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A Revision of the Fossil Genus †*Knightia*, With a Description of a New Genus From the Green River Formation (Teleostei, Clupeidae)

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ABSTRACT

The fossil genus †*Knightia* is revised; †*K. eocaena* Jordan, 1907, and †*K. alta* (Leidy, 1873) are redescribed, and †*K. vetusta*, new species, is described from the Middle Paleocene Tongue River Formation of southeastern Montana. †*Knightia* is placed in the Pellonulinae. It was found that the known geologic range of †*Knightia* is Middle Paleocene to Middle Eocene and its geographic distribution appears to be western North American, or possibly Pacific continental (western United States and possibly China). †*Knightia* is known only from deposits of probable freshwater origin.

A new clupeid genus, †*Gosiutichthys*, is described from early Middle Eocene deposits of the Green River Formation in Wyoming. †*Gosiutichthys parvus*, new species, is a small herring that, unlike †*Knightia* (the other Green River clupeid), has two supramaxillary bones, thin transparent scales, and several other differentiating characters. The interrelationships of †*G. parvus* with other clupeids are not known, but it is placed provisionally in the poorly defined subfamily, Clupeinae. The presence of two supramaxillary bones prevents its placement in Pellonulinae as the subfamily is currently defined.

INTRODUCTION

The generic name †*Knightia* was proposed by Jordan (1907) to consist of "Section II" of †*Diplomystus* Cope, 1877. Partly because †*Knightia* and †*Diplomystus* were originally together in the same genus, and partly because the morphology of the species was poorly known, there has been much confusion over their interrelationships with other clupeomorph fishes. Grande (1982), how-

ever, explained why these two genera are not closely related (also see Taverne, 1975). †*Diplomystus* is not a clupeiform, while †*Knightia* is a clupeid.

The purpose of the present paper is to review the genus †*Knightia*, to redescribe the included species (in particular, the type species, †*K. eocaena* Jordan), to describe a new species of †*Knightia*, and also to describe

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the taxon previously referred to as “†*Knightia* cf. *alta*” by Grande (1980) (it is found not to be in the genus †*Knightia*).

MATERIALS AND METHODS

Fossils used here are deposited in the following institutions: Department of Vertebrate Paleontology, American Museum of Natural History, New York (AMNH); Division of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Department of Paleontology, Science Museum of Minnesota, St. Paul (SMMP); British Museum (Natural History), London (BMNH); Department of Paleontology, California Academy of Sciences, San Francisco (CAS). Skeletal and cleared and stained preparations of extant species are deposited in the Department of Ichthyology, American Museum of Natural History.

All counts and measurements were made as in Grande (1982). Because †*Knightia* and †*Gosiutichthys*, like other clupeoids, have no lateral line scales, a longitudinal row just above the vertebral column was counted instead. Fossils were prepared using needles and microscope. AMNH 10425 was prepared by the transfer technique (Toombs and Rixon, 1959). Skeletons of Recent fishes were cleared and stained following Dingerkus and Uhler (1977). The clupeomorph taxonomy and dorsal scute terminology used in this paper follow Grande (1982).

The locality codes given here (F-1, F-2, etc.) are explained in Grande (1980). The names of all fossil taxa mentioned are preceded by a dagger (†).

Whitehead (1968) divides the family Clupeidae into five subfamilies (Clupeinae, Pellonulinae, Alosinae, Dorosomatinae, and Pristerigasterinae). This classification system will be used here,² but this does not indicate

² Using Whitehead's (1973) key, †*Knightia* and †*Gosiutichthys*, new genus, are excluded from Pristigasterinae by having less than 30 anal rays, excluded from Alosinae and Dorosomatinae because the upper jaw is without a deep median cleft, and excluded from Dussumieriinae and Spratelloidinae because they have abdominal and

acceptance of all these groups as monophyletic. A comprehensive study of the interrelationships of fossil and recent clupeoids is in progress by the author.

ACKNOWLEDGMENTS

I thank Mr. Guido Dingerkus, Drs. Donn E. Rosen, Gareth Nelson, C. Lavett Smith and Colin Patterson for reading and commenting on various drafts of this manuscript. I also thank Dr. Bobb Schaeffer for giving me free access to the field notes of his 1952 collecting trip to the Tongue River Formation of Montana. I thank Mr. Bruce Erickson (SMMP) and Mr. Pete Larson for mailing certain specimens to me. Mr. Guido Dingerkus aided the author with some of the photographic work. Part of the fieldwork for this project was funded by the National Geographic Society grant no. 2339-81 to the author.

ABBREVIATIONS USED IN FIGURES

a, antorbital
 aa, angulo-articular
 af, anterior fontanelle
 c, circulus (surface “ridge”)
 d, dentary
 ecp, ectopterygoid
 ep, epural
 f, frontal
 hs, hemal spine
 hy, hypural
 io, infraorbital
 iop, interopercle
 l, lacrimal
 m, maxilla
 me, mesethmoid
 n, nucleus (focus)
 ns, neural spine
 op, opercle
 p, parietal
 ph, parhypural
 pm, premaxilla
 pop, preopercle
 ps, parasphenoid
 pt, post-temporal
 pu, preural centrum

pelvic scutes with ascending lateral arms. (Dussumieriinae and Spratelloidinae make up the Dussumieriidae of his 1968 classification.)

q, quadrate
 r, retroarticular
 rl, recessus lateralis
 s, symplectic
 sc, sclerotic ring
 sm, supramaxillary
 soc, supraoccipital
 sop, subopercle
 tf, temporal foramen
 u, ural centrum
 un, uroneural

SYSTEMATIC DESCRIPTION

SUBORDER CLUPEOIDEI

FAMILY CLUPEIDAE

SUBFAMILY PELLONULINAE

GENUS †*KNIGHTIA* JORDAN, 1907

TYPE SPECIES (by original designation): †*Knightsia eocaena* Jordan, 1907—a replacement name for the junior primary homonym †*Clupea humilis* Leidy, 1856 (primary homonym is †*Clupea humilis* von Meyer, 1848).

Grande (1980) was incorrect in stating that “[because Cope (1877, 1884) placed Leidy’s (1856) name in †*Diplomystus*] it was no longer a homonym.” According to the Code of Zoological Nomenclature a junior primary homonym cannot be validated by transfer to another genus. Therefore, †*Knightsia humilis* is not the valid name. The name †*Clupea pusilla* Cope, 1870 (synonymized with †*humilis* by Cope, 1884) is not an available replacement name because it is a junior homonym of *C. pusilla* Mitchill, 1814. Therefore †*Knightsia eocaena* Jordan, 1907, is the valid name for this species.

REVISED GENERIC DIAGNOSIS: A double-armored clupeid that differs from all other clupeids in the following combination of characters: only one supramaxillary bone; relatively few vertebrae (36 to 40) and pleural ribs (20–22 pairs); and a series of about 12–14 ovate³ to circular dorsal scutes with smooth unsculptured “wings” and a median crest extending from slightly in front of to slightly

behind the scute (fig. 10). The dorsal scute series is “complete” (running along the dorsal midline from the back of the head to the origin of the dorsal fin) similar to *Hyperlophus*, †*Gosiutichthys*, new genus, and “†*Clupea*” *vectensis* Newton, 1889 (see Grande, 1982). (Some Recent clupeins and alosins also have a similar dorsal scute morphology, but have only a single scute rather than a series.)

ETYMOLOGY: †*Knightsia*, “in honor of the late Wilbur Clinton Knight, of the University of Wyoming, an indefatigable student of the paleontology of the Rocky Mountains” (Jordan, 1907, p. 136). Gender feminine.

DESCRIPTION AND DISCUSSION: Tables 1 and 2 show comparative meristic and morphometric data for the three known North American species of †*Knightsia*, and †*Gosiutichthys parva*, new genus, new species. Like all other clupeiforms, †*Knightsia* has: a recessus lateralis (in which the infraorbital, supraorbital, and preopercular sensory canals converge) (fig. 2A); parietals which are separated by the supraoccipital (fig. 2A and 2B); and no “beryciform foramen” of McAllister (1968, p. 6; Grande, 1982). Like all other clupeoids (at least primitively), †*Knightsia* has: a reduced ural centrum 1 (compared to more primitive clupeomorphs such as †*Ornatogulum* and †*tellimmichthyids*—fig. 3, and Grande, 1982); a free parhypural (not fused to the first preural centrum, see figs. 3, 6, and 9); the first uroneural fused with the first preural centrum (figs. 3, 6, and 9); and no lateral line scale canals. Like pellenulins, †*Knightsia* has a relatively low number of branchiostegals (about seven or eight) and a peculiarly shaped dorsal scute (as described in the diagnosis and illustrated in fig. 10). This same morphological type of dorsal scute also occurs in *Hyperlophus* (illustrated in Grande, 1982), †*Gosiutichthys*, new genus (fig. 18), “†*Clupea*” *vectensis* Newton, 1889 (Grande, 1982), and several Recent clupeins (*Harengula*, *Opisthonema*, and others—Grande and Nelson, in preparation). In Recent dorsal-scuted clupeins, there is only one dorsal scute, which is located just behind the head and anterior to the first predorsal bone. †*Knightsia* has a complete series of dorsal

³ The lateral wings on smaller specimens (where the scutes are extremely thin) are often not fully preserved, or folded along the median crest, giving the scute a narrower appearance.

scutes (about 12–14) running from the back of the head to the origin of the dorsal fin (each scute about equal in length to that of one preural centrum).

†*Knighthia* has seven or eight predorsal bones (†*K. eocaena* and †*K. alta*, usually 7; †*K. vetusta*, new species, usually 8). The bones of the opercular series are smooth, although very large specimens show faint sculpturing of the opercle. The frontals and parietals bear many strong crests (fig. 2B), which are most pronounced in large specimens. There is a median, anterior fontanelle between the mesethmoid and the frontal bones; but no “posterior frontal fontanelles” (terminology as per Whitehead, 1963) were observed (fig. 2B). The skull roof is well preserved in AMNH 11101–11103 (all adult †*K. eocaena* specimens). Many long gill rakers (about equal in length to two preural centra) have been observed in specimens of †*K. eocaena* and †*K. alta* (well preserved on AMNH 10462, for example). (Gill arches were not visible on any of the †*K. vetusta* specimens examined.) No basipterygoid process was observed in this genus. Scales are heavy and make observation of the caudal skeleton and certain other postcranial features difficult, except on very young individuals. Maxilla, premaxilla, and dentary all bear a single row of small conical teeth. Pelvic fin inserts posterior to anterior insertion of dorsal fin and has seven rays.

The placement of †*Knighthia* within the Pellonulinae is based on the absence of the anterior supramaxillary which is cited by Regan (1917, p. 198) as a diagnostic character of “*Pellonula* and its allies.”⁴ Whitehead (1968) lists one species of the Clupeinae [*Platanichthys platana* (Regan, 1917)] without the anterior supramaxilla, but the holotype (his fig. 2B) appears to have one. The only other clupeids known to have a single supramaxillary bone are some gizzard shads

(Whitehead, 1968). †*Knighthia* does not have any of the derived characters for gizzard shads (given in Nelson and Rothman, 1973).

†*Knighthia* is the only known pellonulin in the New World. It is also the oldest known pellonulin. †*Knighthia* is not closely related to the sympatric genus †*Diplomystus*. †*Knighthia* is a clupeid (see below), whereas †*Diplomystus* is not even a clupeiform (Grande, 1982).

Forey (1973, p. 1314) stated that “in *Diplomystus humilis* [=†*Knighthia eocaena*] and *D. analis* [=†*D. dentatus*], the circuli are arranged concentrically as in *Ornategulum*.” Grande (1982) pointed out that this was not true for †*Diplomystus*, and it was found to be untrue also for †*Knighthia*. The circuli on all species of †*Knighthia* run vertically across the scale as in most clupeomorphs (fig. 4).

THE †*K. eocaena*–†*K. alta* COMPLEX: The distinctions between †*Knighthia eocaena* and †*Knighthia alta* are not very clear. Both Leidy (1873) and the first reviewer, Cope (1884), separated the two species on the basis of body depth. Leidy (1873, p. 196) states: “[†*Knighthia alta*] appears to belong to a different species of herring from [†*Knighthia eocaena*], especially distinguished by the greater proportionate depth of the body and the more arched dorsal border. In most other essential characters the two appear to agree.”

Cope (1884, p. 79) states: “[†*Knighthia alta*] is distinguished from . . . [†*Knighthia eocaena*] by the greater relative depth of the body The difference which it presents in this respect is rather too great to permit its union with [†*K. eocaena*]. Nevertheless, intermediate specimens occur, but their characters are sometimes found to be due to distortion.”

In an attempt to find meristic or morphometric characters to separate the “†*K. eocaena*–†*K. alta* complex” into two species, 26 complete specimens (listed below) with a body depth in the †*K. eocaena* range were compared with 25 complete specimens (listed below) with a body depth in the †*K. alta* range. Similar size ranges were selected for each group to eliminate ontogenetic allometric effects (†*K. eocaena*—31 to 135 mm. standard length; †*K. alta*—47 to 144 mm. standard length). The results (tables 1 and 2)

⁴ My use of Regan’s argument does not imply acceptance of his conclusions, but rather sets the stage for a more detailed study of clupeoid interrelationships (in progress). It is quite possible that Pellonulinae like Clupeinae is not a monophyletic group.

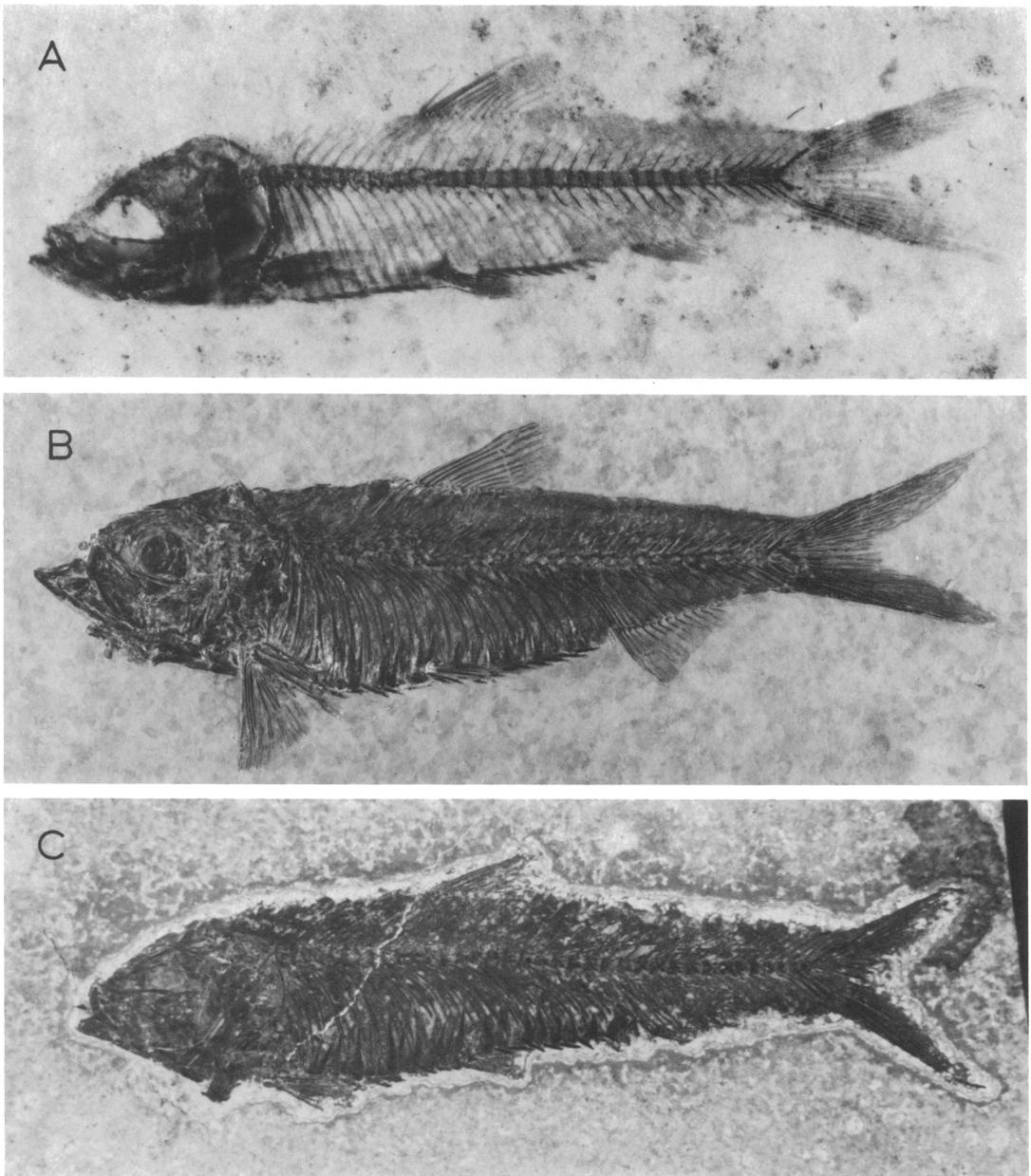


FIG. 1. †*Knightia eocaena* Jordan, 1907, growth series: (A) young juvenile (SMMP 78.9.17), s.l. 2 cm.; (B) average size individual (AMNH 10481), s.l. 7.5 cm.; (C) large specimen (AMNH 4299), s.l. 13.5 cm. Negatives reversed for A and C. All three specimens from locality F-1 of Grande (1980).

did not show any appreciable differences (other than body depth) between †*eocaena* and †*alta*, and it is possible that together they form a single species. They will not be syn-

onymized here because some workers (including Schaeffer, 1947) found a bimodal distribution of relative body depth within the †*K. eocaena*-†*K. alta* complex. †*Knightia*

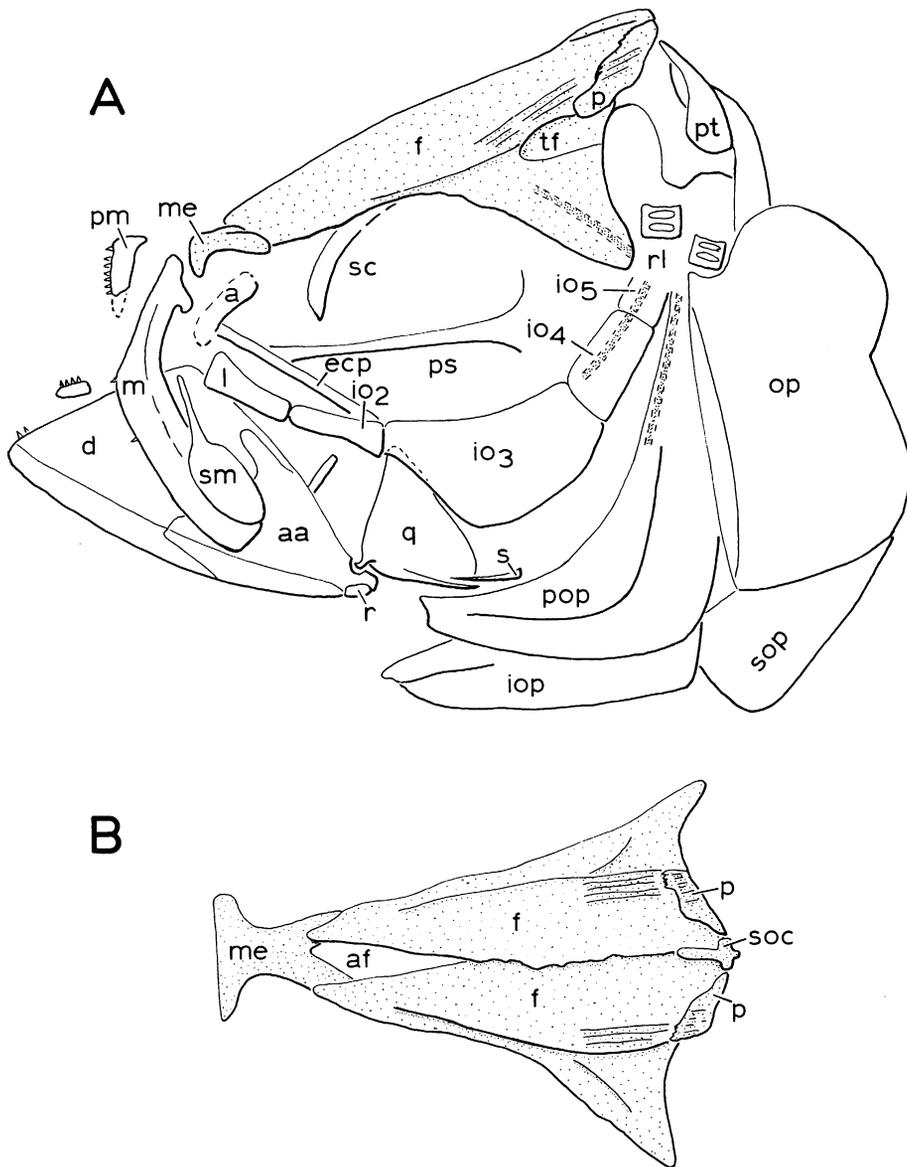


FIG. 2. †*Knightia eocaena* Jordan, 1907, camera lucida drawings of skull: (A) lateral view of SMMP 78.9.9 (s.l. 10 cm.) from locality F-2 of Grande (1980). Anterior half of maxilla restored on the basis of other specimens. Parts of the canal system and the restored margins of the antorbital are indicated by dashed lines; (B) dorsal view of skull (AMNH 11101, s.l. 10 cm.; with supraoccipital restored based on AMNH 11103, s.l. 15 cm.) from locality F-1.

eocaena and †*K. alta* are sympatric, and if they are distinct species, they are probably very closely related. The †*K. eocaena*-†*K.*

alta complex forms a taxon which is very easy to distinguish from †*K. vetusta*, new species (table 1). In addition to the possibility

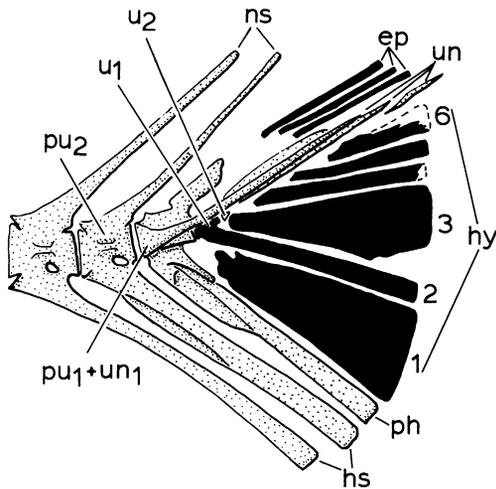


FIG. 3. †*Knightia eocaena* Jordan, 1907, camera lucida drawing of caudal skeleton (AMNH 10461, s.l. 10.5 cm.) from locality F-1. Dashed lines indicate restoration. Hypurals, epurals, and first ural centrum colored black.

of the †*K. eocaena*-†*K. alta* complex being a single species, there is the possibility that it represents several closely related species whose diagnostic characters have yet to be discovered.

†*Knightia eocaena* Jordan, 1907
Figures 1-4, 10A, 11A

†*Clupea humilis* Leidy, 1856.

†*Clupea pusilla* Cope, 1870.

†*Diplomystus humilis*: Cope, 1877.

†*K. humilis*: Grande, 1980.

All the above are invalid because *humilis* and *pusilla* are primary homonyms. (See explanation of homonyms on p. 3.)

TYPE: USNM 87, illustrated in Leidy (1873, pl. 17, fig. 1); nearly complete fish.

REFERENCE SERIES USED HERE FOR TABLES 1 AND 2: AMNH 762, 796, 810a-810f, 1339, 1800, 4299, 4300, 9842, 10425-10427, 10418-10423, and USNM 4022 (illustrated in Cope, 1884, pl. 10, fig. 4).

OTHER REFERRED SPECIMENS: AMNH 795a, 795b, and 11101-11103.

HORIZON AND LOCALITY FOR HOLOTYPE: The Early or Middle Eocene Green River

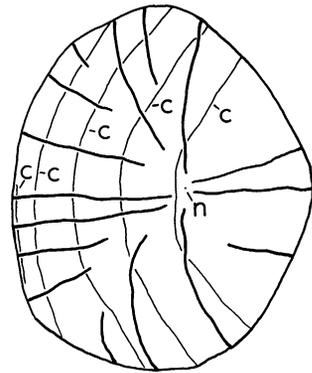


FIG. 4. †*Knightia eocaena* Jordan, 1907, camera lucida drawing of a scale (from SMMP 78.9.9, s.l. 10 cm.), showing the curved, vertically arranged circuli (labeled c). (The thicker unlabeled lines are radii.) Many circuli between the five drawn are omitted. Longest diameter of the scale is 5 mm. From locality F-2. Anterior faces left.

Formation in Wyoming. Exact locality unknown, but probably locality F-1 or G-3 of Grande (1980).

HORIZON AND LOCALITY FOR REFERENCE SERIES: All from the late Early Eocene Fossil Butte Member of the Green River Formation, near and on Fossil Butte National Monument, in southwestern Wyoming at locality F-1 (freshwater deposits) of Grande (1980).

REVISED DIAGNOSIS: †*Knightia eocaena* is more slender-bodied than †*K. alta* [body depth .20-.30 of standard length vs. .33-.41 of standard length in †*K. alta* (based on study sample)]. †*Knightia eocaena* differs from †*K. vetusta* in having: 11-12 (usually 11) principal dorsal fin rays (vs. 12-13, usually 12 in †*K. vetusta*); 11-14 (usually 12 or 13) dorsal pterygiophores (vs. 13 or 14 in †*K. vetusta*); 13-15 (usually 13 or 14) principal anal rays (vs. 17 in †*K. vetusta*); and 13-15 (usually 13 or 14) anal pterygiophores (vs. 16 or 17 in †*K. vetusta*). The dorsal fin is also shorter than in †*K. vetusta*.

ETYMOLOGY: *eocaena*, "changed to dirt" (from Latin) or possibly "dawn of the new" (from Greek) (not specified by original author). Gender feminine.

DESCRIPTION AND REMARKS: Morphometric data are given in table 2. Pectoral fin rays 11–14 (usually 13 or 14) with first ray unbranched; pelvic rays 7⁵ with first ray unbranched; principal dorsal rays usually 11 ($r = 11-12$, $n = 20$, $\bar{X} = 11.10$, $SD = .308$) with first ray unbranched and preceded by two very short “accessory rays” (see definition in Grande, 1980); dorsal pterygiophores usually 12 or 13 ($r = 11-14$, $n = 16$, $\bar{X} = 12.50$, $SD = .817$); principal anal rays usually 13 or 14 ($r = 13-15$, $n = 17$, $\bar{X} = 13.82$, $SD = .728$) with first ray unbranched and preceded by one or two small accessory rays; anal pterygiophores usually 13 or 14 ($r = 13-15$, $n = 16$, $\bar{X} = 14.00$, $SD = .730$); caudal fin rays 1, 9, 8, 1; vertebrae usually 37 or 38 ($r = 37-40$, $n = 21$, $\bar{X} = 37.86$, $SD = .793$); pleural ribs usually 21 or 22 pairs and rarely 23 pairs. Scales cycloid, about 34 or 35 along vertebral column and usually 6 or 7 rows below vertebral column at greatest body depth. One specimen (AMNH 9842) had only five rows below the vertebral column, but this may be an artifact of preservation (the specimen is somewhat twisted). Scales heavy, making observation of caudal skeleton and other internal features difficult. Branchiostegals about 8, predorsal bones usually 7, dorsal scutes (fig. 10A) usually about 13⁶ (11–14), abdominal scutes (which run from anus to below pectoral fin insertion) about 20–22. Small conical teeth on maxilla, premaxilla, and dentary. One supramaxillary bone. Drawings of skull, caudal skeleton, and scale are given in figures 2–4. Maximum total length for this species is about 25 cm., but most specimens do not exceed 15 cm., and specimens greater than 20 cm. are rare. See generic description for additional information. Known only from freshwater deposits. This species is extremely

⁵ Grande (1980, p. 87) reported “usually 6” pelvic rays, but this was due to incomplete preservation on several specimens. Although some specimens appear to have 6 or 8, the normal number of pelvic rays for this species is 7.

⁶ Counts difficult because dorsal scutes are rarely all well preserved.

common in the Green River Formation (see Grande, 1980, p. 84).

†*Knightia alta* (Leidy, 1873)

Figures 5, 6, 10B, 11B

†*Clupea alta* Leidy, 1873.

†*Diplomystus altus*: Cope, 1877.

†*Knightia copei* Tanner, 1925—a subjective junior synonym (Grande, 1980, pp. 86–87).

TYPE: USNM 86, illustrated in Leidy (1873, pl. 17, fig. 2); a nearly complete fish missing part of the lower jaw.

REFERENCE SERIES USED HERE FOR TABLES 1 AND 2: AMNH 1815, 10428–10436, 10442–10447, 10449, 10452, 2682, 2688 (illustrated in Cope, 1884, pl. 9, fig. 9), 10453, 10454, and USNM 4019 (illustrated in Cope, 1884, pl. 10, fig. 5).

OTHER REFERRED SPECIMENS: AMNH 2500.

HORIZON AND LOCALITY FOR HOLOTYPE: The early Middle Eocene Laney Member of the Green River Formation, near Green River, Wyoming at locality G-3 of Grande (1980).

HORIZON AND LOCALITY FOR REFERENCE SERIES: AMNH 1815, 10428–10436, 10442–10444, 2500, 795, and USNM 4019 all from the Fossil Butte Member of the Green River Formation at locality F-1 (freshwater deposits) of Grande (1980); AMNH 2682, 2683, 10445–10447, 10449 and 10452 all from the Laney Member of the Green River Formation at locality G-3 of Grande (1980); AMNH 10453 and 10454 are both from the Laney Member of the Green River Formation at locality G-4 of Grande (1980).

REVISED DIAGNOSIS: †*Knightia alta* is deeper-bodied than †*K. eoacaena* [body depth .33–.41 of standard length vs. .20–.30 of standard length in †*K. eoacaena* (based on study sample)]. †*Knightia alta* differs from †*K. vetusta* in having: 11 principal dorsal fin rays (vs. 12–13, usually 12, in †*K. vetusta*); 11–13 (usually 12) dorsal pterygiophores (vs. 13 or 14 in †*K. vetusta*); 13–15 (usually 14) principal anal fin rays (vs. 17 in †*K. vetusta*); and 13–16 (usually 13 or 14) anal pterygiophores (vs. 16 or 17 in †*K. vetusta*). The dorsal fin is also shorter than in †*K. vetusta*.

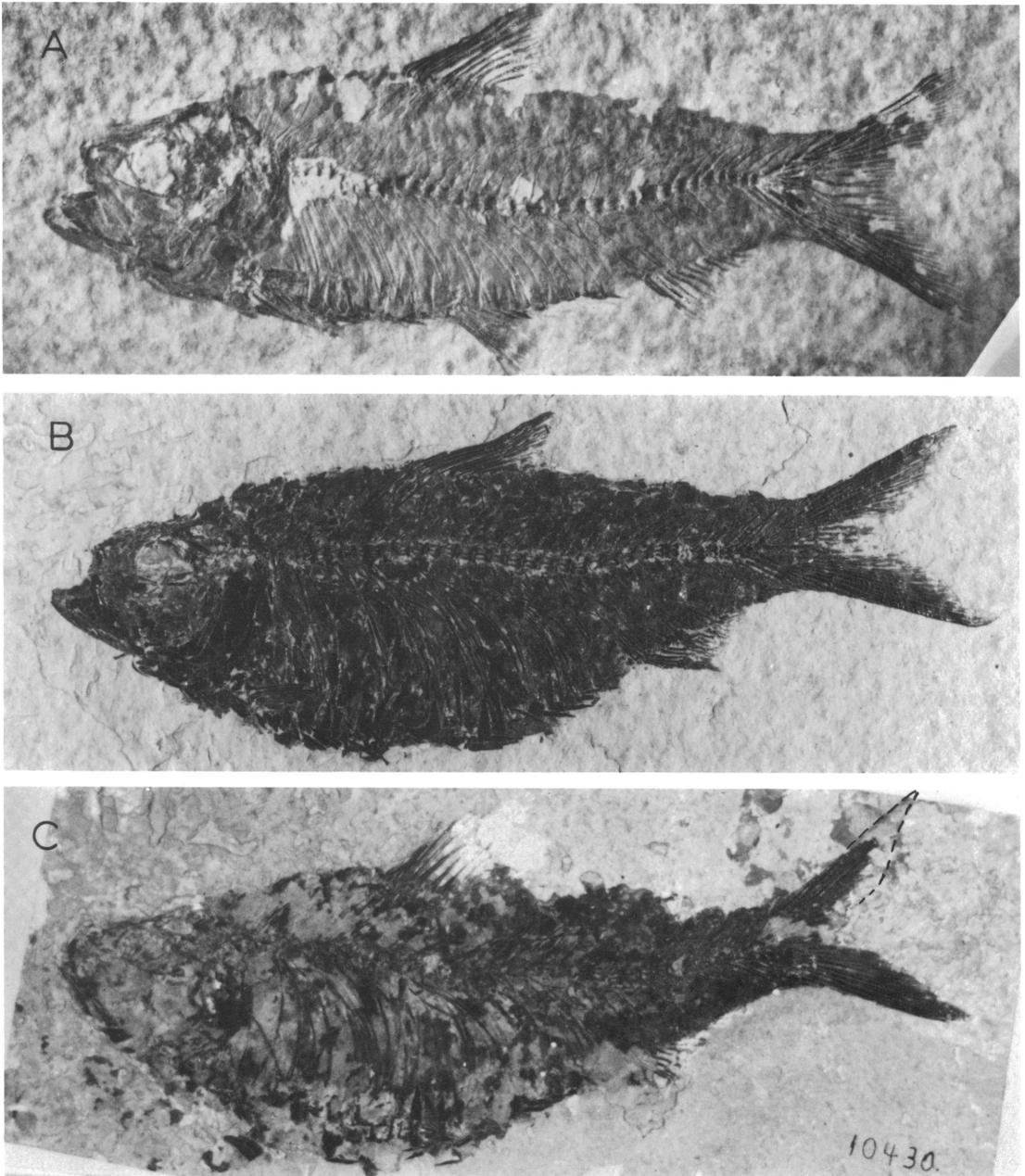


FIG. 5. †*Knightia alta* (Leidy, 1873), growth series: (A) young individual (AMNH 10443), s.l. 4.8 cm.; (B) average sized individual (AMNH 10479), s.l. 7.5 cm.; (C) large specimen (AMNH 10430), s.l. 13.5 cm. Negative reversed for B. All three specimens from locality F-1.

ETYMOLOGY: *alta*, deep (from Latin); gender feminine.

DESCRIPTION AND REMARKS: Morphomet-

ric data are given in table 2. Pectoral fin rays 12–14 (usually 13) with first ray unbranched; pelvic rays seven ($n = 1$); principal dorsal

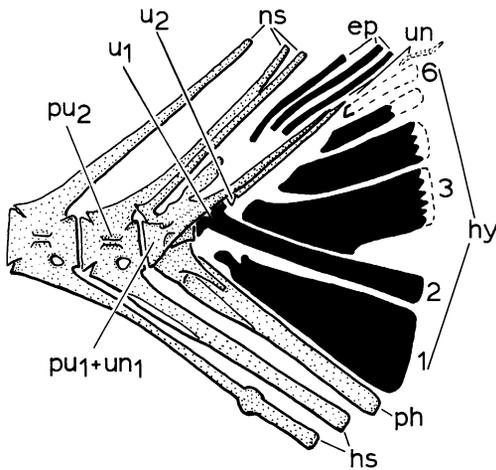


FIG. 6. †*Knightia alta* (Leidy, 1873), camera lucida drawing of caudal skeleton (AMNH 10436, s.l. 10.5 cm.) from locality F-1. The extra neural spine on PU 1 is only rarely found in both †*K. alta* and †*K. eocaena*. Dashed lines indicate restoration. Hypurals, epurals, and ural centrum colored black.

rays 11 ($n = 21$) with first ray unbranched and preceded by two very short accessory rays; dorsal pterygiophores usually 12 ($r = 11-13$, $n = 21$, $\bar{X} = 12.09$, $SD = .302$); principal anal rays usually 14 ($r = 13-15$, $n = 15$, $\bar{X} = 14.07$, $SD = .458$), with first ray unbranched and preceded by one or two very small accessory rays; anal pterygiophores usually 13 or 14 ($r = 13-16$, $n = 16$, $\bar{X} = 14.07$, $SD = .884$); caudal fin rays 1, 9, 8, 1; vertebrae usually 37 ($r = 36-40$, $n = 15$, $\bar{X} = 37.13$, $SD = 1.13$); pleural ribs usually 21 or 22 pairs and rarely 23 pairs. Scales cycloid, about 34 or 35 along vertebral column and about seven rows below vertebral column at greatest body depth. Scales heavy as in †*K. eocaena*. Branchiostegals about eight, predorsal bones usually seven (rarely eight), dorsal scutes (fig. 10B) usually about 12⁶ (10-13), abdominal scutes (which run from anus to below pectoral insertion) about 20-22. Small conical teeth on maxilla, premaxilla, and dentary. One supramaxillary bone. Drawings of part of the opercular series and the caudal skeleton are given in figures 6 and 11B. Maximum known total length for

this species is about 16 cm. (AMNH 10430), but most known specimens are about 6 to 10 cm. See generic description for additional information. Known only from freshwater deposits. This species, although locally abundant at some localities (such as G-3 of Grande, 1980), is not as common as †*K. eocaena*.

It is doubtful that †*K. eocaena* is merely a sexual dimorph of †*K. alta* because †*K. eocaena* frequently occurs in mass mortality zones (see fig. II.41 in Grande, 1980, for example) that can contain up to hundreds of †*K. eocaena* per sq. meter but very few or no specimens of †*K. alta*.

†*Knightia vetusta*, new species

Figures 7-9, 10C, 11C

†*Knightia*, new species A, Grande (1982).

TYPE: AMNH 10404, a nearly complete fish.

DESIGNATED PARATYPE SERIES: AMNH 10406, 10408-10412 (most are nearly complete fish).

ADDITIONAL REFERRED SPECIMENS: AMNH 10413, 10415-10417. The type, paratype series and additional referred specimens were all used to generate the data for tables 1 and 2.

HORIZON AND LOCALITY FOR HOLOTYPE: The late Middle Paleocene Tongue River Formation, near Bay Horse, Montana (Powder River County), SW $\frac{1}{4}$, sec. 4, T9S, R50E. The associated fauna suggests that the fish occur in a freshwater deposit. "Fish occur in a thin, ledge-forming siltstone considered to be about 450' above Lobo-Tongue River contact" (Schaeffer, field notes, 1952). Closer examination of the matrix reveals that it is a limestone rather than a siltstone. The matrix is hard, and not laminated, so the rock frequently breaks across the fish rather than parallel to it. This usually results in damaged and incompletely exposed specimens. More detailed locality information is deposited at AMNH.

About 28 specimens of †*K. vetusta*, new species, were collected by Bobb Schaeffer and Walter Sorenson in 1952. A small fragment



FIG. 7. †*Knightia vetusta*, new species, (A) holotype (AMNH 10404), s.l. 7 cm.; (B) paratype (AMNH 10406), s.l. 5.8 cm., showing the long dorsal fin characteristic of this species. Both from the Middle Paleocene Tongue River Formation of Montana.

of paddlefish skull (AMNH 10478, not identifiable to species) was also found at this locality. No other fish species are known to have been collected there, but poorly preserved plant fossils are common. This locality is similar to many in the Green River Formation (see Grande, 1980) in that †*Knightia* is the most common fish present. This locality is being collected further in the hope of finding other species.

HORIZON AND LOCALITY FOR PARATYPE SERIES AND REFERRED SPECIMENS: As for holotype.

DIAGNOSIS: A medium-sized †*Knightia* that has a higher number of principal anal fin rays (17), anal pterygiophores (16 or 17) and predorsal bones (usually eight) than any other species of †*Knightia*. The dorsal fin is higher (the length of 13 to 14½ anterior vertebrae) and the relative caudal peduncle base length

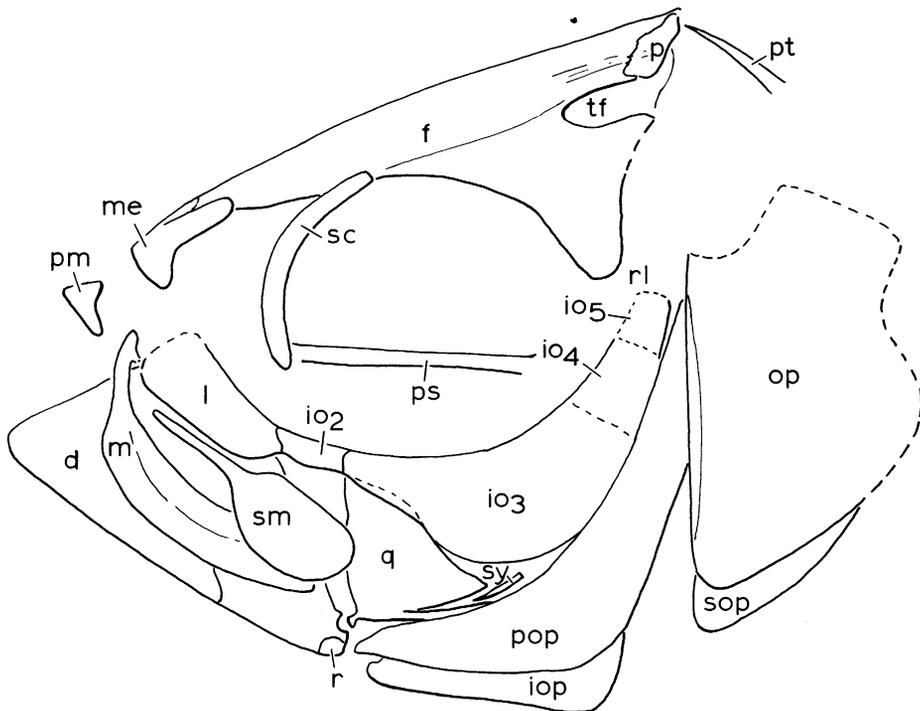


FIG. 8. †*Knightitia vetusta*, new species, camera lucida drawing of skull (AMNH 10408, s.l. 7 cm.). From the Middle Paleocene Tongue River Formation of Montana. Dashed lines indicate restoration. Although not preserved in this specimen, the dentary, maxilla, and premaxilla of †*K. vetusta* bear a single row of conical teeth (as in all known species of †*Knightitia*).

and anal fin base length are greater, than in any other species of †*Knightitia* (see tables 1 and 2).

ETYMOLOGY: *vetusta*, old (from Latin); gender feminine.

DESCRIPTION AND REMARKS: Morphometric data are given in table 2. Pectoral fin rays about 14 or 15; pelvic rays seven with first ray unbranched; principal dorsal rays 12 or 13 (usually 12, $n = 5$, $\bar{X} = 12.20$, $SD = .447$), with first unbranched and preceded by two very short accessory rays; dorsal pterygiophores 13 or 14 ($n = 9$, $\bar{X} = 13.56$, $SD = .527$); principal anal rays 17 ($n = 8$) with first ray unbranched and preceded by one or two very small accessory rays; anal pterygiophores 16–17 ($n = 8$, $\bar{X} = 16.63$, $SD = .518$); caudal 1, 9, 8, 1; vertebrae 38–39 ($n = 8$, $\bar{X} = 38.38$, $SD = .518$); pleural ribs 21 or 22 pairs. Scales cycloid and heavy (when pre-

served), making observation of caudal skeleton difficult. Branchiostegals about eight, predorsal bones usually eight, dorsal scutes (fig. 10C) about 12, abdominal scutes (which run from anus anteriorly to below pectoral fin insertion) about 21–23. Small conical teeth on maxilla, premaxilla, and dentary. One supramaxillary bone. Drawings of skull, opercle, subopercle, and caudal skeleton are in figures 8, 9, and 11C. Maximum total length for this species is about 10 cm. (all study specimens ranged in total length from about 7 to 10 cm.). See generic description for additional information. Known only from freshwater deposits. This species is not very common (the type and reference specimens are the only ones known to the author).

The occurrence of this species suggests that the genus †*Knightitia* inhabited western North American drainage systems for at least most

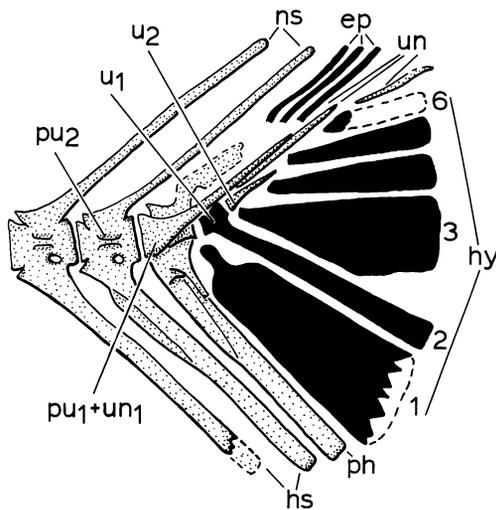


FIG. 9. †*Knightia vetusta*, new species, camera lucida drawing of caudal skeleton (AMNH 10404, s.l. 7 cm.). From the Middle Paleocene Tongue River Formation of Montana. Dashed lines indicate restoration. Hypurals, epurals, and fistular centrum colored black.

of the Paleogene, extending the time range of the genus in that area to Middle Paleocene through Middle Eocene (over 10 million years). This species is the earliest known North American clupeid, and the oldest known pellenulin.

OTHER SPECIES PREVIOUSLY PLACED IN †KNIGHTIA

JUNIOR SYNONYMS, HOMONYMS, AND SPECIES REMOVED FROM †*Knightia*: †*Knightia copei* Tanner, 1925 from the Green River Formation of Wyoming is a junior synonym of †*K. alta* (Grande, 1980, p. 87) and “†*K. humilis* (used in Grande, 1980) is an invalid name for †*K. eocaena* as explained on page 3.

†*Ellimma branneri* (Jordan, 1910), from Tertiary deposits in Riacho Doce, Alagoas (Brazil) was placed in †*Knightia* by Schaeffer (1947) because of similarity in dorsal scute morphology, and some primitive characters (such as large cycloid scales and “general body form”) which are found in many clupeiforms (and other teleosts) and are not de-

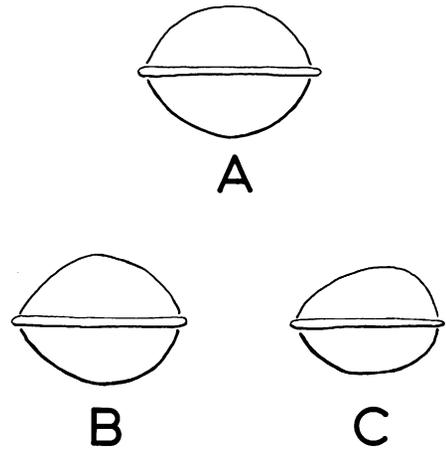


FIG. 10. Dorsal scutes of three species of †*Knightia* (anterior faces left): (A) †*K. eocaena* Jordan, 1907 (drawn from AMNH 2499); (B) †*K. alta* (Leidy, 1873) (drawn from AMNH 10433); (C) †*K. vetusta*, new species (drawn from holotype AMNH 10404, scute inverted to show median crest on dorsal surface). All drawn from average sized adult specimens.

rived characters for †*Knightia*. Grande (1982) shows that the dorsal scute morphology of †*E. branneri* is not similar to that of †*Knightia* as suggested by Schaeffer (1947, fig. 5). Schaeffer drew the inside surface of the scute rather than the dorsal surface; further preparation for this study revealed the true dorsal surface (fig. 22, Grande, 1982). Also, †*E. branneri* was found to have two supramaxillary bones (fig. 19) and is probably a clupeine.⁷

Schaeffer (1947, p. 17) suggested inclusion of †*Ellimma elmodenae* Jordan and Gilbert, 1919, and †*Ellimma barbarae* Jordan and Gilbert, 1919 (both from Miocene deposits of California) but gave no reason for such a placement. The holotype for †*E. elmodenae* (CAS 55404) was examined here and found not to be †*Knightia* (no dorsal scutes, much higher number of vertebrae [at least five more abdominal vertebrae] and other characters).

⁷ This is not to imply acceptance of the Clupeinae as a monophyletic group. Placement there is based only on Whitehead's (1973, p. 12) key.

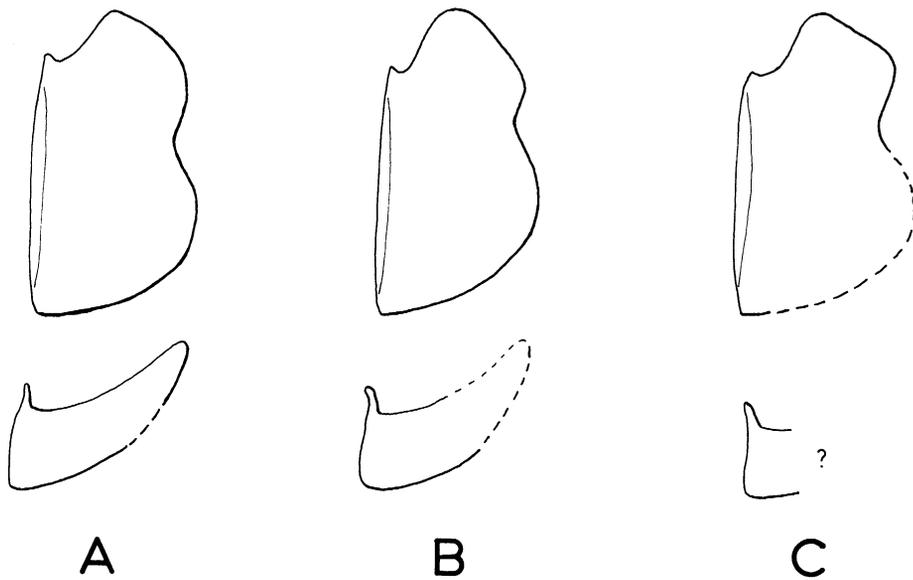


FIG. 11. Opercular and subopercular bones in three species of †*Knightia* (anterior faces left): (A) †*K. eocaena* Jordan, 1907 (OP drawn from AMNH 4300 [s.l. 12 cm.]; SOP drawn from AMNH 10459 [s.l. 8.5 cm.]); (B) †*K. alta* (Leidy, 1873) (OP and SOP drawn from AMNH 10462 [s.l. 9.5 cm.]); (C) †*K. vetusta*, new species (OP and SOP drawn from AMNH 10463 [s.l. 8 cm.]). Dashed lines indicate restoration.

The holotype for †*E. barbarae* is lost, but because no justification has been given to warrant its placement in †*Knightia*, it too is removed from that genus.

SPECIES QUESTIONABLE IN THEIR ASSIGNMENT TO †*Knightia*: “†*Knightia*” *brasiliensis* Woodward, 1939 (from Tertiary deposits of Maranhão, Brazil) and “†*Clupea*” *vectensis* Newton, 1889 (from Oligocene deposits of Isle of Wight) may both belong in the genus †*Knightia*, but the material observed (“cotypes” BMNH 25259 through 25266 for “†*K.*” *brasiliensis* and BMNH 6854 [a slab with about 15 individuals] and two uncatalogued AMNH specimens for “†*C.*” *vectensis*) was insufficiently preserved to determine this (none of the specimens has the supra-maxillary bone (or bones) preserved, none of the “†*K.*” *brasiliensis* specimens has the dorsal scutes preserved). “†*Clupea*” *vectensis* has a dorsal scute morphology like that of †*Knightia*, *Hyperlophus* and †*Gosiutichthys*

(Grande, 1982) and like several clupeins (see explanation of clupein scute on p. 3). The dorsal scute morphology of “†*K.*” *brasiliensis* is unknown. Both “†*K.*” *brasiliensis* and “†*C.*” *vectensis* differ from †*Knightia* in having more principal dorsal fin rays (14 or 15, compared to 11 to 13 in †*Knightia*). These two “Atlantic” continental species (†*brasiliensis* and †*vectensis*) may form their own genus (not named here—work in progress); neither is thought to belong to the “Pacific” continental genus, †*Knightia*.

†*Knightia yuyanga* Liu, 1963, from Eocene (probably freshwater) deposits of Hupei, China, is described on the basis of the anterior portion of a fish, missing the anal, caudal, and most of the dorsal fins, the jaws, the caudal skeleton and other elements (IVPP⁸

⁸ Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, People’s Republic of China.

V.2869 illustrated in fig. 1 of Liu, 1963). Until better material for this species is discovered, its placement in †*Knightsia* remains tenuous.

DISCUSSION: The three North American species of †*Knightsia*, †*K. eocaena* Jordan, 1907, †*K. alta* (Leidy, 1873), and †*K. vetusta*, new species, are the only species that can be placed in the genus with reasonable certainty based on the specimens examined for this study. Those specimens are not only abundant, but well preserved.

“†*Knightsia*” *brasiliensis* and “†*Clupea*” *vectensis* are abundant, but their preservation is not very good. They may be related to each other, but do not appear to belong in †*Knightsia* (see above). †*Knightsia yuyanga* is not only poorly preserved, but known only by one specimen. It is recommended that unless better material is described, with the key characters for †*Knightsia* (see diagnosis), that the genus contain only the three North American species. It may be that the genus †*Knightsia* was endemic to North America, or possibly to Pacific coastal regions (if we include “†*K.*” *yuyanga*). “†*Clupea*” *vectensis* (from Isle of Wight) and “†*K.*” *brasiliensis* (from Brazil) may represent a taxon that was endemic to Atlantic coastal regions.

Another fossil clupeid species from the Green River Formation (known only from “Lake Gosiute” deposits—see Grande, 1980) was originally thought to be a new species of †*Knightsia* (see “†*K. cf. alta*” in Grande, 1980). It was found here not to be in †*Knightsia*, and is described below.

A NEW CLUPEID GENUS FROM THE EOCENE GREEN RIVER FORMATION

SUBORDER CLUPEOIDEI

FAMILY CLUPEIDAE

SUBFAMILY CLUPEINAE?

†*GOSIUTICHTHYS*, NEW GENUS

TYPE SPECIES: †*Gosiutichthys parvus*, new species.

GENERIC DIAGNOSIS: A double armored clupeid that differs from all other clupeids in the following combination of characters: two

supramaxillary bones, low number of vertebrae (34–36) and pleural ribs (20 or 21 pairs), and an ovate⁹ to circular dorsal scute with smooth unsculptured “wings” and a median crest extending from slightly in front of to slightly behind the scute (fig. 18). The dorsal scute series is “complete” (running along the dorsal midline from the back of the head to the origin of the dorsal fin) similar to *Hypertrophus*, †*Knightsia* and “†*Clupea*” *vectensis* Newton, 1889 (see Grande, 1982). Some Recent clupeids have a similar dorsal scute morphology, but have only a single scute rather than a series.

ETYMOLOGY: *gosiute*, referring to the fossil lake which the type species inhabited, Eocene Lake Gosiute; *ichthys*—a fish (from Greek); gender masculine.

DESCRIPTION AND DISCUSSION: This taxon was originally thought to be a new species of †*Knightsia* (=†*K. cf. alta* in Grande, 1980), but more detailed examination showed that it had two supramaxillary bones and several characters (see generic and specific diagnosis) which prevent its placement in that genus. Because of the two supramaxillary bones (fig. 16B), †*Gosiutichthys* is not a pellenuline (as the subfamily is currently defined, by Regan, 1917; Whitehead, 1973; and others).

Like all other clupeiforms, †*Gosiutichthys* has a recessus lateralis (in which the infraorbital, supraorbital, and preopercular sensory canals converge); parietals separated by the supraoccipital. Like all other clupeoids (at least primitively), †*Gosiutichthys* has a reduced ural centrum 1 (compared to more primitive clupeomorphs such as †*Ornategulum* and †*ellimmichthyids* (fig. 17 and Grande, 1982); the first uroneural fused with the first preural centrum (fig. 17); the parhypural unfused with the first preural centrum (fig. 17); and no scales with lateral line canals.

⁹ Like †*Knightsia*, the lateral wings on many specimens are not fully preserved or are folded along the median crest, giving the scute a narrower appearance. Like †*Knightsia*, there is often minor variation in the shape of the scute margin within individuals (i.e., some individuals were observed to have both circular and oval scutes).

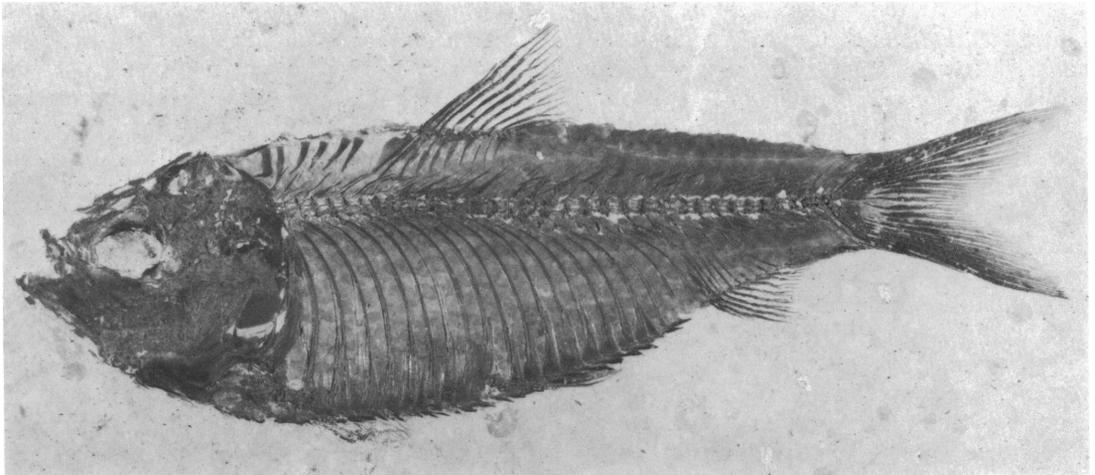


FIG. 12. †*Gosiutichthys parvus*, new genus, new species, a well-preserved individual (AMNH 10480, s.l. 4 cm.) from the Laney Member of the Green River Formation, Wyoming.

†*Gosiutichthys parvus*, new species

Figures 12–18

†*Knightia* cf. *alta* Grande, 1980; and “†New genus and species B” Grande, 1982.

TYPE: AMNH 10458 m., a nearly complete fish on a slab with about 56 referred specimens (fig. 14).

DESIGNATED PARATYPE SERIES: AMNH 10456, a slab with 14 complete specimens

and about 18 partial specimens; and AMNH 10457, a slab with 10 fairly complete specimens and about 20 partial specimens. The data in tables 1 and 2 are taken from the holotype and paratype series only.

ADDITIONAL REFERRED SPECIMENS: AMNH 10458, a slab with about 32 complete specimens and 25 partials, SMMP 78.9.10 and 78.9.11 with two complete specimens each.

HORIZON AND LOCALITY FOR HOLOTYPE:

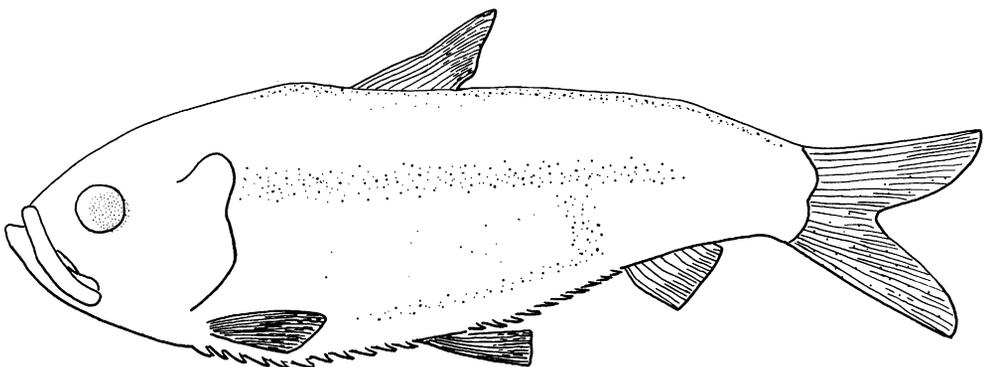


FIG. 13. †*Gosiutichthys parvus*, new genus, new species, camera lucida drawing of the pigmentation pattern preserved on SMMP 78.9.13 (s.l. 3 cm., illustrated in Grande, 1980, fig. II.42). From the Laney Member of the Green River Formation, Wyoming).

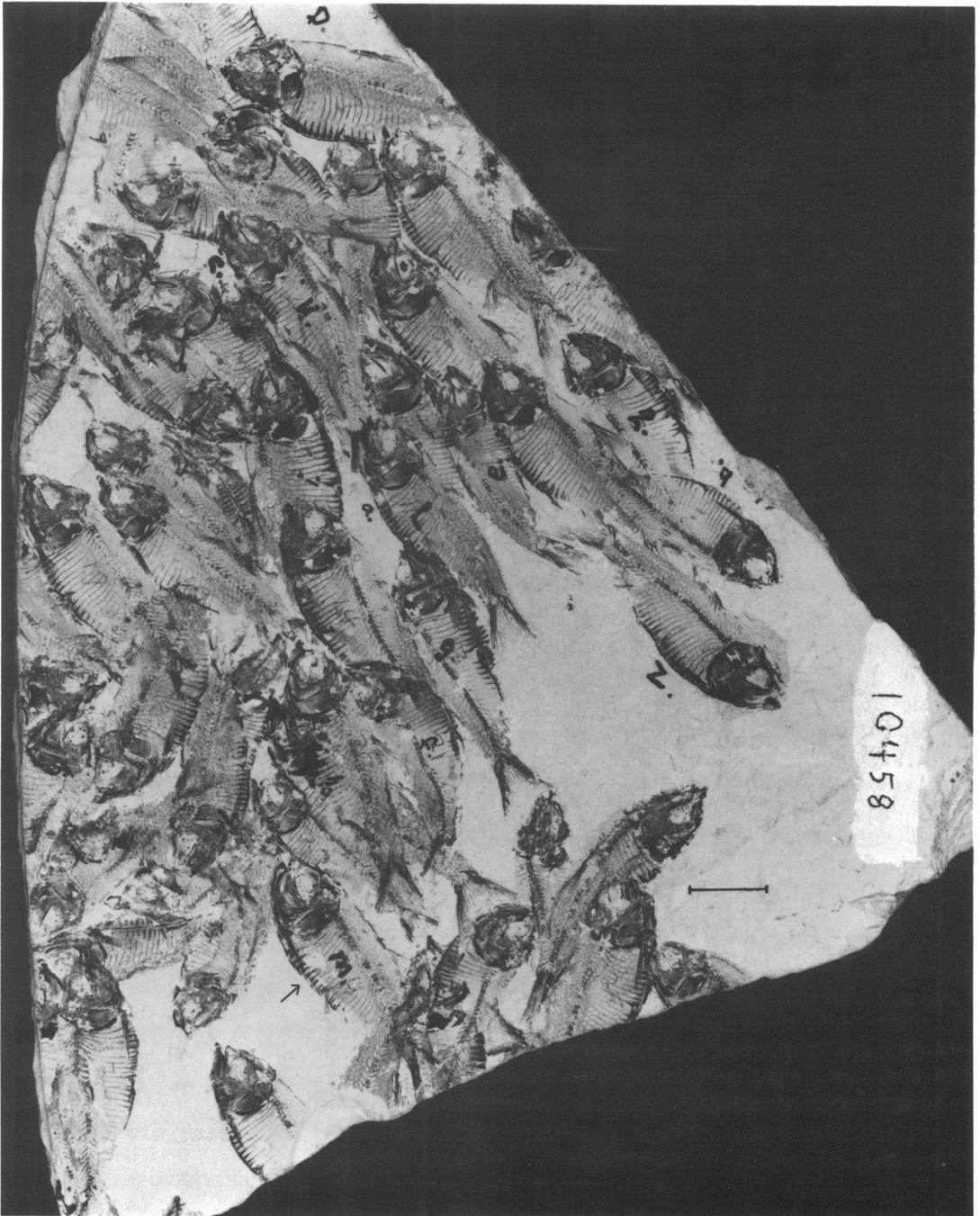


FIG. 14. †*Gosiutichthys parvus*, new genus, new species, mass mortality slab containing holotype (see arrow) and about 56 referred specimens (AMNH 10458). Scale = 1 cm. From the Laney Member of the Green River Formation, Wyoming. Photograph by J. Beckett and AMNH photographic dept.

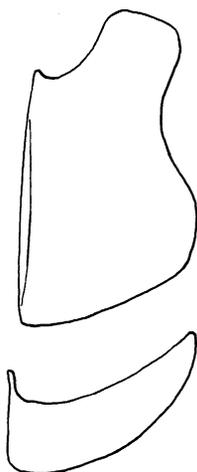


FIG. 15. †*Gosiutichthys parvus*, new genus, new species; opercle (drawn from AMNH 10458h [s.l. 28 mm.]) and subopercle (drawn from AMNH 10458L) [s.l. 27 mm.].

The early Middle Eocene Laney Member of the Green River Formation, about 22 km. north of the Fontenelle Dam, southwestern Wyoming. The insect larvae, amiids, catostomids, and mollusks found closely associated with these fish, together with sedimentological evidence, indicate that these are freshwater deposits (at least at the stratigraphic levels where the fish occur). This species is found in great abundance at the type locality (density as great as thousands per sq. meter). Although other species of fish are proportionately rare at this locality (less than 0.1% of the fish fauna) †*Gosiutichthys* is frequently found associated with large (20–30 cm. long) catostomids (†*Amyzon*, new species—see below).

HORIZON AND LOCALITY FOR PARATYPES AND REFERRED SPECIMENS: As for holotype.

DIAGNOSIS: A relatively small clupeid (rarely exceeding 4 cm. in total length) that differs from †*Knightia*, *Hyperlophus*, and “†*Clupea*” *vectensis* Newton, 1889 (the other clupeids with a complete series of the peculiar dorsal scute type described in the generic diagnosis) in having fewer dorsal fin rays (nine to 10, usually nine); fewer anal fin rays (nine to 12, usually 11); fewer dorsal pterygi-

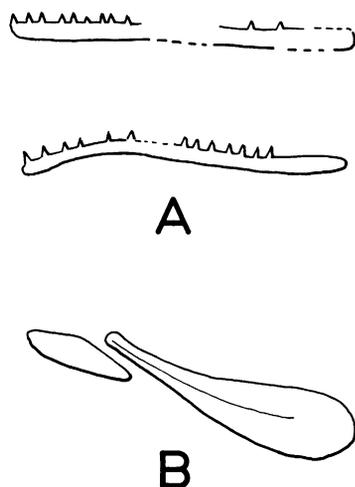


FIG. 16. †*Gosiutichthys parvus*, new genus, new species; elements of the skull and branchial skeleton (anterior to left): (A) basihyal tooth plates (above drawn from AMNH 10458a [s.l. 27 mm.], below drawn from 10458e [s.l. 24 mm.] and reversed); (B) supramaxillary bones (drawn from 10458z [s.l. 28 mm.] and reversed). From the Laney Member of the Green River Formation, Wyoming. Dashed lines indicate restoration.

phores (10 or 11); fewer anal pterygiophores (10 to 13, usually 11 or 12); fewer predorsal bones (usually six or seven); fewer vertebrae (34 to 36, usually 35 or 36); a shorter dorsal and anal fin base length (see table 2); a narrower dorsoposteriorly pointing upper section of the opercle (fig. 15); two supramaxillary bones (fig. 16B); and thinner, more translucent scales.

ETYMOLOGY: *parvus*, small (from Latin); gender masculine.

DESCRIPTION AND REMARKS: Morphometric data are given in table 2. Pectoral fin rays 11–13 (usually 12 or 13) with first ray unbranched; pelvic rays six or seven (which insert posterior to dorsal fin insertion) with the first ray unbranched; principal dorsal rays nine or 10 ($r = 9-10$, $n = 24$, $\bar{X} = 9.33$, $SD = .482$) with first ray unbranched and preceded by two short accessory rays; dorsal pterygiophores 10 or 11 ($n = 19$, $\bar{X} = 10.68$, $SD = .478$); principal anal rays usually 11 ($r = 9-12$, $n = 17$, $\bar{X} = 11.06$, $SD = .899$)

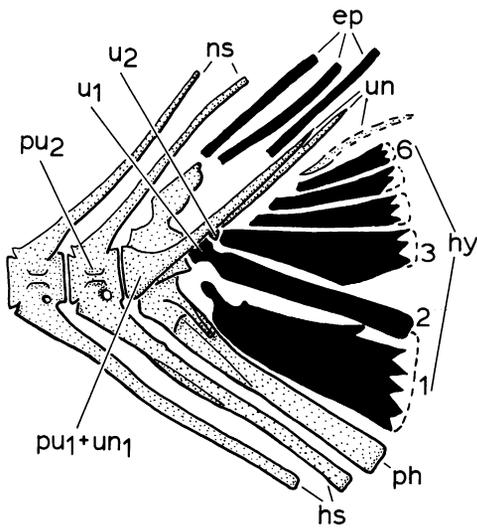


FIG. 17. †*Gosiutichthys parvus*, new genus, new species, camera lucida drawing of caudal skeleton drawn from AMNH 10458h (s.l. 29 mm.). From the Laney Member of the Green River Formation, Wyoming. Dashed lines indicate restoration. Hypurals, epurals, and first ural centrum colored black.

with first ray unbranched and preceded by one or two small accessory rays; anal pterygiophores usually 12 ($r = 10-13$, $n = 24$, $\bar{X} = 11.96$, $SD = .690$); caudal 1, 9, 8, 1; vertebrae 34-36 ($n = 20$, $\bar{X} = 35.35$, $SD = .671$); pleural ribs 20 or 21 pairs. Scales cycloid, thin and transparent, and number about 37 along the vertebral column. Branchiostegals about eight, predorsal bones six or seven, dorsal scutes (fig. 18) usually about 12 or 13 (10-13) (dorsal scute counts often difficult due to lack of preservation), abdominal scutes (which run from anus to just anterior to below pectoral fin insertion) about 20-22. Small conical teeth on maxilla, premaxilla and dentary. Two supramaxillary bones which are well preserved on many specimens including AMNH 10457 a, b, and c and AMNH 10458 b, c, m, q and z. The posterior supramaxillary bone is more slender posteriorly than that of †*Knightsia* (compare fig. 16B with figs. 2A and 8). Maximum total length for this species is about 8 cm. but specimens rarely exceed 4 cm. Basihyal long, with a single row of conical teeth (fig. 16A). The

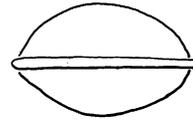


FIG. 18. †*Gosiutichthys parvus*, new genus, new species, camera lucida drawing of a dorsal scute from AMNH 10458. From the Laney Member of the Green River Formation, Wyoming.

gill arches bear many long gill rakers (each about equal in length to two centra). The shape of the opercle is quite distinctive from †*Knightsia* in having a very narrow dorso-posteriorly pointing upper section (compare fig. 15 with fig. 11). Pigmentation patterns are occasionally preserved in †*G. parvus*, and the pattern is illustrated in figure 13. See generic description for additional information. Known only from freshwater deposits. Unlike the two species of †*Knightsia* from the Green River Formation, †*G. parvus* is restricted in its known range to one of the three Tertiary lakes—Lake Gosiute (see Grande, 1980, for a historical discussion of the Green River Lake complex). At the type locality, †*G. parvus* occurs in vast numbers (see fig. 14), sometimes as dense as over 1000 per sq. meter. Other species of fish are extremely rare at this locality (less than 0.1% of total fish fauna) and include †*Amyzon*, new species (a sucker—Grande, Eastman, and Cavender, in press), †*Knightsia*, †*Asineops squamifrons*

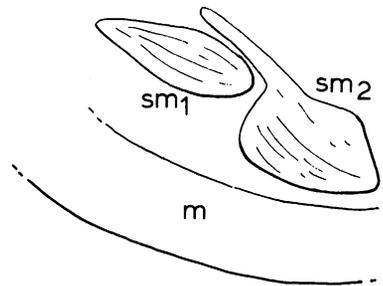


FIG. 19. †*Ellimma branneri* (Jordan, 1910), camera lucida drawing of the two supramaxillary bones, drawn from impressions in AMNH 10050 (s.l. 9 cm.). From Tertiary deposits of Brazil. Anterior faces left, drawing reversed.

TABLE 1
Meristic and Locality Data for the Three North American Species of †*Knightia* and for †*Gosiutichthys*,
New Genus

	† <i>Knightia</i>			† <i>Gosiutichthys</i> , new genus
	† <i>K. eocaena</i>	† <i>K. alta</i>	† <i>K. vetusta</i> , new species	† <i>G. parvus</i> , new species
Principal dorsal fin rays	11–12 (n = 20, \bar{X} = 11.10, SD = .308)	11 (n = 21, \bar{X} = 11.00, SD = 0)	12–13 (n = 5, \bar{X} = 12.20, SD = .447)	9–10 (n = 24, \bar{X} = 9.33, SD = .482)
Dorsal pterygiophores	11–14 (n = 16, \bar{X} = 12.50, SD = .817)	11–13 (n = 11, \bar{X} = 12.09, SD = .302)	13–14 (n = 9, \bar{X} = 13.56, SD = .527)	10–11 (n = 19, \bar{X} = 10.68, SD = .478)
Principal anal fin rays	13–15 (n = 17, \bar{X} = 13.82, SD = .728)	13–15 (n = 15, \bar{X} = 14.07, SD = .458)	17 (n = 8, \bar{X} = 17.00, SD = 0)	9–12 (n = 17, \bar{X} = 11.06, SD = .899)
Anal pterygiophores	13–15 (n = 16, \bar{X} = 14.00, SD = .730)	13–16 (n = 16, \bar{X} = 14.07, SD = .884)	16–17 (n = 8, \bar{X} = 16.63, SD = .518)	10–13 (n = 24, \bar{X} = 11.96, SD = .690)
Vertebrae	37–40 (n = 21, \bar{X} = 37.86, SD = .793)	36–40 (n = 15, \bar{X} = 37.13, SD = 1.13)	38–39 (n = 8, \bar{X} = 38.38, SD = .518)	34–36 (n = 20, \bar{X} = 35.35, SD = .671)
Ribs (pleural) (total number of both sides)	42–46 (usually 42 or 44) (n = 19)	42–46 (usually 42 or 44) (n = 16)	42 or 44 (n = 12)	40 or 42 (n = 25)
Height of dorsal fin (in number of anterior vertebrae)	8½–11 (n = 10, \bar{X} = 9.55, SD = .725)	9–12 (n = 7, \bar{X} = 10.43, SD = 1.02)	13–14½ (n = 4, \bar{X} = 13.88, SD = .750)	9–11 (n = 7, \bar{X} = 9.71, SD = .756)
Locality	Green River Formation, Wyoming, Colorado and Utah (freshwater deposits)	Green River Formation, Wyoming, Colorado and Utah (freshwater deposits)	Tongue River Formation, Montana (freshwater deposits)	Green River Formation, Wyoming (Lake Gosiute freshwater deposits only)
Known geologic range	Early Eocene– Mid-Eocene	Early Eocene– Mid-Eocene	Mid-Paleocene	Mid-Eocene

(a paracanthopterygian of unknown affinity—see Rosen and Patterson, 1969), †*Erismatopterus levatus* (a percopsid) and †*Astephus antiquus* (an ictalurid catfish). Ostracods and mosquito pupae are abundant in the †*G. parvus* beds.

THE RELATIONSHIP OF †*Gosiutichthys parvus* TO OTHER CLUPEIDS: It is not known what clupeid species are most closely related to †*G. parvus*. The dorsal scute series strongly resembles that of *Hyperlophus*, †*Knightia* and “†*Clupea*” *vectensis*, but the morphology

of this scute type is probably primitive for pelloneulines because it is also found (as a single scute—see above) in several clupeins. Because all pelloneulines (including †*Knightia*) have only one supramaxillary bone, and †*Gosiutichthys* has two, †*G. parvus* is placed in Clupeinae. This does not imply that Clupeinae is monophyletic. The Clupeinae is currently a taxonomic repository for clupeoid species that lack diagnostic characters of other clupeoid groups.

TABLE 2
Morphometric Data (Measurements as Fractions of Standard Length) for the Three North American Species of †*Knightsia* and for †*Gosiutichthys*, New Genus

	† <i>Knightsia</i>			† <i>Gosiutichthys</i> , new genus
	† <i>K. eocaena</i>	† <i>K. alta</i>	† <i>K. vetusta</i> , new species	† <i>G. parvus</i> , new species
Body depth	.20-.29 (n = 24, X̄ = .26, SD = .023)	.33-.41 (n = 18, X̄ = .37, SD = .029)	.28-.33 (n = 5, X̄ = .30, SD = .021)	.28-.37 (n = 16, X̄ = .32, SD = .020)
Head length	.25-.29 (n = 22, X̄ = .27, SD = .011)	.25-.30 (n = 17, X̄ = .28, SD = .016)	.28-.31 (n = 6, X̄ = .30, SD = .010)	.29-.37 (n = 14, X̄ = .32, SD = .021)
Predorsal length	.45-.51 (n = 24, X̄ = .48, SD = .021)	.45-.50 (n = 18, X̄ = .47, SD = .020)	.46-.49 (n = 5, X̄ = .48, SD = .013)	.46-.50 (n = 12, X̄ = .48, SD = .018)
Preanal length	.75-.81 (n = 24, X̄ = .78, SD = .018)	.78-.82 (n = 18, X̄ = .80, SD = .016)	.75-.79 (n = 6, X̄ = .77, SD = .019)	.79-.84 (n = 12, X̄ = .81, SD = .017)
Caudal peduncle length	.09-.12 (n = 21, X̄ = .10, SD = .008)	.09-.13 (n = 14, X̄ = .10, SD = .010)	.11-.13 (n = 6, X̄ = .12, SD = .009)	.09-.12 (n = 12, X̄ = .10, SD = .011)
Caudal peduncle depth	.09-.13 (n = 23, X̄ = .11, SD = .011)	.12-.15 (n = 15, X̄ = .13, SD = .012)	.11-.12 (n = 4, X̄ = .12, SD = .005)	.10-.14 (n = 13, X̄ = .11, SD = .011)
Dorsal fin base	.11-.16 (n = 22, X̄ = .13, SD = .014)	.12-.16 (n = 10, X̄ = .14, SD = .017)	.12-.15 (n = 5, X̄ = .13, SD = .012)	.10-.13 (n = 11, X̄ = .12, SD = .009)
Anal fin base	.11-.16 (n = 22, X̄ = .13, SD = .016)	.12-.16 (n = 13, X̄ = .14, SD = .014)	.14-.16 (n = 6, X̄ = .15, SD = .008)	.10-.13 (n = 13, X̄ = .11, SD = .010)

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