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

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

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Table of Contents

ABSTRACT ........................................... 1
INTRODUCTION ...................................... 1
  Anatomical Abbreviations ...................... 4
  Institutional Abbreviations .................... 4
MATERIALS EXAMINED .............................. 4
METHODS ........................................ 5
SYSTEMATICS ..................................... 5
DESCRIPTION ..................................... 11
DISCUSSION ....................................... 16
ACKNOWLEDGMENTS ............................... 17
LITERATURE CITED ............................... 18

3. Three well-preserved skeletons of ↑Paracleupea chetungensis ......................... 8
4. Skull of ↑Paracleupea chetungensis ................. 9
5. Jaws of ↑Paracleupea chetungensis
  a. Photograph .................................... 10
  b. Drawing ....................................... 11
6. Predorsal upper body margin of ↑Paracleupea chetungensis .......................... 12
7. Three species of ↑Ellimmichthys .................... 13
8. Caudal region of ↑Paracleupea chetungensis
  a. Photograph .................................... 14
  b. Drawing ....................................... 15

List of Illustrations

1. Locality map for ↑Paracleupea chetungensis ............................................. 2
2. Holotype of ↑Paracleupea chetungensis .... 3

List of Tables

1. Comparison between ↑Paracleupea chetungensis, ↑Ellimmichthys longicostatus,
   and ↑E. goodi ...................................... 6
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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 †Diplomyctes (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 showchungensis Ping and Yen (1933), another Lower Cretaceous teleost from the same area. †Mesoclupea was later reassigned to †Ichthyodontiformes 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 holotype 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-
dominal scutes, Sun (1956) noted that †Paraclupea was a "double-armored 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 establish a separate family for the double-armored 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-armored 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 paraphenoid, parratals not completely separated from each other by
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 †Armillatus, because there were no synapomorphic characters to tie it to †Diplomystus. The remaining species, †D. dentatus, †D. birdi, †D. dubertrei, were then found to form a monophyletic group, to which the Chinese species †D. shengiensis 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 Diplomys- 

taes.) †Ellimmichthyidae was weakly diagnosed by a single character: the presence of subrectangular dorsal scutes. Grande (1982, 1985) also demonstrated that the “double-armored herrings” (see above) were a nonmonophyletic group, because †Knightia, Hyperlophus, Potamolosa, and Eth- midium all clearly belong to the Clupeidae, while †Diplomystus is not even a clupeiform. Conse- quently, 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), †Hu- ashia (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 nec- essary to review the forms previously reported from southeastern China to clarify their morphol- ogy and taxonomic identity and to better under- stand 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 Chi- nese, it is worthwhile to make this information more accessible by providing a relatively com- plete description of the material in English. After restudying †P. chetungensis and comparing it
with †E. longistatus and †E. goodi we find that the genus †Paraclupea forms the sister group to †Ellimichthys. 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., †Ellimichthys, see text). If †Paraclupea belongs in the same family as †Ellimichthys and †Diplomycterus, then †Ellimichthyidae 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

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>angulo-articular</td>
</tr>
<tr>
<td>AFN</td>
<td>anterior frontal fontanelle</td>
</tr>
<tr>
<td>CS</td>
<td>caudal scute</td>
</tr>
<tr>
<td>D</td>
<td>dentary</td>
</tr>
<tr>
<td>DFR</td>
<td>dorsal fin rays</td>
</tr>
<tr>
<td>DS</td>
<td>dorsal scute</td>
</tr>
<tr>
<td>ECPT</td>
<td>ectopterygoid</td>
</tr>
<tr>
<td>ENPT</td>
<td>entopterygoid</td>
</tr>
<tr>
<td>ENPT.T</td>
<td>entopterygoid teeth</td>
</tr>
<tr>
<td>EP</td>
<td>epural</td>
</tr>
<tr>
<td>FR</td>
<td>frontal</td>
</tr>
<tr>
<td>H</td>
<td>hypural</td>
</tr>
<tr>
<td>HM</td>
<td>hyomandibula</td>
</tr>
<tr>
<td>HS</td>
<td>haemal spine</td>
</tr>
<tr>
<td>IOP</td>
<td>interopercle</td>
</tr>
<tr>
<td>MPT</td>
<td>metapterygoid</td>
</tr>
<tr>
<td>MX</td>
<td>maxilla</td>
</tr>
<tr>
<td>NPU₁</td>
<td>neural arch of first preural centrum</td>
</tr>
<tr>
<td>NS</td>
<td>neural spine</td>
</tr>
<tr>
<td>OP</td>
<td>opercle</td>
</tr>
<tr>
<td>PA</td>
<td>parietal</td>
</tr>
<tr>
<td>PD</td>
<td>predorsal bones</td>
</tr>
<tr>
<td>PH</td>
<td>parhypural</td>
</tr>
<tr>
<td>PMX</td>
<td>premaxilla</td>
</tr>
<tr>
<td>POP</td>
<td>preopercle</td>
</tr>
<tr>
<td>PR</td>
<td>proximal radial</td>
</tr>
<tr>
<td>PT</td>
<td>posttemporal</td>
</tr>
<tr>
<td>PU</td>
<td>preural centrum</td>
</tr>
<tr>
<td>Q</td>
<td>quadrate</td>
</tr>
<tr>
<td>R</td>
<td>retroarticular</td>
</tr>
<tr>
<td>S</td>
<td>symplectic</td>
</tr>
<tr>
<td>SC</td>
<td>sclerotic bones</td>
</tr>
<tr>
<td>SMXA</td>
<td>anterior supramaxilla</td>
</tr>
<tr>
<td>SMXP</td>
<td>posterior supramaxilla</td>
</tr>
</tbody>
</table>

SOC = supraoccipital
U = ural centrum
UN = uroneural
VT = vertebra
† (a dagger) preceding a taxonomic name indicates that this taxon is extinct.

Institutional Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Institution</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>American Museum of Natural History, New York</td>
</tr>
<tr>
<td>BMNH</td>
<td>Department of Palaeontology, Natural History Museum, London</td>
</tr>
<tr>
<td>CMNH</td>
<td>Carnegie Museum of Natural History, Pittsburgh, PA</td>
</tr>
<tr>
<td>FMNH</td>
<td>Department of Geology, Field Museum of Natural History, Chicago, IL</td>
</tr>
<tr>
<td>IGSOF</td>
<td>Institute of Geology, Shengli Oil Field, Dongying, Shandong Province, China (Collections)</td>
</tr>
<tr>
<td>IVPP</td>
<td>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing</td>
</tr>
<tr>
<td>UNAM</td>
<td>Instituto de Geología, Universidad Nacional Autónoma, México</td>
</tr>
</tbody>
</table>

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).

†Ellimichthys

†Ellimichthys longistatus (Cope, 1886). From Lower Cretaceous estuarine deposits of Bahia, Brazil. Three specimens, including two on AMNH 734 and one on BMNH P7109. This is the type specimen for the genus.

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

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

Denticipitidae

Denticips

Denticips 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 Janiero, 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

†Armiagatus

†Armiagatus 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 †Ellimmichthiformes 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.

<table>
<thead>
<tr>
<th>Features</th>
<th>†Paraclupea chetungensis</th>
<th>†Ellimmichthys longicostatus</th>
<th>†E. goodi</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Locality</td>
<td>Early Cretaceous freshwater deposits of eastern China</td>
<td>Early Cretaceous estuarial deposits of Bahia, Brazil</td>
<td>Early Cretaceous freshwater deposits of West Africa</td>
</tr>
<tr>
<td>2. Maximum depth</td>
<td>At origin of dorsal fin</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis</td>
</tr>
<tr>
<td>3. Body depth/standard length</td>
<td>43–48%</td>
<td>63%</td>
<td>52%</td>
</tr>
<tr>
<td>4. Dorsal outline</td>
<td>Obtuse angle at origin of dorsal fin (Fig. 3)</td>
<td>Sharp angle at origin of dorsal fin (BMNH P7109 only) (Fig. 7a)</td>
<td>Prominent angle at origin of dorsal fin (Fig. 7b)</td>
</tr>
<tr>
<td>5. Ventral outline</td>
<td>Markedly convex (Fig. 3)</td>
<td>Extremely convex (Fig. 7a)</td>
<td>Extremely convex (Fig. 7b)</td>
</tr>
<tr>
<td>6. Skull roofing bones</td>
<td>Strongly sculptured with ridges</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis</td>
</tr>
<tr>
<td>7. Anterior frontal fontanelle</td>
<td>Present</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>8. Parietals</td>
<td>Anterior parts meeting at midline</td>
<td>Not meeting at midline</td>
<td>Same as in †Ellimmichthys longicostatus (CMNH 5404)</td>
</tr>
<tr>
<td>9. Supraoccipital crest</td>
<td>Small and low</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Small and low (?)</td>
</tr>
<tr>
<td>10. Supraorbital sensory canal</td>
<td>Enclosed in crest</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis</td>
</tr>
<tr>
<td>11. Supramaxillae</td>
<td>Showing fine, branching grooves on surface</td>
<td>Smooth</td>
<td>Smooth (CMNH 5404)</td>
</tr>
<tr>
<td>12. Entopterygoid teeth</td>
<td>Fine and numerous</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis</td>
</tr>
<tr>
<td>13. Shape of dorsal scutes</td>
<td>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</td>
<td>Same as in †Paraclupea chetungensis, 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</td>
<td>Same as in †Ellimmichthys longicostatus</td>
</tr>
<tr>
<td>14. Ornamentation of dorsal scutes</td>
<td>Posterior third or half covered with radiating ridges with secondary branching (feather-like)</td>
<td>Posterior bigger half covered with radiating ridges</td>
<td>Same as in †Ellimmichthys longicostatus</td>
</tr>
<tr>
<td>15. Number of dorsal scutes</td>
<td>18</td>
<td>12</td>
<td>12 or 13</td>
</tr>
<tr>
<td>16. Number of predorsals</td>
<td>8 or 9</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis</td>
</tr>
<tr>
<td>17. Dorsal fin rays</td>
<td>ii, 18 (actual number might be a bit more)</td>
<td>2, 12 (AMNH 734, BMNH P7109)</td>
<td>2, 14 (FMNH 2163, CMNH 5404)</td>
</tr>
<tr>
<td>18. Dorsal proximal radials</td>
<td>17 or 18</td>
<td>12 (BMNH P7109); 13 or 14 (AMNH 734)</td>
<td>15</td>
</tr>
<tr>
<td>19. Anal fin rays</td>
<td>i, 13 or 14</td>
<td>i, 10</td>
<td>14</td>
</tr>
<tr>
<td>20. Anal pterygiophores</td>
<td>14 or 15</td>
<td>9 (AMNH 734)</td>
<td>13</td>
</tr>
<tr>
<td>21. Pelvic fin</td>
<td>Small, short distance behind origin of dorsal fin</td>
<td>Small, in advance of dorsal fin</td>
<td>Opposite to posterior third of dorsal fin (FMNH 2163, CMNH 38790)</td>
</tr>
<tr>
<td>22. Pectoral fin rays</td>
<td>11 (IVPP V3002.12,13,15) 38–43</td>
<td>13 (BMNH P7109) 32 (BMNH P7109); 28 (incomplete in AMNH 734)</td>
<td>14</td>
</tr>
<tr>
<td>23. Number of abdominal scutes</td>
<td>35 (BMNH P7109); 38 (AMNH 734)</td>
<td>35 (FMNH P7109); 36 (FMNH 2163); 35 (CMNH 38790)</td>
<td>36 (FMNH 2163)</td>
</tr>
<tr>
<td>24. Total number of vertebrae</td>
<td>41</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Features</td>
<td>†Paraclupea chetungensis</td>
<td>†Ellimmichthys longicostatus</td>
<td>†E. goodi</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>--------------------------</td>
<td>-----------------------------</td>
<td>-----------</td>
</tr>
<tr>
<td>25. Abdominal</td>
<td>24</td>
<td>22 (BMNH P7109); 25 (AMNH 734)</td>
<td>20 (FMNH 2163, CMNH 38790)</td>
</tr>
<tr>
<td>26. Caudal</td>
<td>17</td>
<td>13 (BMNH P7109, AMNH 734)</td>
<td>16 (FMNH 2163); 15 (CMNH 38790)</td>
</tr>
<tr>
<td>27. Ribs</td>
<td>23 pairs</td>
<td>22 (AMNH 734)</td>
<td>20 (FMNH 2163, CMNH 38790)</td>
</tr>
<tr>
<td>28. Caudal scutes</td>
<td>2 or 3 on dorsal, 1 on ventral side of peduncle</td>
<td>1 on dorsal side (BMNH P7109)</td>
<td>1 on each side of caudal peduncle</td>
</tr>
<tr>
<td>29. Epural</td>
<td>3</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis</td>
</tr>
<tr>
<td>30. Uroneurals</td>
<td>3, the longest extending to Pu₃</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis (CMNH 38790)</td>
</tr>
<tr>
<td>31. Neural spine on pul</td>
<td>Short</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis (CMNH 38790)</td>
</tr>
<tr>
<td>32. Gap between H₂ and H₃</td>
<td>Present</td>
<td>Same as in †Paraclupea chetungensis</td>
<td>Same as in †Paraclupea chetungensis (CMNH 38790)</td>
</tr>
<tr>
<td>33. Lowermost ray of upper lobe and uppermost ray of lower lobe of caudal fin</td>
<td>Proximal end bifurcated, with median branch prolonged into thin, pointed end</td>
<td>Proximal end enlarged and prolonged, with dorsal and ventral tiny “pegs” (or “buds”)</td>
<td>Same as in †Ellimmichthys longicostatus (CMNH 38790)</td>
</tr>
</tbody>
</table>

primitive features, such as the lack of a recessus lateralis, the presence of a “beryctiform foramen” of the anterior ceratothyal, 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 †paraclupeids 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 anterioriormost dorsal scutes (vs. the primitive clupeomorph condition where the dorsal scutes are nearly all the same size, or the posterioriormost scutes are only slightly larger than the anterioriormost 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 (featherlike) 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

CHANG & GRANDE: REDESCRIPTION OF †PARACLupeA CHETUNGensis
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).
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.
Both authors have examined the †“Diplomystus” material from the Early Cretaceous freshwater 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
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 maximum 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. *Paraclupea 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).
strongly ornamented with irregular ridges radiating from the centers of the bones (Fig. 4). The supraoccipital crest is small and low. The supraorbital 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 supraleithrum 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.
**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 V3002.15) 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 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 anterior most scutes are many times smaller than the posterior most scutes. The lateral wings of the posterior most 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 †Diplomytus, 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 uro-neurals. The first among them is robust and long, extending to the dorsolateral side of the second preural centrum. The second and third uro-neurals 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 †Diplomytus 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 †Diplomytus 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 †Diplomytus form a sister pair. The grouping of the two genera by Grande was based on the subrectangular shape of the dorsal scutes, while †Diplomytus was distinguished by a pectinated posterior margin of the dorsal scutes. Three species of †Diplomytus, 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 "Diplomytus n. sp. A" in Grande, 1985), but †Paraelupea was not included in Grande's study.

From Table 1 we can see †Paraelupea and the two species of †Ellimichthys 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 ridges; 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 †Ellimichthys 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 †Ellimichthys 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 †Ellimichthys 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 †Ellimichthys and †Paraelupea appear to be closely related to each other as sister taxa and are thus placed into their own subfamily here.

†Ellimichthys and †Paraelupea 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., †Diplomytus, †Mawsonia, †Belonostomus, †Ellimichthys [then †Diplomystus] and families, (e.g., †Ichthyodectidae, Chaniidae, Patterson, 1975, table on p. 170; Maisey, 1991, 1993). The amidi †Urocles, also reported in Patterson's (1975) table as present in West Africa and Brazil, does not actually occur in those areas; but other amidiids 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).

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Literature Cited

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

Chang, M.-M. = Zhang, M.-M.
Chou, C.-C. = Chow, C.-C. = Zhou, J. = Zhou, J.-J.


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