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The youngest ellimmichthyiform (clupeomorph) fish to date from the Oligocene of South China

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A new ellimmichthyform, *Guiclupea superstes*, gen. et sp. nov., from the Oligocene Ningming Formation of Ningming Basin, Guangxi Zhuang Autonomous Region, South China is described herein. With relatively large body size, parietals meeting at the midline, anterior ceratohyal with a beryciform foramen in the center, a complete predorsal scutes series of very high number and about equally-size scutes with radiating ridges on dorsal surface, first preural centrum unfused with first uroneural but fused with the parhypural, and first ural centrum of roughly the same size as the preural centrum, *Guiclupea superstes* cannot be assigned to the order Clupeiformes. The phylogenetic analyses using parsimony and Bayesian inference methods with *Chanos*/*Elops* as outgroup respectively suggests that the new form is closer to ellimmichthyiform genus *Diplomystus* than to any other fishes, although there are some discrepancies between the two criteria and different outgroup used. It shares with *Diplomystus* the high supraoccipital crest, pelvic-fin insertion in advance of dorsal fin origin, and number of predorsal scutes more than 20. The new form is the youngest ellimmichthyiform fish record in the world so far. Its discovery indicates that the members of the Ellimmichthyiformes had a wider distribution range and a longer evolutional history than previously known.

Guiclupea superstes, gen. et sp. nov., the youngest ellimmichthyiform (clupeomorph) fish to date from the Oilgocene of South China

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Abstract A new ellimmichthyform, *Guiclupea superstes*, gen. et sp. nov., from the Oligocene Ningming Formation of Ningming Basin, Guangxi Zhuang Autonomous Region, South China is described herein. With relatively large body size, parietals meeting at the midline, anterior ceratohyal with a beryciform foramen in the center, a complete predorsal scutes series of very high number and about equally-size scutes with radiating ridges on dorsal surface, first preural centrum unfused with first uroneural but fused with the parhypural, and first ural centrum of roughly the same size as the preural centrum, *Guiclupea superstes* cannot be assigned to the order Clupeiformes. The phylogenetic analyses using parsimony and Bayesian inference methods with *Chanos*/*Elops* as outgroup respectively suggests that the new form is closer to ellimmichthyiform genus *Diplomystus* than to any other fishes, although there are some discrepancies between the two criteria and different outgroup used. It shares with *Diplomystus* the high supraoccipital crest, pelvic-fin insertion in advance of dorsal fin origin, and number of predorsal scutes more than 20. The new form is the youngest ellimmichthyiform fish record in the world so far. Its discovery indicates that the members of the Ellimmichthyiformes had a wider distribution range and a longer evolutional history than previously known.

Keywords Ellimmichthyiforms, Oligocene, southern China, phylogeny, paleobiology

Introduction

The Ellimmichthyiformes is one of the two major clades of the Clupeomorpha (Nelson et al., 2016). The Recent Clupeomorpha is represented only by the order Clupeiformes, which is amongst the most economically important fish species for food (Zhang, 2001), and containing both fossil and extant herrings, anchovies, and other relatives. The order Ellimmichthyiformes is an extinct cosmopolitan clade (Nelson et al., 2016), established by Grande in 1982. It initially included only a single family Ellimmichthyidae (=Paraclupeidae, see Chang & Grande 1997) with only two genera– *Diplomystus* and *Ellimmichthys*, diagnosed by bearing a series of predorsal scutes expanding laterally then taking a subrectangular-shape, and ~~laking~~ some derived characters of the Clupeiformes, e.g., presence of recessus lateralis, parietal bones completely separated by the supraoccipital, and loss of the 'beryciform' foramen in anterior ceratohyal (Grande, 1982, 1985). Since the founding of Ellimmichthyiformes, especially in the last two decades, many new and previously known genera and species have been added or moved to this order (Silva Santos, 1990, 1994; Bannikov & Bacchia, 2000; Chang & Maisey, 2003; Poyato-Ariza & García-Garmilla, 2000; Forey et al., 2003; Hay et al., 2007; Alvarado-Ortega & Ovalles-Damián 2008; Khalloufi et al., 2010; Newbrey et al 2010; Murray & Wilson, 2011, Malabarba et al., 2004; Bannikov, 2015; Vernygora & Murray, 2015; Murrey et al., 2016; Alvarado-Ortega & Melgarejo-Damián. 2017; ~~Plock~~ et al., 2020; etc), though some of them with the predorsal scutes pattern only partially agree with or completely disagree with this order-level character, e.g., *Ellimma branneri*, whose anterior predorsal scutes is longer than broad; *Scutatospinosus itapagipensis* and *Codichthys carnavalii*, without any subrectangular predorsal scutes at all, completely disagree with the order-level character. Along with the increasing of the members of this order, several families were erected, and the interest in the definition, classification, and intra-relationship of the group has been increasing (Bannikov & Bacchia, 2000; Chang & Maisey, 2003; Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008; Murray & Wilson, 2013; Figueiredo & Ribeiro 2016; Vernygora et al., 2016; Marramà & Carnevale 2017; Boukhalfa et al., 2019; Vernygora & Murray, in press; etc), though no definitive consensus has been reached on these issues. The main differences among the results of previous studies are the relationship of *Armigatus* and *Diplomystus* [some analysis suggested that *Armigatus* is sister to *Diplomystus* (Chang & Maisey, 2003, Murray & Wilson, 2013; others suggested that *Armigatus* is in a more basal (Forey, 2004; Figueiredo & Ribeiro 2016) or derived position than *Diplomystus* (Vernygora & Murray, 2016; Marramà & Carnevale 2017; Boukhalfa et al., 2019), or *Armigatus* is not an ellimmichthyiform member (Zaragüeta-Bagils, 2004)], and *Ornategulum* is an ellimmichthyiforms or not (Murrey & Wilson, 2013; Marrama et al., 2018; Figuereido & Ribeiro 2017; Boukhalfa et al., 2019). To date, reported members of the group have reached 21 genera and 37 species at least, ranging from the Early Cretaceous to middle Eocene marine and non-marine strata of Eastern Asia, Middle East, North and South America, Africa, and Europe (Figure 1). No ellimmichthyiform fish from the strata younger than the Eocene has ever been reported. Accordingly, it was believed that the ellimmichthyiforms have finally become extinct after the middle Eocene. However, recently, an Oligocene ellimmichthyiform fish was discovered from the non-marine deposits of Ningming Basin, Guangxi Zhuang Autonomous

Region, South China. Consequently, this new ellimmichthyiform fish is the youngest one to date. This discovery not only extends the spatial and temporal distribution of ellimmichthyiform, but also shed new light for our understanding of the evolutionary history and paleobiogeography of the order. Herein we provide descriptions of the new form, perform a phylogenetic analysis of the Ellimmichthyiformes, and discuss the taxonomic position and the paleobiographical implications of the new form.

Abbreviations

Institutional Abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. **NHMG**, Natural History Museum of Guangxi Zhuang Autonomous Region, China.

Anatomical Abbreviations—aa, angulo-articular; **ach**, anterior ceratohyal; **as**, autosphenotic; **br**, branchiostegal rays; **cl**, cleithrum; **cor**, coracoid~~s~~; **cs**, caudal scute; **d**, dentary; **ect**, ectopterygoid; **en**, epineural; **enpt**, entopterygoid; **ep**, epural; **epl**, epipleural; **fr**, frontal; **h**, hypural; **hy**, hyomandibula~~r~~; **io**, infraorbital; **iop**, interopercle; **la**, lacrimal; **le**, lateral ethmoid; **met**, metapterygoid; **ms**, mesethmoid; **msc**, mandibular sensory canal; **mx**, maxilla; **ns**, neural spine; **op**, opercle; **pa**, parietal; **pch**, posterior ceratohyal; **pcl**, postcleithr~~a~~; **pd**, predorsal bones; **ph**, parhypural; **pmx**, premaxilla; **pop**, preopercle; **pr**, pleural rib; **ps**, parapophysis; **pt**, posttemporal; **pto**, pterotic; **pu**, preural centrum; **q**, quadrate; **ra**, retroarticular; **sc**, scapula; **scl**, supracleithrum; **scr**, sclerotic bone; **so**, supraorbital; **sop**, subopercle; **smxa**, anterior supramaxilla; **smxp**, posterior supramaxilla; **sp**, sphenotic; **spo**, supraoccipital; **sy**, symplectic; **u**, ural centrum; **uh**, urohyal; **un,** uroneural; **vo**, vomer; **vs**, ventral scutes.

Materials and Methods

Fossil specimens except NHMG 038777, described herein, including articular skeletons and detached bones, were collected from the outcrops about 2.5~3.5 km west of Ningming County, Guangxi, South China (Figure 1), about 40 km away from the boundary of China and Vietnam and about 120 km northwest of the South China Sea, and now housed in the NHMG. The fossil-bearing strata positions in the middle-upper part of the Second Member of the Yongning Group (Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region, 1985), or Ningming Formation (Li et al., 1995), which is a set of fossiliferous lacustrine sediments dominated by light-gray, yellowish mudstones, occasionally containing fine sand grains. This deposition also bears a variety of cyprinid and a few siluriform and perciform fishes, and a large number of plant macrofossils (Chen et al., 2018). No volcanic material which can be used for isotopic dating was found at the locality. The geological age of the Ningming Formation, according to palynologists (Wang et al., 2003), is Oligocene. Paleobotanists accepted this opinion when studied macrofossil plant from the same strata (Li et al., 2003; Shi et al., 2010, 2012, 2014; Wang et al., 2014; Dong et al., 2017; Ma et al., 2017; etc). We applied this geological age also when we studied *Huashancyprinus robustispinus* (Cyprinidae, Cypriniformes) from the same locality and horizon (Chen & Chang, 2011) and adopt it herein. NHMG 038777 is a disarticulated dentary collected from Yongning formation of Santang, Nanning basin, Guangxi. The geological age of Yongning formation is Oligocene (Zhao, 1983, 1993; Quan et al., 2012)

Fossil fish materials were prepared mechanically with steel needles of different sizes under a binocular microscope. Line drawings were made based on the observations of the fossils under an Olympus SZ61 microscope and the photos.

The taxonomy terminology and the methods of counting and measurement used in here follow Grande (1982) and Forey et al. (2003). The descriptions of gill raker follow Bornbusch & Lee (1992). Specimens used for comparison include: 1) *Paraclupea chetungensis* Sun 1956, including IVPP V816, V2986.2, V3002.1, 5-8, 10, 12, 15, 19, from the Lower Cretaceous Chawan Formation, eastern China; 2) *Diplomystus shengliensis* Zhang et al. 1985, including SOF 790001, SOF 790002, and SOF 790003, from top of series 4 to bottom of series 3 of the Shahejie Formation, Middle Eocene, East China; 3) *Knightia bohaiensis* Zhang et al. 1985, including SOF 790003, from top of series 4 to bottom of series 3 of the Shahejie Formation, Middle Eocene, East China; and 4) dried skeleton and disarticular bones of *Ilisha elongate*, NHMG , collected from Nanning Dancun Market.

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The Phylogenetic analyses are based on data matrix (see Appendix 1S-3S) consisted of 55 morphological characters and 40 taxa, including three Recent clupeiform species (~~*Denticep*~~ *clupeoides*, *Chirocentrus dorab*, and *Odaxothrissa vittata* (the first one is the only extant member of the Denticipitoidei; the latter two represent the Clupeoidei), a gonorynchiform or elopomorph (*Chanos chanos* or *Elops saurus*, being used as outgroup alternatively to polarize the characters and root the tree), the enigmatic fossil *Ornategulum sardinioides* Forey 1973, and our new form (to test its position within the Clupeomorpha). Characters are mainly adopted from Chang & Maisey (2003), and Murray & Wilson (2013).

The analyses use both parsimony and Bayesian inference methods, for both methods have advantages and disadvantages for morphological data (Bai et al., 2020). The parsimony analyses were performed with TNT 1.5 (Goloboff et al., 2008), using the Traditional Search method with 1000 replicates and tree bisection and reconnection (TBR) swapping algorithm. All characters are unordered and equally weighted. The most parsimonious trees (MPTs) generated by the analysis were used to construct a strict consensus tree. Tree length, consistency index (CI), retention index (RI), Bremer support and bootstrap values were then calculated for the strict consensus tree.

Bayesian analyses were conducted by MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). For the substitution models, the Mkv model was used with an assumption of gamma rate variation across characters. Markov chain Monte Carlo analysis consists of four chains, which were run simultaneously with 2 000 000 trees, sampling 1/100 trees, with a burn-in value of 5000. The remaining trees were used to build a 50% majority rule consensus tree, and statistical support of each node was assessed by posterior probabilities.

Systematic Paleontology

Infraclass TELEOSTEI Müller, 1845

Cohort CLUPEOCEPHALA Patterson & Rosen, 1977

Superorder CLUPEOMORPHA Greenwood et al., 1966

Order ELLIMMICHTHYIFORMES Grande, 1982

Diplomystus clade

Genus *GUICLUPEA* gen. nov.

Diagnosis: A pretty large-sized, double-armoured ellimmichthyiform fish, differing from other genera of the order with the following combination of characters: dorsal body margin without marked angle at the dorsal fin insertion; posttemporal large; predorsal scutes series complete, with scutes small, numerous (about 55), all about equal in size, and with ridges on dorsal surface; number of predorsal bones ten or more; no diastema between second and third hypural; proximal end of middle principal caudal fin rays enlarged.

Etymology : 'gui', the abbreviation in Chinese of the Guangxi Zhuang Autonomous Region, a province of China from where the fossil materials were collected; 'clupea', from the Latin, to indicate clupeomorph affinities of the new taxon.

Type species : *Guiclupea superstes* gen. et. sp. nov.

Guiclupea superstes gen. et~~.~~ sp. nov.

(Figs. 2–7)

Diagnosis: See generic diagnosis. Pectoral fin rays 18, pelvic fin rays 5~6, dorsal fin rays 14, anal fin rays 38, total number of vertebrae (include ural centra) about 46.

Etymology: 'superstes', Latin 'survivore'. The species name means that the species survived in Oligocene when ~~almost~~ all menbers of the order ~~Eliimmchthyiforms~~ had become extinct.

Holotype: NHMG 005532, a nearly complete skeleton, part and counterpart (Figs. 2A-B).

Paratypes: NHMG 033659 (Fig. 3A), a relatively complete skeleton with the snout and the caudal fin rays missing; NHMG 033658 (Fig. 6), a skeleton from the anterior margin of the orbital to the caudal peduncle, part of the anterior portion and counterpart of the posterior portion; NHMG 011648 (Fig. 7A), caudal peduncle to caudal fin, part and counterpart.

Additional material: NHMG 033660 (Fig. 5), disarticulated bones of skull and anterior part of the body; NHMG 004929, an incomplete skeleton with the posterior part of the body missing; NHMG 033361, disarticulated bones of skull, the anterior ceratohyal and entopterygoid in this specimen were showed in Fig. 4E; NHMG 033680, disarticulated bones of skull and anterior part of the body, the posterior ceratohyals in this specimen were showed in Fig. 4~~F~~; NHMG 033685, premaxilla (Fig. 4C); NHMG 038778, an incomplete skeleton with the head and caudal skeleton and fin missing; NHMG 033681–033683 and NHMG 038777, dentary (NHMG 033681 showed in Fig. 3D); NHMG 011647 and NHMG 011649, caudal skeleton and caudal fin; NHMG 011650–011651, caudal skeleton.

Localities and horizon: Gaoling Village (22º07N, 107º02′E), Ningming County, and Santang (22º52′N, 108º25′E), Nanning, Guangxi province, China; middle to upper portion of the second member of the Yongning Group or Ningming Formation and Yongning Formation; Oligocene.

Description

(1) **General Appearance**. This new form is a pretty large-sized double-armored clupeomorph. The total length of the holotype (Figs. 2A-B) is about 526 mm, and the known largest incomplete specimen, NHMG 033659 (Fig. 3A), with the preserved portion reaches 638 mm in length, and the distance from the anterior margin of the lacrimal to the caudal fin base is about 585 mm. The fish has an elongate fusiform body. The standard length in holotype is about 3.3 times of maximum body depth. The anterior dorsal margin of the fish body is rounded and convex, without a marked angle at the origin of the dorsal fin as the typical members of paraclupeids. The ventral border in front of the insertion of the pelvic fin is also convex, but is straight and obliquely rising upwards behind the insertion, making the posterior part of the body gradually

narrowing caudally. The origin of the dorsal fin is posterior to the level of the insertion of the pelvic. The anal fin has a long base. The caudal fin is deeply forked. There are complete series of predorsal and ventral scutes along the dorsal and ventral margin of the body respectively. The meristic characters are listed in Table 1.

(2) **Skull Roof**. The head is slightly longer than deep (Figs. 2A; 4A). The skull roof above the ~~eye~~ is narrow. The frontal is a long bone, with its posterior one-fourth expanding laterally. There is a longitudinal ridge ~~of~~ the supraorbital sensory canal running along the dorsal surface of this bone (Figs. 4A-B; 5). The frontal sutures with the anterior edge of the parietal posteriorly. Two parietal bones meet at the midline, at least in the anterior part (Fig. 4A-B), as in the case of the primitive clupeomorphs (Grande, 1985). No fontanelle between the anterior portions of the frontals is observed, which is often present in clupeoids and *Paraclupea chetungensis* (Chang and Grande, 1997). Anterior to the frontal is the mesethmoid, which bears a lateral process on each side (Fig. 5). Lateral ethmoid, contacting the frontal at its anteriolateral margin, is situated anterior to the orbit, forming the lateral portion of the anterior wall of the orbit (Figs. 4A-B). The outlines of pterotic and sphenotic are not clear. But the strong ventrally directed process of the autosphenotic can be seen, lying in front of the head of the hyomandibula (Fig. 4A-B). The posttemporal is a very large bone (Figs. 4A-B; NHMG 004929). Supraoccipital is situated posteriorly and sutures with the parietals anteriorly. Supraoccipital crest is well-developed, being high and triangle-shaped, making the lateral profile of the skull roof with a distinct angle between the anterior and the posterior parts (Fig. 4A-B). The external surface of all the skull roof bones lacks ornamentation, except for a longitudinal ridge containing the supraorbital sensory canal (Figs. 2A-B, 4A, 5, 6A). No openings of the recessus lateralis are observed.

(3) **Opercular Series and Cheek Bones**. The opercle is trapezoidal in shape. Its ventral part is

wider than the dorsal part, with the anteroventral corner protrudes downward and a little bit forward. The depth of the opercle is about 1.5 times of its width. No ornamentation on the surface of the opercle can be observed (Figs. 4A, 6). Two arms of the preopercle, with the dorsal branch slightly longer than the ventral branch, form an obtuse angle. The preopercular sensory canal runs along the mid-line of the bone sending out several branches backwards and downwards. Interopercle and subopercle are long and thin, with smooth surface (Figs. 4A-B, 6A). About 8-9 branchiostegal rays can be detected in the holotype, although the outline of each ray is not very clear (Fig. 2A). In NHMG 033659, five of the posterior branchiostegal rays of the right side can be counted below the interopercular bone, while four displaced, slender anterior branchiostegal rays are discernible in the position anterior to the interopercle (Fig. 4A-B).

(4) **Circumorbital Bones**. There is an arched, long bone above the frontal bone in NHMG 033659 (Fig. 4A-B), we guess that it ought to be the supraorbital bone displaced from its original position. The sclerotic ring, consisting of two halves, can be observed in the posterior and anterior part of the orbit. Anterior to the orbit, there are two bones, which seem to bear sensory canals. The large, sub-trianglular, anterior thin bone is the lacrimal, whereas the posterior rectangle one may be the infraorbital 2 (Fig. 4A-B). Detached infraorbital bones are preserved in NHMG 033660 (Fig. 5).

(5) **Jaws and Palate**. The mouth is somewhat superterminal based on NHMG 004929. The oblique gap is relatively short, with the lower jaw articulation under the anterior border of the orbit (Fig. 4A; NHMG 004929). The upper jaw consists of a premaxilla, a maxilla and two supramaxillae. The premaxilla is a small, long, triangular bone, with a row of small conical teeth on its oral margin (Fig. 4C). The maxilla is a long bone, with its anterior part narrow and thick while its posterior part broadening into a thin blade and bearing a rounded ventral profile. The

oral margin of the thin blade is finely serrated. The anterior end of the maxilla develops into a round ethmoid head and a round palatine head (Fig. 5, NHMG 004929, 033684, 033686, 033689). Along the dorsal edge of the maxilla two supramaxillae can be detected in NHMG 004929 and 033659 (Fig. 4A). In NHMG 033689, two disarticulated supramaxillae bones seem to be roughly equal in size and similar in shape, and their external surfaces are smooth, except for a low ridge extending along its midline.

The dentary has a well-developed coronoid process. In NHMG 033681-3 and NHMG 038777, there is a single row of small conical teeth along the short tooth oral margin of the dentary (Fig. 4D-E). Teeth close to the symphysis of the two dentaries are slightly stouter than that in the rear. But in specimen NHMG 033660, no teeth can be seen on the oral margin of the dentary, which are probably missing during preparation or fossilization. Along the lower lateral margin of the dentary, the mandibular sensory canal is well developed with 6~7 pores (Fig. 5). The angulo-articular is a triangular bone with mandibular sensory canal running along ~~it~~ lower margin of lateral surface. Length of angulo-articular is about half of that of the dentary. Its posterior end forms the articular ~~process~~ for the quadrate (Figs. 4A-B, 5). The very small retroarticular bone is located below the postarticular head of the angulo-articular bone (Fig. 4A-B).

The parasphenoid can be partly observed in NHMG 033658 and 004929. It is difficult to judge if a basipterygoid process and the “osteoglossid” tooth patch of the bone is present or not due to the preservation. The quadrate, as is generally for teleosts, consists of a fan-like plate at its dorsal side and a rod-like posterior process at its ventral side. The articular head of the quadrate fits into the socket at the postero-dorsal end of the angulo-articular (Fig. 4A-B).

(6) **Hyoid Arch**. The area for hyomandibular articulation with the braincase is broad. The hyomandibula~~r~~ bears a thin, broad anter~~i~~o-dorsal plate and a long, narrow ventral shaft, which

ventrally connects the upper end of the symplectic (Figs. 4A-B, 5). The condyle for articulation with the opercle is large. From that level, a prominent ridge runs ventrally along the posterior margin of the inner surface of the shaft. The foramen for hyomandibular branch of facial never (VII.hm) is clear. The symplectic inserts the notch between the plate of the quadrate and its ventral process with its anterior end to complete the suspension of the lower jaw to the braincase (Figs. 4A-B). Detached entopterygoid is ~~shown~~ in NHMG 033660 and 033661. It is a broad, triangular bone, with numerous fine conical teeth covering its buccal side (Figs. 4F, 5). The metapterygoid is an expansive, trapezoid bone. Its anterior margin is posterior to the anterior margin of the quadrate, and its posterior margin reaches a relatively more dorsal position, almost in line with the hyomandibular condyle (Figs. 4A-B, 6A).

The anterior ceratohyal is a thick, sub-rectangular plate with its length about two times of its depth. Its dorsal margin is slightly convex, whereas its ventral margin is slightly concave. Its central part is pierced by a large elongated oval foramen (Figs. 4F, 5) as in primitive clupeomorphs (Grande, 1985). The posterior ceratohyal is a triangle plate without foramen within it. There is a small notch on its dorsal-posterior margin (Fig. 4G). The urohyal shows a narrow ventral keel and a vertical crest. Height of the crest gradually increases posteriorly (Fig. 5). Gill arches are not well-preserved, but many dislocated, long and pointed gill rakers with a bifid base which embraced the gill arches are observed in several specimens (Figs. 3A, 4F-G, 5). Length of the gill rakers varies from about one vertebral centrum to 2~3 time as long as a vertebral centrum or even more. There are numerous fine conical denticles recurved posteriorly throughout almost the upper edge of the gill rakers, differing from the situation in *Diplomystus* sp. from English chalk in which the rakers appear to be smooth throughout most of their length (Forey, 2004)

(7) **Paired Fins and Girdles.** Supracleithrum is small, lying below and posterior to the very developed posttemporal. The cleithrum is a long and S-shaped bone, with its upper end covered by the supracleithrum. Below the cleithrum is the developed, laminate coracoid with a large notch on its anterior margin (Figs. 4A, 5-6). The pectoral fin is located rather high in the flank. The fin is long, extending over the insertion of the pelvic fin in NHMG 033658 (Fig. 6A). In other specimens, the fin rays do not look so long, probably because of the distal ends of the fin rays were missing during the process of fossilization. Eighteen pectoral fin rays can be counted (Fig. 6A).

The pelvic girdle cannot be observed due to the covering of the abdominal scutes. The pelvic fin is small, with about 5~6 fin rays, inserted at the level in front of the origin of the dorsal fin (Figs. 2A, 6A). The length of the longest pelvic fin ray is equivalent to the span of 6~7 postpelvic scutes.

(8) **Dorsal and Anal Fins**. The origin of the dorsal fin is situated slightly posterior to the mid-point of standard body length. There are about 14 dorsal fin rays (Figs. 2A, 6A). The first two are short and unbranched, while the third to the fifth rays are the longest ones. Twelve pterygiophores are preserved in the holotype. The first is comparatively long and broad, inserted between the tenth and eleventh neural spines, whereas those posterior to it are much narrower (Fig. 2A).

The origin of the anal fin lies behind the end of the dorsal fin base, closer to the pelvic fin insertion than to the caudal fin base. The anal fin base is comparatively long, containing about 38 rays, of which the anterior six are longer than the posterior ones. At least 36 pterygiophores are preserved in the holotype. In specimen NHMG 038778, 38 pterygiophores can be counted. Anterior pterygiophores are longer than the posterior ones. The first pterygiophore inserts between the last pleural rib and the first hemal spine (Figs. 2A, 3A).

(9) **Vertebral Column**. Twenty-three caudal vertebrae, not including two ural centra, and nineteen abdominal vertebrae are recognized in the holotype (Fig. 2A-B). We added two to our counts for the vertebrae that normally lie under the superficial bones of the skull and pectoral girdle (e.g., opercle, cleithrum), thus, the total number of the preural vertebrae is about 44 in the holotype. The length and depth of the vertebra ~~is~~ about equal, except the last several ones which are shorter than the anterior ones (Figs. 2A, 3A). There are two longitudinal ridges along the lateral side of each vertebra, forming two pits on their lateral side (Fig. 3A). Halves of the neural arches fused medially. The hemal spines start from the 21st or 22nd centrum, and their length decreases gradually until the fourth or fifth preural centrum where they increase greatly to support the fin rays of the lower caudal lobe (Fig. 7).

Nineteen pairs of ribs are present in the holotype, but in NHMG 033659 only 18 pairs of ribs could be counted. All the pleural ribs insert deeply into the centra. Ventrally, these ribs touch the lateral wings of the abdominal scutes. There are numerous thin and long epineural and epipleural intermuscular bones. The epineural series extends from the occiput to the first preural centrum. The epipleural series starts from approximately under the last three abdominal vertebrae and extends to about the first preural centrum. Longest epineural reaches the length about five to six centra, and the epipleural is about the length of four to five centra (Figs. 2A-B, 3A, 6).

(10) **Caudal Skeleton and Fin**. Caudal skeleton and fin are preserved relatively well in specimens NHMG 011646-011651. The neural and haemal spines of the second to the fourth or fifth preural centrum are elongated and somewhat flattened in that of the second and third preural centrum, and support a few caudal fin rays and procurrent rays. The structure of the caudal skeleton, collectively, differs from that in clupeiforms but closely resembles that in

ellimmichthyiforms, i.e., bearing at least two autogenous uroneurals, and the first one without fusing with the first preural centrum as in clupeoidei, though it is long and thick, extending anteriorly to reach the anterodorsolateral side of that centrum. The second uroneural is much shorter than the first one, extending anteriorly only to the anterior end of the second ural centrum, although its distal end reaches that of the first one. It cannot be confirmed if a third uroneural is present or not. There are two free ural centra, the first one is about equal in size to the first preural centrun, but the second one is much shorter than the first one. Six hypurals are present. The proximal end of first hypural is in contact with but not fused to the first ural centrum, although the narrow second hypural is fused to this centrum with its proximal end. The hypural 3 is the largest. Anteriorly, its enlarged proximal end contacts with the distal end of the second ural centrum entirely constraining the hypurals above it to go forwardly to contact with this centrum; posteriorly, it expands, filling the entire space between the second and the fourth hypurals, then there is no diastema between them, as the case in *Armigatus brevissimus* and the Eocene *Diplomystus* species. The fourth to sixth hypurals are narrower and shorter in turn. The proximal end of parhypural fused with the first preural centrum, which has a long and broad neural arch and spine. There are three epurals (NHMG 011650). The caudal fin is deeply forked with the upper and lower lobes of about equal in length, containing 19 principal fin rays (I. 9-8, I), and eleven and nine procurrent rays above and below the principal caudal fin rays, respectively (Figs. 2A, 7). The proximal ends of the middle principal fin rays are preserved as impressions in NHMG 011648, but relatively well-preserved in NHMG 011649, from which we can see that these ends enlarge obviously. Caudal scutes can be seen in NHMG 011647.

(11) **Predorsal Bone and Scutes**. There are ten or eleven predorsal bones with thin anterior and posterior bony expansions. The anterior bones are broader than the posterior ones, and the

first three stretches almost vertically (Figs. 2A-B, 3A) or somewhat postero-ventrally (Fig. 6), whereas the rest antero-ventrally.

There is a series of scutes along the dorsal margin from the occiput to the origin of the dorsal fin in the holotype. The entire series includes about 55 small, equally-sized scutes (Fig. 2). For poor preservation, the details of the scutes cannot be observed in this specimen. In specimen NHMG 038778, about six predorsal scutes from just behind the occiput and about nine ones just anterior to origin of the dorsal fin can be recognized. The detail of the scutes cannot be observed for poorly preserved also. However, it can be detected in NHMG 033658 (Fig. 6), in which numerous small dorsal scutes are preserved along the dorsal margin from the occiput to the seventh predorsal bone. Most of the scutes are displaced, some of them are even upside-down and showing their smooth ventral surface, but many scutes show their dorsal surface ornamented with several radial ridges. In NHMG 033659, a few predorsal scutes with weak ridges are preserved anterior to the dorsal fin. In NHMG 033680, several displaced dorsal scutes bearing radial ridges as NHMG 033658 can be detected. No dorsal scutes are seen behind the dorsal fin base.

About 24 prepelvic scutes are counted from the posterior edge of the coracoid to the insertion of pelvic fin in the holotype (Fig. 2A-B) and in NHMG 033658 (Fig. 6). Fourteen postpelvic scutes are present in the holotype. Only first 11 postpelvic scutes are preserved in NHMG 033658. Several much smaller ventral scutes can be detected below the coracoids in the holotype or displaced in the lower part of the head in NHMG 033659. The scutes behind the coracoid bear strong ventral spine and much higher lateral wings. The lateral wings are wider at their ventral edges, but get narrower gradually dorsally, extending from the ventral edge of the body up to about one quarter of the way to the vertebral column (Figs. 2A, 3A, 6).

(12) **Squamation/Scales**. In NHMG 038778, impression of some ~~squamations~~ can be seen in the body above the vertebral column. The squamation is small in shape. The detail of it is not clear.

DISCUSSION

Phylogenetic Relationships of the New Form

Although the predorsal scutes of the new form do not expand laterally as in the diagnosis given by Grande (1982) of the Ellimmichthyiformes when he established the order, the presence of two parietals meeting at the midline, a beryciform foramen within the anterior ceratohyal, ornamentations on the predorsal scutes, and the structure of the caudal skeleton suggest that it apparently differs from clupeiforms but resembles ellimmichthyiforms (Grande, 1982, 1985). To further assess the systematic position of the new form, phylogenetic analyses are conducted.

Two data matrices were constructed for the phylogenetic analyses. Data matrix 1 (D1) used *Chanos chanos* as outgroup taxon, whereas data matrix 2 (D2) used *Elops~~e~~ saurus* taking the place of *Chanos chanos* as outgroup taxon. Each data matrix includes 55 morphological characters and 40 taxa (see Apeendix 2S-3S), being analyzed using parsimony and Bayesian inference methods respectively.

The analysis of the D1, using parsimony criteria, generated 4 equally most parsimonious trees (PMTs). A strict consensus tree of 189 steps was built, with a consistency index (CI) of 0.323 and retention index (RI) of 0.670 (Fig. 8, Appendix Figure 1S). The cladogram of the strict consensus tree (SCT1) shows two main clades of Clupeomorpha: Clupeiformes and Ellimmichthyiformes. The monophyly of the Ellimmichthyiformes, including *Ornategulum* as the most basal taxon, is supported by the following features: two parietals meeting at the midline (2:0), two supramaxillary bones (8:0), presence of the “basipterygoid” process (9:1), anterior ceratohyal with foramen (11:1), and three epurals (38:0). *Gasteroclupea* and *Sorbinichthys* lie in the basal position of the Ellimmichthyiformes, but do not form sister groups as suggested by Marramà et al. (2019) and Boukhalfa et al. (2019). Sorbinichthyidae *sensu* Murrey and Wilson 2013 including only two *Sorbinichthys* species, is strongly supported by a number of derived characters: broad dorsal process of the posttemporal (15:2), posterior predorsal scutes laterally expanded (41:1), the most posterior predorsal scutes enlarged (44:1), high number of abdominal scutes (51:2), but less number of postpelvic scutes (52:1). Monophyly of *Armigatus* is supported by sharp proximal end of first hypural (27:1), predorsal scute series incomplete (39:0). Monophyly of *Diplomystus* (exclude *D. solignaci* Gaudant 1971) is supported by the presence of sub-rectangular scutes in anterior and posterior predorsal series (40:1 and 41:1), and presence of series of spines on posterior margin of lateral wings of predorsal scutes (42:1). *Diplomystus solignaci* is a member of the paraclupeid clade as suggested by many previous studies (Alvarado-Oetega et al., 2008; Murrey & Wilson 2013; Figuereido & Ribeiro 2016; Marramà et al., 2019; Boukhalfa et al., 2019). *Armigatus* is in a more basal position than that of *Diplomystus* as suggested by Alvarado-Oetega et al. (2008) and Figuereido & Ribeiro (2016). Our new form, *Guiclupea*, forms sister group to *Diplomystus*. The synapomorphies of the two are high supraoccipital crest (4:1), pelvic-fin insertion in advance of dorsal-fin origin (22:0), number of predorsal scutes more than twenty (46:1). The membership of Paraclupeidae, not include *Kwangoclupea* and *Codoichthys* as some previous studies suggested (e.g., Murrey and Wilson, 2013; Francisco and Figueiredo, 2016; Marrama et al., 2018; Boukhalfa et al., 2019) but in some way consistent with the recent analysis conducted by Vernygona and Murray (in press), is supported by the dorsal outline forming a marked angle at dorsal-fin insertion (1:1), first uroneural extending forward to second preural centrum (32:0), and predorsal scutes with ridges on the dorsal surface (44:1).

The analysis of the D1 using Bayesian inference method, generated a Bayesian Inference tree (BIT) (Fig. 9). As in SCT1, the monophyly of *Sorbinichthys*, *Armigutus*, *Diplomystus*, and Paraclupeidae were supported, and *Guiclupea* is sister to *Diplomystus*. Unfortunately, the monophyly of the Clupeiformes cannot be supported, and *Gasteroclupea*, *Sorbinichthys*, and *Kwangoclupea* lies in a more derived position than that in SCT1.

The analysis of the D2, using parsimony criteria, recovered 16 PMTs. The SCT of the 16 PMTs (see Appendix Figure 3S) is 188 in step, the CI is 0.324, and the RI is 0.671. The cladogram of the SCT2 shows that *Ornategulum* is in a basalmost position of the superorder, i.e., *Ornategulum* does not belong to the Ellimmichthyiformes as suggested by SCT1 and BIT1. The monophyly of the Clupeiformes, *Sorbinichthys*, and the remaining members of the Ellimmichthyiformes clade exclusive of *Gasteroclupea* was all supported, and the last one has the same topology as in SCT1.

The topology of the BIT2, resulted from the analysis of D2, is very similar with that of the BIT1 except for the position of *Ornategulum* and *Denticeps*. In BIT2, *Ornategulum* lies in the most basal position as in SCT2, and *Denticeps* is sister group to the two clupeoid genera. It seems that the applying different outgroup taxa effects the position or the assignment of *Ornategulum*, as demonstrated by previous analyses (Murrey and Wilson, 2013; Marramà et al., 2019; Figuereido and Ribeiro 2017; Boukhalfa et al., 2019). In addition, the positions of *Armigatus*, *Gasteroclupea*, *Sorbinichthys*, *Kwangoclupea*, and *Codoichthys* are the same in the two SCTs and in the two BITs respectively, but different between the SCTs and the BITs. In BITs, *Armigatus* lies in the basalmost position of the order but it is not so in SCTs. In BITs, *Gasteroclupea* belongs to the Sorbinichthyidae as suggested by Marramà et al. (2019) and

Boukhalfa et al. (2019); but in SCTs, *Gasteroclupea* does not form sister group to *Sorbinichthys. Kwangoclupea* forms sister group to *Codoichthys* and lies in a relatively basal position in the two SCTs, whereas it lies in a relatively derived position and belongs to the Paraclupeidae in the two BITs. These differences between the general topologies of the SCTs and BITs probable due to that the information contained in the dataset is insufficient to draw firm conclusions about their relationships as pointed out in the recent analyses of the phylogeny of Ceratomorpha (Bai et al., 2020). To improve the understanding of relationships of the group, more phylogenetically informative fossils and more complete data are needed.

Although there are discrepancies between the MPTs and BITs, and between the trees with alternative outgroups, the general topologies of the four trees mentioned above are basically similar, and all the four trees suggest that the new form is a member of the ellimmichthyiforms and forms a sister group to *Diplomystus*. The close relationship of them is supported by high supraoccipital crest (4:1), pelvic-fin insertion in advance of dorsal fin origin (22:0), and number of predorsal scutes ≥20 (46:1). Actually, in addition to these synapomorphies, the new form and *Diplomystus*, especially the Eocene species, i.e., *D.dentatus* and *D. shengliensis*, share many more similar characters, such as having an elongated fusiform body form, dorsal outline curved gently, no ornamentation on the skull bones, with teeth on entopterygoid, high number of anal fin rays (23-25 in *D. birdi*, 27 in *D. dubertreti*, 38-41 in *D. dentatus*, about 39 in *D. shengliensis* and 55 in *Guiclupea superstes*), and no diastema between second and third hypural (but there is a gap between second and third hypural in the Later Cretaceous species, i.e., *D. birdi* and *D. dubertreti* (Chang & Maisey 2003, p27)). The last character also occurs in pristigasteroids, and osteoglossids, some elopomorphs, and a number of ostariophysans (Chang & Maisey, 2003). The differentiation between *Diplomystus* and *Guiclupea* is in the shape and ornamentation of the predorsal scutes (sub-rectangular vs. ovate, presence vs. absence of pectinate posterior border, dorsal surface smooth vs. with radial ridges), and the number of predorsal bones (6-8 vs. 10-11). Accordingly, the new form is a distinct genus and species, and can be easily distinguished from *Diplomystus*. Comb-like teeth along the posterior edges of the dorsal scutes is a derived character of *Diplomystus*. In addition to *Diplomystus*, sub-rectangular predorsal scutes also occur in most members of the Paraclupeidae. As far as the radial ridges on the dorsal surface of predorsal scutes is concerned, they usually occur in paraclupeids, such as *Paraclupea*, *Ellimmichthys*, *Ellimma*, *Triplomystus*, etc., these forms usually have a marked angle at the insertion of dorsal fin, and sub-rectangular dorsal scutes at least in the posterior part of the scute series. The new form is distinct from them in the shape of the body and predorsal scutes. Among species with ornamentation on predorsal scute, the new form resembles *Scutatuspinosus itapagipensis* in the shape of body and predorsal scutes (not laterally expanded), and posterior expansion of the third hypural, leaving no gap or notch between the second and third hypurals. However, there are obvious differences between the two forms in the number of predorsal scutes and anal fin rays, ornamentation on the skull roof bones, and the size and shape of the abdominal scutes. On the whole, the new form displays a mosaic combination of characters. It bears radial ridges on the dorsal surface of predorsal scutes as the paraclupeids, but the scutes are all about the same size as in *Armigatus* and *Diplomystus*. Consequently, *Guiclupea* can easily be distinguished from all known ellimmichthyiforms in number and morphology of the dorsal scutes. So that predorsal scutes with ridges on the dorsal surface are not unique to Paraclupeidae.

Body shape and size of the Ellimmichthyiformes

The ellimmichthyiforms are diverse both in general morphology and body size. Generally, ellimmichthyiforms show two types of body form. One bears a deep body, with the maximum depth/standard length (MD/ST) larger than 50%, some of them even with the MD roughly equal to, or slightly larger than the ST in adult specimens, e.g., in *Tycheroichthys dunveganensis* and *Rhombichthys intoccabilis* (Hay et al., 2007; Khalloufi et al., 2010). Most of this kind of fishes are referred to paraclupeids. The other kind of fishes have an elongate fusiform shape, the MD/ST often lower than 50%. They occupy a relatively basal position in the Ellimmichthyiformes, such as *Armigatus*, *Diplomystus*, and *Guiclupea*.

Body size of ellimmichthyiforms ranges from several centimeter to about 65 cm in TL. The known smallest fish is *Eoellimmichthys superstes* with the TL and ST about 17.5 mm and 13.7 mm, respectively (Marramà et al., 2019). Many species are with the TL shorter than 100 mm, such as *Armigatus alticorpus*, *A. dalmaticus*, *A. oligodentatus*, *Codoichthys carnavalii*, *Diplomystus shengliensis*, "*Diplomystus*" *trebicianensis*, *Ellimmichthys maceioensis*, *Eoellimmichthys superstes*, *Gasteroclupea branisai*, *Scutatuspinosus itapagipensis*, *Sorbinichthys africanus*, *Thorectichthys marocensis*, *T. rhadinus*, and *Tunisiaclupea speratus*. Species with TL larger than 200 mm are rare. The TL of *Rhombichthys intoccabilis* reaches about 230 mm in the holotype (Khalloufi et al., 2010, fig. 3). The predorsal length of *Horseshoeichthys armigserratus*, from the Maastrichtian of Canada, is 172 mm, with the estimated SL about 260-280 mm (Newbrey et al., 2010). Specimens with SL over 300 mm are only seen in *Diplomystus dentatus* from the Eocene of the eastern coast of the Pacific and *Guiclupea superstes* from the Oligocene of the western coast of the Pacific so far. The former reaches a TL of about 650 mm (Grande, 1982) while the latter reaches a ST about 600 mm. They should be the largest ellimmichthyiform fishes. It is noted that the order or the *Diplomystus* clade seems to show a trend to enlarge their body size. In the Cretaceous, members of this order usually have a small body length; it is until the end of the Cretaceous, some member (e.g., *Horseshoeichthys armigserratus*) became relatively large body-sized; in the late Paleogene, some members developed large body size. It is worth mentioning that the fishes with large body size all are members of *Diplomystus* clade (*Horseshoeichthys* forms sister group to *Diplomystus* species (Veryngora & Murray, in press)) and occur along the coast of the Pacific.

A recent study based on a comparative analysis indicates that across the Clupeiformes diadromous species are larger than non-diadromous species (Bloom et al., 2018). Another study based on over 4500 migratory and non-migratory species of ray-finned fishes also shows that migratory species are larger than non-migratory relatives in nearly all clades and across all modes of migration (Burns & Bloom, 2020). No association of body size with trophic position was found (Bloom et al., 2018). From these two studies, we have reason to speculate that the wide-spread *Diplomystus* clade possibly involve some diadromous or migratory species which have large-sized body and are able to be widely distributed along the coast of the Pacific, for increased body size is an adaptation to mitigate the energetic expense of long-distance migration (Bloom et al., 2018). Then the restriction of the species of the Sorbinichthyidae and Armigatidae to the circum-Mediterranean region may be associated with their small body size.

Paleobiogeographic history of the Ellimmichthyiformes

The Ellimmichthyiformes is an extinct cosmopolitan group of fishes, with members known from marine and non-marine sediments of South and North America, Africa, coastal regions of Mediterranean, and East Asia (Fig. 1). The oldest known so far are from Hauterivian-Barremian. It includes *Scutatuspinosus itapagipensis* and ~~*Eillmmichthys*~~ *longicostatus* from northeastern Brazil (Figueiredo & Ribeiro 2017; Cope, 1886), *Ezkutuberezi carmenae* from northern Spain (Poyato-Ariza et al., 2000), *Tunisiaclupea speratus* from southern Tunisia (Boukhalfa et al., 2019), and *Paraclupea chedungensis* from eastern China (Sun, 1956; Chang & Grande, 1997; Hu et al., 2017). All these species belong to the Paraclupeidae. The paraclupeid fishes are abundant during late Early Cretaceous (Aptian-Albian). There are *Ellimma branneri* and *Ellimmichthys maceioensis* from Alagoas (Schaeffer, 1947; Chang and Maisey 2003; Malabarba et al., 2004), and *Ellimma longipectoralis* from Santos Basin (Polck et al., 2019) of Brazil; *Ellimmichthys goodi* from Equatorical Guinea (Eastman, 1912); and *Paraclupea seilacheri* from Puebla, Mexico (Alvarado-Ortega and Melgarejo-Damián 2017). In addition to paraclupeids, there are *Codoichthys carnavalii* from the Aptian of Brazil (de Figueiredo and Ribeiro, 2016) and *Foreyclupea loonensis* from the Albian of Canada (Vernygora et al., 2016, the authors thought this species should be closely related with *Scutatuspinosus itapagipensis*). The close relationship between the Early Cretaceous fish faunas from northeastern South America and from western Africa might have resulted from the contiguous margins of Brazil and West Africa during the Early Cretaceous (Chang and Grande, 1997). But there is little geologic evidence to support an Early Cretaceous non-marine paleogeographic connection between the eastern Asiatic margin and western Gondwana. Consequently, the distribution pattern of paraclupeids in the Early Cretaceous arouses a biogeographic conundrum. No favorable hypothesis well deciphers this distribution pattern to date. Chang and Maisey (2003) suggested that either a substantial portion of their non-marine fossil record is missing or their distribution involved marine dispersal.

During the early Late Cretaceous, the Ellimmichthyiformes reaches its greatest diversity. Not only the Paraclupeidae is highly diversified in the Mediterranean region and extended their range to North America (*Tycheroichthys dunveganensis* from Canada, Hay et al., 2007), but all other main ellimmichthyiform clades, i.e., Sorbinichthydae, Armigatidae or *Armigatus*, and *Diplomysus*, occurred and flourished in the Cenomanian with their oldest record from the eastern Tethys (Lebanon) (Woodward, 1895; Signeux, 1951; Grande, 1982; Zhang et al., 1985; Bannikov & Bacchia, 2000; Murray & Wilson, 2011; 2013; Murray et al., 2016). With all main clades first occurring there, undoubtedly, the circum-Mediterranean region is a hotspot of the evolution of ellimmichthyiforms. Species of *Diplomysus* are also found from the Cenomanian English chalk (Forey, 2004). The diversity of ellimmichthyiforms during the early Late Cretaceous was probably resulted from the global sea-level rising and the consequential land-sea distribution which increased food input, dispersal routes, and habitat fragmentation for these fishes (Boukhalfa et al., 2019). In the end of the Cretaceous, the diversity of the Ellimmichthyiformes suddenly declined. Only *Gasteroclupea branisai* from South America and *Horseshoeichthys armigserratus* from North America are known to date.

Rare ellimmichthyiforms survived after the Cretaceous-Tertiary boundary. *Gasteroclupea branisai*, *Eoellimmichthys superstes*, and *Diplomystus* clade are the exception. *Gasteroclupea branisai* firstly occurred in the Late Cretaceous of South America and survived to the Danian of Argentina and Bolivia (Signeux, 1964; Marramà & Carnevale, 2017). *Eoellimmichthys superstes* is a paraclupeid from the marine Eocene of Italy. Interestingly, *Diplomystus* clade not only survived up to the Oligocene, but also had a relatively wide distribution range along both sides of the Pacific coast (see Fig. 1). *Horseshoeichthys armigserratus* occurred on west coast of North America in the end of the Cretaceous (Newbrey et al., 2007). The Eocene *Diplomystus* occurred on both sides of the Pacific Ocean (along the coast of the Bohai Gulf, east China and the west coast of North America) bearing striking similarity in morphology (Zhang et al., 1985; Chang & Maisey, 2003). Their sister group, *Guiclupea superstes*, survived to the Oligocene as the youngest ellimmichthyiform fish. The Eocene “transpacific” distribution pattern of *Diplomystus* and other fishes and terrestrial vertebrates has long been noted by paleontologists (Chang & Chow, 1978; Grande, 1982, 1985; Zhang et al., 1985). A broad connection between Asia and North America in the Bering Strait area and temporary desalination of the Arctic Ocean could have facilitated the dispersal of these fishes (Chang & Maisey, 2003). It is interesting to find that all ellimmichthyiform fossil localities (Fig. 1) are near to the recent coast. Many contemporaneous fish fauna have been found from inland areas of China, Mongolia, and East Kazakhstan (Tang, 1959; Liu et al., 1962; Wang et al., 1981; Sytchevskaya, 1986), but no ellimmichthyiforms have been reported from there to date. In addition, most Recent Clupeomorpha inhabit in the sea. It seems reasonable to suggest that the origin and dispersal of these fishes must have something to be related with the sea.

CONCLUTION

Guiclupea superstes from the Oligocene of southern China is the youngest ellimmichthyiform known to date. Its occurrence indicates that the Ellimmichthyiformes had a wider distribution range and a longer evolutionary history than previously knew. *Guiclupea superstes* is closely related to *Diplomystus*, which suggests that the dorsal scutes with ridges on dorsal surface is not a character unique to paraclupeids.

Paraclupeids is very diverse and widely distributed during the Early Cretaceous, and survived to the Eocene in circum-Mediterranean area. *Sorbinichthys* and *Armigatus* are restricted to the Mediterranean region in the early Late Cretaceous. *Diplomystus* clade might originated not later than early Late Cretaceous, and disappeared from Europe and Middle East after early Late Cretaceous, but still prosperous in the Pacific coast in the end of the Cretaceous to Eocene and survived there until the Oligocene. This made the Ellimmichthyiformes to obtain a particularly long distribution range along the West Pacific.

There is still no consensus among ichthyologists on the phylogenetic relationships of the Ellimmichthyiformes, especially the relationship of *Armigatus* and *Diplomystus*, the position of *Gasteroclupea* and *Codoichthys.* Besides, there are discordances between the most parsimonious tree and the Bayesian Inference tree. To solve those problems, more informative specimens and characters are needed to add to the dataset.

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Figure 1

Map of the main localities of ellimmichthyiform fossils

Map of the main localities of ellimmichthyiform fossils

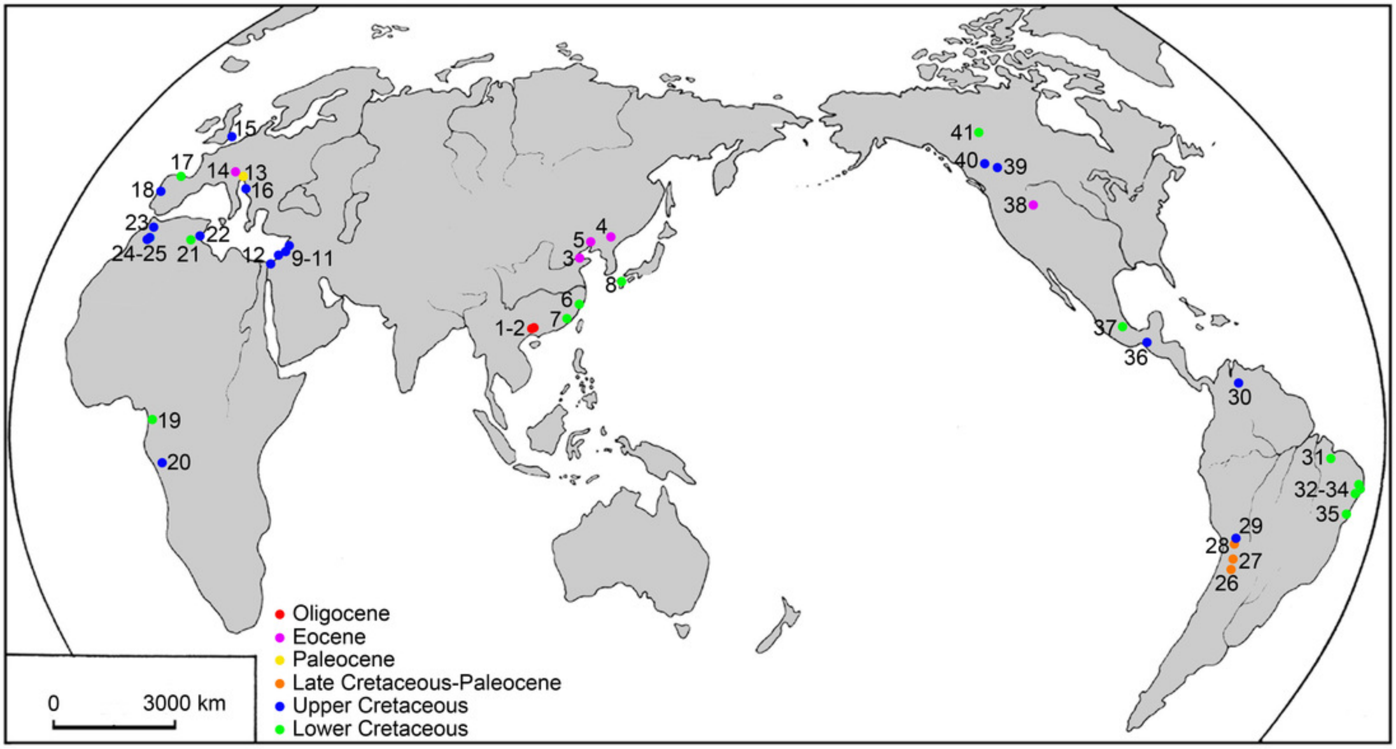

Figure 2

Guiclupea superstes, gen. et sp. nov

Guiclupea superstes, gen. et sp. nov. **A**, and **B**, photograph of the holotype (NHMG 005532); **C**, close up of the complete predorsal scutes series maeked by the ~~white~~ box in A.

Figure 3

Guiclupea superstes, gen. et sp. nov

A, photograph of the NHMG 033659; **B**, tentative restoration mainly based on the holotype and paratypes.

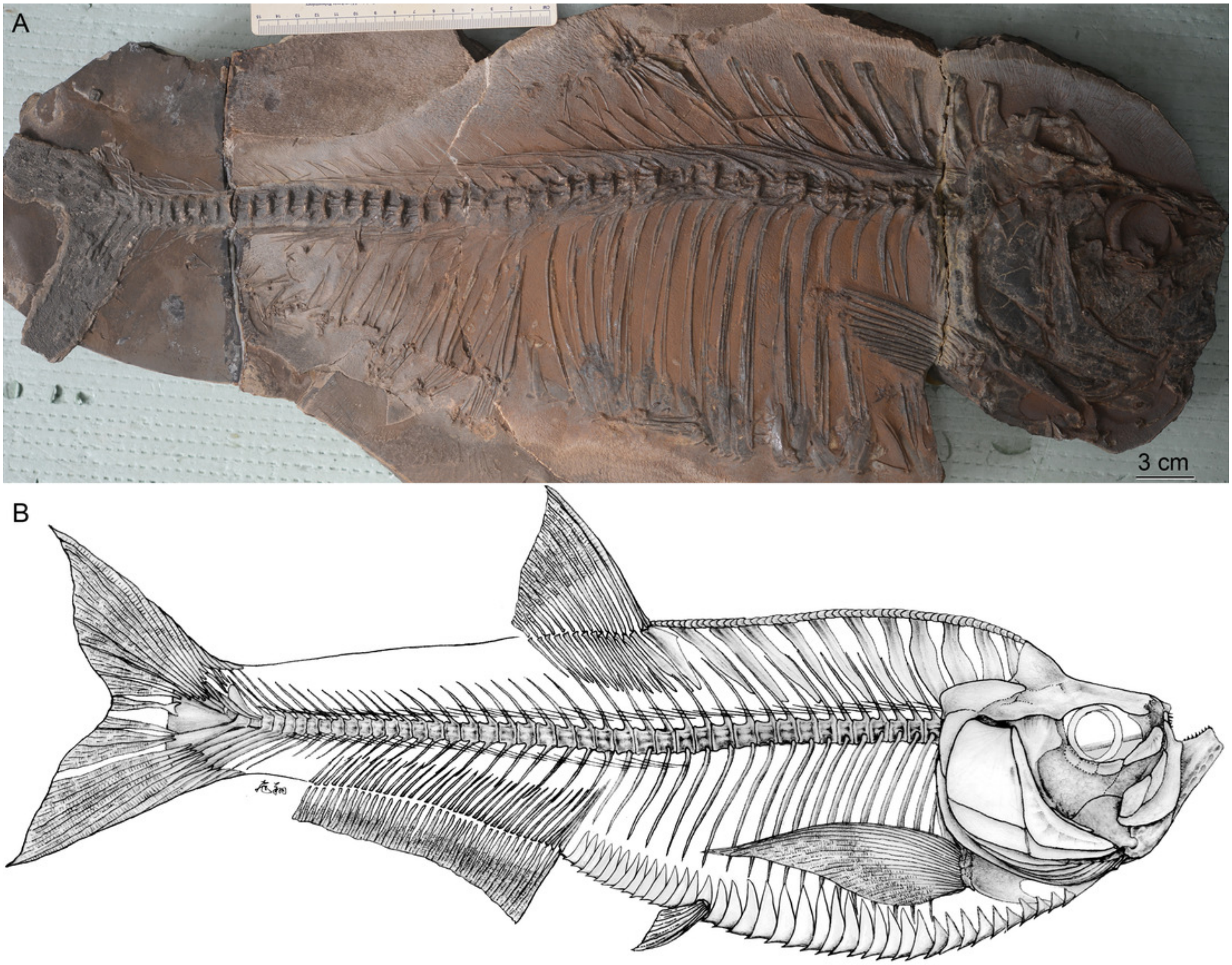

Figure 4

Guiclupea superstes, gen. et sp. nov

A, photograph, and **B**, line drawing of the head in NHMG 033659. Anterior facing right. **C**, photograph of a left premaxilla, NHMG 033685; **D**, photograph of an incomplete dentary, NHMG 033682, showing the oral teeth; **E**, photograph of a dentary, NHMG 033683; **F**, photograph, showing anterior ceratohyal and entopterygoid in NHMG 033661; **G**, photograph, showing posterior ceratohyals in NHMG 033680.

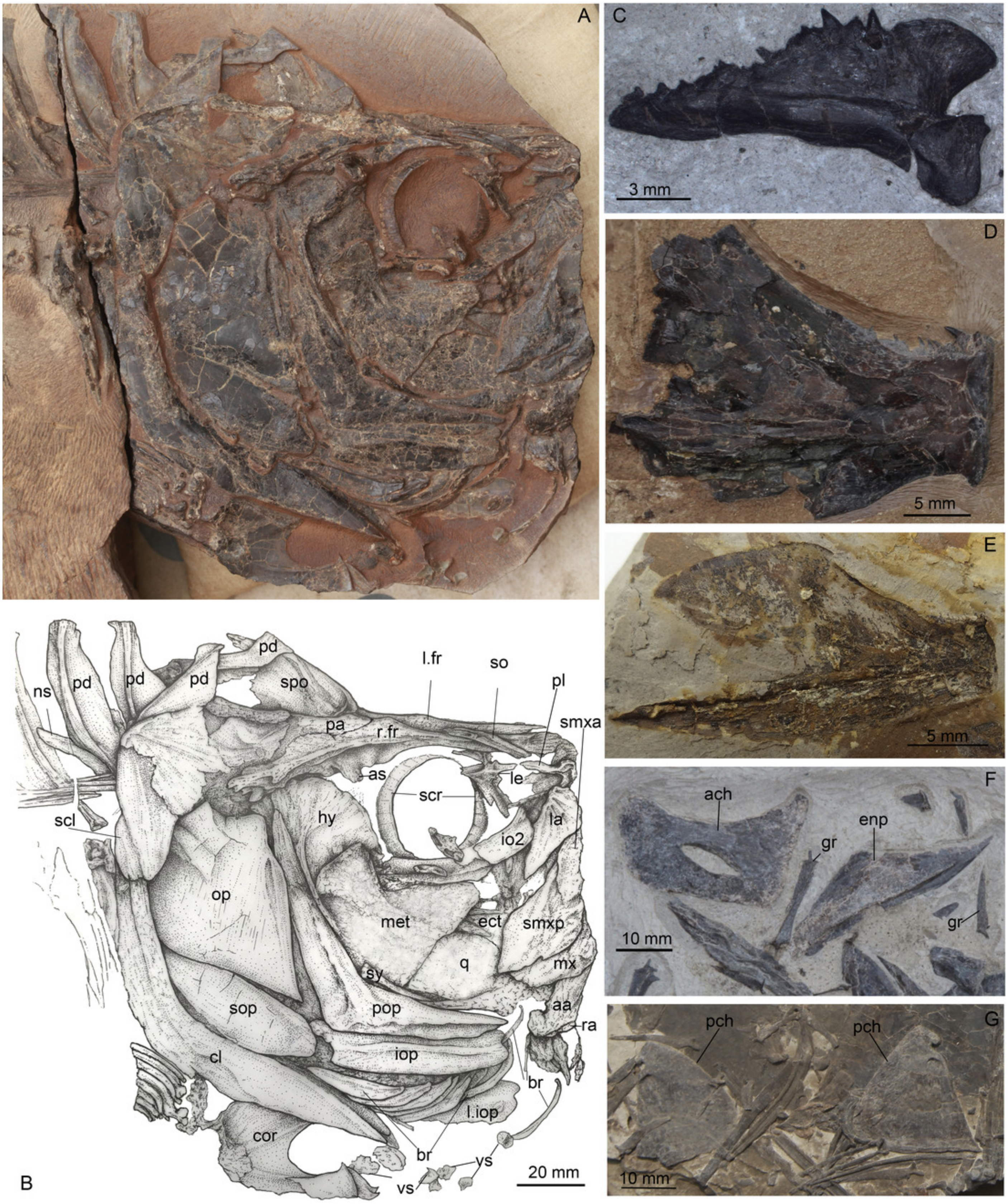
A
C
3 mm
D
5 mm
E
5 mm
F
ach
enp
gr
gr
10 mm
G
pch
pch
10 mm
B
pd
ns
pd
pd
pd
spo
l.fr
so
pl
smxa
pa
r.fr
as
scr
le
scl
hy
la
io2
op
met
ect
smxp
q
mx
sy
sop
pop
aa
ra
iop
cl
br
l.iop
cor
br
ys
vs
20 mm

Figure 5

Guiclupea superstes, gen. et sp. nov.

A, photograph and **B**, line drawing of the disarticular skull and anterior trunk bones of NHMG 033660.

Figure 6

Guiclupea superstes, gen. et sp. nov

A, photograph of NHMG 033658, **B**, and **C**, close up of the predorsal scutes in the black boxes of B and C in A, respectively.

Figure 7

Guiclupea superstes, gen. et sp. nov.

A, photograph and **B**, line drawing of NHMG 011648. Anterior facing left.

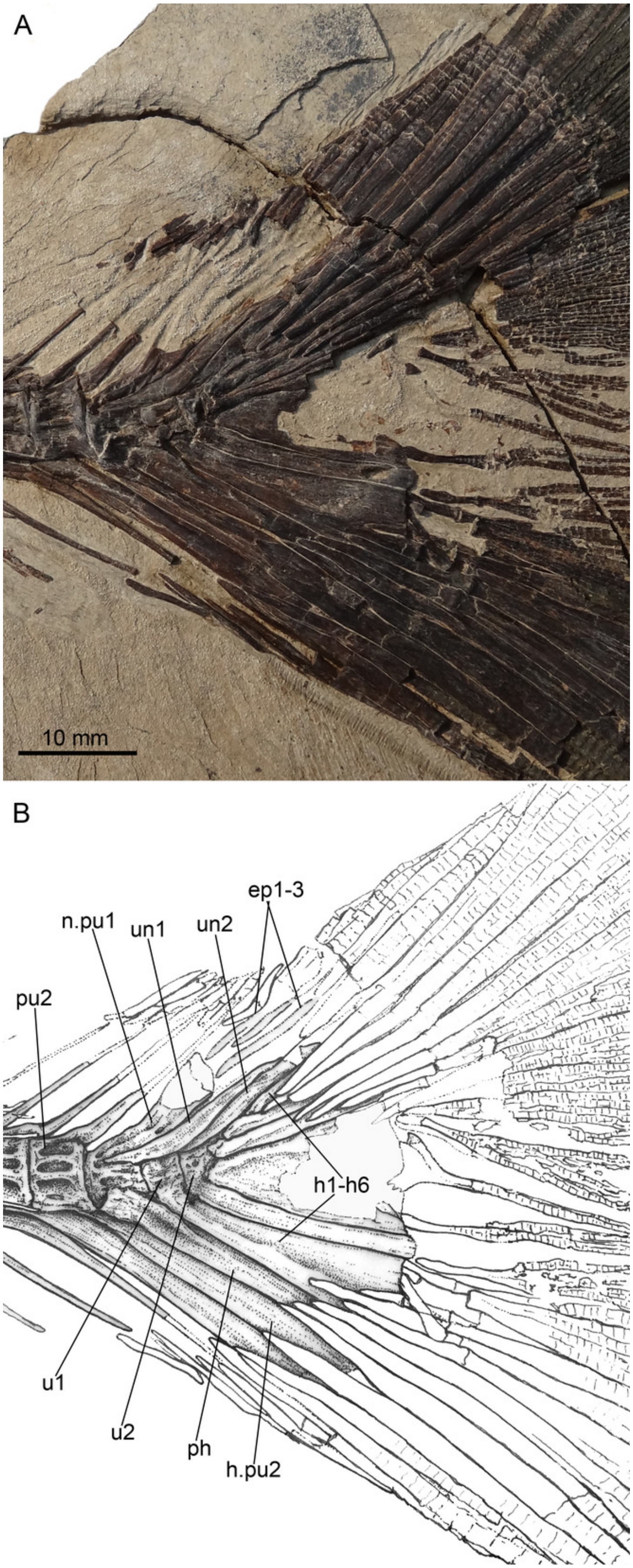
A
10 mm
B
ep1-3
n.pu1
un1
un2
pu2
h1-h6
u1
u2
ph
h.pu2

Figure 8

Strict consensus of most parsimonious trees

Strict consensus of most parsimonious trees retrieved in TNT 1.5 based on 55 morphological characters and 40 taxa, with *Chanos chanos* being used as outgroup taxa. Characters supporting each node are listed along corresponding branches. Characters above black spot have consistency index of 1. Numbers at each node represent Bremer support/bootstrap values. Only bootstrap values higher than 50% are shown on the tree.

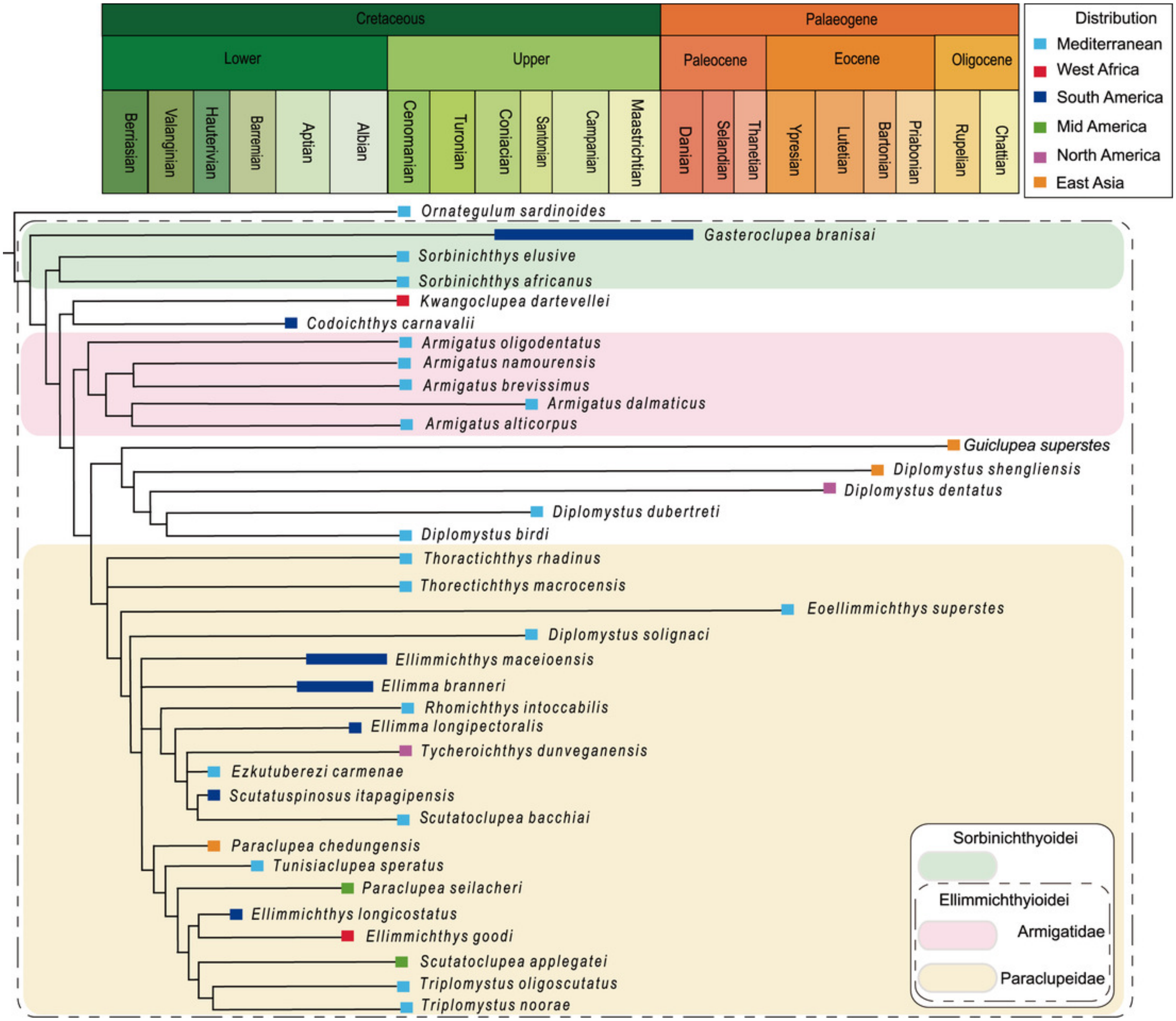
Cretaceous
Palaeogene
Lower
Upper
Paleocene
Eocene
Oligocene
Berriasian
Valanginian
Hauterivian
Barremian
Aptian
Albian
Cenomanian
Turonian
Coniacian
Santonian
Campanian
Maastrichtian
Danian
Selandian
Thanetian
Ypresian
Lutetian
Bartonian
Priabonian
Rupelian
Chattian
Distribution
Mediterranean
West Africa
South America
Mid America
North America
East Asia
Ornategulum sardinoides
Gasteroclupea branisai
Sorbinichthys elusive
Sorbinichthys africanus
Kwangoclupea dartevellei
Codoichthys carnavalii
Armigatus oligodentatus
Armigatus namourensis
Armigatus brevissimus
Armigatus dalmaticus
Armigatus alticorpus
Guiclupea superstes
Diplomystus shengliensis
Diplomystus dentatus
Diplomystus dubertreti
Diplomystus birdi
Thoractichthys rhadinus
Thorectichthys macrocensis
Eoellimmichthys superstes
Diplomystus solignaci
Ellimmichthys maceioensis
Ellimma branneri
Rhomichthys intoccabilis
Ellimma longipectoralis
Tycheroichthys dunveganensis
Ezkutuberezi carmenae
Scutatuspinosus itapagipensis
Scutatoclupea bacchiai
Paraclupea chedungensis
Tunisiaclupea speratus
Paraclupea seilacheri
Ellimmichthys longicostatus
Ellimmichthys goodi
Scutatoclupea applegatei
Triplomystus oligoscutatus
Triplomystus noorae
Sorbinichthyoidei
Ellimmichthyioidei
Armigatidae
Paraclupeidae

Figure 9

Cladogram

Cladogram resulting from Bayesian phylogenetic analyses based on 55 morphological characters and 40 taxa, with *Chanos chanos* ~~was~~ used as outgroup taxon. The numbers at the internal nodes are the posterior probabilities of the corresponding clades.

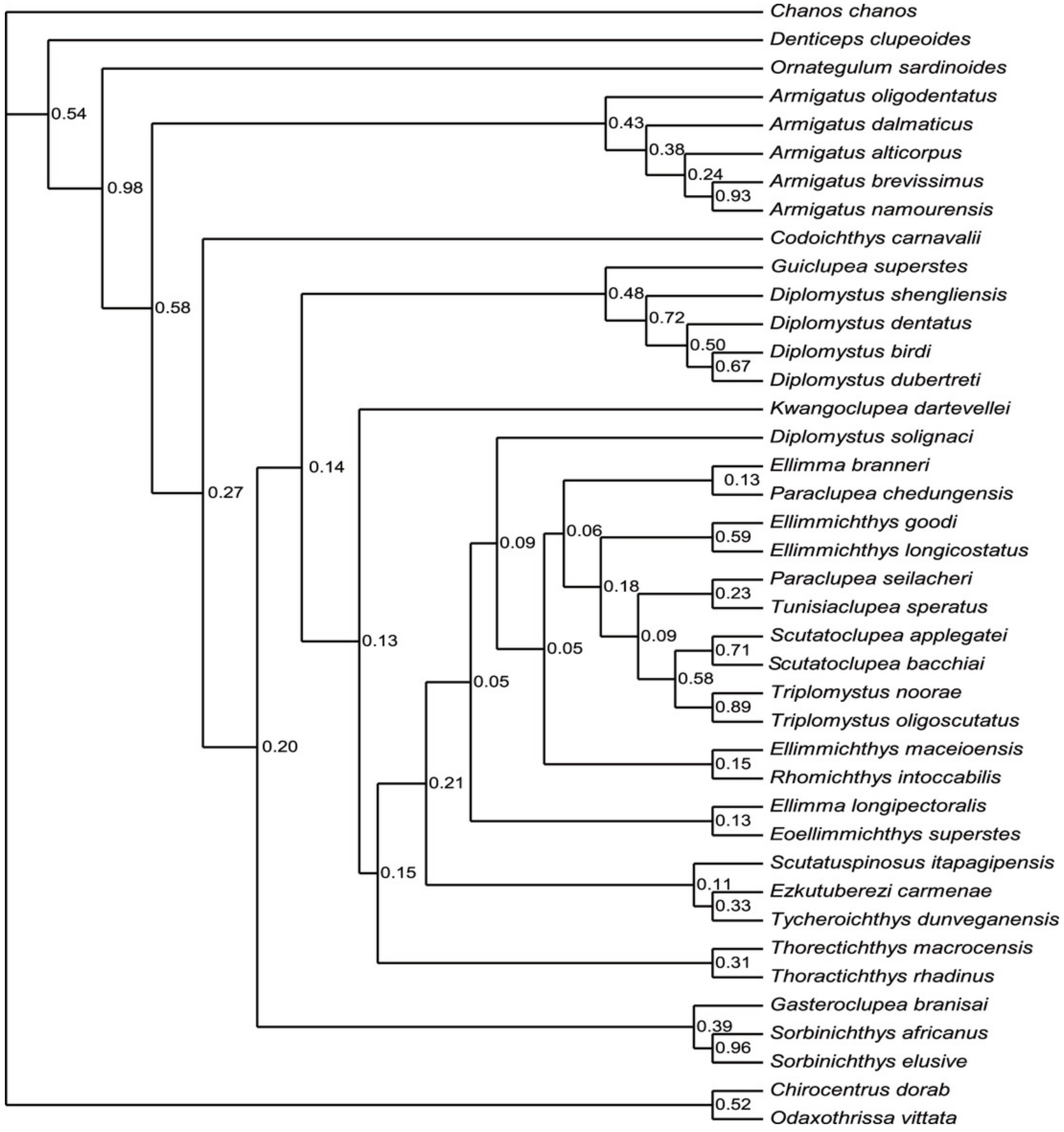
Chanos chanos
Denticeps clupeoides
Ornategulum sardinoides
Armigatus oligodentatus
Armigatus dalmaticus
Armigatus alticorpus
Armigatus brevissimus
Armigatus namourensis
Codoichthys carnavalii
Guiclupea superstes
Diplomystus shengliensis
Diplomystus dentatus
Diplomystus birdi
Diplomystus dubertreti
Kwangoclupea dartevellei
Diplomystus solignaci
Ellimma branneri
Paraclupea chedungensis
Ellimmichthys goodi
Ellimmichthys longicostatus
Paraclupea seilacheri
Tunisiaclupea speratus
Scutatoclupea applegatei
Scutatoclupea bacchiai
Triplomystus noorae
Triplomystus oligoscutatus
Ellimmichthys maceioensis
Rhomichthys intoccabilis
Ellimma longipectoralis
Eoellimmichthys superstes
Scutatuspinosus itapagipensis
Ezkutuberezi carmenae
Tycheroichthys dunveganensis
Thorectichthys macrocensis
Thoractichthys rhadinus
Gasteroclupea branisai
Sorbinichthys africanus
Sorbinichthys elusive
Chirocentrus dorab
Odaxothrissa vittata
0.54
0.98
0.58
0.27
0.43
0.38
0.24
0.93
0.14
0.48
0.72
0.50
0.67
0.13
0.20
0.13
0.09
0.06
0.59
0.18
0.23
0.09
0.71
0.58
0.89
0.05
0.15
0.05
0.13
0.21
0.15
0.11
0.33
0.31
0.39
0.96
0.52

Table 1(on next page)

TABLE

Measurements and counts for the specimens of the † *Guiclupea superstes*, gen. et sp. nov.

Measurements are in millimeters.

TABLE 1. Measurements and counts for the specimens of the †*Guiclupea superstes*, gen. et sp. nov. Measurements are in millimeters.

	004929	005532	033658	033659
total length		526.0		630+
standard length (SL)	502+*	453.0	410+	585+
head length	175	132.0		140+
head length/SL		29.1%		
head depth	169.0	116.0		165+
body depth	213	137.0	150	210
body depth/SL		30.2%		
predorsal length	333.5	252.8		310+
predorsal length/SL		55.8%		
prepelvic length	293.7	242.0		260+
prepelvic length/SL		53.4%		
preanal length	387.0	309.3		358+
Preanal length/SL		68.3%		
dorsal fin rays		Ii, 12	at least 13	
anal fin rays		~35		
pterygophores of anal fin		~36	29+	22+
pectoral fin rays		at least 12	18	12+
pelvic fin rays		5~6	5~6	
abdominal vertebrae	20	22	20	20
caudal vertebrae (exclude u1, u2)	12+	23		24
total vertebrae (exclude u1, u2)	32+	45		44
predorsal bones	10	10 or 11	10	10
abdominal scutes	at least 36	~38	35+	27+
pre-pelvic scutes	~24	~24	~24	16+
post-pelvic scutes	at least 12	14	11+	11+
pre-dorsal scutes		55	27+	
pairs of ribs	18	20	18	19

*: "+" stand for the actual digital larger than this digital because of the specimen is incomplete or not well-preserved.