FIELDIANA

Geology

NEW SERIES, NO. 37

Redescription of †*Paraclupea chetungensis*, an Early Clupeomorph from the Lower Cretaceous of Southeastern China

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DEC 31 1997
PUBLICATION 1489

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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Redescription of †*Paraclupea chetungensis*, an Early Clupeomorph from the Lower Cretaceous of Southeastern China

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**Accepted October 22, 1996
Published December 31, 1997
Publication 1489**

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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Redescription of †*Paraclupea chetungensis*, an Early Clupeomorph from the Lower Cretaceous of Southeastern China

Mee-man Chang Lance Grande

Abstract

A reexamination and redescription of the Early Cretaceous clupeomorph †*Paraclupea chetungensis* from southeastern China based on newly prepared specimens reveals a number of characters it shares with †*Ellimmichthys longicostatus* (Cope, 1886) from eastern Brazil and †*Ellimmichthys goodi* (Eastman, 1912) from West Africa (Equatorial Guinea) but not with †*Diplomystus* (from western North America, eastern China, and the Middle East). These characters are summarized in a differential diagnosis of †Paraclupeinae, a new subfamily within †Paraclupeidae Chang and Chou, 1977. Revised diagnoses for †Paraclupeidae and †*Paraclupea* are also provided. Among the three †paraclupeine species revised here, †*Ellimmichthys longicostatus* and †*Ellimmichthys goodi* share more putatively derived characters with each other than either does with †*Paraclupea chetungensis*, thus indicating the monophyly of †*Ellimmichthys*. Because of the close relationship between †*Paraclupea* and †*Ellimmichthys*, we find the family name †Ellimmichthyidae Grande, 1982 to be a subjective junior synonym of †Paraclupeidae Chang and Chou, 1977.

Introduction

The primitive clupeomorph †*Paraclupea chetungensis* is known from the Pacific coast of eastern China in Lower Cretaceous freshwater deposits of Zhejiang and Fujian provinces (Fig. 1; Chang & Chou, 1977; Zhang & Zhou, 1978; Chang & Chow, 1986). The species was originally reported and named by Du (1950) and was assigned by him to Clupeidae, together with †*Mesoclupea showchangensis* Ping and Yen (1933), another Lower Cretaceous teleost from the same area. †*Mesoclupea* was later reassigned to †Ichthyodectiformes by a number of authors (e.g., Bardack, 1965; Patterson & Rosen, 1977).

The initial assignment of †*Paraclupea* to Clupeidae was unwarranted, based solely on primitive clupeomorph characters (i.e., characters common to most or all clupeomorphs), such as the jaw possessing fine teeth and the presence of abdominal scutes. Du (1950) provided no diagnosis or figures in his description, and there was no ho-

lotype designated. Thus his name was unavailable, according to the rules of zoological nomenclature (International Commission on Zoological Nomenclature, 1985). Later, Sun (1956) provided a description of specimens of the same species collected from the same area. In Sun's description she reported the loss of what she referred to as Du's "type specimen" of †*P. chetungensis* (not actually designated in Du's paper) and provided a picture of it (Sun, 1956, pl. 1.4; not shown in Du, 1950). Sun (1956) also designated her own type specimen (IVPP V816, illustrated here in Fig. 2) and used the generic and species name given by Du. She considered her specimen to be a neotype for the species, but we consider it the holotype, because Du (1950) did not fulfill the requirements of availability for the name (e.g., International Commission on Zoological Nomenclature, 1985). Consequently Sun (1956) is the author of the available use of the name, and her designated type is the holotype rather than a neotype.

Based on the presence of both dorsal and ab-

FIG. 1. A map of eastern China showing the localities of Anxi and Linhai (indicated with stars).

dominal scutes, Sun (1956) noted that †*Paraclupea* was a “double-armed herring” (*sensu* Schaeffer, 1947). She described the dorsal scutes as “broadly cordate in shape, a little wider than long” (Sun, 1956, p. 417). Based on this character she suggested that †*Paraclupea* belonged to the “*Diplomystus* group” (*sensu* Schaeffer’s, 1947, nonmonophyletic use of the term), very close to †“*Diplomystus*” *brevissimus* (= †*Armigatus brevissimus*, *sensu* Grande 1982), †“*D.*” *longicostatus* (= †*Ellimmichthys longicostatus*, *sensu* Grande 1982) and possibly †“*D.*” *goodi* (= †*Ellimmichthys goodi*, see below).

Following the suggestions of Schaeffer (1947) that “in many respects it appears desirable to es-

tablish a separate family for the double-armed herrings” (p. 24) and of Patterson (1967), “*Diplomystus brevissimus* . . . can hardly be included in the Clupeidae” (p. 104), Chang and Chou (1977) erected a new family †Paraclupeidae to include all “double-armed herrings”—†*Paraclupea*, †*Diplomystus* (some species now in †*Ellimmichthys* and †*Armigatus*), †*Knightia*, and the three Recent genera *Hyperlophus*, *Potamolosa*, and *Ethmidium*. The characters Chang and Chou (1977) used to diagnose the new family were mostly plesiomorphic and not diagnostic for the family (e.g., presence of dorsal scutes, presence of basipterygoid process of parasphenoid, parietals not completely separated from each other by

FIG. 2. †*Paraclupea chetungensis* Sun, 1956, holotype. Specimen is IVPP V816, SL = 55 mm. From freshwater deposits of the Lower Cretaceous Chawan Formation of eastern China.

supraoccipital, posterior extension of supraorbital sensory canal into parietal and absence of its junction with infraorbital sensory canal, and first uro-neural extended anterior to ural centra to over the first two preural centra but not fused with them). Also, some of these characters do not occur in the Recent genera or †*Knightia*. Thus, this group, as defined by Chang and Chou (1977), was non-monophyletic.

In his revision of †*Diplomystus*, Grande (1982) referred all species of †*Diplomystus* from the Green River Formation to †*D. dentatus*, justified Jordan's (1919) removal of †*D. longicostatus* from the genus †*Diplomystus* into the new genus †*Ellimmichthys*, and removed a number of other nominal species from †*Diplomystus* for various reasons (e.g., some of the species removed were clupeids, while others were Clupeomorpha incertae sedis). Grande (1982, 1985) also placed †*D. brevissimus* into the new genus †*Armigatus*, because there were no synapomorphic characters to tie it to †*Diplomystus*. The remaining species, †*D. dentatus*, †*D. birdi*, †*D. dubertreti*, were then found to form a monophyletic group, to which the Chinese species †*D. shengliensis* was later added by Zhang et al. (1985) and Grande (1985, p. 314, referred to as "†*Diplomystus* n. sp. A"). Grande (1982) also found †*Diplomystus* to be the sister group of †*Ellimmichthys* and established a new family †*Ellimmichthyidae* to contain the two genera. (*Diplomystidae* could not be used for this group because it is preoccupied by a South American catfish family with the type genus *Diplomystes*.) †*Ellimmichthyidae* was weakly diagnosed by a single character: the presence of subrectangular

dorsal scutes. Grande (1982, 1985) also demonstrated that the "double-armed herrings" (see above) were a non-monophyletic group, because †*Knightia*, *Hyperlophus*, *Potamolosa*, and *Ethmidium* all clearly belong to the Clupeidae, while †*Diplomystus* is not even a clupeiform. Consequently, the "†*Paraclupeidae*," as initially defined by Chang and Chou (1977), were not a natural group.

Zhang and Zhou (1978) and Chang and Chow (1986) noted a resemblance between the Early Cretaceous fish fauna from southeastern China (which contains †*P. chetungensis*) and the Early Cretaceous fish fauna from Brazil (which contains †*E. longicostatus*). Besides †*Paraclupea*, the Early Cretaceous fish fauna from southeastern China also includes †*Neolepidotus* (†*Semionotidae*), †*Mesoclupea* (possible †*ichthyodectiform*), †*Huashia* (possible Chanidae or gonorynchiform), and a few other taxa probably comparable to those from Brazil (Chang & Chow, 1986). However, before we can draw more definitive conclusions on faunal comparisons and biogeography, it is necessary to review the forms previously reported from southeastern China to clarify their morphology and taxonomic identity and to better understand the phylogenetic interrelationships of the groups to which they belong. We choose †*P. chetungensis* as the first form to be reviewed for this purpose. Because most previous descriptions of these Chinese fossil fishes are published in Chinese, it is worthwhile to make this information more accessible by providing a relatively complete description of the material in English. After restudying †*P. chetungensis* and comparing it

with †*E. longicostatus* and †*E. goodi* we find that the genus †*Paraclupea* forms the sister group to †*Ellimmichthys*. It is clear that a more comprehensive phylogenetic study of all primitive clupeomorph fishes is still needed. Our preliminary work suggests the past existence of a widespread monophyletic group including Lower Cretaceous forms from China and possibly Japan (i.e., †*Paraclupea*), Africa, South America, and Mexico (i.e., †*Ellimmichthys*, see text). If †*Paraclupea* belongs in the same family as †*Ellimmichthys* and †*Diplomystus*, then †*Ellimmichthyidae* Grande, 1982 and †*Paraclupeidae* Chang and Chou, 1977 are synonyms, and †*Paraclupeidae* has priority. Thus we adopt the family name †*Paraclupeidae* in the following description.

Anatomical Abbreviations

AA	= angulo-articular
AFN	= anterior frontal fontanelle
CS	= caudal scute
D	= dentary
DFR	= dorsal fin rays
DS	= dorsal scute
ECPT	= ectopterygoid
ENPT	= entopterygoid
ENPT.T	= entopterygoid teeth
EP	= epural
FR	= frontal
H	= hypural
HM	= hyomandibula
HS	= haemal spine
IOP	= interopercle
MPT	= metapterygoid
MX	= maxilla
NPU ₁	= neural arch of first preural centrum
NS	= neural spine
OP	= opercle
PA	= parietal
PD	= predorsal bones
PH	= parhypural
PMX	= premaxilla
POP	= preopercle
PR	= proximal radial
PT	= posttemporal
PU	= preural centrum
Q	= quadrate
R	= retroarticular
S	= symplectic
SC	= sclerotic bones
SMXA	= anterior supramaxilla
SMXP	= posterior supramaxilla

SOC	= supraoccipital
U	= ural centrum
UN	= uroneural
VT	= vertebra

† (a dagger) preceding a taxonomic name indicates that that taxon is extinct.

Institutional Abbreviations

AMNH	= American Museum of Natural History, New York
BMNH	= Department of Palaeontology, Natural History Museum, London
CMNH	= Carnegie Museum of Natural History, Pittsburgh, PA
FMNH	= Department of Geology, Field Museum of Natural History, Chicago, IL
IGSOF	= Institute of Geology, Shengli Oil Field, Dongying, Shandong Province, China (Collections)
IVPP	= Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
UNAM	= Instituto de Geología, Universidad Nacional Autónoma, México

Materials Examined

†*Paraclupeidae*

†*Paraclupea*

†*Paraclupea chetungensis* Sun, 1956. From Lower Cretaceous Chawan Formation, eastern China. Ten specimens (see materials listed in Systematics section). These fishes are thought to have been deposited in fresh water (Chang & Zhou, 1993).

†*Ellimmichthys*

†*Ellimmichthys longicostatus* (Cope, 1886). From Lower Cretaceous estuarine deposits of Bahia, Brazil. Three specimens, including two on AMNH 734 and one on BMNH P.7109. This is the type specimen for the genus.

†*Ellimmichthys goodi* (Eastman, 1912). From Lower Cretaceous deposits of the Cocobeach series of Spanish Guinea, West Africa. This formation is thought by some authors to be freshwater (Grekoff & Krömmelbein, 1967; Patterson, 1975). Five specimens, including FMNH UC2163, 2164; CMNH 5404, 38790; and AMNH 6146.

†*Ellimmichthys* sp. (undescribed). From Lower Cretaceous marine deposits of the Morelos Formation, Puebla, Mexico. Four specimens, including UNAM IGM4738 and FMNH PF13582 and 13585.

†*Diplomystus*

†*Diplomystus dentatus* Cope, 1877. From Lower Eocene freshwater deposits of the Green River Formation, Wyoming. Five specimens, including FMNH PF12504, 12917, 11793–11795. This is the type species of the genus.

†*Diplomystus shengliensis* Zhang, Zhou, and Qin, 1985. From Middle Eocene freshwater deposits of eastern China. Three specimens, IGSO 790001–790003.

†*Diplomystus birdi* Woodward, 1895. From Upper Cretaceous marine deposits of Hakel and Hajula, Lebanon. Five specimens, including FMNH PF13586–13592.

†*Diplomystus dubertreti* Signeux, 1951. From Upper Cretaceous marine deposits of Sahel Alma, Lebanon. One specimen, FMNH PF706.

Denticipitidae

Denticeps

Denticeps clupeoides Clausen, 1959. From a freshwater stream on the Dahomey–Nigerian border, Africa. Two cleared and double-stained specimens, including FMNH 96513 and AMNH 53082. This is the type and only species of this genus.

Pristigasteridae

Pellona

Pellona harroweri (Fowler, 1917). From freshwater, Rio de Janeiro, Brazil. Two cleared and double-stained specimens from lot AMNH 20759SW.

Clupeidae

Dorosoma

Dorosoma cepedianum (LeSueur, 1818). From a freshwater stream in Macystown, Illinois. One cleared and double-stained specimen from lot FMNH 48065.

Family *incertae sedis*

†*Armigatus*

†*Armigatus brevissimus* (Blainville, 1818). Upper Cretaceous marine deposits of Hakel, Lebanon. Five specimens, including FMNH PF13451–13456. This is the type species of this genus.

Methods

The specimens of †*P. chetungensis* preserved in argillaceous shales were prepared first with needles to remove the strongly weathered remains of bone in order to get clean impressions. Then black-colored latex peels were made from the impressions. The peels show much more detail than the specimens with fragments of bone. The black latex peels were coated with ammonium chloride to bring out the relief for the photographs used here. The specimens of †*D. dentatus* were prepared with needles and an air-abrasive machine.

Systematics

Cohort Clupeocephala Patterson and Rosen, 1977

Subcohort Clupeomorpha Greenwood et al., 1966

Order †*Ellimmichthyiformes* Grande, 1982

Family †*Paraclupeidae* Chang and Chou, 1977

[= *Diplomystidae* Patterson, 1970 (preoccupied),

= †*Ellimmichthyidae* Grande, 1982 (subjective junior synonym)]

GENERA CONTAINED IN FAMILY—†*Paraclupea*, †*Ellimmichthys*, and †*Diplomystus* (*sensu* Grande, 1985).

FAMILY DIAGNOSIS—A family of nonclupeiform clupeomorphs (*sensu* Grande, 1985) that differs from all other clupeomorphs by the presence of laterally expanded, subrectangular dorsal scutes, each bearing a median keel. At least some of the scutes have the keel extending posteriorly over the next scute in the form of a pointed spine.

This family is also distinguishable from Clupeiformes (*sensu* Grande, 1982, 1985) by several

TABLE 1. Comparison between †*Paraclupea chetungensis*, †*Ellimmichthys longicostatus*, and †*E. goodi*. This table is not meant to represent a phylogenetic data matrix but is instead a list of general comparisons to aid in the redescription of †*Paraclupea chetungensis*.

Features	† <i>Paraclupea chetungensis</i>	† <i>Ellimmichthys longicostatus</i>	† <i>E. goodi</i>
1. Locality	Early Cretaceous freshwater deposits of eastern China	Early Cretaceous estuarine deposits of Bahia, Brazil	Early Cretaceous freshwater deposits of West Africa
2. Maximum depth	At origin of dorsal fin	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i>
3. Body depth/standard length	43–48%	63%	52%
4. Dorsal outline	Obtuse angle at origin of dorsal fin (Fig. 3)	Sharp angle at origin of dorsal fin (BMNH P.7109 only) (Fig. 7a)	Prominent angle at origin of dorsal fin (Fig. 7b)
5. Ventral outline	Markedly convex (Fig. 3)	Extremely convex (Fig. 7a)	Extremely convex (Fig. 7b)
6. Skull roofing bones	Strongly sculptured with ridges	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i>
7. Anterior frontal fontanelle	Present	Unknown	Unknown
8. Parietals	Anterior parts meeting at midline	Not meeting at midline	Same as in † <i>Ellimmichthys longicostatus</i> (CMNH 5404)
9. Supraoccipital crest	Small and low	Same as in † <i>Paraclupea chetungensis</i>	Small and low (?)
10. Supraorbital sensory canal	Enclosed in crest	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i>
11. Supramaxillae	Showing fine, branching grooves on surface	Smooth	Smooth (CMNH 5404)
12. Entopterygoid teeth	Fine and numerous	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i>
13. Shape of dorsal scutes	Broader than long, with median keel; posterior margin not pectinate, nearly straight, with small median notch; keel of last 2–3 scutes protruding into stout spines	Same as in † <i>Paraclupea chetungensis</i> , with minor differences—as in having more extensive median emargination on posterior margin and keel of more scutes (last 4–5) protruding into stout spines	Same as in † <i>Ellimmichthys longicostatus</i>
14. Ornamentation of dorsal scutes	Posterior third or half covered with radiating ridges with secondary branching (feather-like)	Posterior bigger half covered with radiating ridges	Same as in † <i>Ellimmichthys longicostatus</i>
15. Number of dorsal scutes	18	12	12 or 13
16. Number of predorsals	8 or 9	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i>
17. Dorsal fin rays	ii, 18 (actual number might be a bit more)	2, 12 (AMNH 734, BMNH P.7109)	2, 14 (FMNH 2163, CMNH 5404)
18. Dorsal proximal radials	17 or 18	12 (BMNH P.7109); 13 or 14 (AMNH 734)	15
19. Anal fin rays	i, 13 or 14	i, 10	14
20. Anal pterygiophores	14 or 15	9 (AMNH 734)	13
21. Pelvic fin	Small, short distance behind origin of dorsal fin	Small, in advance of dorsal fin	Opposite to posterior third of dorsal fin (FMNH 2163, CMNH 38790)
22. Pectoral fin rays	11 (IVPP V3002.12,13,15)	13 (BMNH P.7109)	14
23. Number of abdominal scutes	38–43	32 (BMNH P.7109); 28 (incomplete in AMNH 734)	35 (FMNH 2163)
24. Total number of vertebrae	41	35 (BMNH P.7109); 38 (AMNH 734)	36 (FMNH 2163); 35 (CMNH 38790)

TABLE 1. Continued.

Features	† <i>Paraclupea chetungensis</i>	† <i>Ellimmichthys longicostatus</i>	† <i>E. goodi</i>
25. Abdominal	24	22 (BMNH P.7109); 25 (AMNH 734)	20 (FMNH 2163, CMNH 38790)
26. Caudal	17	13 (BMNH P.7109, AMNH 734)	16 (FMNH 2163); 15 (CMNH 38790)
27. Ribs	23 pairs	22 (AMNH 734)	20 (FMNH 2163, CMNH 38790)
28. Caudal scutes	2 or 3 on dorsal, 1 on ventral side of peduncle	1 on dorsal side (BMNH P.7109)	1 on each side of caudal peduncle
29. Epural	3	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i>
30. Uroneurals	3, the longest extending to Pu ₂	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i> (CMNH 38790)
31. Neural spine on pul	Short	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i> (CMNH 38790)
32. Gap between H ₂ and H ₃	Present	Same as in † <i>Paraclupea chetungensis</i>	Same as in † <i>Paraclupea chetungensis</i> (CMNH 38790)
33. Lowermost ray of upper lobe and uppermost ray of lower lobe of caudal fin	Proximal end bifurcated, with median branch prolonged into thin, pointed end	Proximal end enlarged and prolonged, with dorsal and ventral tiny "pegs" (or "buds")	Same as in † <i>Ellimmichthys longicostatus</i> (CMNH 38790)

primitive features, such as the lack of a recessus lateralis, the presence of a "beryiciform foramen" of the anterior ceratohyal, and the midline contact of the parietals.

†*Paraclupeinae* Chang and Chou, 1977
(First use as a subfamily of †*Paraclupeidae*)

TYPE GENUS—†*Paraclupea*.

GENERA CONTAINED IN SUBFAMILY—†*Paraclupea* and †*Ellimmichthys*.

SUBFAMILY DIAGNOSIS—A subfamily of †paraclopeids that differs from the rest of the family †*Paraclupeidae* (i.e., †*Diplomystus sensu* Grande, 1985) by the following characters: (1) The absence of multiple pectinate or comblike teeth along the posterior edges of the dorsal scutes. The absence of this character is the primitive clupeomorph condition. (2) Posteriormost dorsal scutes are many times the size of the anteriormost dorsal scutes (vs. the primitive clupeomorph condition where the dorsal scutes are nearly all the same size, or the posteriormost scutes are only slightly larger than the anteriormost ones).

†*Paraclupea*, Sun, 1956

[†*Paraclupea* Du, 1950 is a *nomen nudum*]

TYPE SPECIES—†*Paraclupea chetungensis* Sun, 1956, only species.

REVISED GENERIC DIAGNOSIS—A genus of †*Paraclupeinae* that differs from the other genus in the subfamily (†*Ellimmichthys*) by the following characters (taken mostly from Table 1): (1) slightly slimmer in body outline (43–48% vs. 52–63% in †*Ellimmichthys*); (2) supramaxillae showing fine, branching grooves on surface (vs. smooth-surfaced in †*Ellimmichthys*); (3) more numerous dorsal scutes (18 vs. 12–13 in †*Ellimmichthys*); (4) more numerous dorsal fin rays and proximal radials (ii, 18 and 18 vs. ii, 12–14 and 12–15 in †*Ellimmichthys*); (5) more numerous abdominal scutes (38–43 vs. 32–35 in †*Ellimmichthys*); (6) more numerous vertebrae (41 vs. 35–38 in †*Ellimmichthys*); (7) lowermost ray of upper lobe and uppermost ray of lower lobe of caudal fin with thin elongate median branch on proximal end. Besides, in †*Paraclupea* the number of dorsal scutes in which the keel protrudes into stout spine is less than in †*Ellimmichthys*, and the posterior area of the dorsal scutes covered by secondarily branching ridges (feather-like) is less extensive than in the latter. Some of the above counts and measurements are based on very small sample sizes, and the ranges could

FIG. 3. †*Paraclupea chetungensis*: three nearly complete skeletons from the Lower Cretaceous Chawan Formation of eastern China. **a**, Specimen ivpp V3002.6 (73 mm SL). **b**, Specimen ivpp V3002.7 (58 mm SL). **c**, Specimen ivpp V3002.8 (90 mm SL).

FIG. 4. †*Paraclupea chetungensis*. Photograph and line drawing of skull. Photograph is of a black latex peel coated with ammonium chloride. Specimen is IVPP V3002.12. Scale is in millimeters; negative reversed so anterior faces left.

obviously be increased with additional material. Collectively, they should form an applicable diagnosis.

REMARKS—The above diagnoses (taken largely from Table 1) represent a first step in sorting out the taxonomy of †*Paraclupeidae*. Once additional

taxa are studied sufficiently to include them (e.g., undescribed †*paraclupeids* from Mexico and the Middle East), the hierarchical groupings within the family will probably become more complex, and some of these generic characters may have to be moved to new suprageneric levels.

FIG. 5a. †*Paraclupea chetungensis*, photograph of a well-preserved jaw region (IVPP V3002.3), most bones with anterior facing left. Black latex peel coated with ammonium chloride. This specimen is drawn in Figure 5b. Scale in millimeters.

Both authors have examined the †“*Diplomystus*” material from the Early Cretaceous fresh-water deposits of Kyushu, Japan (e.g., Yabumoto, 1994). We find no evidence linking these specimens to †*Diplomystus* (*sensu* Grande, 1982, 1985) and observed dorsal scutes strongly resembling those of †paraclupeines in some of the specimens, suggesting the possibility of another species of †*Paraclupea*. This material is in need of additional study.

ETYMOLOGY—*Para-* (Latin), closely related to, and *Clupea* (Latin), type genus of Clupeidae comprising the typical herrings.

†*Paraclupea chetungensis* Sun, 1956
Figures 2–6, 8

HOLOTYPE—IVPP V816, a nearly complete skeleton. The dorsal border is not preserved and the skull bones are not distinct (Fig. 2).

ADDITIONAL MATERIAL—IVPP V2986.2; IVPP V3002.1, 3, 5–8, 10, 12, 15, 19.

HORIZON AND LOCALITIES FOR REFERENCE SPECIMENS AND HOLOTYPE—Chawan Formation (Bureau of Geology and Mineral Resources of Zhejiang Province, 1989), Lower Cretaceous; Shantouho, Shantouxu, and Lingxiachen, 18 km NW

FIG. 5b. †*Paraclupea chetungensis*, line drawing of specimen shown in Figure 5a.

of Linhai County, Zhejiang Province, China. Specimens of the same species are also found near Anxi County, Fujian Province. See Figure 1.

REVISED DIAGNOSIS—As for genus.

ETYMOLOGY—*Chetung*-, east part of Zhejiang province; *che*, abbreviation for Zhejiang Province according to the Wade-Giles romanization system of the Chinese language (Chekiang) used until 1979, when it was replaced by the Pinyin (Chinese phonetic alphabet) system of romanization in the mainland of China; *tung*, Mandarin Chinese for “east.”

Description

BODY SHAPE—The body is similar to that of †*Ellimmichthys* in that it was laterally compressed in life, deep in the abdominal region, with maxi-

mum depth at the origin of the dorsal fin. The dorsal body margin rises steeply from behind the head to the origin of the dorsal fin, then descends gradually from this point to the caudal peduncle, forming a distinct angle at the origin of the dorsal fin. The ventral outline is markedly convex (Fig. 3). Body depth of †*P. chetungensis* is usually 43–48% of standard length ($N = 4$), but one specimen had a body depth of 36% of the standard length.

SKULL ROOF—Only one specimen (IVPP V3002.12, see Fig. 4) has a well-preserved skull roof. It shows a small elongated-rhombic fontanelle between the anterior portions of the frontals comparable to the anterior frontal fontanelle often present in clupeoids (AFN, Fig. 4). The anterior third to one-half of the parietals meet along the midline while posteriorly they are separated by the dorsal portion of the supraoccipital. The posterior portion of the frontals, the parietals, and the triangular roofing portion of the supraoccipital are

FIG. 6. †*Paralupea chetungensis*, photograph and line drawing of predorsal region of upper body margin, showing well-preserved dorsal scutes. Specimen is ivpp V2982.2. Compare these scutes to those of †*Ellimichthys* species in Figure 7. Scale in millimeters. Anterior facing left.

FIG. 7. Species of the widespread Lower Cretaceous genus, †*Ellimmichthys*. Inset box for each showing closeup of dorsal scutes. a, †*Ellimmichthys longicostatus* (Cope, 1886), from Lower Cretaceous deposits of eastern Brazil (BMNH P7109, 104 mm SL). b, Closeup of posterior dorsal scute series from a. c, †*Ellimmichthys goodi* (Eastman, 1912), from Lower Cretaceous deposits of Zaire (FMNH UC2163, 138 mm SL). d, Closeup of posterior dorsal scute series from c. e, †*Ellimmichthys* sp. (undescribed), from Lower Cretaceous marine deposits of the Tlayua Formation, southern Mexico. Specimen is FMNH PF13582 (112 mm SL). f, Closeup of posterior dorsal scute series of another specimen of the undescribed species illustrated in e. Dorsal scutes from FMNH PF13585 (est. SL = 103 mm).

FIG. 8a. †*Paraclupea chetungensis*, photograph of caudal region from IVPP V3002.19, anterior facing left. Line drawing of this specimen in Figure 8b. Scale in millimeters.

strongly ornamented with irregular ridges radiating from the centers of the bones (Fig. 4). The supraoccipital crest is small and low. The supra-orbital sensory canal is extended from the frontal backward into the parietal and seems to be contained in the crest. The supratemporal commissure can be traced on IVPP V3002.6 passing through the parietals and the supraoccipital.

The posttemporal and supracleithrum are also ornamented with long ridges more or less parallel to the long dimension of the bones.

ORBITAL REGION—Only pieces of the sclerotic ring are visible (SC, Fig. 4).

PARASPHENOID AND ENTOPTERYGOID—No teeth were observed on the parasphenoid. On quite a

few specimens (e.g., IVPP V3002.1), the basipterygoid process is preserved as an outgrowth pointing somewhat ventrolaterally from the parasphenoid in the posterior region of the orbit. Fine teeth covering the buccal side of the entopterygoid are clearly shown on IVPP V3002.1 and IVPP V3002.13. On the former specimen they appear to be divided by fine grooves into oblique rows.

JAWS (Fig. 5)—The premaxilla and dentary bear a single row of small conical teeth while the margin of the maxilla is finely serrated. There are two supramaxillary bones, with the posterior one being the larger of the two (SMXP, Fig. 5). The supramaxillae show a network of fine, branching grooves over their external surfaces.

FIG. 8b. †*Paraclupea chetungensis*, line drawing of specimen shown in Figure 8a.

OPERCULAR SERIES AND HYPOBRANCHIAL APPARATUS—The opercular bones are smooth. The vertical arm of the preopercular bone is longer than the horizontal one (Fig. 4). The preopercular sensory canal sends out five or six branches in the horizontal arm. The number of branchiostegal rays is not clear. The anterior ceratohyal is rectangular in shape, showing a large foramen in the center and a deep groove leading from the foramen to its anterior border. The posterior ceratohyal is subtriangular in shape.

VERTEBRAL COLUMN AND FINS—The total number of vertebrae is about 41, 24 of them abdominal (IVPP V3002.6). There are 23 pairs of ribs.

The dorsal fin (based on IVPP V3002.8 and 3002.15) contains one unbranched and 18 branched fin rays and is supported by 17 or 18 pterygiophores. The anal fin shows one unbranched and 13 or 14 branched fin rays, and 14

or 15 pterygiophores on IVPP V3002.6 and IVPP V3002.19.

The pelvic fin is very small and inserts posterior to the origin of the dorsal fin. The pectoral fin is much larger and has about 12 fin rays.

PREDORSAL BONES AND SCUTES—There are about eight (IVPP V3002.15) to nine (IVPP V3002.6) predorsal bones with thin anterior and posterior bony expansions.

The dorsal scute series is complex, containing several distinct characters (Fig. 6). The anteriormost scutes are many times smaller than the posteriormost scutes. The lateral wings of the posteriormost scutes are greatly expanded laterally. The distal expansion area of the scute lacks the strong ornamentation of the more median surface area. The anterior margin of each scute is usually overlain by the scute anterior to it. The posterior margin of most scutes is straight, with a small, shal-

low median notch with the posterior sharp tip of the median keel sticking out over the notch. The posterior end of the keel of the last two to three scutes is modified into a spine, with the spines successively increasing in size backward. The last much prolonged and enlarged spine pointing posterodorsally is just in front of the origin of the dorsal fin and is ornamented with long ridges along its lateral side. The posterior third to half portion of the dorsal surface of the scutes shows prominent ridges starting from the posterior end of the keel, extending laterally and anterolaterally, sometimes branching secondarily. There are approximately 18 dorsal scutes based on IVPP V3002.6. The peculiar dorsal scutes of †*P. chetungensis* are very similar to those of species of †*Ellimmichthys* (Fig. 7), differing from the latter only in smaller median notch at the posterior margin, and a smaller area covered with secondarily branching ridges and fewer posterior scutes protruding into stout spines.

The abdominal scutes are similar to those found in other clupeiforms. They are 38–43 in number.

CAUDAL SKELETON AND FIN (Fig. 8)—The caudal skeleton shows six hypurals as in many clupeomorphs. The third hypural is striplike, its posterior portion is much narrower than in †*Diplomystus*, thus leaving a distinct gap between the second and third hypural (seen on specimens V3002.6, V3002.19, and others). One specimen (Fig. 8) may have thin bone filling this gap, but additional material is needed to verify this. As in other nonclupeoid clupeomorphs, the first hypural is in close contact with the first ural centrum, and the second is fused to it (Fig. 8). The parhypural and more anterior haemal spines are fused with their respective centra. The neural arch of the first preural centrum is short. There are three epurals, the first being the longest. There are three free uroneurals. The first among them is robust and long, extending to the dorsolateral side of the second preural centrum. The second and third uroneurals are much shorter.

The caudal fin is deeply forked with the lower lobe slightly longer than the upper. As in nearly all clupeomorphs, the upper lobe contains one unbranched and nine branched principal fin rays, while the lower contains one unbranched and eight branched. In front of the principal rays there are approximately eight procurent rays in the upper lobe and five in the lower lobe. IVPP V3002.19 shows three caudal scutes on the upper side of the peduncle in front of the procurent rays and one on the lower side. Two scutes on the upper side

have cleft anterior tips. As is seen on IVPP V3002.19, the proximal end of the lowermost hemilepidotrichia of the upper lobe and that of the uppermost ray of the lower lobe are bifurcated, with the median branch longer than the other and prolonged into a thin, pointed end.

SCALES—Scales small, oval in shape, deeper than long, with concentrically arranged, fine growth rings around the nucleus, which is situated a little bit posterior to the center of the scale. No semicircular or vertical circuli, as seen in †*Diplomystus* from Green River (Grande, 1982, fig. 8), were observed. A partial scale count on the preserved portion of specimen IVPP V3002.6 would suggest an estimate of approximately 60 rows of scales along the body length from the posterior margin of the opercular to the base of the caudal fin.

Discussion

Among the known clupeomorphs †*P. chetungensis* appears to be most closely related to the genus †*Ellimmichthys*, including †*E. longicostatus* from Lower Cretaceous deposits along the coast near Itacaranha, Province of Bahia, Brazil, and †*E. goodi* from Equatorial Guinea (formerly Spanish Guinea), West Africa. For the purpose of general comparison we provide a summary of certain features for the three species in Table 1. This should not be interpreted as a comprehensive data matrix, and a large-scale phylogenetic study of primitive clupeomorphs is still needed.

†*Paraclupea* was grouped with †*Diplomystus* and †*Ellimmichthys* (included as †*D. longicostatus*) by Chang and Chou (1977; see also Sun, 1956) without further specification of the relationships between the taxa. Grande (1982, 1985) provided a cladogram of Clupeocephala in which †*Ellimmichthys* and †*Diplomystus* form a sister pair. The grouping of the two genera by Grande was based on the subrectangular shape of the dorsal scutes, while †*Diplomystus* was distinguished by a pectinated posterior margin of the dorsal scutes. Three species of †*Diplomystus*, i.e., †*D. dentatus* from the Eocene Green River Formation of Wyoming, †*D. birdi* from the Upper Cretaceous marine limestone deposits at Hakel, Mount Lebanon, and †*D. dubertreti* from the Upper Cretaceous marine chalk deposits at Sahel Alma, Lebanon, were contained in the cladogram, and †*D. shengliensis*, from Eocene freshwater deposits

of China, was later added to the genus (Zhang et al., 1985, and “†*Diplomystus* n. sp. A” in Grande, 1985), but †*Paraclupea* was not included in Grande’s study.

From Table 1 we can see †*Paraclupea* and the two species of †*Ellimmichthys* mentioned above share several putatively derived characters, including: maximum depth at origin of dorsal fin with dorsal outline forming here an angle or apex; skull roofing bones strongly sculptured with radiating ridges; supraoccipital ridge small and low; eight to nine predorsals; dorsal scutes broader than long, ornamented with ridges¹; gap between hypural 2 and hypural 3; uroneural 2 extending to preural 2. Thus, the suggestion of the close relationship between †*P. chetungensis* and †*E. longicostatus* is indicated and additional characters are added to Sun’s dorsal scute character to group the two genera together. Among the three species under discussion here the two †*Ellimmichthys* species share a few characters that they do not share with †*P. chetungensis*. The body is much deeper in †*E. longicostatus* and †*E. goodi* than in †*P. chetungensis*. There is an extensive emargination in the posterior margin of the dorsal scute (Grande, 1982, fig. 8) and the keel of the last four to five scutes protrudes into a stout spine in †*E. longicostatus* and †*E. goodi*, while the margin is just slightly notched in the middle and the keel of only two to three scutes protrudes into a stout spine in †*P. chetungensis*. In the two former species the posterior half or sometimes nearly the entire length of the dorsal scute is covered by radiating ridges without secondary branching, while in †*P. chetungensis* only the posterior third or at most half of the scute is covered by ridges, often with secondary branching. The proximal ends of the lowermost ray of the upper lobe and the uppermost ray of the lower lobe of the caudal fin are enlarged and prolonged, with dorsal and ventral tiny “pegs” in the two former species, while those in the latter are bifurcated and the median branch is prolonged into a thin pointed end (Fig. 8b). In addition, the surface of the supramaxillae in †*P. chetungensis* bears fine, branching grooves while in the two †*Ellimmichthys* species the supramaxillae are smooth. Furthermore, in †*P.*

chetungensis the anterior parts of the parietals appear to meet at the midline with the insertion of the supraoccipital between their posterior parts (Fig. 4), while in †*E. longicostatus* and †*E. goodi*, as far as we can observe from AMNH 734 and C.M.5404, the supraoccipital separates the two parietals completely. An anterior frontal fontanelle which is usually present in many clupeoids (Ride-wood, 1905; Grande, 1985) is found in one specimen of †*P. chetungensis* (AFN, Fig. 4), but the information is lacking in †*E. longicostatus* and †*E. goodi*. The meristic characters also show obvious differences (see Table 1, characters 15, 17, 18, 23, 24, 28). Thus, it appears that among the three taxa dealt with here, †*E. longicostatus* and †*E. goodi* must be more closely related to each other than to †*P. chetungensis*. Whether the two †*Ellimmichthys* species and †*P. chetungensis* should be treated as belonging to the same genus, or in two separate genera as they are, is, to some extent, a matter of subjectivity. More important is that among known clupeomorphs †*Ellimmichthys* and †*Paraclupea* appear to be closely related to each other as sister taxa and are thus placed into their own subfamily here.

†*Ellimmichthys* and †*Paraclupea* are primarily from Lower Cretaceous nonmarine deposits, †*E. longicostatus* and †*E. goodi* from the western and eastern coasts of the southern Atlantic, respectively, while †*P. chetungensis* is from the west coast of the north Pacific. The close relationship between the Lower Cretaceous fish faunas from northeastern South America and from western Africa has long been demonstrated by the sharing of several genera (e.g., †*Mawsonia*, †*Lepidotus*, †*Belonostomus*, †*Ellimmichthys* [then †*Diplomystus*]) and families (e.g., †Ichthyodectidae, Chanidae, Patterson, 1975, table on p. 170; Maisey, 1991, 1993). The amiid †*Urocles*, also reported in Patterson’s (1975) table as present in West Africa and Brazil, does not actually occur in those areas; but other amiids show the same South American–African biogeographic connection, based on studies in progress by Grande and Bemis. It is reasonable to consider these faunal similarities as an artifact of Cretaceous geography (hypothesized Brazil–African land connection), because these data are congruent with evidence provided by invertebrates, such as ostracods (Patterson, 1975).

Acknowledgments

We thank John Maisey, Mike Gottfried, and Xiaobo Yu for reading and commenting on the

¹ Dorsal scutes ornamented with ridges have also been described from †*Ellimma branneri* Jordan (Grande, 1982, fig. 23) from Brazil and †*Ellimma* (misspelling?) *guinensis* Gayet (1989, fig. 1) from Equatorial Guinea. Both are from Lower Cretaceous nonmarine deposits. The former possesses wider than long dorsal scutes. The latter is probably an †*Ellimmichthys* rather than †*Ellimma*.

manuscript, Mrs. Hu Huiqing for making most of the drawings, Steve McCarroll for helping us make the casts, Colin Patterson and Peter Forey (BMNH), Shelly Applegate (UNAM), and Mary Dawson (CMNH) for loaning us material, and Yoshitaka Yabumoto (Kitakyushu Museum of Natural History) for showing us his specimens. For her work at the Field Museum of Natural History, Chang is indebted to the Robert O. Bass Visiting Scientist Fund, to the Field Museum Scholarship Committee for making the award, and to the Department of Geology for providing facilities. She is also indebted to Richard Tedford, Department of Vertebrate Paleontology, AMNH, for providing the facilities and time to finish this work. The work is also supported by the Chinese National Science Foundation.

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NOTE: There are several different published spellings of the names of the following two authors:

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