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Redescription of †*Ellimma branneri* and †*Diplomystus shengliensis*, and Relationships of Some Basal Clupeomorphs

MEE-MANN CHANG[1] AND JOHN G. MAISEY[2]

ABSTRACT

Two extinct clupeomorphs, †*Ellimma branneri* from the Cretaceous of Brazil and †*Diplomystus shengliensis* from the Eocene of China, are redescribed. †*Ellimma branneri* was formerly classified within the Clupeiformes, but it lacks derived characters of clupeiforms and clupeoids. Dorsal scute ''wings'' are expanded and subrectangular in †*Ellimma* and other members of the family †Paraclupeidae Chang and Chou (1977), approximately equal to †Ellimmichthyidae Grande (1982a). Consequently, †*Ellimma branneri* is classified here within the family †Paraclupeidae. †Paraclupeidae are known from the Lower Cretaceous to the middle Eocene.

In the present work, two monophyletic groups are identified within the †Paraclupeidae. One group (subfamily †Paraclupeinae of Chang and Grande, 1997), known only from the Lower Cretaceous (Hauterivian–Albian), includes †*Paraclupea*, †*Ellimmichthys*, and †*Ellimma*. These taxa are united by strongly sculptured, skull-roofing bones with ridges radiating from the growth center, and a dorsal scute ornament of prominent ridges. †*Scutatuspinosus* may also belong in this group. The other group includes †*Diplomystus* (Upper Cretaceous–Eocene) and †*Armigatus* (Upper Cretaceous), which are united by a single homoplaseous character (presence of a posteriorly expanded third hypural, leaving no gap between hypurals 2 and 4): this character also occurs in pristigasteroids, †*Erichalcis*, osteoglossids, some elopomorphs (†*Lebanichthys lewisi*, and most *Albula* spp.), and a number of ostariophysans not included in our analysis. †Paraclupeines are customarily regarded as being more closely related to the Clu-

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peiformes than to other teleosts (i.e., as clupeomorphs), although no derived characters are uniquely shared by †*Ellimma branneri* and modern Clupeiformes. The relationships of †*Ellimma* and certain other extinct herring-like teleosts (including other †paraclupeines) with the Clupeiformes are unclear, and they may collectively form a paraphyletic assemblage.

No biogeographical hypothesis satisfactorily explains the known distribution of nonmarine †paraclupeine fishes in the Cretaceous. A substantial portion of their nonmarine fossil record is missing (as evidenced by the recent discovery of a possible †paraclupeine, †*Ezkutuberezi carmeni* Poyato-Ariza et al., 2000, in Spain), and some aspects of their early distribution pattern may have involved marine dispersal. Eocene †*Diplomystus* occurs on both sides of the Pacific Ocean, but the ‘‘Pacifica’’ hypothesis (which lacks empirical support) is abandoned as an explanation for such Eocene (and younger) trans-Pacific distribution patterns of nonmarine fishes. Instead, a ‘‘freshwater Arctic Ocean’’ hypothesis is favored. According to this hypothesis (for which there are several independent lines of geological evidence), temporary desalination of the Arctic Ocean occurred during the Paleocene and early Eocene, which may have permitted freshwater fishes to move unimpeded by salt-water barriers between Asia and North America; this temporary desalination event may eventually become recognized as a significant factor in the holarctic distribution patterns of various Tertiary-Recent freshwater fishes.

INTRODUCTION

The primary purpose of our study is to reexamine †*Ellimma branneri*, an Early Cretaceous (Upper Aptian) clupeomorph from Riacho Doce, in the Sergipe Basin of Alagoas, Brazil. The original material was collected by J.C. Branner in 1907 and was deposited in the Carnegie Museum, Pittsburgh. It formed the basis for Jordan's (1910) description under the name *Ellipes*, where it was referred to the family Clupeidae. Unfortunately the name *Ellipes* is preoccupied by a genus of orthopteran (Scudder, 1902), requiring that another name be created for the fish taxon (†*Ellimma*; Jordan, 1913).

†*E. branneri* was restudied by Schaeffer (1947) using additional material collected by Euphrasio Borges in 1917–1918. In 1931 Euzebio Paulo de Oliveira donated this material to the Department of Vertebrate Paleontology at the American Museum of Natural History from the Geological Survey of Brazil. Schaeffer (1947) transferred the species to the clupeid genus †*Knightia*, effectively making †*Ellimma* a synonym of that genus. His proposal implied a significant stratigraphic range extension for †*Knightia*, as the genus had previously been recognized only in the Eocene deposits of western North America (Jordan, 1907). Schaeffer's proposal was subsequently reversed by Grande (1982a, 1982b, 1985a), who excluded †*E. branneri* from the genus †*Knightia*, noting that †*Ellimma* can be distinguished from other clupeid taxa by the presence of two supramaxillae and a complex pattern of sculpture on the surface of its dorsal scutes. He restored the generic name †*Ellimma* and referred it to the family Clupeidae, subfamily Clupeinae.

Our further preparation and observation of the original specimens of †*E. branneri*, from both the American Museum and Carnegie Museum collections, has provided new information supporting the view that †*Ellimma* is a distinct taxon, but also suggesting that it does not belong in the Clupeidae. Instead, we propose that it is a more primitive clupeomorph, closely related to three other Early Cretaceous taxa, †*Ellimmichthys longicostatus* (Cope, 1886), †*E. goodi* (Eastman, 1912), and †*Paraclupea chetungensis* Sun (1956). The collective geographical distribution of these taxa is of considerable interest. †*Ellimmichthys longicostatus* is from the Marfim Formation (late Hauterivian–early Barremian, Recôncavo Basin) of Brazil (Maisey, 2000), and †*Ellimmichthys goodi* is from Aptian–Albian strata of Equatorial Guinea, West Africa (Eastman, 1912), while †*Paraclupea chetungensis* is from the Lower Cretaceous of southeastern China (Sun, 1956). A close relationship between †*Ellimmichthys* and †*Paraclupea* was established by Chang and Grande (1997), who erected the subfamily †Paraclupeinae for these two genera, within the family †Paraclupeidae of Chang and Chou (1977). The family was defined by a single character (dorsal scutes broader than long), which also occurs in the genus †*Di-*

plomytus. Grande (1982a) had previously related †*Ellimmichthys* and †*Diplomystus* within his family †Ellimmichthyidae on the basis of a similar character (‘‘lateral wings of the dorsal scute elongated and blunted at the lateral edges, giving the scute a subrectangular outline’’), and Chang and Grande (1997) also included †*Diplomystus* within the †Paraclupeidae.

The pattern of the dorsal scutes in †*Ellimma branneri* only partially agrees with this family-level character, because the anterior dorsal scutes are longer than broad in this species, whereas the posterior ones are broader than long. Inclusion of this form within the †Paraclupeidae on the basis of scute shape is therefore not straightforward and necessitates a reevaluation of characters supporting paraclupeid monophyly. In searching for characters other than scute shape, we addressed wider issues such as the relationships between these taxa and other basal clupeomorphs, including †*Santanaclupea*, †*Armigatus*, †*Diplomystus*, and †*Knightia*.

A redescription of the Chinese species of †*Diplomystus*, that is, †*D. shengliensis* Zhang et al. (1985), is also incorporated in this paper. According to its original description (in Chinese), †*Diplomystus shengliensis* is an Eocene teleost first collected from drilling cores of the Sheng-li Oil Field situated on the southern coast of Bohai Gulf along the western coast of the Pacific Ocean. The species is very similar to †*Diplomystus dentatus* from the Eocene Green River Formation of North America, and hardly any differences exist between them except for a few minor meristic characters (Zhang et al., 1985), a remarkable situation considering the widely separated occurrences of these species on opposite sides of the Pacific.

Besides the taxa considered here, there are a few other records of Cretaceous ‘‘double-armoured’’ clupeomorphs, such as †*Scutatuspinosus itapagipensis* from the Neocomian of Brazil (Silva Santos and Correa, 1985), an undescribed species of †*Ellimmichthys* from the Tlayua Formation of southern Mexico (Chang and Grande, 1997: fig. 7e, f), and †*Ezkutuberezi carmeni* from Spain, said to be related to paraclupeids (Poyato-Ariza et al., 2000). There are also records of a supposed paraclupeid in the Cabo Formation (Lower Cretaceous, Aptian–Albian?) from the Cabo Basin of northeastern Brazil. This form was identified originally as †*Ellimmichthys longicostatus* (Costa et al., 1979), but it was subsequently referred to †*Ellimma* and named †*E. cruzi* by Silva Santos (1990). The same horizon has produced a small gonorhynchiform which was referred to †*Dastilbe*.

The Cretaceous and Eocene paraclupeids each present a puzzling biogeographic pattern for freshwater fishes. The Early Cretaceous ‘‘southern transatlantic’’ pattern (i.e., restricted to western Gondwana, and represented by †*Ellimmichthys longicostatus* and †*Ellimma branneri* from northeastern Brazil and †*Ellimmichthys goodi* from West Africa) is now extended into southeastern China (†*Paraclupea chetungensis*) and will perhaps be expanded farther by the new Spanish discovery (Poyato-Ariza et al., 2000). The Eocene forms have a ‘‘transpacific’’ distribution, with the two sister species (†*Diplomystus shengliensis* and †*D. dentatus*) on opposite sides of the northern Pacific. Possible origins of this pattern are reexamined below in the light of recent discoveries concerning the history of the Arctic region in the early Cenozoic.

ABBREVIATIONS

Anatomical

AA	angulo-articular
br.r	branchiostegal rays
BT?	basibranchial toothplate?
Ch	ceratohyal
Cs	caudal scute
D	dentary
Enpt	entopterygoid
Ep	epural
Fr	frontal
H_3	hypural 3
Hm	hyomandibular
Io_2, Io_3	infraorbital 2, infraorbital 3
Iop	interopercle
msc	mandibular sensory canal
Mx	maxilla
Op	opercle
P	parasphenoid
Pa	parietal
Pd	predorsal bones
Ph	parhypural
Pmx	premaxilla
Pop	preopercle
Psp	parasphenoid

Pt	posttemporal
Pu$_1$	preural centrum 1
Q	quadrate
S	symplectic
Sc	sclerotic bone
Smxa	anterior supramaxilla
Smxp	posterior supramaxilla
Soc	supraoccipital
U$_1$	ural centrum 1
Ur	urohyal
Un$_1$	uroneural 1

Institutional

AMNH	American Museum of Natural History, New York
CM	Carnegie Museum of Natural History, Pittsburgh, PA
FMNH	Field Museum of Natural History, Chicago
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
SOF	Shengli Oil Field, Dongying, Shandong Province, China

MATERIALS AND METHODS

This study primarily involves specimens of †*Ellimma branneri* from the collections of the AMNH and CM, and of †*Diplomystus shengliensis* from the Shengli Oil Field. Specimens of †*Paraclupea chetungensis* from the IVPP, as well as those of †*Armigatus brevissimus*, †*Diplomystus dentatus*, a few species of †*Knightia*, plus dried skeletons and cleared-and-stained specimens of *Clupea harengus* and *Onchorhynchus mykiss* from the AMNH, were compared, as were some specimens of †*Diplomystus dentatus* from the FMNH.

The specimens of †*E. branneri* examined are all preserved in bituminous shales of the Muribeca Formation and are in a laterally compressed and flattened state. In all these specimens the braincase is badly crushed, and their study was further impaired by broken surfaces and weathering of exposed surfaces, which frequently makes it difficult to examine features such as sutures between bones and other structures. The poor state of preservation also helps explain why features such as dorsal scute ornamentation, the structure of the caudal skeleton, and various other anatomical details have not been described previously, for they are almost impossible to observe without some cleaning of the material. Fortunately the bituminous matrix has a very low carbonate content, and so for the present study we were able to use dilute HCl to dissolve and clean broken bone from the matrix in order to obtain clean impressions of the skeleton. Latex peels were made from these cleaned impressions, and both reveal much more detail then unprepared specimens.

SYSTEMATICS

SUBCOHORT CLUPEOMORPHA GREENWOOD ET AL., 1966

ORDER †ELLIMMICHTHYIFORMES GRANDE, 1982

FAMILY †PARACLUPEIDAE CHANG AND CHOU, 1977

= †ELLIMMICHTHYIDAE GRANDE, 1982

SUBFAMILY †PARACLUPEINAE CHANG AND GRANDE, 1997

†*ELLIMMA* JORDAN, 1913

†*Diplomystus* Cope, 1877: 811 (in part).
†*Knightia* Jordan, 1907: 136.
†*Ellipes* Jordan, 1910: 24 (Brazilian species only).
†*Ellimma* Jordan, 1913: 79 (new name for *Ellipes* Jordan, 1910, preoccupied).
†*Ellimma*, Jordan and Gilbert, 1919: 26.
†*Knightia*, Schaeffer, 1947: 17.
†*Ellimma*, Grande, 1982a: 22.
†*Ellimma*, Grande, 1982b: 13.
†*Ellimma*, Grande, 1985a: 250.

EMENDED DIAGNOIS: Paraclupeine with comparatively low body depth. Surface of opercle with striations. Teeth on jaws and palate very weakly developed. Anterior dorsal scutes slightly longer than broad and ornamented with ridges; posterior ones broader than long and ornamented with tubercles or tubercles plus ridges. Sharp spine extending from median keel of posterior few dorsal scutes pointing posteriorly rather than posterodorsally. Origin of pelvic fin opposite to middle point of base of dorsal fin. Procurrent rays 5 and 6 on each side of base of caudal fin.

TYPE SPECIES: †*Ellipes branneri* Jordan, 1910, the only species (based on page priority).

†*Ellimma branneri* (Jordan), 1910

Figures 1–8

†*Ellimma branneri* Jordan, 1910: 25, pl. 8, fig. 3.
†*Ellimma riacensis* Jordan, 1910: 28, pl. 10.
†*Ellimma branneri* Jordan, 1913: 79.
†*Knightia branneri*, Schaeffer, 1947: 17.
†*Ellimma branneri*, Grande, 1982a: 22; 1982b: 13; 1985a: 250.

HOLOTYPE: CM 5249/1 and CM 5249/2. Note that only CM 5249/1 was designated the type by Schaeffer (1947), and this was also the type specimen chosen by Jordan for †*Ellimma branneri*. In fact, CM 5249/2 is the counterpart to CM 5249/1, although this was not noticed in previous descriptions. The holotype is a small fish, with a standard length of 38.5 mm (measured from the counterpart CM 5249/2, which is more complete than CM 5249/1).

ADDITIONAL MATERIAL: AMNH 10046–10062; CM 5248/10, 11, 21, 36, 39; 5249/2 (counterpart of 5249/1), 3, 25, 27, 33, 49, 52, 54, 55, 56 (counterpart of 5248/11), 125, 130 (counterpart of 5249/125), 175 (counterpart of 5249/52).

DIAGNOSIS: As for genus.

HORIZON AND LOCALITIES: From Riacho Doce, Sergipe Basin, Brazil (Muribeca Formation, Lower Cretaceous, Aptian–Albian, = “Alagoan” local stage). The age of this unit is well established from palynomorphs and foraminifers (Feijó, 1994).

COMMENTS: The type specimen of †*Ellimma riacensis* (CM 5248/4) has a standard length of 102.2 mm and is therefore a somewhat larger individual than the type of †*E. branneri*. It is also much better preserved, and it consequently shows more morphological details than the type of †*E. branneri*. We were however unable to identify any unequivocally unique features of †*Ellimma riacensis*, and we consequently agree with Schaeffer (1947) that †*Ellimma riacensis* is a synonym of †*E. branneri*. We regard †*E. branneri* as the type species of the genus on the basis of page priority. Our observations led us to the conclusion that all the †*Ellimma* specimens studied by Schaeffer indeed represent a single species, but we must also admit that the holotype of †*E. riacensis* (CM 5248/4) provides some morphological information, including details of the skull roof ornamentation, dorsal scute morphology, and entopterygoid teeth, that are not discernible in the holotype of †*E. branneri*. There is inevitably some circularity in our inclusion of these features in our description of †*E. branneri*, but we found no evidence to retain †*Ellimma riacensis* as a distinct species, and this taxon is regarded here as a subjective synonym of †*E. branneri*. Thus, we conclude there is only one species of †*Ellimma* represented in the Riaco Doce material, rather than two sympatric species.

DESCRIPTION

GENERAL SHAPE: The overall outline of †*E. branneri* resembles that of †*Paraclupea chetungensis* (Chang and Chou, 1977; Chang and Grande, 1997), with a markedly convex ventral outline and a gently curved dorsal outline rising to an apex at the origin of the dorsal fin (figs. 1A, B, 2A–C). The maximum body depth occurs at the origin of the dorsal fin. The standard length of individuals in our samples varies from 20.8 (CM 5249/125) to 102.2 mm (CM 5248/4); in other words, our largest specimens are five times longer than the smallest. The proportion between the body depth and the standard length is therefore somewhat variable, usually being approximately 41–44% standard length, but rarely 36 or 50%.

SKULL ROOF: The bones of the braincase in †*E. branneri* are usually so badly crushed that it is impossible to recognize bone margins or even various recesses, fossae, and bullae within the bones; importantly, it has not been possible to determine whether a recessus lateralis was present (an important clupeiform character absent in primitive clupeomorphs; Grande, 1985a). Few features of the braincase can be described. In the anterior part of the skull roof, the posterior portion of the dermethmoid (seen in CM 5249/49) bears a lateral process on both sides and a pair of processes extending posteriorly above the frontals. In larger specimens the posterior one-third of the frontals, as well as the parietals, are strongly ornamented with ridges radiating from their growth centers. The dorsal part of the supraoccipital (seen in CM 5249/56) is small and triangular and shows indications of ridges radiating from

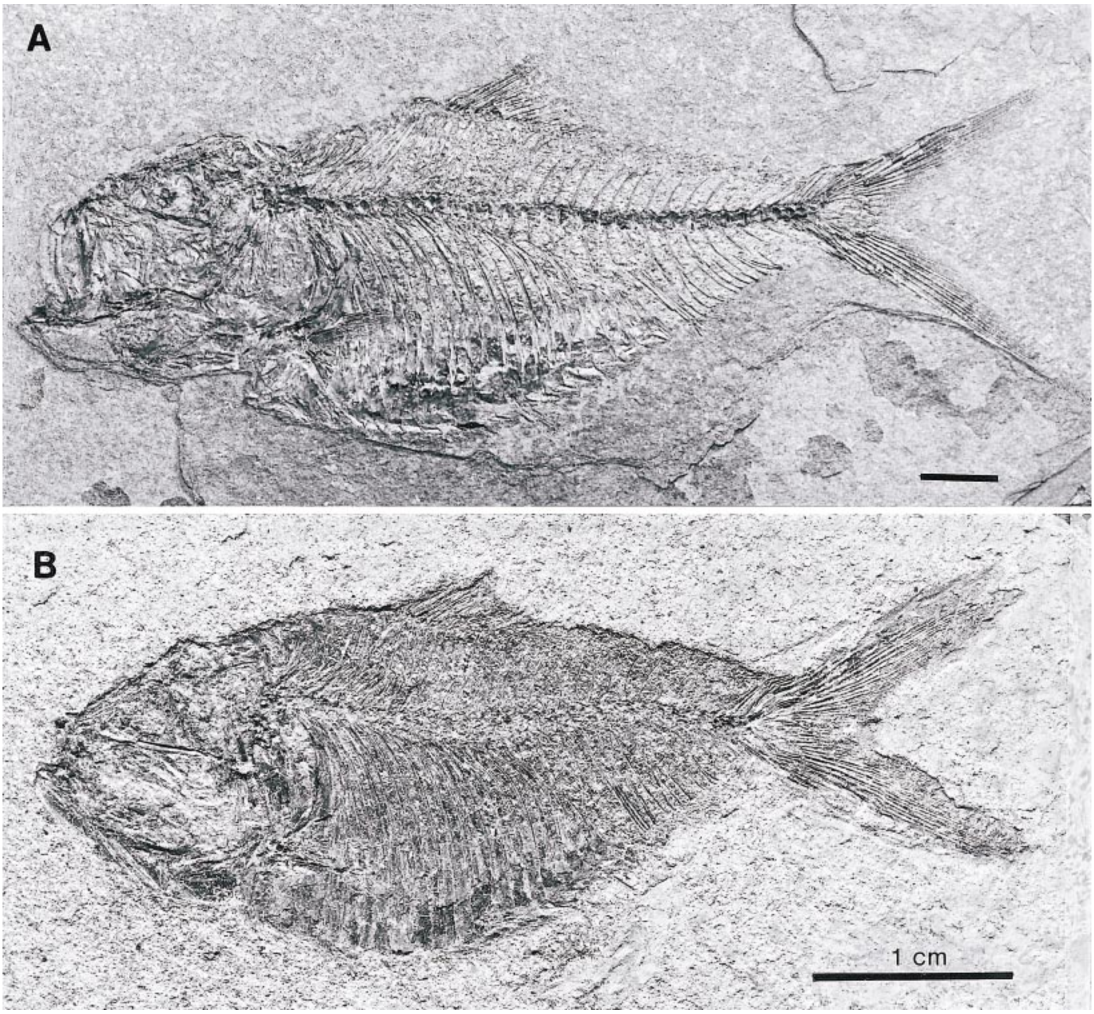

Fig. 1. †*Ellimma branneri*, Muribeca Formation, Riaco Doce, Sergipe Basin, Brazil. **(A)** CM 5248/4; **(B)** CM 5249/2, the holotype. Both scale bars = 1 cm.

the posteromedian point of the bone anterolaterally. In smaller individuals (e.g., CM 5248/39, standard length approximately 51 mm) the skull roof bones are smooth and without sculpture (fig. 3). Unlike in †*Paraclupea chetungensis* there is no anterior fontanelle between the frontals. The parietals meet at the midline and are not separated by the supraoccipital (in clupeiforms the supraoccipital separates the parietals; Grande, 1985a). As far as can be determined the supraoccipital crest is small and low (CM 5249/56, 5248/11, and 5248/39). The supraorbital sensory canal is enclosed in a bony ridge and extends from the frontal to the parietal. The supratemporal commissure passes through the parietals.

A comparatively broad and flat ridge runs the length of the posttemporal along its midline, and its broader posterior part is ornamented with ridges in larger individuals. The dorsal (epiotic) limb of the posttemporal is long and narrow anteriorly but becomes broader posteriorly, while the ventral limb of this bone is thin. The lateral line sensory canal runs diagonally through the supracleithrum.

Orbital Region: Faint impressions of three infraorbital bones can be seen in a few specimens, for example, AMNH 10048 (fig.

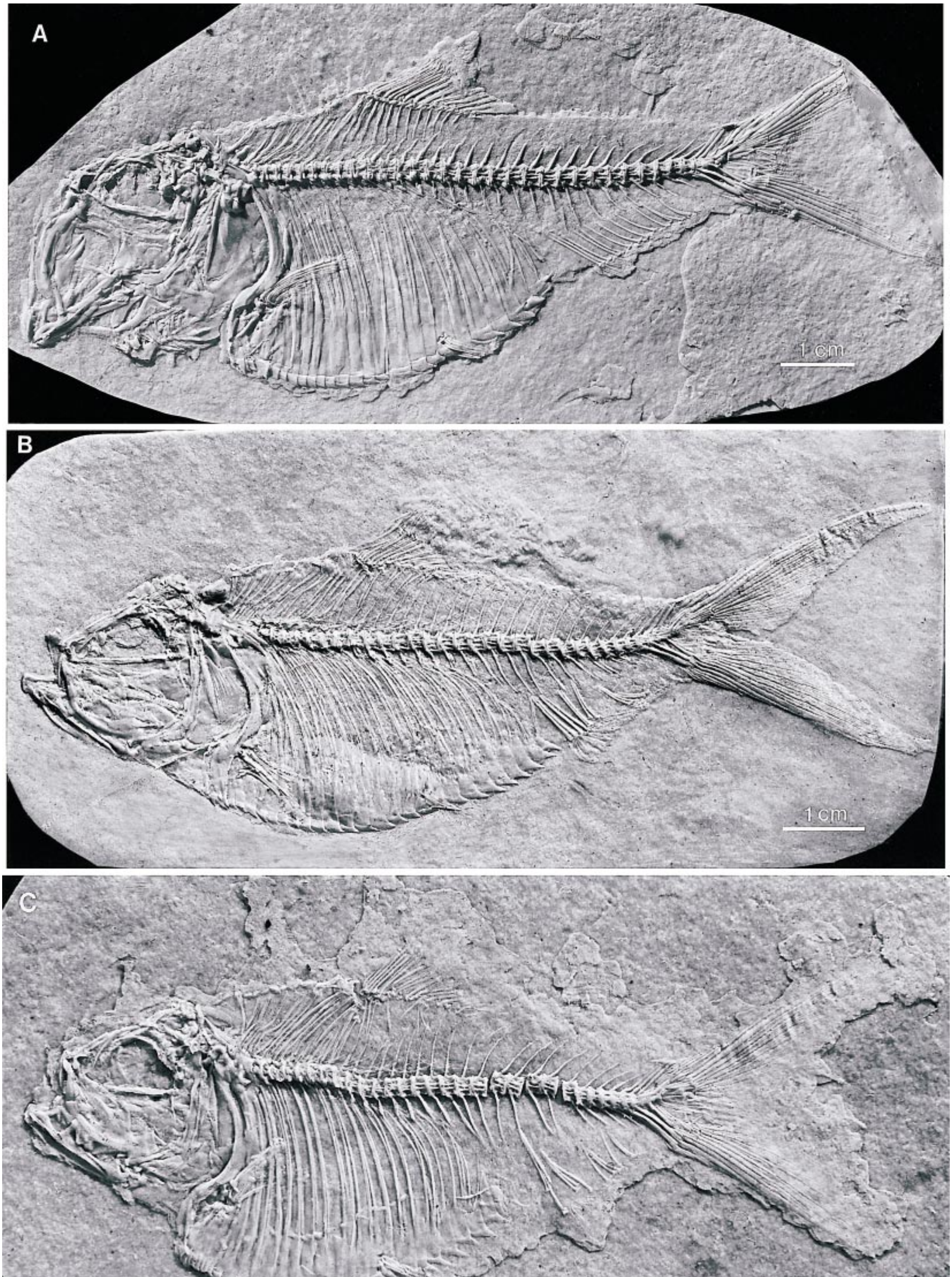

Fig. 2. †*Ellimma branneri*, Muribeca Formation, Riaco Doce, Sergipe Basin, Brazil. Silicone peels prepared from AMNH specimens. **(A)** AMNH 10048; **(B)** AMNH 10057; **(C)** AMNH 10060.

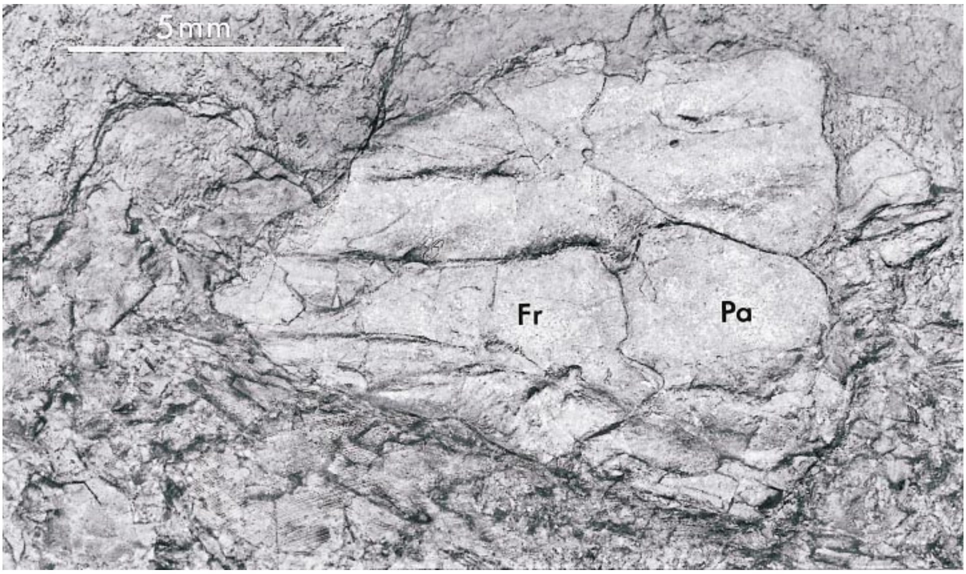

Fig. 3. †*Ellimma branneri*, CM 5248/39 to show skull roof.

2A) and 10050. Two detached infraorbitals (perhaps the second and third) are exposed on CM 5249/52 and 5249/175 (part and counterpart; fig. 4). The first two infraorbitals seem to be narrow and elongated, but the third is broader and shorter. The infraorbital sensory canal runs along the orbital margin of all three bones. Parts of the sclerotic ring were seen in several specimens, although no details were evident.

PARASPHENOID AND ENTOPTERYGOID: No teeth are present on the parasphenoid. A basipterygoid process is recognizable on the latex cast of AMNH 10051. In most specimens of †*Ellimma branneri* no teeth were observed on the entopterygoid, although faint traces of tiny broken tips of teeth are sometimes present (e.g., AMNH 10047, 10048 and CM 5248/4). In contrast, †*Ellimmichthys* and †*Paraclupea* have an entopterygoid dentition that is relatively better developed, and the reduced dentition in †*Ellimma* is a distinguishing feature of the genus within paraclupeids.

JAWS: In †*Ellimma branneri* the articulation of the lower jaw is positioned more or less below the posterior margin of the orbit (figs. 2A–C, 5B). The dentary, angulo-articular, and retroarticular are seen clearly in AMNH 10048 (fig. 5A). A well-developed coronoid process is present on the dentary. The mandibular sensory canal runs above the lower margin of both the dentary and the angulo-articular (fig. 5B). The maxilla is long and extends behind the jaw joint. In most specimens of †*Ellimma branneri* the jaw teeth are not visible, but a few fine, conical teeth are recognizable on the oral margin of the premaxilla and dentary in the latex peel of AMNH 10057. Very fine serrations are also present on the oral margin in one detached maxilla (CM 5248/11 and CM5249/56, part and counterpart; fig. 6C, D).

Collectively, these observations suggest that the entire jaw dentition of †*Ellimma branneri* consists only of very small teeth, and is much reduced in comparison with both †*Ellimmichthys longicostatus* and †*Paraclupea chetungensis*, where a well-developed dentition is present both on the jaws and the palatal surface of the entopterygoid (Chang and Chou, 1977; Chang and Grande, 1997). The presence of very small entopterygoid teeth in †*Ellimma branneri* may be related to a microphagous diet, as in many Recent clupeomorphs. †*Ellimma branneri* possesses two supramaxillae (a primitive teleostean state), of which the posterior one is larger. Both supramaxillae are ornamented by

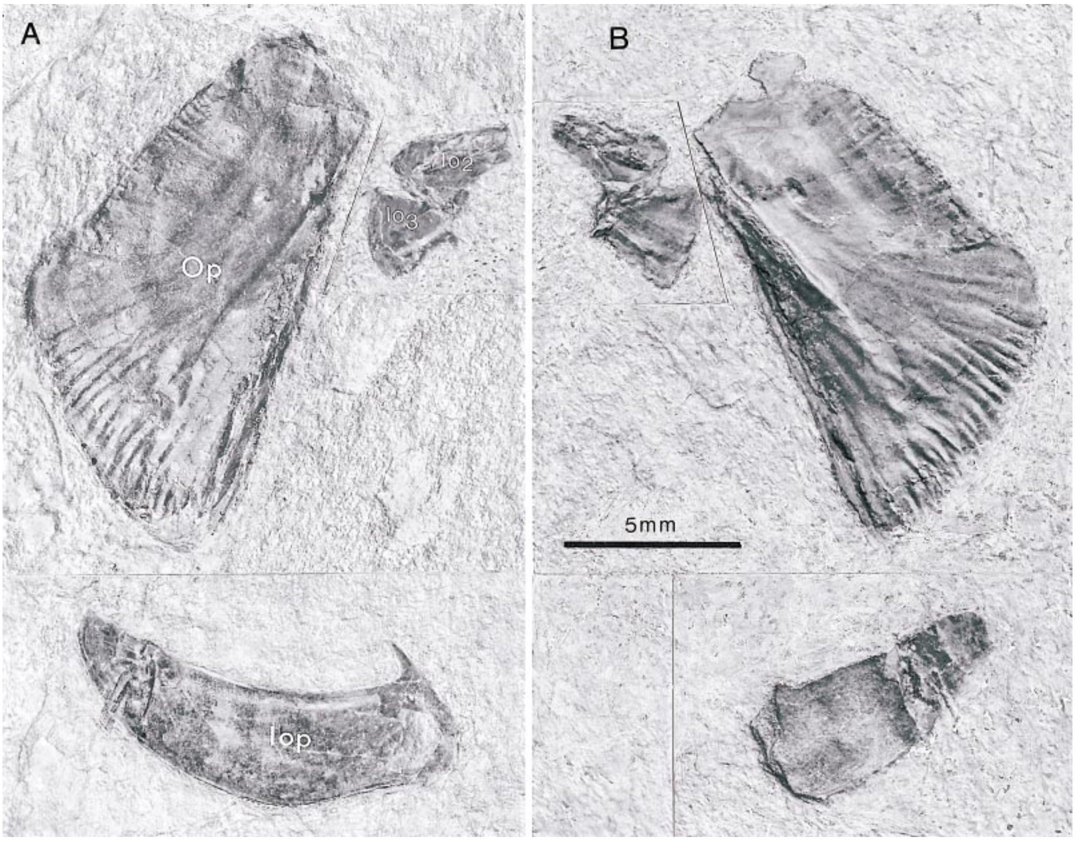

Fig. 4. †*Ellimma branneri*, to show detached opercle, subopercle (at bottom) and two small infraorbitals. **(A)** CM 5249/52 (part) and **(B)** CM 5249/175 (counterpart).

fine shallow grooves on their external surface.

Opercular Series and Hypobranchial Apparatus: A detached but well-preserved opercle with an almost complete margin is present in CM 5249/52 and 175. It is deep and rectangular in shape, with a protruding anteroventral corner. The ventral part of the opercle in most specimens of †*Ellimma branneri* is ornamented on its lateral surface by striations which radiate ventrally from the area of attachment (fig. 4A, B), but the surface of the opercle in the smallest specimen is smooth, with no striations (CM 5249/125 and 130, standard length 20.8 mm). The subopercle shows the anterior ascending process which is usually covered by the opercle (CM 5249/52; fig. 4A). The preopercle has two arms forming an obtuse angle; its vertical arm is longer than the horizontal one, which contains three or four branches of the preopercular sensory canal (fig. 5B).

The hyomandibular shaft is narrow, with a single head and no anterodorsal process. The quadrate is thick, with the symplectic inserted in a notch above its posteroventral margin, as in teleosts generally (fig. 5A, B). The anterior ceratohyal is rectangular in shape, longer than deep, and contains an elongated oval bericiform foramen (AMNH 10048, 10050; fig. 5A). This opening is traversed by a groove for the hyoidean artery on the outer face of the anterior ceratohyal. Absence of the bericiform foramen is considered to be a synapomorphic character of clupeiforms by Grande (1985a). There are approximately 10 branchiostegal rays (AMNH 10048; fig. 5A). An outline of the urohyal was detected on AMNH 10048, but few details are discernible because the bone

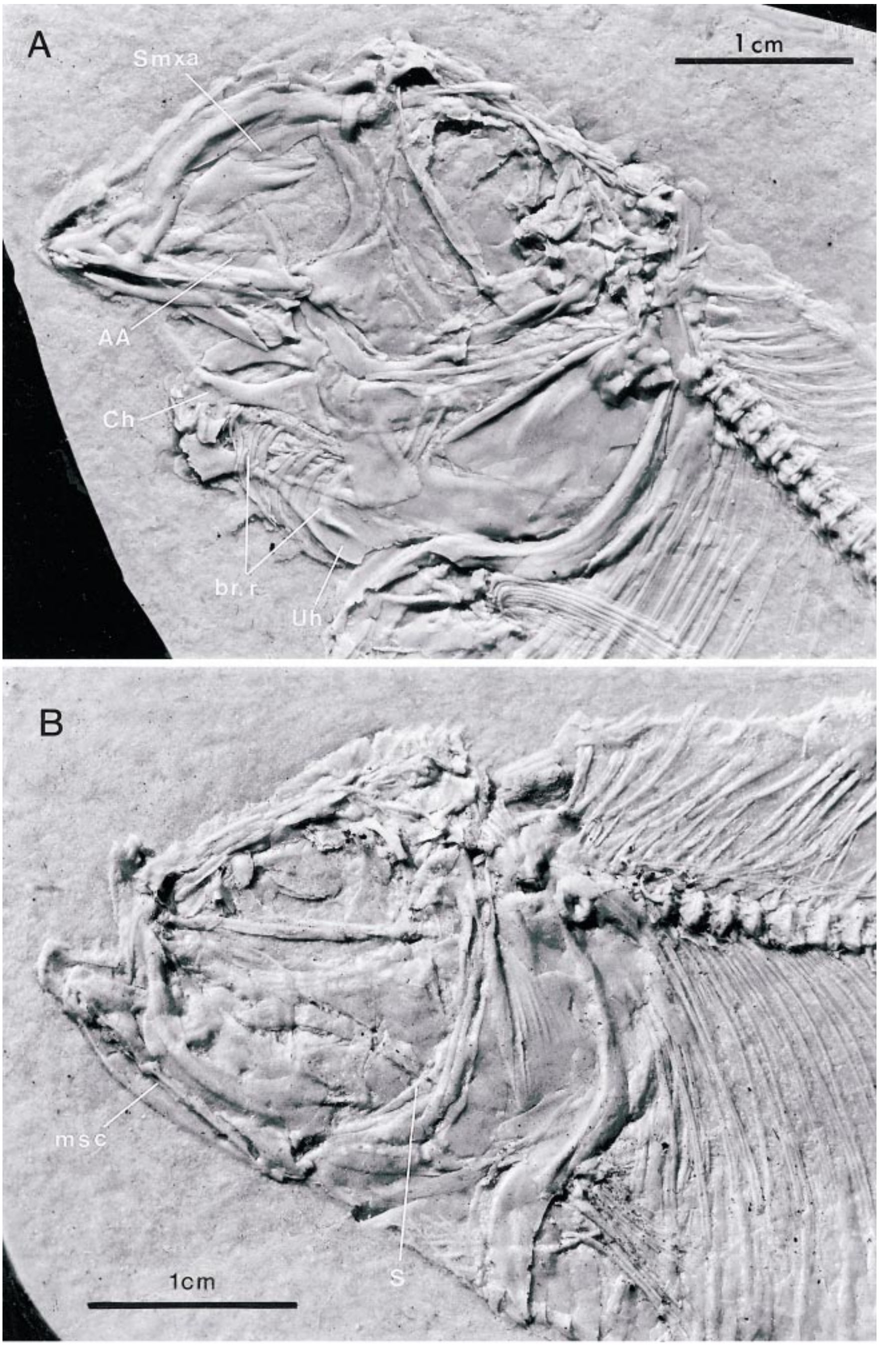

Fig. 5. †*Ellimma branneri*, silicone peels showing detail of the head in **(A)** AMNH 10048; **(B)** AMNH 10057. Both scale bars = 1 cm.

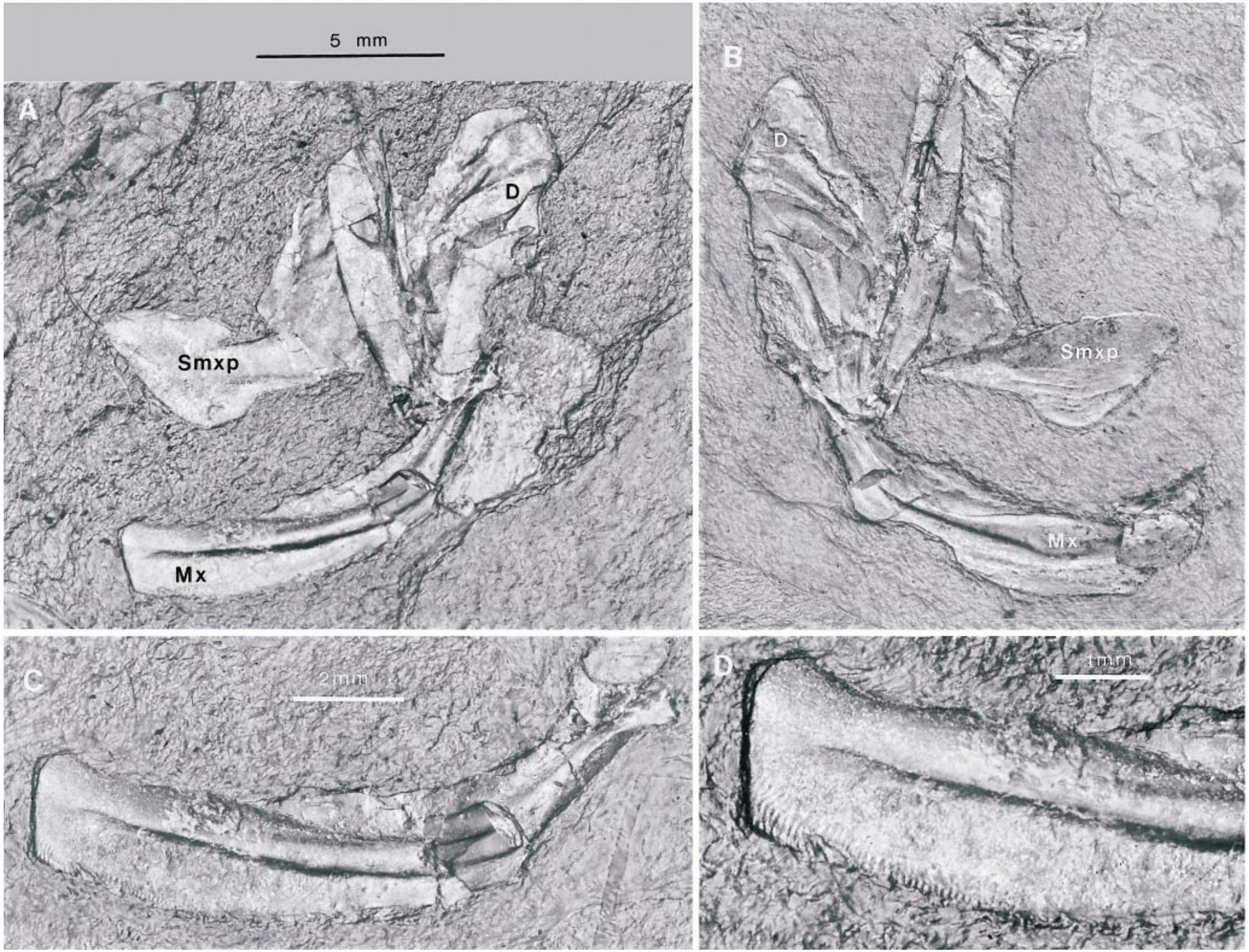

Fig. 6. †*Ellimma branneri*, detached jaw elements in **(A)** CM 5249/56 and its counterpart **(B)** CM 5248/11, both to same scale; **(C, D)** enlarged details of maxilla in CM 5249/56, showing the finely serrated oral margin.

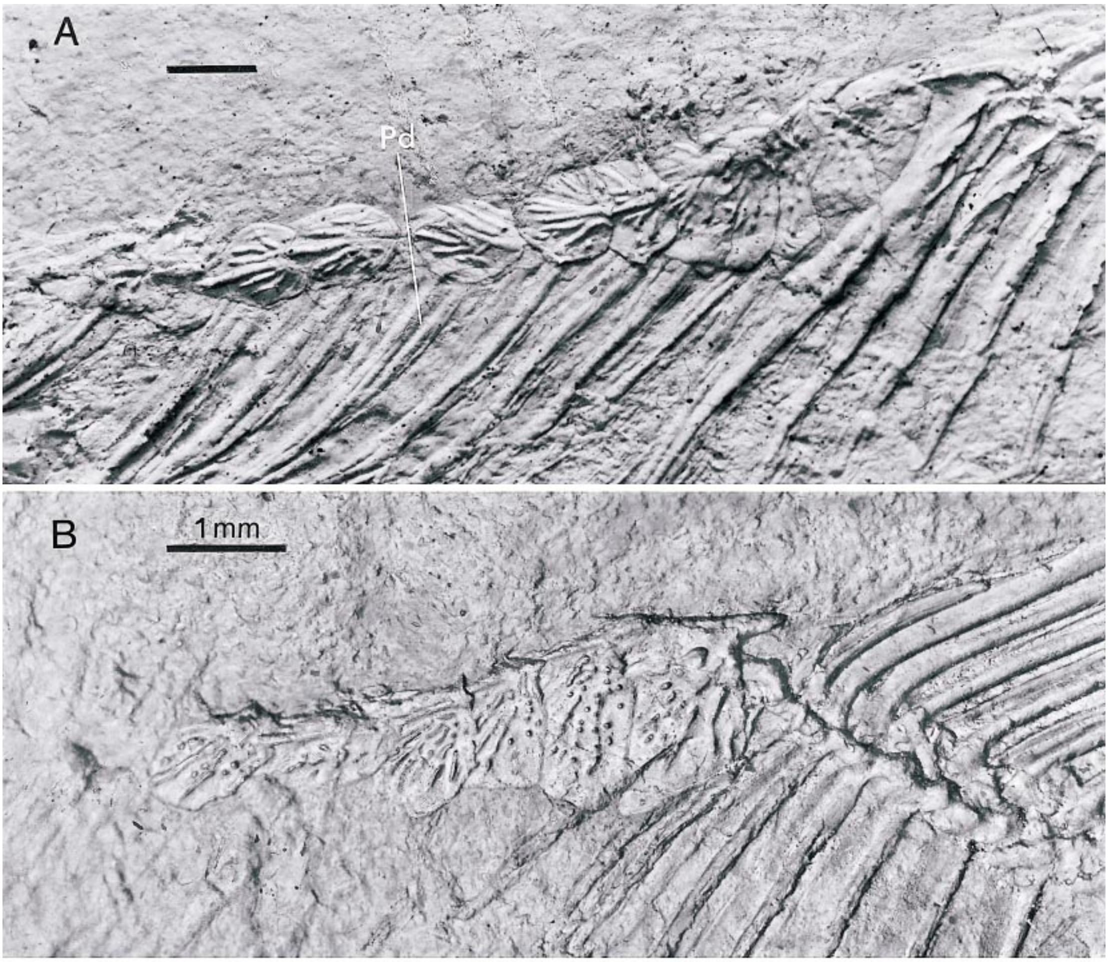

Fig. 7. †*Ellimma branneri*. Detail of dorsal scutes in (A) AMNH 10048 and **(B)** AMNH 10057 (both from silicone peels). Anterior scutes are better preserved in A, whilst the posterior scutes are clearer in B. Ornamentation of anterior scutes is mostly ridges, whereas the posterior scutes have ridges and tubercles. Both scale bars = 1 mm.

lies beneath the branchiostegal rays; it is narrow and triangular, with a long, narrow anterior process.

Vertebral Column and Fins: Two longitudinal ridges are present along the lateral side of each vertebra (fig. 2). The total vertebral count in †*Ellimma branneri* could only be estimated because the anteriormost centra are covered by the opercle in all the available specimens. We estimate that the vertebral column originally comprised 36–38 centra, of which 20–22 are abdominal (based on the number of pairs of ribs) and 15–16 are caudal. There are eight predorsal bones with thin anterior and posterior bony expansions (fig. 5A, B).

In †*Ellimma branneri* the dorsal and anal fins are of more or less equal size (figs. 1, 2). The dorsal fin contains 2 unbranched and 14 branched rays, and is supported by 14–16 pterygiophores. In both AMNH 10048 and 10050 the anal fin has 15 rays and 14–15 pterygiophores. The pelvic fin is small and contains about six or seven rays (seven are present in CM 5249/27). Its insertion is approximately opposite to the middle point

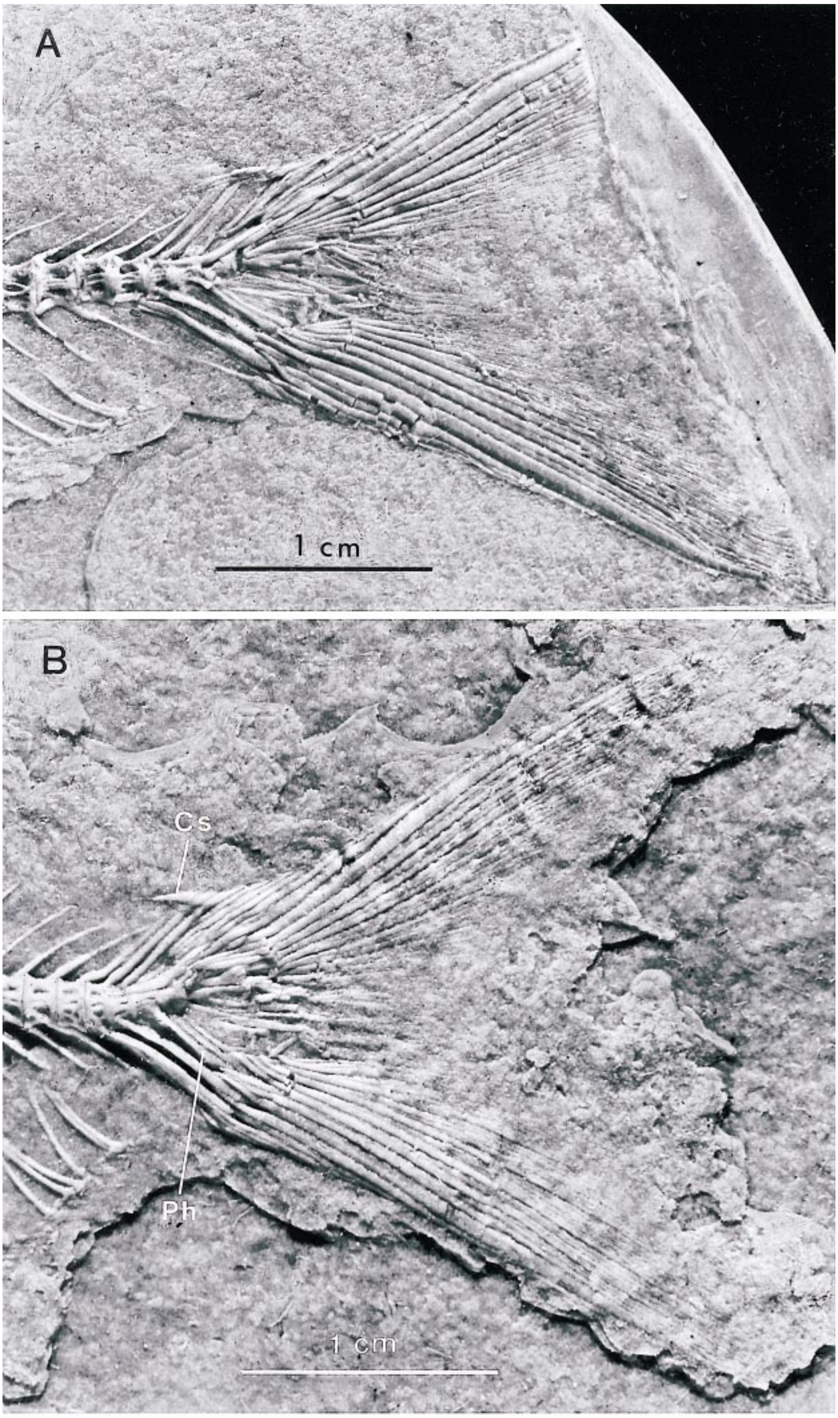

Fig. 8. †*Ellimma branneri* caudal fin skeleton, silicone peels. **(A)** AMNH 10048; **(B)** AMNH 10060. Both scale bars = 1 cm.

of the base of the dorsal fin. The pectoral fin is large but does not reach the origin of the pelvic, and has at least 12 fin rays. The cleithrum is large and curved. No postcleithra have been recognized in the available specimens.

SCUTES: †*Ellimma branneri* possesses a complete dorsal scute series (unlike in †*Armigatus*), extending from the back of the head to the origin of the dorsal fin (figs. 1A, 2A, C, 7). The entire series includes 12–14 scutes, each of which is overlapped anteriorly by the next (AMNH 10048, 10060, and CM 5249/2). The more anterior scutes are generally rounded in shape and are slightly longer than broad (like those illustrated by Grande, 1982a: fig. 23), but those farther posteriorly tend to be broader than long. The last three or four scutes in the dorsal series are expanded laterally and are much broader than those farther anteriorly. All the dorsal scutes in †*Ellimma branneri* have a median keel, but scute margins are not always well preserved, and it is therefore uncertain whether the keel of every scute was extended as a spine (as in †*Ellimmichthys* and †*Paraclupea*; Chang and Grande, 1997). The last few scutes in †*Ellimma branneri* are extended into a sharp spine pointing posteriorly. This arrangement is slightly different from that seen in †*Ellimmichthys* and †*Paraclupea*, where the spine projects from the scute in a more posterodorsal direction. In †*E. branneri* most of the scutes are ornamented with ridges, which arise laterally from the posterior end of the keel and then turn posteriorly to pass almost parallel to the keel. The ornamentation of the posteriormost scutes is rather different, however, as some are covered with tubercles arranged in rows, and others have both tubercles and ridges (fig. 7A, B). Almost the entire upper surface of each scute is ornamented in †*E. branneri*; by contrast, in †*Paraclupea chetungensis*, only the posterior half or third of the scute upper surface is ornamented.

The abdominal scutes in †*E. branneri* form a continuous series extending from the lower end of the cleithrum to just in front of the origin of the anal fin (fig. 2A–C). There are 27–30 abdominal scutes, of which 8–10 lie behind the origin of the pelvic fin. The abdominal scutes behind the pelvic fin are smaller than in †*Ellimmichthys longicostatus* (see Jordan, 1910: pl. XI).

SCALES: The scales are thin, with fine concentric growth lines, although no vertical circuli were observed like those in †*Diplomystus* and many other clupeiforms. From the material available it could not be determined whether lateral line scales are present.

CAUDAL SKELETON AND TAIL (FIG. 8A, B): The structure of the caudal skeleton in †*E. branneri* closely resembles that of †*Ellimmichthys* and †*Paraclupea*. Collectively, all these taxa have a caudal fin morphology that differs from the clupeiform condition. There are two free ural centra, the first ural centrum is approximately equal in size to the first preural centrum, and there are six hypurals. The first hypural is in close contact with (but not fused to) the first ural centrum, although the second hypural is fused to this centrum. The third hypural is comparatively narrow, not expanded posteriorly, and there is a gap between the second and third hypurals. The parhypural is fused with the first preural centrum, which has a short neural arch. As many as three epurals are present (e.g., AMNH 10060), although in most specimens only one or two are visible. There are three uroneurals, all of which are autogenous. The first uroneural is long and thick, extending to the posterodorsolateral side of the second preural centrum, but the second and third uroneurals are much smaller.

The caudal fin is deeply forked (figs. 1, 2, 8). Its upper lobe contains one unbranched and nine branched rays, and its lower lobe has one unbranched and eight branched rays. The proximal end of the lowermost branched ray from the upper lobe is bifurcated into upper and lower branches, as is the uppermost branched ray from the lower lobe. In both cases, the upper branches are longer, broader, and more flattened than the lower ones. There are five or six procurrent rays on both the upper and lower margins of the peduncle in front of the caudal fin, and one caudal scute is present on the upper margin of the peduncle anterior to the procurrent rays.

†PARACLUPEIDAE INCERTAE SEDIS

†*Diplomystus* Cope, 1877

EMENDED DIAGNOSIS: Differs from other genera of †Paraclupeidae in having a high number of dorsal scutes; posterior border of dorsal scutes pectinate; supraoccipital crest very well developed and high; posttemporal with long and slender epiotic branch; entopterygoid with robust teeth along dorsal margin of buccal surface; seven or eight predorsal bones; H_3 much expanded posteriorly. No gap between H_2 and H_3, lowermost ray of upper caudal fin lobe bifurcates proximally, with two branches of more or less equal size, uppermost ray of lower caudal fin lobe slightly bent and enlarged.

TYPE SPECIES: †*Diplomystus dentatus* Cope, 1877

OTHER INCLUDED SPECIES: †*D. shengliensis* Zhang et al., 1985; †*D. birdi* Woodward, 1895; †*D. dubertreti* Signeux, 1951.

†*Diplomystus shengliensis* Zhang et al., 1985

Figures 9–12

HOLOTYPE: SOF 790001, first illustrated in Zhang et al., 1985: pl. 1, fig. 1 (see figs. 9, 10A, 11, 12A here).

ADDITIONAL MATERIAL: SOF 790002 (fig. 10B), 790003 (fig. 12B).

HORIZON AND LOCALITIES: Top of series 4 to bottom of series 3 of the Shahejie Formation, Middle Eocene; SOF 790001 and 790002 from Bore Lai 38–8, depth from the ground surface 2628m and 2668m, respectively, SOF 790003 from Bore Lai 1–9, depth from the ground surface 2622 m, Kenli county, Shandong Province, East China.

EMENDED DIAGNOSIS: †*Diplomystus* with elongate fusiform body, depth and standard length ratio of about 40%; with number of dorsal scutes (41) and dorsal fin rays (1, 13) slightly higher than in †*D. dentatus* (highest number of dorsal scutes 40 and that of dorsal fin rays 1, 12), but number of ribs (15 pairs) and number of vertebrae (around 42), namely number of abdominal vertebrae (around 17), lower than in the latter (17–18 pairs of ribs and 20 abdominal vertebrae).

ETYMOLOGY: *sheng-li-*, transliteration of the Chinese word ‘‘victory’’, the species named after Sheng-li Oil Field.

DESCRIPTION

GENERAL SHAPE: The only more or less complete specimen of †*D. shengliensis* is the holotype SOF 790001 (fig. 9), which fortuitously lies entirely within the diameter of a drilling core. This example is nevertheless somewhat distorted in the abdominal region, and its scale cover is missing. Data from this specimen are supplemented by SOF 790002, in which the anterior portion of vertebral column and ribs is better preserved; and SOF 790003, which has a well preserved caudal skeleton and fin rays. Some skeletal features cannot be observed in any of the available material, and our description is therefore incomplete.

The total length of the holotype of †*D. shengliensis* (SOF 790001, the only complete specimen) is 5.5 cm. The other fragmentary specimens evidently represent larger individuals, although their original size is uncertain. In the holotype, the body is elongate and fusiform, reaching a maximum depth (approximately 40% of standard length) a short way behind the head (fig. 9). The dorsal margin of the body curves upward a short distance behind the head, and then descends gradually to the caudal peduncle, without an abrupt angle at the origin of the dorsal fin. The ventral outline is moderately convex.

SKULL ROOF: The head can be studied in the holotype and in SOF 790002 (fig. 10). It is not easy to determine the arrangement of the bones along the midline of the skull roof in †*D. shengliensis* because the specimens are all laterally compressed. The supraoccipital is situated far posteriorly and probably did not separate the parietals, which therefore may have met at the dorsal midline. The external surfaces of the frontals and parietals are generally smooth, apart from ridges containing the sensory canals. The supraorbital sensory canal extends from the frontal into the parietal, where it meets a prominent curved ridge which appears to contain part of the supratemporal commissure. The supraoccipital crest is well-developed, being high and triangular in shape (fig. 10B), but it cannot be determined whether this bone contained part of the supratemporal commissure. The posttemporal has a long and slender epiotic limb (fig. 11).

ORBITAL REGION: Nothing is preserved except part of the sclerotic ring (SOF 790002; fig. 10B).

PARASPHENOID AND ENTOPTERYGOID: No

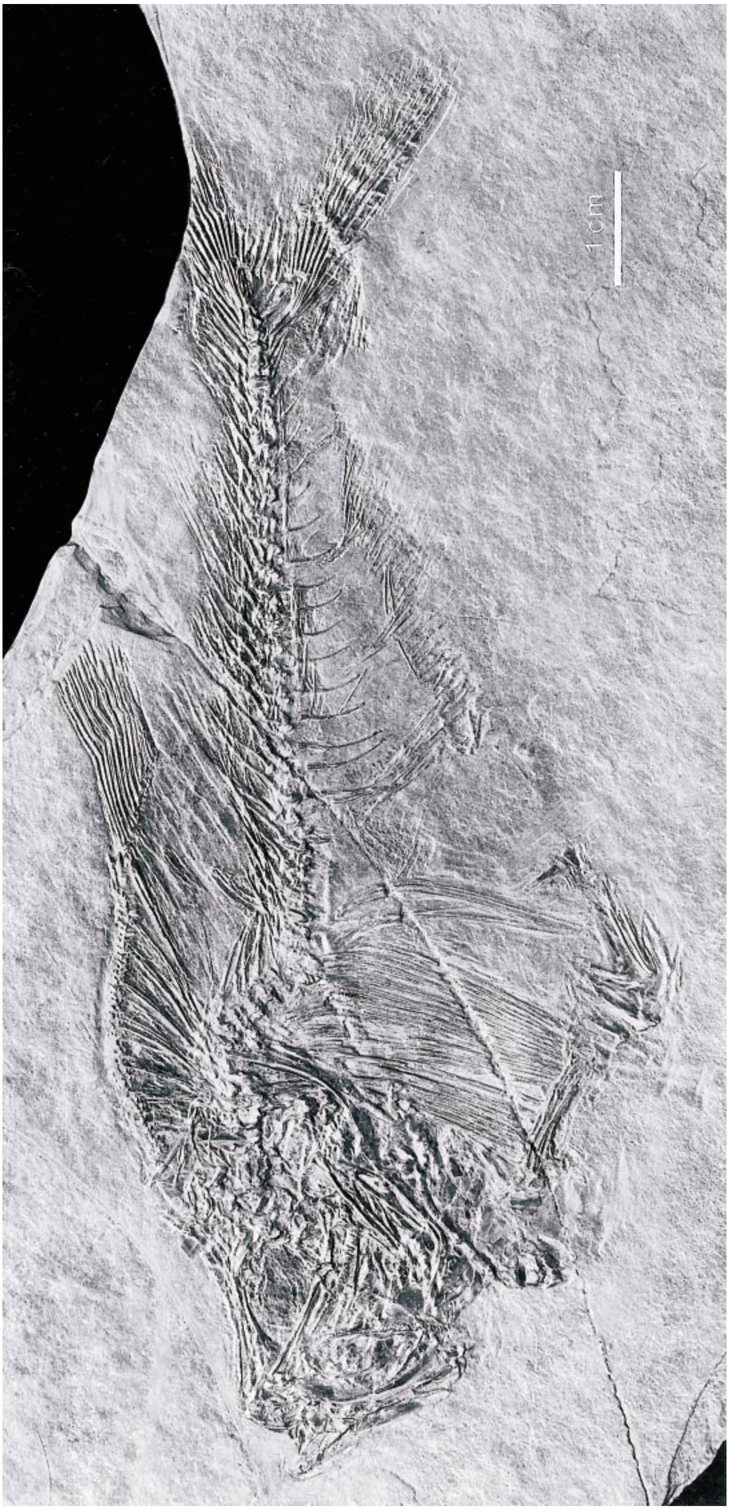

Fig. 9. †*Diplomystus shengliensis*. Lower Cretaceous, Sheng-li Oil Field, China. The holotype, SOF 790001.

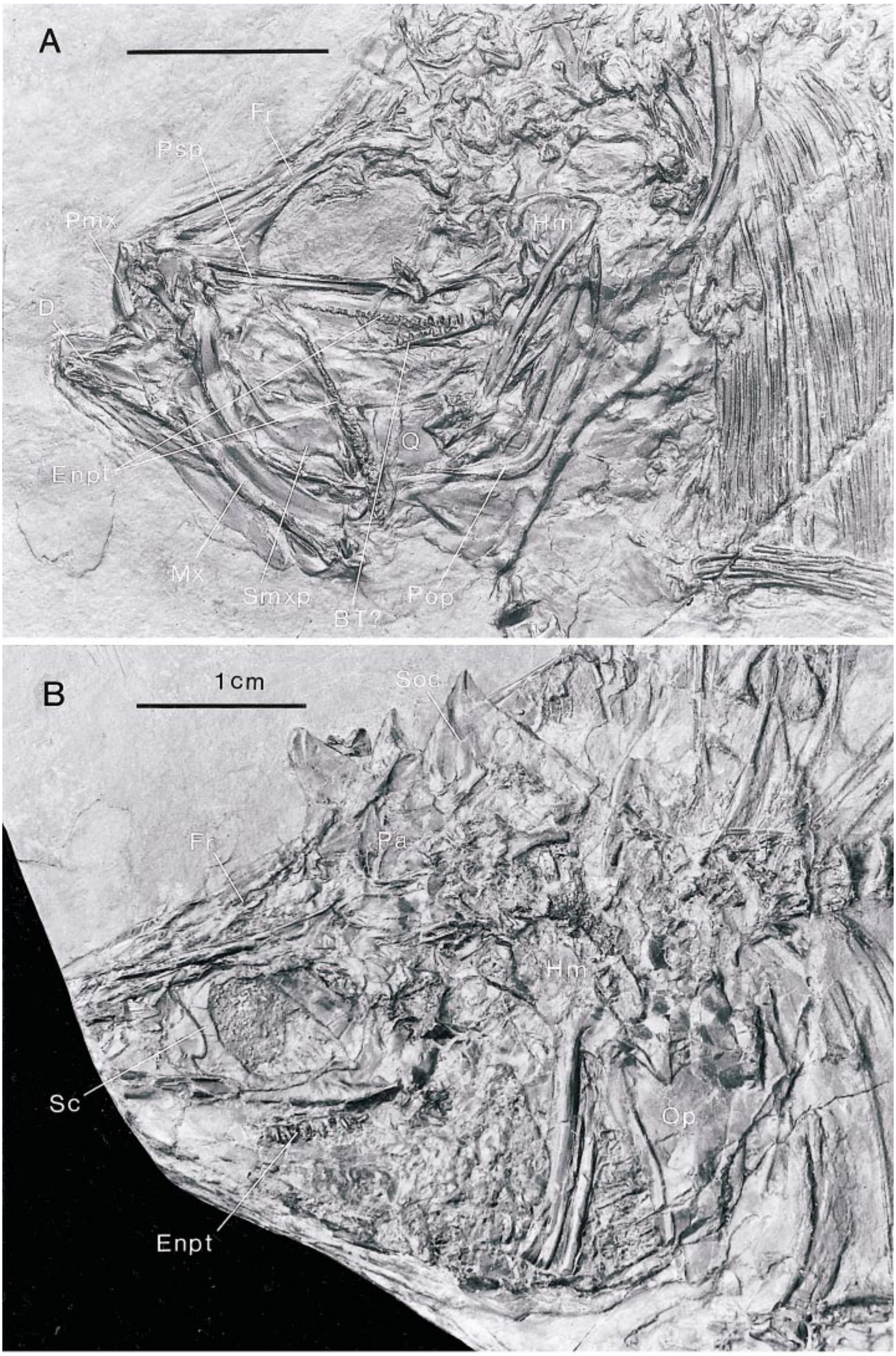

Fig. 10. †*Diplomystus shengliensis*. Detail of the head in **(A)** the holotype, SOF 790001; and **(B)** SOF 790002. Both scale bars = 1cm.

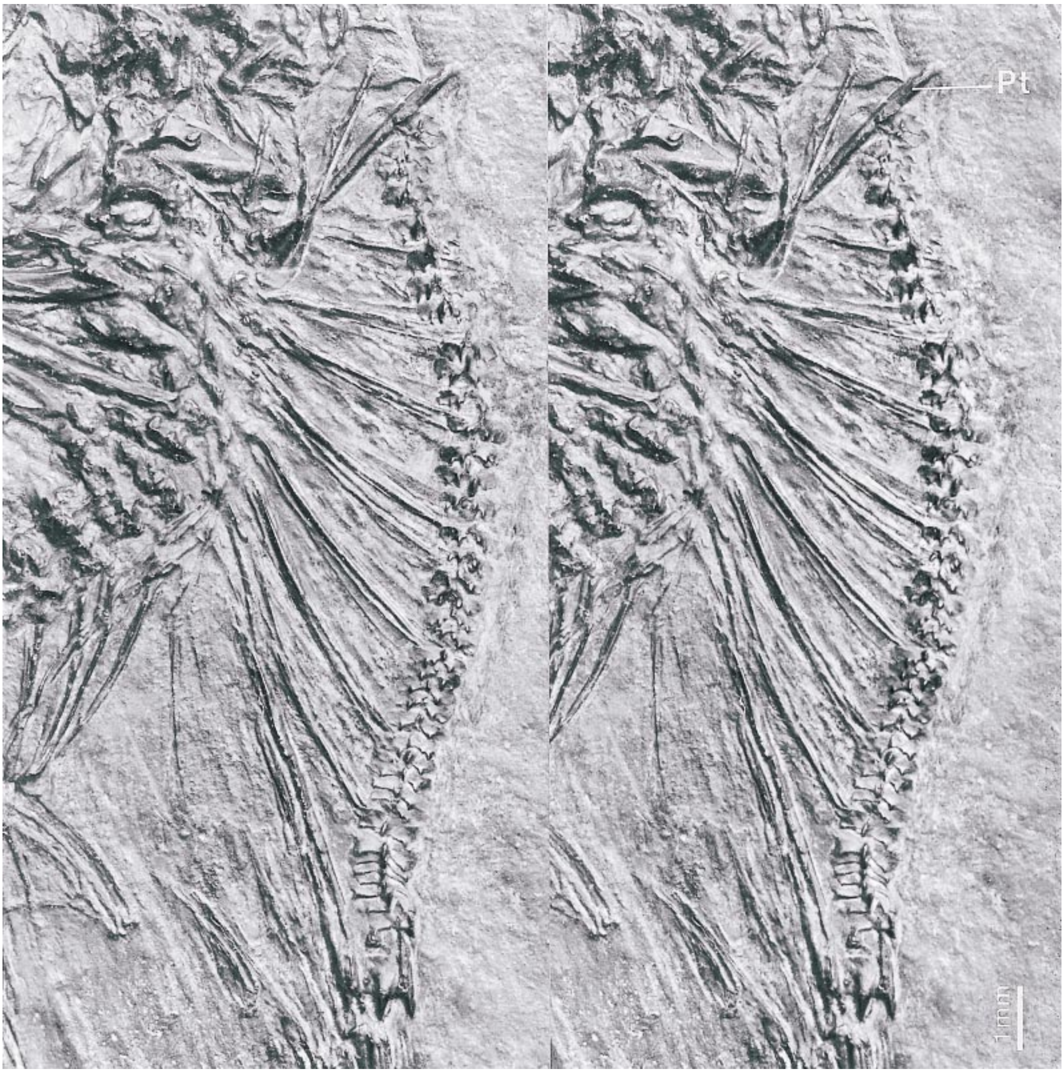

Fig. 11. †*Diplomystus shengliensis*. Stereophotographs showing the predorsal bones and dorsal scute series in the holotype, SOF 790001 (specimen oriented vertically).

teeth were observed on the parasphenoid, and it is apparently edentulous in †*D. shengliensis*. A basipterygoid process is present in the holotype SOF 790001 (fig, 10A), although no features are descernible. In this specimen, the left entopterygoid is observed in situ against the parasphenoid margin, while the right entopterygoid has its buccal side turned outward and its posterior end displaced downward. This bone therefore occupies an oblique position, and it was mistakenly identified as the ectopterygoid by Zhang et al. (1985). The buccal surface of the entopterygoid bears numerous teeth, of which the posterodorsal ones adjacent to the parasphenoid are much stouter than the rest.

JAWS: The dentary and premaxilla bear small conical teeth, and the oral margin of the maxilla is finely serrated. There are two supramaxillae, but unlike in †*Paraclupea* and †*Ellimma* these bones both have smooth surfaces.

OPERCULAR SERIES AND HYPOBRANCHIAL APPARATUS (FIG. 10A, B): The bones of the

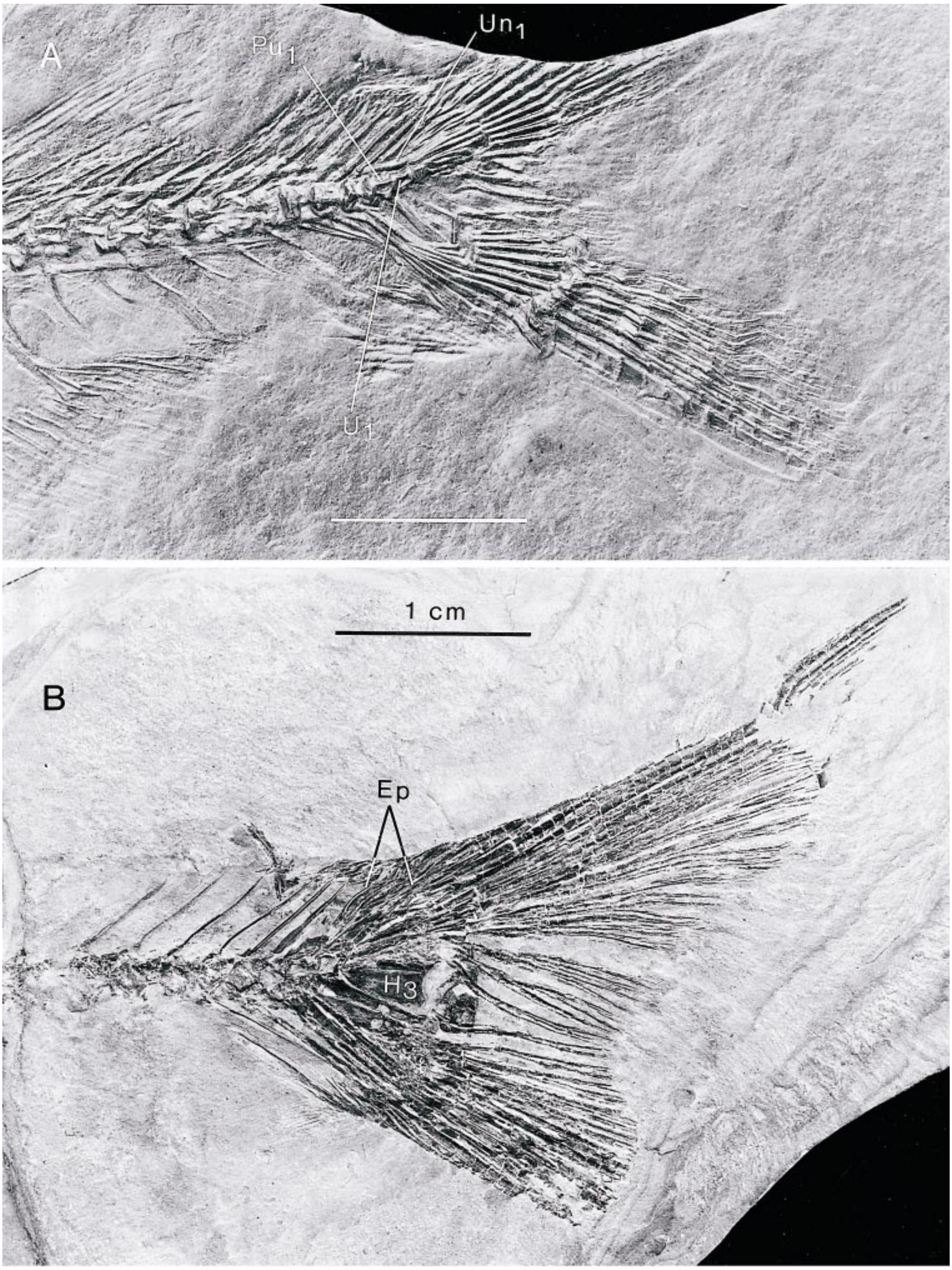

Fig. 12. †*Diplomystus shengliensis*. Detail of caudal fin skeleton in **(A)** the holotype, SOF 790001; and **(B)** SOF 790003. Both to same scale.

opercular series are smooth in †*D. shengliensis*. The vertical branch of the preopercle is much longer than the horizontal branch. In SOF 790001 there is a bone covered with stout teeth, in occlusion with the left entopterygoid; we interpret this as the basibranchial bone and its associated toothplate.

VERTEBRAL COLUMN AND FINS: The vertebral column is fairly well preserved in the holotype of †*D. shengliensis*, but the exact number of abdominal vertebrae cannot be determined because the anterior portion of the vertebral column is distorted (fig. 9). We estimate that there were 42 vertebrae, 25 of which are caudal. In SOF 790002 (where the anterior portion of the vertebral column is better preserved) there are 17 abdominal vertebrae and 15 paired ribs. There are seven predorsal bones on the holotype of †*D. shengliensis*, with both anterior and posterior bony expansions (fig. 11).

The dorsal fin of †*D. shengliensis* contains one unbranched and 13 branched fin rays (fig. 9). The anal fin is very long and contains at least 39 fin rays. The pterygophores of both dorsal and anal fins are badly preserved in all the available specimens.

SCUTES: The dorsal scute series in the holotype, SOF 790001 is shown in figure 11. As the stereophotographs illustrate, the dorsal scutes of †*D. shengliensis* are much broader than long, with a prominent median keel and a pectinate posterior margin, but the scute surface is smooth and lacks ornamentation. There are 41dorsal scutes on the holotype of †*D. shengliensis*, but the number of abdominal scutes is uncertain because of poor preservation. These scutes are quite similar in shape to those of other clupeiforms, and as in †*D. dentatus* the ventral part of the posterior border is pectinate in the anteriormost few scutes.

SCALES: Scale morphology cannot be determined in any of the specimens of †*D. shengliensis*, but detached scales associated with them resemble those referred to †*Knightia bohaiensis* by Zhang et al. (1985: fig. 16).

CAUDAL SKELETON AND TAIL: Only parts of the caudal skeleton and fin are preserved in the holotype, SOF 790001, but more can be seen in SOF 790003 (fig. 12). There are seven hypurals in †*D. shengliensis*, of which the first is in contact with the first ural centrum and the second is fused to it. The third hypural fills the entire space between the second and the fourth hypurals, unlike in †*Paraclupea*, †*Ellimma*, and †*Ellimmichthys*, where there is a gap. The parhypural in †*D. shengliensis* is apparently fused with the first preural. The latter carries a short neural arch protruding backward into a very sharp spine. There are three epurals and three uroneurals in †*D. shengliensis*, the first of which extends anteriorly to the second preural.

The caudal fin is deeply forked in †*D. shengliensis*, and the lower lobe is slightly longer than the upper. There are 19 principal fin rays (as in primitive teleosts generally), of which the 2 lateral ones are unbranched. The proximal end of the lowermost ray from the upper lobe bifurcates into two short branches of approximately equal size. The corresponding end of the uppermost ray of the lower lobe is slightly bent and spatulate.

PHYLOGENETIC ANALYSIS

The data we assembled (see table 1 and appendix 1) are mainly based on characters from Grande (1985a), Forey (1975), Patterson and Rosen (1977), Maisey (1993), Arratia (1996), and Chang and Grande (1997), plus a few new observations. Our phylogenetic analysis involved 30 osteological characters and 11 taxa, 7 of which are extinct (†*Armigatus*, †*Diplomystus*, †*Ellimma*, †*Ellimmichthys*, †*Knightia*, †*Paraclupea* and †*Santanaclupea*). Two Recent clupeomorphs were included (*Clupea* and *Denticeps*), which, together with †*Knightia*, are representatives of either Clupeoidei or Denticepitoidei. Two other Recent taxa (*Elops* and *Oncorhynchus*) represent successive outgroups (Elopomorpha and Euteleostei, respectively). Taxa only known from very incomplete fossils such as †*Spratticeps* (Patterson, 1970) are not included in our analysis because data are too limited. Characters for †*Diplomystus* are taken from the type species †*D. dentatus* and †*D. shengliensis*. The Late Cretaceous species †*D. birdi* Woodward and †*D. dubertreti* Signeux need further investigation before they can be meaningfully included in a phylogenetic analysis.

The dataset was analyzed by using Swofford's (2000) Phylogenetic Analysis Using

TABLE 1

Data Matrix

Taxon	11111111112222222223 123456789012345678901234567890
Armigatus	00100100100011010001010001 00?0
Clupea	1111111001111 0-111000111101110
Denticeps	1101010101111 0-110011110100000
Diplomystus	001001001000120100010100010100
Ellimma	0??0010001?01211000101000000?0
Ellimmichthys	0??001?001?01211000101000000?0
Elops	0000000000110 0-000000000000000
Knightia	11?111110111120101000101101110
Paraclupea	0??01100010012110001 01000000?0
Onchorhynchus	0000000001111 0-010100000000001
Santanaclupea	0111?1001100?0-100010100101000

Parsimony (PAUP Version 4.0). All characters are unordered and unweighted. Our analysis (using the branch-and-bound search) generated two equally short trees (fig. 13A, B), each 45 steps long and with a consistency index (excluding uninformative characters) of 0.6585, a homoplasy index (excluding uninformative characters) of 0.3111, and a retention index of 0.7255 (with rescaled consistency index of 0.4998). The two trees agree in recognizing two groups within the Clupeomorpha. One consists of (†*Armigatus* + †*Diplomystus*) + (†*Ellimma* + †*Ellimmichthys* + †*Paraclupea*), which corresponds approximately to the †Paraclupeidae of Chang and Grande (1997) or †Ellimmichthyiformes (Grande, 1982a). The other group comprises (*Clupea* + †*Knightia*) + *Denticeps* and is equivalent to Clupeiformes. In both trees †*Ellimma*, †*Ellimmichthys*, and †*Paraclupea* collectively form a monophyletic group, but their interrelationships are unresolved. This group is referred to below as the subfamily †Paraclupeinae. Differences between the two most parsimonious trees mainly involve the position of †*Santanaclupea*. In tree 1 (fig. 13A), †*Santanaclupea* is grouped with †*Clupea* + †*Knightia* (i.e., Clupeoidei), but in tree 2 (fig. 13B) †*Santanaclupea* is the closest extinct stem taxon to Clupeiformes.

The overall grouping of taxa within these trees largely agrees with the phylogeny proposed by Grande (1982a: fig. 20; 1985a: fig.1A) in which †*Diplomystus* + †*Ellimmichthys* and Denticipitoidei + Clupeoidei form two monophyletic sister groups. Our results differ from his in three respects: (1) the position of †*Armigatus*; according to Grande (1985a), this forms an unresolved trichotomy with two monophyletic groups (†Ellimmichthyiformes, Clupeiformes), whereas here it is grouped with †*Diplomystus*; (2) †*Paraclupea* and †*Ellimma* were not included in Grande's (1985a) analysis, although †*Paraclupea* was later placed in the subfamily †Paraclupeinae along with †*Ellimmichthys* by Chang and Grande (1997); (3) †*Santanaclupea* (a clupeomorph from Santana Formation, Northeast Brazil; Maisey, 1993) is also included in our analysis and appears to be closer to Clupeiformes than to †Paraclupeidae (= †Ellimmichthyiformes). It may form a sister taxon to Clupeoidei, represented by †*Clupea* and †*Knightia* in our analysis (fig. 13A), or it may be a sister taxon to Clupeiformes, represented by (†*Clupea* + †*Knightia*) + †*Denticeps* (fig. 13B).

Despite some uncertainties both in the data and in our phylogenetic analysis, the present study confirms the monophyly of Clupeomorpha and also its subdivisions into two major groups: (1) †Paraclupeidae (= †Ellimmichthyiformes) including (†*Armigatus* + †*Diplomystus*) + †Paraclupeinae; and (2) Clupeiformes. Our analysis also supports monophyly of the Denticipitoidei and Clupeoidei within the Clupeiformes, as proposed by Grande (1982a, 1985a). The Clupeomorpha, Clupeiformes and Clupeoidei are well supported by shared derived characters (e.g., Clupeomorpha by characters 6, 16, 20, 22, node 1 in fig. 13A, B; Clupeiformes by characters 2, 4, 25, node 5; and Clupeoidei by characters 1, 5, 7, 18, 20, 24, 28, 29, node 7). The monophyly of the †Paraclupeidae (†Ellimmichthyiformes) is less robust, being supported only by characters with low consistency (i.e., characters which are shared with taxa outside the group, or which are lacking in some of the in-group taxa, 11, 12, 14, node 2). In Grande's (1985a) analysis, †*Armigatus*, †Ellimmichthyiformes (including †*Diplomystus*), and Clupeiformes formed an unresolved trichotomy. In our analysis this trichotomy is resolved so that †*Armigatus* and †*Diplomystus* form a sister pair (node 3 in fig. 13A, B). Among the characters uniting these taxa (3, 9, 10, 26) only 26 (pres-

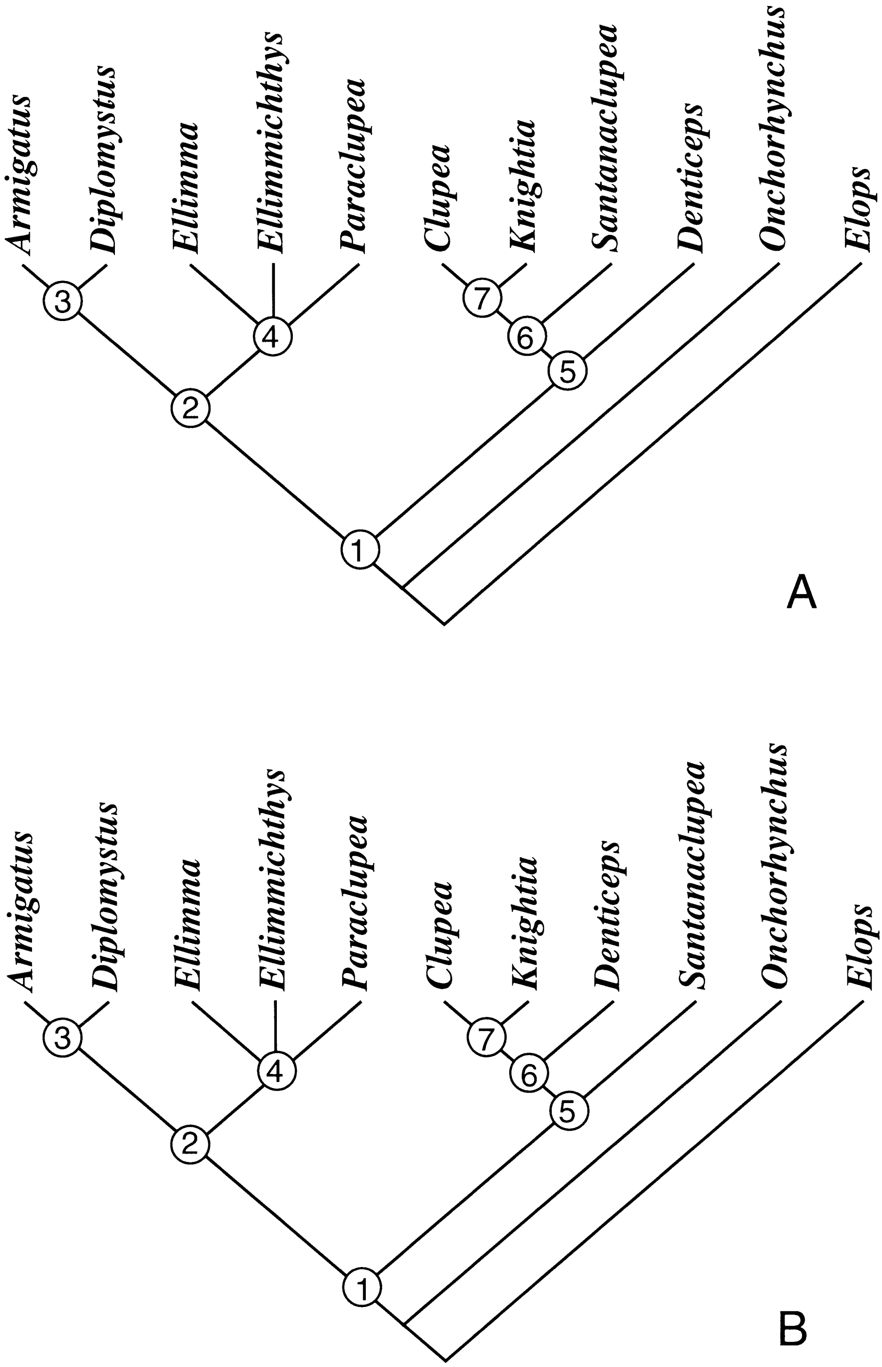

Fig. 13. Results of the phylogenetic analysis discussed in the text, with the two most parsimonious trees generated by our characters. **(A)** †*Santanaclupea* is grouped with Clupeoidei. Characters supporting nodes: **1** (6, 16, 20, 22); **2** **(**11, 12, 14); **3** **(**3, 9, 10, 26); **4** (15); **5** (2, 4, 25); **6** (3, 27); **7** (1, 5, 7, 18, 20, 24, 28, 29). **(B)** †*Santanaclupea* is grouped more generally with Clupeiformes. Characters supporting nodes: **1** (3, 6, 16, 20, 22); **2** (11, 12, 14); **3** (9, 10, 26); **4** (15); **5** (2, 4, 25); **6** (1); **7**(5, 7, 18, 20, 24, 27, 28, 29).

ence of a posteriorlyexpanded third hypural leaving no gap between hypurals 2 and 4) is uniquely shared by two of the 11 taxa under our analysis. Among clupeoids it also occurs in pristigasteroids (Grande, 1985a). Our principal findings are discussed further below.

DISCUSSION

PHYLOGENETIC COMMENTS. Jordan (1910: 23) noted that the herringlike fishes he recognized among fossils collected in 1907 by John Casper Branner from Riaco Doce, Brazil ''. . . have the general traits of †*Diplomystus dentatus*, with the short anal and fewer vertebrae of †*Knightia*, while at the same time their squamatiom seems to be different from both . . . ''.

Schaeffer (1947) placed the genus †*Ellimma* into synonymy with †*Knightia*, which considerably extended the stratigraphic range of the latter (until then it had only been discovered in Eocene strata of western North America; Jordan, 1907). He also placed †*Ellimmichthys* into synonymy with †*Diplomystus*, despite admitting there were similarites between †*Ellimma branneri* and †*Diplomystus* in the ovate shape of the dorsal scutes and the absence of scute lateral wings (Cope, 1877), as well as similarities in the size and shape of body scales. Schaeffer (1947) also concurred with Jordan (1910) that the dorsal scutes of †*Knightia branneri* differ from those of North American †*Knightia* in being wider and in lacking a posterior median spine.

It is possible that such morphological differences, however slight, might have been given greater emphasis had it been realized that the Brazilian taxa were in fact far older than those from North America. Jordan (1910) commented that the age of the Riacho Doce shales is ''. . . Lower Eocene, possibly but not probably Upper Cretaceous'', and Schaeffer (1947) also considered them to be Eocene. †*Ellimmichthys* from Bahia was nevertheless considered to be of Upper Cretaceous age by both Jordan (1910) and Schaeffer (1947). In fact, the fossils from both Alagoas and Bahia are Lower Cretaceous in age; †*Ellimma* from the Riacho Doce shales of Alagoas (Muribeca Formation) dates from the Aptian–Albian (Alagoan local stage), and †*Ellimmichthys* from the sedimentary sequence in Bahia (Marfim Formation) is even older (late Hauterivian–early Barremian) (for references, see Maisey, 2000).

Grande (1982a, 1982b, 1985a) restored the generic name †*Ellimma* and removed †*E. branneri* from the genus †*Knightia* on morphological grounds: (1) †*Ellimma* has two supramaxillae, whereas †*Knightia* has only one; and (2) the dorsal scutes of †*Ellimma* show a complex pattern of sculpture, whereas in †*Knightia* they do not. Grande (1982a, 1985a) also resurrected the genus †*Ellimmichthys*, again on morphological grounds, and thus he essentially restored the systematic distinctions recognized by Jordan (1910, 1913), albeit within a far more comprehensive and refined phylogenetic framework for clupeomorph fishes. In Grande's (1985a) phylogenetic analysis †*E. branneri* is not closely related to †*Ellimmichthys* or †*Diplomystus*, and is placed instead within Clupeidae (i.e., within Clupeiformes, rather than †Ellimmichthyiformes); as such, †*Ellimma* would be the only clupeine having dorsal scutes.

Unfortunately, there is little evidence in support of that conclusion. Grande's (1985a) single morphological character supporting monophyly of the Clupeidae (presence of two long, rodlike postcleithra; Grande, 1985a: character 23) has not been identified in †*E. branneri*. Clupeids are nested within the Clupeoidea, whose single synapomorphy (increase in pleural rib to preural vertebrae ratio; Grande, 1985a: character 22) is certainly present in †*E. branneri*, but is also a feature of †*Ellimmichthys* (where it was regarded as convergent by Grande, 1985a: 263). †*Ellimma branneri* also lacks three of the derived characters of clupeoids (fusion of the first uroneural with the first preural centrum, reduction in relative size of the first ural centrum, separation of the parhypural from the first preural centrum; Grande, 1985a: characters 14, 15 17) and is unknown with respect to the fourth (absence of lateral line scales; Grande, 1985a: character 16). Finally, †*Ellimma branneri* lacks two of the three synapomorphies shared by the Clupeiformes (parietals separated by supraoccipital, beryciform foramen lost; Grande, 1985a:

characters 10, 11) and the third (presence of a recessus lateralis, Grande, 1985a: character 9) is unknown.

Thus, none of Grande's (1985a) characters support the inclusion of †*Ellimma* within the Clupeidae, Clupeoidei, or Clupeiformes, and its inclusion within Clupeoidea is only supported by a single ambiguous character which could be convergent with clupeoids, as in †*Ellimmichthys*. Grande (1985a) found a single character to unite his †Ellimmichthyidae (lateral expansion of dorsal scute ''wings'' which give scute a subrectangular shape; Grande, 1985a: character 7; this feature is also shared with †*Diplomystus*). In †*Ellimmichthys* and †*Paraclupea*, all the dorsal scutes are broader than long, as are the posterior dorsal scutes in †*Ellimma branneri* (although its anterior dorsal scutes are slightly longer than broad); thus, lateral expansion of dorsal scutes remains a synapomorphy of † Paraclupeidae (= †Ellimmichthyidae), including †*Ellimma*, but the condition is clearly variable. In addition, †*Ellimma* shares several generalized clupeomorph characters with †*Ellimmichthys* and †*Paraclupea*, such as presence of abdominal and dorsal scutes, enclosure of the supratemporal commissure within the parietals, and fusion of the second hypural with the first ural centrum, although these similarities do not help elucidate its relationship within clupeomorphs.

Two derived characters are shared by †*Ellimma*, †*Ellimmichthys*, and †Paraclupea and distinguish them collectively from †*Diplomystus*: strongly sculptured skull roofing bones, with ridges radiating from the growth center, and dorsal scute ornament of prominent ridges. It is concluded from this that †*Ellimma branneri* (Jordan, 1910) is closely related to †*Ellimmichthys longicostatus* (Cope, 1886), from the Hauterivian–Barremiam of Brazil, †*E. goodi* (Eastman, 1912), from the late Aptian of Equatorial Guinea, and †*Paraclupea chetungensis* Sun, 1956, from the Lower Cretaceous of southeastern China. All these taxa are grouped here in the subfamily †Paraclupeinae.

†*Ellimma* can be distinguished at generic level from these other taxa by the ornamentation on the last few dorsal scutes, where there are tubercles (or tubercles plus ridges); in †*Ellimmichthys* and †*Paraclupea* the ornamentation of all dorsal scutes consists only of ridges. Additionally, the jaw and palatal dentition of †*Ellimma* is reduced in comparison with †*Ellimmichthys* and †*Paraclupea*. The origin of the pelvic fin also differs. In †*Ellimma* it is opposite to the middle point of the dorsal fin base, whereas in †*Ellimmichthys longicostatus* it is in advance of the dorsal fin, and in †*Ellimmichthys goodi* the pelvic fin inserts opposite to the posterior third of the base of the dorsal fin; in †*Paraclupea chetungensis* the pelvic fin lies behind the origin of the dorsal fin. There are also fewer procurrent rays on each side of the peduncle (approximately five in †*Ellimma*; in †*Ellimmichthys* and †*Paraclupea* there are eight or nine rays on the upper side and four to six on the lower side). These differences suggest that †*Ellimma* is a distinct genus from †*Ellimmichthys* and †*Paraclupea*.

Observed meristic characters of †*Ellimma branneri* agree more closely with those of the two species of †*Ellimmichthys* than with †*Paraclupea* (see table 2) The number of vertebrae, dorsal fin rays, dorsal scutes and abdominal scutes in †*Ellimma* are respectively, 36–38, ii, 12–14, 12–14, and 27–30. Those in †*Ellimmichthys* are 35–38, 12–15, 12–13, and 28–32. In †*Paraclupea* the number is noticeably higher (41, 17–18, 18, and 38–43). Furthermore, in †*Ellimma* and †*Ellimmichthys* almost the entire surface of each dorsal scute is ornamented, whereas in †*Paraclupea* only the posterior third or half is ornamented.

†*Ellimna guineensis* from Equatorial Guinea, West Africa (apparently misspelled as ''†*Ellimna*''; Gayet, 1989), was referred to Clupeidae and has been considered close to †*Diplomystus goodi*. Grande (1982a) previously noted that the characters of †''*Diplomystus*'' *goodi* mentioned by Taverne (1975) are all primitive for clupeomorphs, however, and do not clearly place this taxon in †*Diplomystus*; he consequently removed it from †*Diplomystus* and placed it in Clupeomorpha, incertae sedis. Gayet (1989) regarded two characters (presence of two supramaxillae and ornamented dorsal scutes) as diagnostic of the genus †*Ellimna*, but the first is a primitive teleost feature and the other is

TABLE 2

Comparison of Characters Between †*Diplomystus shengliensis* and †*D. dentatus*

Characters	†*Diplomystus shengliensis*	†*D. dentatus*
1. Body form	elongate fusiform	same as in †*D. shengliensis*
2. Maximum depth	between head and dentary	same as in †*D. shengliensis*
3. Body depth/standard length	40% (790001, slightly distorted)	35–37% (PF11776, 11780–11782)
4. Dorsal outline	gently curved	same as in †*D. shengliensis*
5. Ventral outline	convex	same as in †*D. shengliensis*
6. Supraorbital sensory canal	enclosed in crest	same as in †*D. shengliensis*
7. Supraoccipital crest	well developed, high	same as in †*D. shengliensis*
8. Parietals	meet at midline	same as in †*D. shengliensis*
9. Posttemporal	with long, slender anterior branches	same as in †*D. shengliensis*
10. Entopterygoid teeth	those next to dorsal margin robust	same as in †*D. shengliensis*
11. Shape of dorsal scutes	broader than long, posterior border pectinate	same as in †*D. shengliensis*
12. Number of dorsal scutes	41	33–36 (Grande, 1982) 40 (PF 11780) 30 (PF 11781)
13. Predorsals	7 or 8	same as in †*D. shengliensis*
14. Dorsal fin rays	i, 13	I-ii, 11 or 12
15. Anal fin rays	39	39–40 (36–42) (Grande, 1982)
16. Pelvic fin	unknown	slightly anterior to dentary, with six or seven rays
17. Abdominal scutes	number unknown, anteriormost few with pectinate posterior border	32–34 (Grande, 1982), anteriormost few with pectinate posterior border
18. Total number of vertebrae	around 42 (including urocentra)	43–45 (including urocentra)
19. Abdominal	17 (790002)	20 (PF11780, 11782)
20. Caudal	25 (790001)	24 (PF11776, 11782), 25 (PF11780, 11781)
21. Ribs	15 pairs (790002)	17–18 pairs
22. Number of hypurals	6 or 7	same as in †*D. shengliensis*
23. Hypural 1	articulated with ural centrum 1	same as in †*D. shengliensis*
24. Hypural 2	fused to ural centrum 1	same as in †*D. shengliensis*
25. Parhypural	fused to preural centrum 1	same as in †*D. shengliensis*
26. Epural	3	same as in †*D. shengliensis*
27. Uroneural	3	same as in †*D. shengliensis*
28. Preural centrum 1	short	same as in †*D. shengliensis*
29. Lowermost ray of upper lobe and uppermost of lower lobe of caudal fin	proximal end of lowermost ray of upper lobe bifurcated, that of uppermost ray of lower lobe slightly bent and somewhat spatulate	same as in †*D. shengliensis*
30. Gap between hypurals 2 and 3	absent	same as in †*D. shengliensis*
31. Scales	unknown	with semicircular or vertical circuli
32. Number of scales	unknown	80–90 along lateral line

present in †*Ellimmichthys* and †*Paraclupea*. Chang and Grande (1997) considered that both †*Ellimna guineensis* and †''*Diplomystus*'' *goodi* should be placed within †*Ellimmichthys*.

Based on the original description by Silva Santos and Correa (1985), †*Scutatuspinosus itapagipensis* displays some features suggesting paraclupeine affinity. Its dorsal scutes are progressively larger and wider caudally (as in †*Ellimmichthys*, †*Paraclupea*, and †*Ellimma*). They are also ornamented with ridges (a paraclupeine character), but lack tubercles (as in †*Ellimmichthys* and †*Paraclupea*). It is unknown whether the skull roofing bones are sculptured with ridges, as in paraclupeines. The origin of the pelvic fin is anterior to the dorsal fin in †*Scutatuspinosus itapagipensis*, as in †*Ellimmichthys longicostatus*, not beneath it, as in †*Ellimma branneri*. Unfortunately few of the described features in this taxon are phylogenetically informative, and it would benefit from a revision, but our observations suggest that †*Scutatuspinosus* is also a paraclupeine. Its caudally-expanded dorsal scute series is an unusual feature and may represent a synapomorphy with †*Ellimma*. According to Silva Santos and Correa (1985), †*Scutatuspinosus itapagipensis* has 32 vertebral centra and 12 dorsal fin rays (comparable with paraclupeines other than †*Paraclupea* itself), 10 dorsal scutes, and 25 ventral scutes (the lowest number of each for any paraclupeine).

As far as †*Diplomystus* is concerned, although several nominal North American species have been recognized, it has long been suspected that their taxonomic diversity is exaggerated. Woodward (1901) suggested that †*D. analis*, †*D. pectorosus*, and †*D. theta* were synonyms of †*D. dentatus*, while Eastman (1912) pointed out that species of †*Diplomystus* from the Green River were almost indistinguishable. In his revision of †*Diplomystus*, Grande (1982a) also concluded that the only valid species from the Green River shales is †*D. dentatus*, and that the others are all junior synonyms of that taxon. Two other species were retained by Grande (1982a) in the genus †*Diplomystus*: †*D. birdi* and †*D. dubertreti* from the Upper Cretaceous of Lebanon (Woodward, 1895; Signeux, 1951). Grande (1982a, 1985a) united these three †*Diplomystus* species by the presence of dorsal scutes with a pectinate posterior border, more numerous dorsal scutes (22–36) than in †*Ellimmichthys*, and reduction or loss of a median recess in the posterior edge of the scute (present in †*Ellimmichthys*). Grande (1982a) regarded the two Cretaceous species from Lebanon as closer to each other than to †*D. dentatus*, because they both have more dorsal fin rays and fewer vertebrae.

Zhang et al. (1985) noted that †*D. shengliensis* is very similar to †*Diplomystus dentatus* from the Green River shales. In fact, they are so similar that it is difficult to distinguish them as separate species, despite their widely separated occurrences today on opposite sides of the Pacific. A list of characters comparing †*D. shengliensis* and †*D. dentatus* is provided in table 2. Despite the small sample size for †*D. shengliensis* (with merely three specimens), information is lacking in only 4 out of 32 characters (data are missing for the pelvic fin, the number of abdominal scutes, and scale morphology).

†*Diplomystus shengliensis* resembles †*D. dentatus* in 22 of the 28 characters that can be compared. The ratio of depth/standard length is slightly greater in †*D. shengliensis* (40%) than that in †*D. dentatus* (35–37%), but this may be a taphonomic rather than morphological distinction related to deformation of the ventral portion of the body in available specimens of †*D. shengliensis*. There are 41 dorsal scutes in †*D. shengligensis*, only one more than the maximum number observed in †*D. dentatus*, although the majority of specimens have fewer (between 33 and 36; Grande, 1982a). There are 13 branched rays in the dorsal fin of †*D. shengligensis*, again one more than the maximum count in †*D. dentatus*. An estimated 42 vertebrae are present in †*D. shengligensis*, only one fewer than the minimum count from †*D. dentatus* (most individuals have more than 44). Greater apparent differences are found in the number of abdominal vertebrae (17 in †*D. shengligensis*, 20 in †*D. dentatus*) and ribs (15 pairs in †*D. shengligensis*, 17–18 in †*D. dentatus*. Given the extent to which these features vary in †*D. dentatus*, and the very small available sample of †*D. shengliensis*, the meristic distinctions be-

tween them are best regarded as provisional. Whether †*D. shengliensis* is a distinct species, however, the presence of †*Diplomystus* in China during the Eocene is confirmed by the present observations.

The morphological similarity of †*Diplomystus dentatus* and †D. shengliensis is further emphasized by comparison with the two Lebanese Cretaceous species †*D. birdi* and †*D. dubertreti*, both of which have dorsal scutes like those of †*D. dentatus* in their adult morphology and presumed ontogenetic development, but which differ from †*D. dentatus* in having many more dorsal fin rays and far fewer dorsal scutes, abdominal scutes, anal fin rays, vertebrae, and ribs (Grande, 1982a). There is also a gap between the second and third hypurals in the two Cretaceous species, unlike in †*D. dentatus* and †*D. shengliensis*. Some other potentially useful systematic features, such as the supraoccipital crest and entopterygoid dentition, are unknown in the Lebanese species. While both species agree in most respects with the generic diagnosis of †*Diplomystus* presented earlier, their relationships are left unresolved and require further analysis.

According to Greenwood et al. (1966), Patterson (1970), and Nelson (1973), the modern Clupeomorpha are monophyletic and share derived features of the ear-swimbladder connection, the recessus lateralis, the cranial morphology, the caudal skeleton, the abdominal scutes, and the structure of gill arches (see also Nelson, 1967, 1970). With the inclusion of extinct taxa (especially at basal levels), however, monophyly of the Clupeomorpha becomes increasingly tenuous. Forey (1975) conducted a comprehensive analysis of clupeomorph characters while studying †*Erichalcis*, and paid particular attention to the morphology of the recessus lateralis, the position and size of the dermosphenotic, and the sensory canal arrangement around the recessus. He found that presence of an upper division of the levator arcus palatini muscle in clupeoids can be correlated with presence of a ridge on the frontal and an anterodorsal process on the hyomandibular. Both features are present in †*Knightia*, leading Forey (1975) to include it in clupeoids, but they are absent in †*Denticeps*, †*Ornategulum*, and †*Diplomystus brevissimus* (Patterson, 1967; now †*Armigatus*, Grande, 1982a).

The relationships between the two Recent clupeiform suborders (Denticepitoidei, Clupeioidei) and some putative clupeomorph fossils have been investigated by Forey (1975) and Grande (1982a, 1985a), while the problem of clupeomorph relationships generally within teleosts has been discussed by Patterson and Rosen (1977) and Arratia (1996). †*Diplomystus*, †*Armigatus*, and †*Ellimmichthys* all seem to be close extinct relatives of modern clupeomorphs (i.e., Clupeiformes sensu Grande, 1985a; in his phylogeny there is an unresolved trichotomy between †*Armigatus*, the group †*Diplomystus* + †*Ellimmichthys*, and Clupeiformes). There are differences of opinion regarding the inclusion of certain other extinct taxa within clupeomorphs. †*Ornategulum* was included in clupeomorphs by Forey (1975), Patterson and Rosen (1977), and Grande (1982a), but was excluded by Grande (1985a). †*Erichalcis* was placed in the Clupeomorpha by Forey (1975) and Grande (1985a), but was regarded as the sister taxon of *Esox* + salmonids by Arratia (1996). Part of the uncertainty is due to the incomplete preservation of the material, and in the case of †*Erichalcis* the type series may include more than one taxon (Mark Wilson and Lance Grande, personal commun., 2000). †*Santanaclupea* shares at least two synapomorphies with clupeiforms, but cannot be placed unambiguously within any of the modern clupeiform groups (Maisey, 1993).

In Grande's (1985a) revision of Recent and fossil clupeomorphs, †*Diplomystus* and †*Ellimmichthys* form a monophyletic group (order †Ellimmichthyiformes) supported by a single character (dorsal scutes broader than long or of rectangular shape). Clearly this character also unites †*Ellimma branneri* with these genera, although it is developed only in the posterior part of the scute series in this form.

Chang and Grande (1997) referred †*Paraclupea chetungensis* to an equivalent monophyletic group (family Paraclupeidae = Ellimmichthyidae). They concluded that †*Paraclupea* is more closely related to †*Ellimmichthys* than to †*Diplomystus*, and should be included with †*Ellimmichthys* in the subfamily †Paraclupeinae. Our investigation of †*Ellimma branneri* from Brazil suggests that it is also a paraclupeine, in which case the ornamentation of dorsal scutes becomes a synapomorphy of the subfamily. †*Ellimma*, †*Ellimmichthys*, and †*Paraclupea* form an unresolved trichotomy in our phylogenetic analysis, but meristic data for †*Ellimma* and †*Ellimmichthys* are similar whereas those for †*Paraclupea* are different. Our conclusions regarding †*Diplomystus shengliensis* agree with those of Chang and Chow (1978) and Zhang et al. (1985) that it is most closely related to †*D. dentatus* from North America.

Our analysis (fig. 13) supports the main conclusions reached by previous workers, especially those of Grande (1985a), although some aspects of our results require critical comment. First, our morphological evidence that the †Ellimmichthyiformes form a monophyletic group is not as strong as we would wish. Second, some extinct ‘‘double-armored’’ clupeomorph taxa (e.g., †*Scutatospinosus*, †*Ezkutuberezi carmeni*) were excluded from our analysis, because we were unable to examine material or retrieve sufficient data from the published descriptions; their inclusion in future phylogenetic analyses is clearly desirable and may provide a useful test of the conclusions reached here. Third, although the trichotomy formed by †*Armigatus*, †Ellimmichthyiformes, and Clupeiformes in Grande’s (1985a) cladogram seems to be resolved here, our grouping of †*Armigatus* and †*Diplomystus* is actually supported by ambiguous characters (3, 9, 10, and 26 in our character list). Even the most convincing synapomorphy (a posteriorly expanded third hypural, leaving no gap between hypurals 2 and 4) also occurs in some clupeiforms not included in our analysis. For all these reasons the phylogenetic hypothesis presented here is considered tentative, as it reflects current uncertainties concerning paraclupeine relationships.

Two interesting paleobiogeographical puzzles involving China have emerged from this work. First, an apparent sister-group relationship has emerged between †*Paraclupea* and Early Cretaceous paraclupeines of western Gondwanan. Second, the presence of very similar †*Diplomystus* fossils in China and North America during the Eocene is curious. According to our analysis, paraclupeines and †*Diplomystus* are closely related (as members of the family †Paraclupeidae), but their respective distribution patterns are fundamentally different and may be the result of quite unrelated biogeographic histories. In both cases the fossil record is undoubtedly incomplete, and the known distributions of these forms may be so strongly biased as to make them biogeographically unintelligible. We restrict our remarks to a few salient points that may be worthy of further investigation.

BIOGEOGRAPHIC OBSERVATIONS. All the genera included here within the †Paraclupeinae (†*Ellimmichthys*, †*Ellimma*, †*Paraclupea*, and perhaps †*Scutatospinosus*) are Early Cretaceous in age. †*Ellimmichthys* and †*Ellimma* both occur in Brazil, but †*Ellimmichthys* is also known from Africa and Mexico. The two better known species of †*Ellimmichthys* are †*E. longicostatus* (Hauterivian–Barremian, Marfim Formation, Recôncavo Basin, Brazil) and †*E. goodi* (late Aptian–Albian, West Africa). The genus †*Ellimma* contains three nominal species, all from Brazil: †*E. branneri* and †*E. riacensis* (considered synonymous; Schaeffer, 1947; Grande, 1985a) from the late Aptian (Muribeca Formation, Sergipe Basin; Jordan, 1910); and †*E. cruzi* from the Aptian–early Albian (Cabo Formation, Cabo Basin; Silva Santos, 1990; previously identified as †*Ellimmichthys* by Costa et al., 1979). The undescribed Albian species of †*Ellimmichthys* from Mexico mentioned by Chang and Grande (1997) represents a western Tethyan (Caribbean) rather than Gondwanan occurrence, and is the only marine paraclupeine record. Another double-armored clupeomorph, †*Scutatospinosus itapagipensis*, occurs along with †*Ellimma branneri* in the Marfim Formation of Brazil (Silva Santos and Correa, 1985).

Today there is little doubt that the margins of Brazil and West Africa were contiguous during the Early Cretaceous (Pitman et al., 1993). The earliest record of †*Ellimmichthys* (and consequently the minimum postulated age of divergence between †*Ellimma* and †*Ellimmichthys*) is Hauterivian–Barremian, which predates the formation of an equatorial seaway by a considerable margin, although

†*Ellimmichthys goodi* from Africa and all records of †*Ellimma* are Aptian or younger (approximately contemporary with permanent emplacement of the seaway in the late Aptian; Maisey, 2000). All Gondwanan paraclupeines are from strata deposited within rift basins that were involved in the final tectonic separation of Africa and South America. At that time these basins were intracontinental, but subsequent rifting, crustal extension, and drifting transformed them into parts of the new continental margins. Their distribution pattern differs from those of some other Early Cretaceous fishes from western Gondwana, such as †*Mawsonia* and †*Calamopleurus*, which occur more widely across interior localities of Africa and Brazil (including nonrift settings), although these occurrences probably also represent former regions of endemism which were disrupted by formation of the Equatorial Atlantic seaway (Maisey, 2000).

The habitats and history of Gondwanan paraclupeine fishes were undoubtedly affected by the early (predrift) phases of these momentous tectonic processes. The distribution of Gondwanan †*Ellimmichthys* (and †*Scutatuspinosus*?) may reflect vicariant isolation of lacustrine populations along the tectonically active Recôncavo-Tucano-Jatobá and Gabon-Sergipe-Alagoas (GSA) rift trends (Maisey, 2000), and †*Ellimma* may be an endemic South American genus which perhaps evolved as a result of vicariant isolation within lakes of the GSA trend (Sergipe and Cabo basins). Albian occurrences of †*Ellimmichthys* are restricted to freshwater deposits within African marginal rift basins, but have not been documented from the marine strata overlying them. The genus has nevertheless been identified in marine sediments from Mexico, suggesting that a salt-tolerant form reached western (Caribbean) Tethys by the Albian–Cenomanian.

The distribution of †*Paraclupea* is a biogeographic conundrum (Chang and Chow, 1986; Chang and Chen, 2000). †*Paraclupea* is not known from any Gondwanan locality; †*P. chetungensis* is found in freshwater deposits near the western Pacific coast of China, but an Early Cretaceous freshwater paraclupeid from Japan (described as †*Diplomystus*; Uyeno, 1979; Uyeno and Yabumoto, 1980; Yabumoto, 1994) is rather similar to the Chinese form and may extend the range of †*Paraclupea*. These discoveries considerably expand the distribution of paraclupeines beyond western Gondwana and nearby western Tethys, far into eastern Asia. At this stage we can only speculate about the overall paraclupeine distribution pattern in the Cretaceous.

There is little geologic evidence to support an Early Cretaceous nonmarine paleogeographic connection between the eastern Asiatic margin and western Gondwana that would account for the observed distribution of paraclupeine fishes. We could plead for more widespread distribution and earlier occurrences of freshwater paraclupeine than is presently realized, especially since the †*Diplomystus* + †*Armigatus* clade represents the sister group to paraclupeines and is presumably of equal antiquity (in which case there should be relatives of that clade in the Barremian–Hauterivian). Another possibility is that paraclupeines may have marine origins and their distribution may reflect a largely unknown marine history. Unfortunately, both scenarios involve sweeping ad hoc assumptions, for example that the remains of a widespread fauna are still to be found elsewhere, or that their traces in other areas have been obliterated by later geological events.

†*Diplomystus shengliensis* from Bohai Gulf and †*D. dentatus* from Green River are morphologically so similar that there is little doubt they represent closely related sister species. Interestingly, besides †*Diplomystus*, four other genera of fishes (†*Eohiodon*, †*Knightia*, †*Amyzon*, and *Esox*) supposedly are shared by the Green River and Bohai Gulf faunas (Chang and Chow, 1986; Chang and Zhou, 1993, 2002; Chang et al., 2001), and several other lineages from the Bohai Gulf deposits are also represented in the Green River ichthyofaunas (e.g., ‘‘Dasyatidae’’, Amiidae). As pointed out by Grande and Bemis (1998: 337), the Chinese amiid is still inadequately known and cannot yet be assigned either to *Amia* or †*Cyclurus*, although it is almost certainly an amiine. †*Diplomystus*, †*Eohiodon*, †*Knightia*, †*Amyzon* and *Esox* have an Eocene transpacific distribution pattern, but amiines and dasyatids are more broadly distributed.

Interestingly, similar faunal distribution patterns have been noticed among Eocene terrestrial vertebrates of Asia and North America. These have been used to suggest that a land bridge existed between these areas in the vicinity of the Bering Straits, permitting mammals and other tetrapods to pass freely between these regions (Russell and Zhai, 1987). McKenna (1975, 1980, 1983, 1984) has also proposed that arctic connections between the continents have played a significant role in such dispersals.

Grande (1985b, 1989, 1994) noted this repeating pattern of area relationship in the early Tertiary between western North America and east Asia, based on the phylogenetic relationships of teleosts from Green River and the west Pacific region (including China, Indonesia, and Australia). He characterized this distribution as a ''transpacific'' pattern that could be explained by the Pacifica hypothesis (Grande, 1994). While we do not question these observations, note that much of the similarity in ichthyofaunas is restricted to the Eocene fossil assemblages of Bohai Gulf and Green River, whereas other areas on the western side of the Pacific share far fewer taxa with Green River (known examples include osteoglossids of Australia and Indonesia; osteoglossids and catostomids of South China; amiines and catostomids of inland North China; amiines, hiodontids and catostomids of East Khazakstan).

More recent geophysical and geochemical studies (some still in progress) have raised a startling and radically different alternative to the Pacifica hypothesis. There is mounting evidence that, for a brief period (approximately 2 million years, during the late Paleocene and early Eocene), the Arctic Ocean was almost completely landlocked, with a terrestrial corridor between North America, Iceland, and Europe and another through Beringia, and a single outlet to the sea via the Turgai Strait (McKenna, 1998). With several major river systems draining northward into the Arctic, net runoff/evaporation may have caused dramatic lowering in salinity, sufficient perhaps to allow freshwater fishes to move unimpeded by a saltwater barrier between Asia and North America.

Such a rapid dispersal event could certainly account for the sister-group relationship between †*Diplomystus* from China and North America. It would also offer a partial explanation for some Eocene fish distribution patterns, and perhaps even the holarctic distribution of some modern fishes (e.g., paddlefishes). †*Eohiodon falcatus* occurs in the Green River Formation, and hiodontids are represented in eastern China and East Khazakstan (Central Asia). Eocene catostomids also occur in both these areas and are widely spread in the vast plains area of East Asia, from Mongolia in the north to Guangdong Province at the very south of China (Chang et al., 2001). The osteoglossid †*Phareodus* occurs in the Green River Formation, as well as in Australia (†*Phareodus queenslandicus*; Hills, 1934; Li, 1994). Eocene osteoglossids are found in Sichuan Province (†*Sinoglossus*, Su, 1986) and Hubei provinces, South China (Song, in prep.) and Eocene or Oligocene of Indonesia (†*Musperia radiata*; Sanders, 1934). Eocene hiodontids, catostomids, and osteoglossids are also reported from British Columbia (Wilson, 1977). The wide boreal distribution of amiines during the Eocene (including North America, northern China, East Khazakstan, and Europe) is remarkably similar to the pan-Arctic distribution of many riparian and terrestrial vertebrates during the Late Cretaceous and early Cenozoic (Estes and Hutchison, 1980). Freshwater Arctic connections between the northern continents may therefore have played a significant role in amiine dispersal.

On the other hand, in the vast area between the Bohai Gulf and Green River occurrences there are several other Eocene freshwater deposits with abundant fossil fishes, yet these ichthyofaunas do not yet include dasyatids, †*Diplomystus*, or clupeids (e.g., middle Eocene of Washington State, U.S., and British Columbia, Canada; inland areas of South China and East Khazakstan; Wilson, 1977, 1978; Tang, 1959; Liu et al., 1962; Wang et al., 1981; Sytchevskaya, 1986). In addition, some taxa occur in one region but not the other (e.g., Eocene lepisosteids in Green River and western Canada but not Asia; Eocene cyprinids in Bohai Gulf, South China, and East Khazakstan but not in North America or Europe). Such absences from the fossil record may reflect a preservational bias against certain taxa in one area or the other, or it could indicate a real absence, suggesting that some taxa did not participate in any holarctic dispersal event during the late Paleocene and early Eocene.

Quite probably, there is no single factor responsible for the Eocene ''transpacific'' distribution pattern. A broad connection between Asia and North America in the Bering Strait area could have played a role, as could temporary desalination of the Arctic Ocean. Both hypotheses provide equally plausible biogeographic alternatives to the Pacifica model and are certainly more in accordance with geological data than the latter. At present the only common link between the Early Cretaceous distribution of paraclupeines and the Eocene distribution of †*Diplomystus* is China, for only there have both taxa been discovered.

CONCLUSIONS

1. No derived characters are uniquely shared by †*Ellimma branneri* and the Clupeiformes. Thus, while modern Clupeiformes may be monophyletic, the inclusion of extinct forms such as †*Ellimma* and other †paraclupeines may potentially create a paraphyletic assemblage.

2. One derived character (lateral expansion of dorsal scute ''wings'' which give scutes a subrectangular shape) is shared by †*Ellimma* and other members of the family †Paraclupeidae Chang and Chou (1977); = †Ellimmichthyidae Grande (1982a).

3. The Paraclupeidae is divided into two subfamilies: Paraclupeinae Chang and Grande (1997) and an unnamed sistergroup. Paraclupeids are known from the Lower Cretaceous–middle Eocene.

4. The Paraclupeinae include †*Paraclupea*, †*Ellimmichthys*, and †*Ellimma*. These taxa are united by strongly sculptured skull roofing bones, with ridges radiating from the growth center, and by dorsal scute ornament of prominent ridges. †*Scutatuspinosus* may also belong in the †Paraclupeinae. Paraclupeine fishes are at present only recognized from the Lower Cretaceous (Hauterivian–Albian).

5. No biogeographical hypothesis satisfactorily explains the known distribution of nonmarine paraclupeine fishes in the Cretaceous. Either a substantial portion of their nonmarine fossil record is missing (as is evidenced by the recent discovery of a possible paraclupeine *Ezkutuberezi* from Spain; Poyato-Ariza et al., 2000), or their distribution involved marine dispersal.

6. A ''freshwater Arctic Ocean'' hypothesis (supported by several lines of geological evidence) is preferred over the ''Pacifica'' hypothesis (which lacks empirical support from geological data) to account for Eocene (and younger) trans-Pacific distribution patterns of nonmarine fishes (the hypothesis may also explain distribution patterns among certain Recent fishes).

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REFERENCES

Arratia, G. 1996. Reassessment of the phylogenetic relationships of certain Jurassic teleosts and their implications on teleostean phylogeny. *In* G. Arratia and G. Viohl (editors), Mesozoic fishes—systematics and paleoecology: 219–242. München: Verlag Dr. F. Pfeil.

Chang, M.M., and Y.Y. Chen. 2000. Late Mesozoic and Tertiary ichthyofaunas from China and some puzzling patterns of distribution. Vertebrata PalAsiatica 38(3): 161–175.

Chang, M.M., and J.J. Chou. 1977. On Late Mesozoic fossil fishes from Zhejiang Province, China. Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica Memoirs 12: 1–60. [in Chinese with English summary]

Chang, M.M., and J.J. Chou. 1978. On the fossil fishes in Mesozoic and Cenozoic oil-bearing strata from east China and their sedimentary environment. Vertebrata PalAsiatica 16(4): 229–237. [in Chinese]

Chang, M.M., and J.J. Chou. 1986. Stratigraphic and geographic distributions of the late Mesozoic and Cenozoic fishes of China. Indo-Pacific fish biology. *In* T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (editors), Proceedings of the Second International Conference of Indo-Pacific Fishes: 529–539. Tokyo: Ichthyological Society of Japan.

Chang, M.M., and L. Grande. 1997. Redesciption of †*Paraclupea chetungensis*, an early clupeomorph from the Lower Cretaceous of southeastern China. Fieldiana Geology New Series, (37) 1489: 1–19.

Chang, M.M., D.S. Miao, Y.Y. Chen, J.J. Zhou, and P.F. Chen. 2001. Suckers (fish, Catostomidae) from the Eocene of China account for the family's current disjunct distributions. Science in China 31: 577–586.

Chang, M.M., and J.J. Zhou. 1993. A brief survey of the Chinese Eocene ichthyofauna. Darmstädter Beiträge zur Naturgeschichte Heft 2: 157–162.

Chang, M.M., and J.J. Zhou. 2002. First discovery of *Esox* (Teleostei) in China. Vertebrata PalAsiatica 39(2): 81–96. [in Chinese with English summary]

Cope, E.D. 1874. Supplementary notices of fishes from the freshwater Tertiaries of the Rocky Mountains. Bulletin of the U.S. Geological and Geographical Survey of the Territories 1(2): 49–51.

Cope, E.D. 1877. A contribution to the knowledge of the ichthyological fauna of the Green River shales. Bulletin of United States Geological and Geographical Survey 3(34): 807–819.

Cope, E.D. 1886. A contribution to the vertebrate paleontology of Brazil. Proceedings of the American Philosophical Society 23(121): 3–4.

Costa, A.C., V.A. Mendes, and D. E.G. Rocha. 1979. Sintese preliminar da Geologia do Projecto Extremo Nordeste do Brasil. Boletim do Núcleo do NE Sociedade Brasileira de Geologia 7: 421–440.

Eastman, C.R. 1912. Tertiary fish-remains from Spanish Guinea in West Africa. Annals of Carnegie Museum 8(2): 370–378.

Estes, R., and J.H. Hutchison. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology 30: 325–347.

Feijó, F.J. 1994. Bacias de Sergipe e Alagoas. Boletim Geociências da PETROBRÁS, Rio de Janeiro 8(1): 149–161.

Forey, P.L. 1975. A fossil clupeomorph fish from the Albian of the Northwest Territories of Canada, with notes on cladistic relationships of clupeomorphs. Journal of Zoology (London) 175: 151–177.

Gayet, M. 1989. Note préliminaire sur le matérial paléoichthyologique éocrétacique du Rio Benito (sud de Bata, Guinée Équatoriale). Bulletin du Muséum national d'Histoire Naturelle, Section C, Sciences de la Terre Paleontologie Geologie Mineralogie 11(1): 21–31.

Grande, L. 1982a. A revision of the fossil genus †*Diplomystus*, with comments on the interrelationships of clupeomorph fishes. American Museum Novitates 2728: 1–34.

Grande, L. 1982b. A revision of the fossil genus †*Knightia*, with a description of a new genus from the Green River Formation (Teleostei, Clupeidae). American Museum Novitates 2731: 1–22.

Grande, L. 1985a. Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. Bulletin of the American Museum of Natural History 181(2): 231–372.

Grande, L. 1985b. The use of paleontology in systematics and biogeography, and a time control refinement for historical biogeography. Paleobiology 11(2): 234–243.

Grande, L. 1989. The Eocene Green River Lake system, Fossil Lake, and the history of the North American fish fauna. *In* J. Flynn (editor), Mesozoic/Cenozoic vertebrate paleontology: classic localities, contemporary approaches. 28th International Geological Congress Fieldtrip Guidebook T 322: 18–28. Washington DC: American Geophysical Union.

Grande, L. 1994. Repeating patterns in nature, predictability, and ‘‘impact’’ in science. *In* L. Grande and O. Rieppel (editors), Interpreting the hierarchy of nature: from systematic patterns to evolutionary process theories: 61–84. New York: Academic Press.

Grande, L., and W.E. Bemis. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Society of Vertebrate Paleontology Memoir 4: i–x, 1–690; Supplement to Journal of Vertebrate Paleontology 18(1).

Greenwood, P.H., D.E. Rosen, S.H. Weitsman, and G.S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131: 339–456.

Hills, E.S. 1934. Tertiary fresh water fishes from southern Queensland. Memoirs of the Queensland Museum 10: 157–174.

Jordan, D.S. 1907. The fossil fishes of California, with supplementary notes on other species of extinct fishes. University of California Publications in Geological Sciences 5: 95–144.

Jordan, D.S. 1910. Description of a collection of fossil fishes from the bituminous shales at Riaco Doce, State of Alagoas, Brazil. Annals of Carnegie Museum 7(1): 23–34.

Jordan, D.S. 1913. *Ellimma*, a genus of fossil herrings. Proceedings of the Biological Society of Washington 26: 79.

Li, G.Q. 1994. Systematic position of the Australian fossil osteoglossid fish †*Phareodus* (=*Phareoides*) *queenslandicus* Hills. Memoirs of the Queensland Museum 37(1): 287–300.

Liu, T.S., H.T. Liu, and X. Tang. 1962. A new pecoid fish from South China. Vertebrata PalAsiatica 6: 121–127. [in Chinese with English summary]

Maisey, J.G. 1993. A new clupeomorph fish from the Santana Formation (Albian) of NE Brazil. American Museum Novitates 3076: 1–15.

Maisey, J.G. 2000. Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretaceous Research 21: 281–314.

McKenna, M.C. 1975. Fossil mammals and early Eocene North Atlantic land continuity. Annals of Missouri Botanical Garden 62: 335–353.

McKenna, M.C. 1980. Eocene paleolatitude, climate, and mammals of Ellemere Island. Palaeogeography, Palaeoclimatology, Palaeoecology 30: 349–362.

McKenna, M.C. 1983. Cenozoic paleogeography of North Atlantic land bridges. *In* M.H.P. Bott, S. Saxov, M. Talwani, and J. Thiede (editors), Structure and development of the Greenland-Scotland Ridge: 351–399. New York: Plenum.

McKenna, M.C. 1984. Holarctic landmass rearrangement, cosmic events, and Cenozoic terrastrial organisms. Annals of the Missouri Botanical Garden 70: 459–489.

McKenna, M.C. 1998. Semi-isolation of the Arctic Ocean in the late Thanetian to earliest Ypresian time. Geological Society of America Abstracts with Programs 30(7): 118.

Nelson, G.J. 1967. Gill arches of teleostean fishes of the family Clupeidae. Copeia 1967: 389–399.

Nelson, G.J. 1970. The hyobranchial apparatus of teleostean fishes of the families Engraulidae and Chirocentridae. American Museum Novitates 2410: 1–30.

Nelson, G.J. 1973. Relatiohships of clupeomorphs, with remarks on the structure of the lower jaw in fishes. *In* P.H. Greenwood, R.S. Miles, and C. Patterson (editors), Interrelationships of fishes. Zoological Journal of Linnean Society 53(Suppl. 1): 333–349.

Patterson, C. 1967. Are the teleosts a polyphyletic group? Colloques Internationaux du Centre National de la Recherche Scientifique 163: 93–109.

Patterson, C. 1970. A clupeomorph fish from the Gault (Lower Cretaceous). Zoological Journal of Linnean Society 49(3): 161–182.

Patterson, C., and D.E. Rosen. 1977. A review of ichthyodectiform and other Mesozoic teleost fishes, and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158(2): 81–172.

Pitman, W.C., S. Cande, J. LaBreque, and J. Pindell. 1993. Fragmentation of Gondwana: the separation of Africa from South America. *In* P. Goldblatt (editor), Biological relationships between Africa and South America: 15–34. New Haven, CT: Yale University Press.

Poyato-Ariza, F.J., M.A. López-Horgue, and F. Garcia-Garmilla. 2000. A new early Cretaceous clupeomorph fish from the Arratia Valley, Basque County, Spain. Cretaceous Research 21: 573–585.

Russell, D.E., and R.J. Zhai. 1987. The paleogene of Asia: mammals and stratigraphy. Memoires du Muséum National d'Histoire Naturelle, Serie C, Sciences de la Terre, 52: 1–488.

Sanders, M. 1934. Die fossilen Fische der altertiären Süsswasserablagerungen aus Mittel-Sumatra. Verhandelingen van het Geologisch-Mijnbouwkundig Genootschap voor Nederland en Koloniën Geologische Serie 11(1): 1–143.

Schaeffer, B. 1947. Cretaceous and Tertiary actinopterygian fishes from Brazil. Bulletin of the American Museum of Natural History 89(1): 1–40.

Scudder, S.H. 1902. On the United States Orthoptera which have been referred to the genus *Tridactylus*. Psyche, A Journal of Entomology. 9: 308–310.

Signeux, J. 1951. Notes paléoichthyologiques. V. *Diplomystus dubertreti*, une nouvelle espèce du Sénonien du Liban. Bulletin du Muséum National d'Histoire Naturelle 23(2): 692–693.

Silva Santos, R.Da. 1990. Clupeiformes e Gonorhynchiformes de Cretáceo Inferior (Aptiano) da Formação Cabo, Nordeste do Brasil. Anais da Academia brasileira de Ciências 62(3): 261–268.

Silva Santos, R.Da., and V.L.S. Correa. 1985. Contribução ao conhecimento da paleoictiofáunula do Cretáceo no Brasil. *In* D. De A. Campos, C.S. Ferreira, I.M. Brito, and C.F. Viana (editors), Coletânea de Trabalhos Paleontológicos Série Geologia 27(2): 169–174. Rio de Janeiro: Ministério das Minas e Energia–Departamento Nacional de Produção Mineral.

Su, D.Z. 1986. The discovery of a fossil osteoglossid fish in China. Vertebrata PalAsiatica 24(1): 10–19. [in Chinese with English summary]

Sun, A.L. 1956. *Paraclupea*—a genus of double-armored herrings from Chekiang. Acta Palaeontologica Sinica 4: 413–418.

Swofford, D.L. 2000. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland, MA: Sinauer Associates.

Tang, X. 1959. A new fossil fish from Linli, Hunan. Vertebrata PalAsiatica 1: 211–213. [in Chinese]

Taverne, 1975. A propos du genre fossile *Knightia* Jordan, D.S., 1907, Clupéidé à double carène de l'Eocène des Etats-Unis et du Brésil. Biologisch Jaarboek Dodonaea 43: 246–251.

Uyeno, T. 1979. Early Cretaceous freshwater fishes from Northern Kyushu, Japan. 1. Description of two new species of the clupeid genus *Diplomystus*. Bulletin of the Kitakyushu Museum of Natural History 1: 11–24.

Uyeno, T., and Y. Yabumoto. 1980. Early Cretaceous freshwater fishes from northern Kyushu, Japan. Bulletin of the Kitakyushu Museum of Natural History 2: 25–31.

Wang, J.K., G.F. Li, and J.S. Wang. 1981. The Early Tertiary fossil fishes from Sanshui and its adjacent basin, Guangdong. Palaeontologia Sinica 160; New Series C 22: 1–90. [in Chinese with English summary]

Wilson, M.V.H. 1977. Middle Eocene Freshwater fishes from British Columbia. Royal Ontario Museum Life Sciences Contributions 113: 1–61.

Wilson, M.V.H. 1978. *Eohiodon woodruffi* n. sp. (Teleostei, Hiodontidae), from the Middle Eocene Klondike Mountain Formation near Republic, Washington. Canadian Journal of Earth Sciences 15(5): 679–686.

Woodward, A.S. 1895. On two deep-bodied species of the clupeoid genus *Diplomystus*. Annals and Magazine of Natural History ser. 6, 15: 3.

Woodward, A.S. 1901. Catalogue of fossil fishes in the British Museum (Natural History). Volume 4: 696 pp. British Museum (Natural History), London.

Yabumoto, Y. 1994. Early Cretaceous freshwater fish fauna in Kyushu, Japan. Bulletin of the Kitakyushu Museum of Natural History 13: 107–254.

Zhang, M.M., J.J. Zhou and D.R. Qing. 1985. Tertiary fish fauna from coastal region of Bohai Sea. Academia Sinica Institute of Vertebrate Paleontology and Paleoanthropology Memoirs 17: 1–60.

APPENDIX 1

CHARACTER LIST

1. Recessus lateralis absent (0), present (1).
2. Otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase, absent (0), present (1).
3. Preepiotic fossa absent (0), present (1).
4. Parietals meeting at midline (0), separated completely by supraoccipital (1).
5. Frontal fontanelle absent (0), present (1).
6. Supratemporal commissure not passing through parietals or parietals and supraoccipital (0), passing through these bones (1).
7. Anterodorsal process of hyomandibular absent (0), present (1).
8. Supramaxillae, two (0), less than two (1).
9. Teeth on entopterygoid fine or absent (0), strong (1).
10. Tooth patch on posterior part of parasphenoid present (0), absent (1).
11. Basipterygoid process present (0), absent (1).
12. Bericiform foramen in anterior ceratohyal present (0), absent (1).
13. Angular fused with retroarticular (0), with articular (1).
14. Dorsal scutes, absent (0), scute series incomplete (1) or complete (2).
15. Ornamentation on dorsal scutes, absent (0), present (1).
16. Abdominal scutes absent (0), present (1).
17. Caudal scutes present (0), absent (1).
18. First ural centrum about equal in size with first preural centrum (0), much smaller (1).
19. Neural spine of first preural centrum short or lacking (0), long (1).
20. Parhypural not fused to first preural centrum (0), fused to first preural centrum (1).
21. Number of hypurals: six or more (0), less than six (1).
22. Second hypural not fused with first ural centrum (0), fused with first ural centrum (1).
23. Number of epurals: three (0), less than three (1).
24. First uroneural independent (0), fused with first preural (1).
25. First uroneural extending forward to second preural centrum (0), failed to extend to second preural centrum (1).
26. Third hypural not expanded posteriorly, leaving a gap or notch between second and third hypurals (0), expanded posteriorly, leaving no gap or notch between second and third hypurals (1).

27. First hypural articulating with first ural centrum (0), not articulating with (1).
28. Semicircular to almost vertical fine surface ridges (circuli) on scales absent (0), present (1).
29. Lateral line scales present (0), absent (1).
30. Neural spines of a few posterior preurals without laminar outgrowth (0), with laminar outgrowth and leaflike (1).

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