type and paratypes. All are from the Olson Ranch, Butte County, South Dakota. A. SDSM 110292. Holotype. skull and anterior body preserved in three dimensions. B. SDSM 110286 Paratype skull preserved in three dimensions. Bones of the suspensorium are visible in this specimen. C. SDSM 110296. Paratype. skull in right lateral view. Palatal teeth are visible on this specimen. D. SDSM 110291. Paratype. This paratype includes a fragment of the caudal fin.*

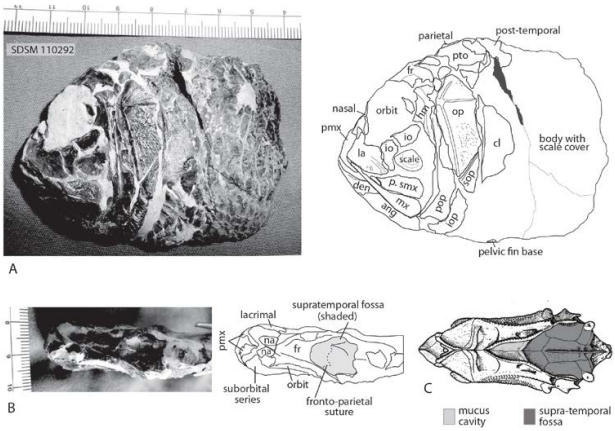

Figure 3. SDSM 110292. Holotype. Skull and anterior portion of body in left-lateral view. 3A. Lateral view of the fish as preserved, showing mainly bones of the dermal skull and jaw, plus opercular and shoulder girdle elements. Scales are represented mainly by molds of the internal surface of the scale. An interpretive sketch with individual bones identified is shown on the right. The ornament represented on the bones in this sketch was traced from the photograph on the right. 3B. Dorsal view of the skull of SDSM 110292 to show the supratemporal fossa. An interpretive sketch is shown to the right of the photograph. 3C. Dorsal view of the skull roof in **Hoplopteryx lewesiensis** *showing the relationship between the mucus cavity (light gray) and supratemporal fossa (dark gray). Modified from Patterson (1964). Abbreviations: ang, angular; cl, cleithrum; den, dentary; fr, frontal; hm, hyomandibular; io, infraorbital; iop, interopercular; la, lachrymal; mx, maxilla; na, nasal; op, opercular; p. smx, posterior supramaxillary; pmx, premaxilla; pop, preopercular; pto, pterotic; sop, subopercular. Anterior is to the left in all views*

the articulated skull; other specimens preserve only a small region of the body just caudal to the opercular apparatus. Only the superficial bones of the skull are visible in many specimens, but elements of the suspensorium can be seen at the surface in several specimens (Figure 4 – SDSM 110286).

Geologic setting. The South Dakota fishes were recovered from the Pool Creek Member of the Carlile Shale Formation (Figure 5) close to its type area north of Belle Fourche in Butte County, South Dakota (Knechtel and Patterson 1962). The Pool Creek Member is a dark gray to blackish-gray shale with thin calcareous partings and thin lenses of buff-weathering limestone. All of the South Dakota fish remains are preserved in buff limestone, and probably came from limestone lenses in the lower part of the Pool Creek Member (Knechtel and Patterson 1962). Field notes with several of the specimens state that they come from dark shale with a prominent yellow-orange concretion zone. The beryciform remains which Cobban (1951a) reported were recovered from the upper part of what is now known as the Pool Creek Member of the Carlile Shale Formation, also in Butte County, South Dakota. The Carlile and its Pool Creek Member are correlated to the middle Turonian Stage of the Cretaceous System (Merewether 1996) based on its molluscan (Cobban 1951b), decapod (Bishop & Williams 1991), and foraminiferal (Fox 1954) paleofaunas (Figure 6).

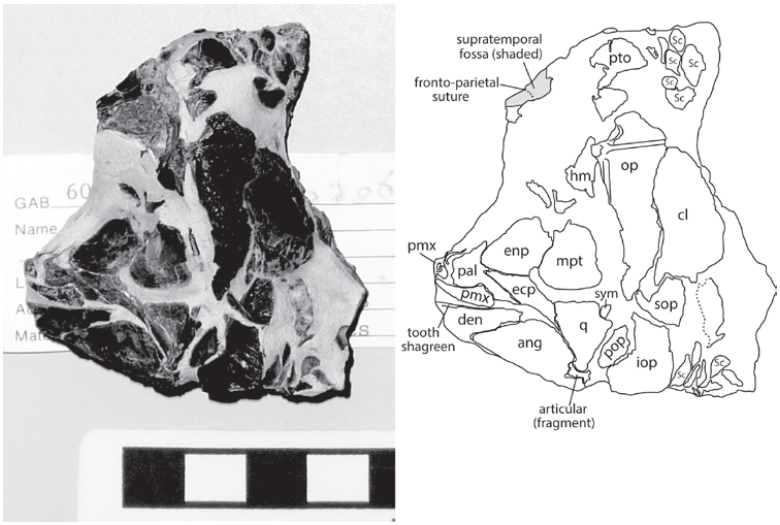

Figure 4. SDSM 110286. Paratype. Skull in left-lateral view. Several bones of the suspensorium are visible in this skull. This skull is slightly crushed dorsally so that the supratemporal fossa faces toward the left side of the skull. It is visible near the top of this image. An interpretive sketch of SDSM 110286 with individual bones identified is to the right of the photograph. The darker interior of the concretion in which this skull is preserved is visible in the area below the supratemporal fossa. Abbreviations: ang, angular; cl, cleithrum; den, dentary; ecp, ectopterygoid; enp, entopterygoid; fr, frontal; hm, hyomandibular; iop, interopercular; la, lachrymal; mpt, metapterygoid; na, nasal; op, opercular; p. smx, posterior supramaxillary; pal, palatine; pmx; premaxilla; pop, preopercular; pto, pterotic; q, quadrate; Sc,scale; sop, subopercular; sym, symplectic. Anterior is to the left in both images.

The South Dakota *Hoplopteryx* come from a paleolatitude about 47 degrees north of the Turonian paleoequator. Their latitudinal location can be seen in the paleogeographic map in Figure 1.

Figure 5. A. Geologic map of the Black Hills region of South Dakota. The star indicates the general location from which the fossils were collected. B. Detailed geologic map of the Butte and Meade County area. The star indicates the Carlile Shale Formation outcrop area where Dr. Bishop collected invertebrates and the* Hoplopteryx *specimens described herein. Map A is taken from King and Beikman (1974). Map B is a detail from Martin et al. (2004). North is toward the top in both views.

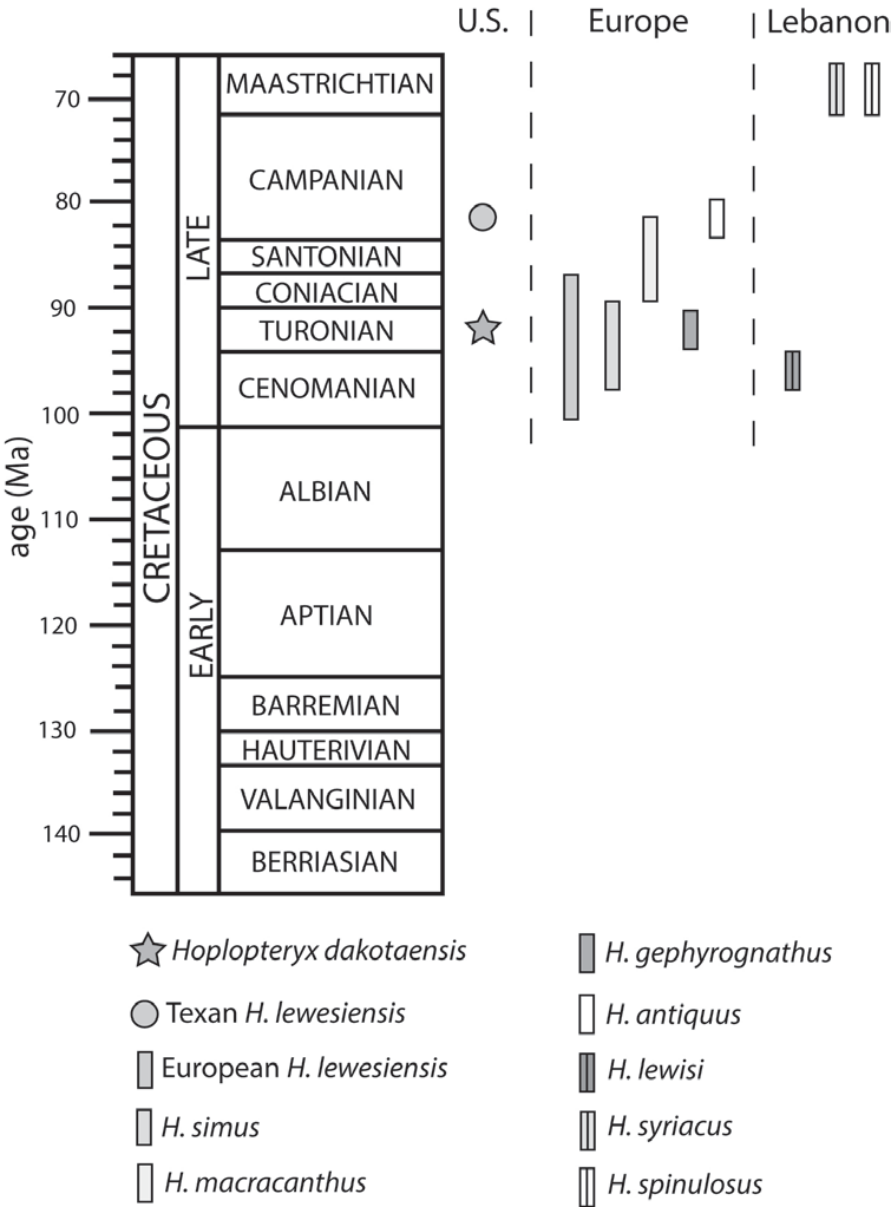

Figure 6. Stratigraphic distribution of* Hoplopteryx *species. Age ranges of the various species are based on Patterson (1964) and Friedman et al. (2015). Geologic time scale based on Walker et al. (2012).

METHODS

We examined the fish at low to moderate magnification as needed using a Bausch and Lomb dissection microscope and used a Mitutoyo Absolute Digimatic bar caliper to measure them. We took photographs of the fossil fishes with a Panasonic DCM-TZ4 digital camera with a Leica DC Vario-Elmar lens. We used Adobe Illustrator to create the figures included in this paper.

RESULTS

SYSTEMATIC PALEONTOLOGY

Order Beryciformes Regan (1911)
Suborder Berycoidei (Patterson 1964)
Family Trachichthyidae (Patterson 1964)
Genus *Hoplopteryx* (Agassiz 1838)

Diagnosis for the genus follows Patterson (1964:305).

Hoplopteryx dakotaensis sp. nov.

Etymology: the species name honors the state of South Dakota and the Dakota-speaking peoples for whom the state was named.

Holotype specimen: SDSM 110292, major portion of anterior skeleton, with skeleton in three-dimensional preservation and impressions of scales.

Paratypes: SDSM 110286, SDSM 110296, SDSM 110291.

Referred Material: SDSM 110293, SDSM 110287, SDSM 110288, SDSM 110290, SDSM 110278.

Diagnosis: *Hoplopteryx* reaching an estimated standard length of 15 to 20 cm; no distinct mucus cavity on the frontals; suture between frontal and parietal bones located near antero-posterior midpoint of supratemporal fossa; supratemporal fossa not divided by a high supraoccipital crest; ridges lateral to supratemporal fossa unornamented; supraoccipital crest low or absent; supraorbital sensory canal not covered by a bony bridge; maxilla with deepened and rounded caudal end; teeth extending onto lateral face of dentary along most of its oral length; cranial ornamentation subdued, consisting of fine, low ridges ornamented with small tubercles; body not deeper than opercular region of head; pelvic fin located well forward relative to cleithrum.

Some of the characters observed for the South Dakota specimens are characteristic of *Hoplopteryx* (or Beryciformes) in general. Among these is a short, deep head with a short snout. This characteristic is seen in all members of the genus *Hoplopteryx*, but is also present in other beryciforms and may be a family-level character. The head is large relative to standard length in *Hoplopteryx*; this could also be true in *H. dakotaensis*, but we do not as yet have any complete specimens. The pelvic fin is located nearly under (ventral to) the pectoral fin in the South Dakota specimens. This derived, anterior location of the pelvic fin is also seen in other species of *Hoplopteryx*, and cannot be considered unique to the South Dakota specimens.

Based on visual and microscopic examination of eight specimens from Olson Ranch and one from the Kudlock Ranch, the South Dakota *Hoplopteryx* specimens differ from all other described species of the genus in the following characters: *Hoplopteryx dakotaensis* does not have a distinct mucus cavity on the frontals, unlike all other species of *Hoplopteryx*. There is a single large depression on the skull roof in *H. dakotaensis*. The suture between frontal and parietal bones is located near the anteroposterior midpoint of this depression, and there is no low transverse ridge separating the anterior part of this depression from its posterior part. All other *Hoplopteryx* species have a mucus cavity located entirely on the frontals that is separated from the supratemporal fossa by a low transverse ridge (Figure 3C). The frontals anterior to the supratemporal fossa in *H. dakotaensis* are convex both anteroposteriorly and mediolaterally; they lack the hollow bordered laterally by high crests that is present on all other species of *Hoplopteryx*. Absence of a distinct mucus cavity on the frontals distinguishes *H. dakotaensis* from *H. lewesiensis* and all other species of *Hoplopteryx* (Figure 3B). The ridges that form the lateral margins of the large supratemporal fossa and set it apart from the rest of the skull roof are smooth (unornamented) in *H. dakotaensis*. In other species of *Hoplopteryx* the ridges that border both the mucus cavity and the supratemporal fossa are ornamented (Patterson 1964).

The supraoccipital crest is low to absent in *H. dakotaensis*. The low supraoccipital crest lies caudal to the supratemporal fossa in those specimens on which the supraoccipital crest is present. It does not divide the supratemporal fossa into left and right halves in any of the South Dakota specimens. A high, well-developed supraoccipital crest does effectively divide the supratemporal fossa in all other species of *Hoplopteryx*.

The supraorbital sensory canal in *H. dakotaensis* is not covered by a bony bridge in the anterior part of the frontals. Patterson (1964) shows this bony bridge in *Hoplopteryx lewesiensis* in his figure 46, and in *H. simus* in his figure 54.

The maxilla is deepest at its posterior end in all specimens of *Hoplopteryx dakotaensis* in which it is preserved. In this it most resembles *Hoplopteryx antiquus*, and differs from *H. lewesiensis* and *H. lewisi* (Patterson 1964). The caudal end of the maxilla is typically more rounded and less rectilinear in *H. dakotaensis* than in other species of *Hoplopteryx* (Figure 3, 4).

Dentary teeth on the lateral side of the dentary are not confined to the symphyseal area in *Hoplopteryx dakotaensis*. A narrow band of minute (0.1-0.2 mm in diameter) columnar, blunt-tipped teeth is present on the lateral surface of the dentary all the way to the caudal end of the oral opening. Lateral dentary teeth are known in *H. lewesiensis* (Patterson 1964), but are reported only in the symphyseal area of the dentary. Teeth do not extend onto the lateral side of the dentary in *H. antiquus*.

Cranial ornamentation in *H. dakotaensis* is generally fine and sparse. Ornamentation consists of fine, low ridges ornamented with small tubercles. Sculpture on the bones is less strongly developed than in *H. lewesiensis* and is definitely less robust than sculpture in *H. simus, H. macracanthus, H. antiquus, H. lewisi,* and *H. spinulosus*. The subdued sculpture, and most notably its radiating pattern on the opercular, is probably diagnostic for *H. dakotaensis*.

The pelvic fin is located ventral to the pectoral fin in all South Dakota specimens which retain the base of the pelvic fin. In *H. antiquus* it is located under the pectoral (Smith-Woodward 1901, 1902). It is described as "thoracic" in *H. simus* (Patterson 1964) and as lying at the anterior part of the cleithrum in *H. spinulosus* (Patterson 1964). Its location may be only slightly different in *H. dakotaensis* than in other *Hoplopteryx* species; the main point here is that the pelvic fin position is highly derived in this early acanthomorph fish.

The scales are typically large in all species of *Hoplopteryx*. The scales of the South Dakota specimens vary in size in different parts of the body. Scales in a longitudinal row a short distance below the lateral line are the largest on the body and reach heights of around 10 mm. Scales on the face and above the lateral line are smaller than those on the body below the lateral line.

The body is not deeper than the opercular region of the head in *H. dakotaensis* (Figure 3A). The body does deepen caudal to the operculum in *H. lewesiensis* (Smith-Woodward 1902; Patterson 1964; Bardack and Teller-Marshall 1982).

DISCUSSION

Based on the fossil record, Patterson (1993) states that acanthomorph fishes first appear by the Cenomanian (Figure 6). Near et al. (2013) used time-calibrated molecular phylogeny to place the origin of acanthomorphs in the Early Cretaceous and pushed the origin of the Beryciformes back before 100Ma. Chen et al. (2014) placed the origin of beryciform fishes at between 99.6 and 95.9Ma. Patterson (1964) placed *Hoplopteryx* in the Order Beryciformes, Family Trachyichthyidae, and reported the earliest appearance of this genus as Cenomanian. Nelson (2006) elevated Trachyichthyoidei to a suborder within the Order Beryciformes. The Trachyichthyidae have been removed from the Beryciformes by some authors (Moore 1993; Miya et al. 2003), but these authors still consider them to be relatively derived acanthomorphs. Other authors (Wiley and Johnson 2010) still view the Trachyichthyidae as a family within a monophyletic Order Beryciformes.

Hoplopteryx ranges through essentially the entire Late Cretaceous, having been recovered from rocks of Cenomanian to Maastrichtian age. The genus is known from Europe, the eastern Mediterranean, and North America (Agassiz 1838; Patterson 1964: Applegate 1970; Bardack and Teller-Marshall 1982; Russell 1988; Ekrt et al. 2008). The genus is represented by seven species within 20 million years after the first appearance of acanthomorph fishes (Figure 6), and by nine species before the end of the Cretaceous. This relatively low diversity supports the observation that Late Cretaceous acanthomorphs were not diversifying particularly rapidly. Patterson (1993) found little evidence for rapid acanthomorph diversification within the Late Cretaceous fossil record. Near et al. (2013) came to the same conclusion based on their time-corrected acanthomorph molecular phylogeny.

Hoplopteryx first appears in Europe during the Cenomanian. The known range of the genus extended as far as Lebanon by the late Cenomanian. Its greatest di-

versity remained in Europe, but by Turonian time the genus had even reached the western side of the proto-Atlantic; it has now been found in Turonian rocks in the northern reaches of the North American Western Interior Seaway, as well as in Campanian rocks at the southern end of the Seaway. The genus is not yet known from the east coast of North America. This could be because its remains have not yet been recognized among the isolated skeletal elements which are typical of many east coast deposits, but may also be due to the scarcity of marine rocks of mid-Cretaceous age in the east (Russell 1988; Weishampel 2006).

Bishop found the South Dakota specimens in association with decapod crustaceans (Bishop and Williams 1991; Parris et al. 2005). Extant beryciforms are known to eat shrimps (Woods and Sonoda 1973), and the association of these fossil beryciforms with decapods suggests that they also may have consumed crustaceans. The small teeth in *H. dakotaensis* completely cover the oral surface of the palate, and had bluntly-pointed tips. They could easily have been used to crush the exoskeletons of small shrimps or other crustaceans with non-mineralized shells.

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