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A primitive clupeomorph from the Albian Loon River Formation (Northwest Territories,
Canada)

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Abstract: *Foreyclupea loonensis*, gen. et sp. nov., is described from the early/middle Albian Loon River Formation of the Northwest Territories, Canada. The only specimen of the new species was originally described as a part of an enigmatic taxon *Erichalcis arcta* in 1975, which was assigned to the Clupeomorpha. Since then, *E. arcta* has proven to be a composite taxon, made up of clupeomorph and non-clupeomorph specimens. The non-clupeomorph material was redescribed as a Euteleostei *incertae sedis* and retained the species name.

Described herein is the fossil clupeomorph specimen originally assigned to *Erichalcis arcta*. As in other members of the superorder Clupeomorpha, the ventral margin of the body in the specimen is covered with spiny scutes and the supratemporal commissural sensory canal passes through the parietals. Along with these diagnostic characters, the new taxon also shows primitive traits of the basal members of the group, including a medioparietal skull roof, unfused halves of the neural spines of the abdominal vertebrae, and no evidence of presence of the *recessus lateralis*. When included in a phylogenetic analysis of the Early Cretaceous clupeomorphs, the new species forms a clade with the Early Cretaceous clupeomorphs from Mexico and Brazil, *Ranulfoichthys dorsonudum* and *Scutatuspinosus itapagipensis* respectively.

Key Words: Osteichthyes, phylogeny, Early Cretaceous, Ellimmichthyiformes, *Erichalcis*

30

31 Introduction

32 The extant members of the superorder Clupeomorpha (herrings and allies), all in the order
 33 Clupeiformes, include more than 400 species in both marine and freshwater habitats, and include
 34 some of the most numerically abundant and commercially most important fishes, but little is
 35 known about their early evolutionary history. The majority of fossil members of this group are
 36 placed in the extinct order Ellimmichthyiformes. The earliest fossil record of the clupeomorph
 37 fishes dates from the early Early Cretaceous deposits of Europe, Asia, and South and North
 38 America. Already at that time clupeomorphs had a broad environmental distribution, occurring in
 39 freshwater, marine, and brackish water settings. Their remarkable ecological plasticity
 40 apparently allowed for a successful dispersal worldwide. The most diverse and abundant fossil
 41 material of this group of fishes is known from the Aptian–Albian deposits of Brazil and from
 42 Late Cretaceous deposits of the Mediterranean region (e.g. Poyato-Ariza et al. 2000; Taverne
 43 2002; Chang and Maisey 2003; Forey et al. 2003; Malabarba et al. 2004; Murray and Wilson
 44 2013; Silva Santos and Silva Correa 1985). These deposits have yielded a large number of
 45 ellimmichthyiform taxa.

46 In Canada, the early fossil record of the Clupeomorpha is limited to only a few mid- to
 47 Late Cretaceous species: *Horseshoeichthys armaserratus* Newbrey et al. 2010, from the
 48 Maastrichtian Horseshoe Canyon Formation, *Tycheroichthys dunveganensis* Hay et al. 2007,
 49 from the Cenomanian Dunvegan Formation, and an enigmatic taxon, *Erichalcis arcta*, first
 50 described by Forey (1975) from the early/mid Albian deposits of the Loon River Formation.
 51 Description of the last taxon was based on sixty nine specimens collected in 1972 that showed a
 52 perplexing combination of characters. Forey (1975) recognized *Erichalcis* as Clupeiformes

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incertae sedis mainly based on the presence of abdominal scutes; however, he noted that unlike other clupeomorphs the new taxon had enlarged modified scales along the lateral midline of the body and showed specialized features of the caudal skeleton—fusion of the upper hypurals, first preural centrum without a neural arch, and laminar flanges associated with the haemal spine of the second preural centrum and neural spines of the third and second preural centra. This perplexing combination of characters led Forey (1975) to the conclusion that *Erichalcis* represented a primitive clupeomorph and could not be classified as a member of either Denticipitoidei or Clupeoidei.

In his monograph on the classification of the clupeomorph fishes, Grande (1985) placed *Erichalcis* in his monotypic Division I as the sister group to all known recent and fossil clupeomorphs. He referred to a few specimens from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) collections, including the holotype (UALVP 8606) showing enlarged lateral line scales, paratypes UALVP 8598 and UALVP 8629 with modified caudal skeletons, and UALVP 17535 showing a complete series of abdominal scutes (Grande, 1985, fig. 5D).

Subsequent re-examination of the holotype and a number of paratype specimens of *Erichalcis arcta* led Arratia (1997) to the conclusion that this taxon belongs to the Euteleostei and is more closely related to salmoniforms than to clupeomorphs. Later, Hermus et al. (2004) described another species of *Erichalcis*, *E. conspicua*, from the middle Albian Christopher Formation, Nunavut, Canada. Similar to the type species, *E. conspicua* has enlarged, modified lateral mid-line scales diagnostic for the genus. These studies showed that the original *Erichalcis arcta* was a composite of euteleost and clupeomorph taxa; however, they did not investigate further the clupeomorph material originally assigned to *Erichalcis arcta sensu* Forey (1975).

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In the present study, we describe the clupeomorph specimen that was originally a paratype of *Erichalcis arcta*. This work includes morphological and phylogenetic analyses of specimen UALVP 17535, which represents the oldest known clupeomorph from Canada.

Geological setting

The fossil fish material was recovered from the Loon River Formation cropping out along the Hay River, southern Northwest Territories (60°01' N, 116°57' W). This formation is part of the Fort St. John Group and is dominated by black marine shales and limestones. This locality has yielded a number of vertebrate taxa including a holostean, an aspidorhynchiform, an ananogmiid, euteleosts, and at least two genera of ichthyosaurs (Forey 1975; Hermus et al. 2004; Maxwell and Caldwell 2006). The Loon River Formation has been dated as early to middle Albian (Rudkin 1964; Singh 1971). The most recent biostratigraphic revision of the Loon River Formation indicates that the upper interval of the formation may be late Albian in age, based on the presence of the foraminiferan *Miliammina manitobensis* and age-indicative dinocysts (Hathway et al. 2013).

Material and Methods

Description of the new taxon is based on a single specimen preserved in part and counterpart in black laminated shales. The specimen is incomplete, with only the anterior part of the fish preserved. This is the only specimen showing the abdominal series of scutes in the original collection of the fossil fish material from the locality catalogued in the collections of the University of Alberta Laboratory for Vertebrate Paleontology (UALVP). The specimen is catalogued as UALVP 17535, the part being 17535a and the counterpart 17535b.

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The morphological description is based on examination of the original specimen and of a latex peel of the part, using a Wild M3 stereomicroscope. All drawings and reconstructions of the specimen are based on microscopic examination and digital photographs of the specimen.

Comparative material

The following taxa of extinct and recent clupeomorphs were examined for the purpose of morphological analysis and comparative study: *Alosa sappidissima* (Wilson, 1811): Z-366; *Armigatus brevissimus* (Blainville, 1818): UALVP 5087, 17620, 47258; *Diplomystus dentatus* (Cope, 1877): UALVP 17731, 21163, 22860, TMP 1986.224.0081, 1986.224.0083 – 0086, 1986.224.0088 – 0091; *Dorosoma cepedianum* (Lesueur, 1818): Z-441; *Horseshoeichthys armaserratus* Newbrey et al., 2010: TMP 2001.045.00931; *Sorbinichthys africanus* Murray and Wilson, 2011: UALVP 51640 (holotype), 47186, 51641; *Thorectichthys marocensis* Murray and Wilson, 2013: UALVP 47178 (holotype), 51647, 51649, 51657, 51659; *T. rhadinus* Murray and Wilson, 2013: UALVP 51653 (holotype), 51664.

Institutional abbreviations: UALVP , University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada; TMP, Royal Tyrrell Museum, Drumheller, Alberta, Canada; Z, zooarchaeology collections of the Canadian Museum of Nature, Ottawa, Ontario, Canada.

Phylogenetic analysis

Cladistic analysis was performed using TNT 1.1 (Goloboff et al. 2008) employing a heuristic search method with 1000 replicates and tree bisection and reconnection (TBR) swapping algorithm. The most parsimonious trees (MPTs) retrieved by the initial analysis were

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used to construct strict consensus tree. Mesquite v 3.03 (Maddison and Maddison 2011) was used to construct a character matrix for the analysis and calculate tree length, and consistency (C.I.) and retention (R.I.) indices for the consensus tree. Ancestral state reconstruction was also carried out in Mesquite v 3.03 (Maddison and Maddison 2011).

The character matrix used for the phylogenetic analysis includes a total of 17 taxa and 62 characters (Appendix 1). We used ten early Cretaceous ellimmichthyiform taxa along with two Early Cretaceous putative clupeiforms (*Pseudoellimma gallae*, *Santanaclupea silvasantosi*), three extant clupeiform taxa (*Chirocentrus dorab*, *Odaxothrissa vittata*, and *Denticeps clupeoides*), and the gonorhynchiiform *Chanos chanos* (Forsskål 1775) (as a representative member of the Ostariophysii, sister group to the Clupeomorpha) for the purpose of out-group comparison.

Character descriptions and states were adopted from previously published works by Zaragüeta-Bagils (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013). The new taxon was scored based on the morphological description provided in this study and included to the character matrix (Appendix 2). All characters are unordered and equally weighted. Missing data for the characters are coded by question marks; inapplicable characters are coded by dashes.

Fossil taxa included in the phylogenetic analysis

Ellimma branneri (Jordan, 1910); *Ellimmichthys goodi* (Eastman, 1912), *Ellimmichthys longicostatus* (Cope, 1886), *Ellimmichthys maceioensis* Malabarba et al., 2004; *Ezcutuberezi carmenae* Poyato-Ariza et al., 2000; *Paraclupea chetungensis* Sun, 1956; *Pseudoellimma gallae* Figueiredo, 2009; *Ranulfoichthys dorsonudum* Alvarado-Ortega, 2014; *Santanaclupea*

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145 *silvasantosi* Maisey, 1993; *Scutatuspinosus itapagipensis* Silva Santos and Silva Correa, 1985;
146 *Triplomystus applegatei* Alvarado-Ortega and Ovalles-Damian, 2008.

147

148 **Systematic Paleontology**

149 Subdivision Teleostei Müller, 1845

150 Cohort Clupecocephala Patterson and Rosen, 1977

151 Superorder Clupeomorpha Greenwood et al., 1966

152 Order Ellimmichthyiformes Grande, 1982

153 Family Scutatuspinosidae Silva Santos and Silva Corrêa, 1985, new rank

154 Genus *Foreyclupea*, gen. nov.

155 DIAGNOSIS: as for type and only known species.

156 ETYMOLOGY: the genus is named in honor of Dr. Peter L. Forey in recognition of his great

157 contributions to paleoichthyology and his first description of the fossil fish material from the

158 Loon River Formation; and from the Latin ‘clupea’ to indicate clupeomorph affinities of the new

159 taxon.

160 TYPE AND ONLY KNOWN SPECIES: *Foreyclupea loonensis*, sp. nov.

161

162 ***Foreyclupea loonensis***, sp. nov.

163 (Figs. 1–3)

164 DIAGNOSIS: clupeomorph fish with a shallow body differing from other ellimmichthyiforms

165 (except *Ranulfoichthys dorsonudum*) in having at least two broad postcleithra and lacking

166 predorsal series of scutes; distinguished from *R. dorsonudum* by the pelvic fin insertion anterior

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to the origin of the dorsal fin and abdominal scutes with spine-like ascending lateral wings with strengthening ridge at the posterior margin.

ETYMOLOGY: the specific epithet is derived from the name of the formation where the specimen was found.

HOLOTYPE: UALVP 17535 (a, b) a single specimen in part and counterpart. The part showing the specimen in left lateral view (UALVP 17535a) preserves the complete head and anterior part of the body; the counterpart (UALVP 17535b) has only the postorbital part of the skull and the anterior part of the body preserved.

LOCALITY: Loon River Formation, Hay River, Northwest Territories, Canada.

AGE: Early/middle Albian (Early Cretaceous).

Description

General body form

This is a slender fish with a shallow body similar to that of some other Early Cretaceous clupeomorphs — *Scutatuspinosus itapagipensis*, *Ranulfoichthys dorsonudum*, and *Santanaclupea silvasantosi* (Silva Santos and Silva Correa 1985; Maisey 1993; Alvarado-Ortega 2014). The dorsal margin of the body, although distorted, seems to run in a smooth and straight line from the back of the head to the origin of the dorsal fin (Fig. 1). The predorsal part of the trunk appears to be uniformly deep with the body depth equal to 19 mm. The posterior part of the fish, including the anal and caudal fins, is missing and thus the standard length (SL) of the fish cannot be determined. The total length of the preserved portion is 56 mm. We estimate the SL of this fish would have been about 100 mm, if the proportions of this fish were similar to those of the three other Early Cretaceous clupeomorphs mentioned above (Fig. 2). The head is preserved

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in lateral view; it is relatively narrow, triangular and about 1.4 times longer than deep. The dorsal profile of the skull is a straight line from the tip of the snout to the back of the skull. Only the dorsal, pectoral, and pelvic fins are preserved in the specimen. The pelvic fin insertion is slightly farther anterior than the dorsal fin origin. Measurements and counts of the specimen are summarized in Table 1.

Skull

Skull bones are not well preserved, with many elements crushed, displaced or preserved only as impressions. The head, as is typical for clupeomorphs, is triangular and relatively narrow with a pointed snout (Fig. 3).

The ethmoid region of the skull is partially preserved with only the mesethmoid and lateral ethmoid visible in the specimen. The mesethmoid is a well-ossified bone with a blunt and bilobed anterior end that contacts the maxillary and premaxillary bones; however, details of the articulation cannot be determined. Posteriorly, the mesethmoid has two elongate processes that suture with the frontal bones. The lateral ethmoid is only partially visible in the specimen; it appears to be large, extending from the frontals to reach the parasphenoid.

The frontal bones are long, extending over the entire orbital and anterior part of the otic regions of the skull; they are narrow anteriorly and gradually expand posteriorly where they suture with the parietal and pterotic bones. The frontals contact each other in the midline leaving no frontal fontanelle; there is also no posttemporal fossa. In the posterior part, the frontal bones are ornamented with deep sinuous ridges similar to those in *Pseudoellimma gallae* (Figueiredo 2009; Fig. 3).

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The supraorbital sensory canal runs through the frontal bones. It is visible in the posterior part of the left frontal where the sensory canal becomes bone-enclosed. At the suture between the frontal, parietal and pterotic bones, the supraorbital canal gives off at least two branches.

The pterotic is a relatively large, wedge-shaped bone that contains the bone-enclosed supratemporal sensory canal. There are no openings for a *recessus lateralis* in the pterotic. The parietals are relatively small trapezoidal bones, located just above the posterior portion of the orbit. They are not separated by the supraoccipital and so contact each other in the midline (medioparietal condition). The suture between the parietals is not deeply sinuous as in *Ranulfoichthys dorsonudum* (Alvarado-Ortega 2014). The right parietal is marked with a transverse groove for the supratemporal commissure that is one of the diagnostic characters of the Clupeomorpha (Grande 1985). The parietal bones are ornamented with only a few sinuous ridges, much less pronounced than those of the frontals.

The supraoccipital is poorly preserved and only a low crest is distinguishable behind the parietals. The lateral surface of the braincase is distorted and it is impossible to determine details of the individual bones. Presence or absence of the *recessus lateralis* in the specimen cannot be confirmed.

Orbital region and hyopalatine bones

Circumorbital bones are not preserved in the specimen; only impressions of infraorbitals 3 and 4 can be identified. Infraorbital 3 is located in the posteroventral part of the orbit and appears to be a relatively large and expanded bone with an open groove for the infraorbital sensory canal (Fig. 3). The sensory canal continues dorsally where only a partial impression of infraorbital 4 is visible. A partially preserved bone in the posterodorsal portion of the orbit is

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identified as the sphenotic. Presence of the antorbital and supraorbital bones cannot be confirmed.

The parasphenoid is narrow and edentulous. Its anterior and posterior ends are obscured and the presence of the basipterygoid process, which would be expected in basal clupeomorphs (Chang and Maissey 2003; Zaragüeta-Bagils 2004; Alvarado-Ortega et al. 2008), is uncertain.

The hyomandibula is large; it has a single head and the shaft appears to be the same width as the head. No other hyopalatine bones are preserved in the fossil; there is fragmentary bone material present in the area where the ectopterygoid and endopterygoid bones would be expected, but details cannot be determined.

Jaws

The jaw bones are only partially preserved, with most bones displaced or preserved only as impressions. The premaxilla, maxilla, and two supramaxillae comprise the upper jaw. The premaxilla is only partially preserved; it is relatively short and small. The maxilla is a long and curved bone with a longitudinal ridge running at least half the length of the bone. It is very narrow anteriorly with a well-defined head that articulates with the premaxilla and mesethmoid; however, the details of the articulation cannot be determined. From its anterior tip, the maxilla widens as it extends posteriorly to just under the anterior margin of the orbit.

There are two supramaxillae above the maxilla (Fig. 3). The posterior supramaxilla is large, with a long antero-dorsal process that projects over the smaller anterior supramaxilla. Both supramaxillary bones bear fine longitudinal ridges.

The lower jaw is missing; there is only a partial impression of the right dentary in the specimen, suggesting that the mouth was most likely terminal or slightly upturned.

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258 There is no evidence of teeth on any of the jaw bones, but this may be an artifact of preservation.

259

260 **Opercular series and branchial arches**

261 The opercle is large, with a convex posteroventral margin; it is about twice as high as
262 long. The opercular bone is thickened anteriorly where it contacts the preopercle; just posterior
263 to the robust anterior ridge, there are fine striations in a form of four straight lines along the
264 anterior edge of the opercle. The subopercle is an elongate bone with a rounded ventral margin;
265 the surface of the subopercle is smooth, with no ridges or striations.

266 The preopercle is L-shaped with both limbs well developed; the dorsal limb is slightly
267 longer than the ventral limb. The surface of the bone is smooth. The preopercular sensory canal is
268 enclosed in bone and runs close to the anterior margin of the preopercle, giving off at least six
269 secondary branches. The interopercle is elongate, with a prominent longitudinal groove close to
270 the dorsal margin of the bone.

271 The ceratohyal elements are not preserved in the specimen. At least six branchiostegal
272 rays are visible below the interopercle but 'clupeoid' projections (McAllister 1968) cannot be
273 distinguished on them. The branchiostegals gradually become wider and more robust from the
274 anterior to the posterior ones.

275

276 **Vertebral column**

277 The vertebral column is incompletely preserved and obscured in the specimen and so the
278 total number of vertebrae as well as details of the individual vertebral centra cannot be
279 determined (Fig. 1). Based on the number of ribs and neural spines visible, there are
280 approximately 25 vertebrae present. Abdominal vertebrae are cylindrical, about 1.5 times longer

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than high. Neural spines associated with the abdominal vertebrae are paired. There are 22 or 23 pairs of pleural ribs. The ribs are very long and thin; the anterior ten ribs are curved while the posterior 12 or 13 ribs have a sinuous shape. It is difficult to determine details of the rib articulations in the fossil, but it appears that the anterior-most ribs articulate in deep pits of the abdominal centra.

Intermuscular bones are well developed in the specimen and present in at least two series: epineurals, and epipleurals; epicentral may also be present in the specimen, but due to the poor preservation this cannot be concluded with certainty. The epineurals are associated with all vertebral centra visible; they are thin and long, reaching the length of approximately 2 centra. The epipleurals are shorter than the epineurals; their length is equal to 1.5 vertebral centra.

Paired fins and girdles

The pectoral girdle is partially preserved. The posttemporal is present; however, its details cannot be accurately determined. The ventral arm of the posttemporal is expanded and ovoid, but very little can be inferred about the antero-dorsal process of the bone. Just below and posterior to the posttemporal, an elongated supracleithrum is visible; it has been displaced during preservation and appears as a flat and slightly curved bone.

The cleithrum is L-shaped, similar to that of *Ranulfoichthys dorsonudum* (Alvarado-Ortega 2014) and *Pseudoellimma gallae* (Figueiredo 2009), but with a more slender and pointed dorsal limb (Fig. 3). The ventral limb of the cleithrum is poorly preserved but it appears to be broader than the dorsal limb. There are at least two flat, ovoid postcleithra in the specimen, preserved well behind the cleithrum, that have been displaced posteriorly during preservation. Both postcleithra are broad, unlike the rod-like postcleithra described in some

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ellimmichthyiforms (*Armigatus*, *Diplomystus*, and *Sorbinichthys*) and most clupeiforms; the ventral postcleithrum is slightly elongated and pointed. The right coracoid is preserved overlying the left pectoral fin; it is a subtriangular bone with a convex dorsal margin. The scapula and radials are not preserved in the specimen. The pectoral fin is long, approximately equal to the length of seven abdominal vertebrae. There are 14 pectoral fin rays; the third and fourth rays are the longest in the series.

The pelvic fin is small and positioned anterior to the level of the origin of the dorsal fin (Fig. 1). The pelvic girdle is not preserved in the specimen. Both pelvic fins are visible in the specimen, with a total of 12 fin rays preserved; however, the left and right pelvic fins are clumped together and the number of rays in each fin is not clear. Based on the total fin ray counts, there are approximately 6 pelvic fin rays in each.

Median fins

Only the dorsal fin is preserved in the specimen; it originates approximately above vertebral centrum 20 or 21. The fin is almost complete but the last few rays are missing due to the partial preservation of the specimen. There are 11 dorsal fin rays preserved; the first two or three are unbranched and the first fin ray is shorter than the following rays. Distal ends of the third and fourth dorsal fin rays are not preserved, making it impossible to determine whether they are branched. Posterior to the fourth ray, the dorsal fin rays are branched and gradually become shorter.

The dorsal fin is supported by at least 12 pterygiophores. The first pterygiophore is a large and complex element that appears to be made by the first three bones in the series which

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are connected by a lamina. The anterior ten pterygiophores are long and interdigitate with the neural spines.

Supraneural bones, dorsal and abdominal scutes

Supraneural bones are for the most part not preserved in the fossil and only the proximal ends of the bones can be identified. They are long and thin bones without the antero-posterior laminar expansions found in *Diplomystus* (Grande 1982). The supraneurals interdigitate with the neural spines of the anteriormost vertebrae. The exact number of the supraneural bones cannot be determined; there are two or three bones visible just in front of the dorsal fin in UALVP 17535a and at least three bones close to the occiput in the counterpart of the specimen, UALVP 17535b.

The dorsal margin of the body is largely obscured and the presence of a dorsal series of scutes cannot be determined. However, in the areas that are clearly visible in the specimen, just behind the occiput and anterior to the dorsal fin origin, there is no evidence of dorsal scutes.

The abdominal series of scutes is partially well preserved in the specimen (Fig. 1). There are approximately 19 ventral scutes, with 13 anterior to the pelvic fin insertion and six posterior to the fin. Additional scutes likely would have been present in the living fish anterior to the anal fin, but the fossil does not preserve this region. Each abdominal scute has a median keel that partially overlaps the succeeding scute in an antero-posterior direction, and a spine-like ascending lateral arm. These lateral arms are relatively short and cover less than one third of the distance between the vertebral column and the ventral margin of the body; each lateral spine is marked with a thick posterior margin forming a strengthening ridge.

Phylogenetic results

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In the present study, we performed a phylogenetic analysis of the Early Cretaceous (Berriasian – Albian) clupeomorphs with the purpose of clarifying interrelationships and early diversification patterns within the group. We included 12 fossil clupeomorph taxa from Europe, Asia, and South and North America that have been assigned to either *Ellimmichthyiformes*, *Clupeiformes*, or *Clupeomorpha incertae sedis*. Some of the taxa used in the present study (*Pseudoellimma gallae* and *Ranulfoichthys dorsonudum*) have never been included before in the phylogenetic analysis of the *Clupeomorpha*.

The analysis retrieved two most-parsimonious trees that were used to construct a strict consensus tree. The resulting strict consensus tree has a length of 135 steps, a consistency index (CI) of 0.519, and a retention index of 0.588 (Fig. 4). The bootstrap and Bremer support analyses revealed weak support for most clades (Fig. 4); only one clade (*Ellimmichthys longicostatus* + *E. goodi*) had a bootstrap support value higher than 50%. The strict consensus tree contains three polytomies: a basal trichotomy includes a clade consisting of the recent clupeiforms (*Odaxothrissa vittata*, *Chirocentrus dorab*, and *Denticeps clupeoides*), two fossil taxa that have been described as putative clupeiforms (*Santanaclopea silvasantosi* and *Pseudoellimma gallae*) and a large group containing ellimmichthyiforms and clupeomorphs of uncertain affinities (*Ornategulum sardinoides*). Another polytomy within the latter group includes three Early Cretaceous clupeomorphs, *Scutatuspinosus itapagipensis*, *Ranulfoichthys dorsonudum*, and *Foreyclupea loonensis*. The third polytomy is within the *Paraclupeidae* and includes *Ellimmichthys maceioensis*, *Paraclupea chetungensis*, and *Triplomystus applegatei*.

Results of the analysis suggest that *Ellimmichthys* is a polyphyletic genus, with *E. maceioensis* not forming a natural group with the type species, *E. longicostatus*, on any of the most parsimonious trees retrieved by the analysis. This agrees with the general pattern recovered

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by previous phylogenetic analyses that grouped *E. longicostatus* and *E. goodi* as sister-taxa (Zaragüeta-Bagils 2004; Alvarado-Ortega et al. 2008) and revealed *E. maceoiensis* as being closely related to the Late Cretaceous ellimmichthyiforms *Diplomystus solignaci* and *Rhombichthys intoccabilis* (Murray and Wilson 2013). However, none of the previous analyses included all three species of *Ellimmichthys* to provide a better comparison with the present results.

The new species, *Foreyclupea loonensis*, was recovered as a member of a clade that also includes *Scutatuspinosus itapagipensis* and *Ranulfoichthys dorsonudum*. This is the first time such a clade has been recovered in a phylogenetic analysis.

Discussion

Morphological examination of UALVP 17535 provides conclusive evidence that the new species, *Foreyclupea loonensis*, is a member of the superorder Clupeomorpha: the specimen shows a complete abdominal series of scutes and the supratemporal commissural sensory canal passing through the parietals. The former character has been regarded by many authors as a diagnostic feature exclusive to clupeomorph fishes (Whitehead 1963; Patterson 1970; Grande 1982, 1985; Arratia 1997). Unfortunately, because the specimen is missing its posterior part, no conclusions can be made about the structure of the caudal skeleton. In clupeomorphs, the caudal skeleton is characterized by an autogenous hypural 1 and the second hypural fused to the first ural centrum. These features, although not exclusive to the Clupeomorpha, in combination with other clupeomorph traits provide a reliable diagnosis for the group.

Along with the general clupeomorph characteristics mentioned above, *Foreyclupea loonensis* shows a mosaic of primitive and derived features that make further classification of the

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new taxon within the Clupeomorpha problematic. The cranial skeleton of *F. loonensis* shows the following plesiomorphic conditions: parietals contacting each other in the midline and absence of the *recessus lateralis*.

The parietal bones contacting each other medially (medioparietal condition of the skull roof) is a common plesiomorphic condition present in ellimmichthyiforms and many other groups of teleost fishes including ichthyodectiforms, osteoglossomorphs, elopiforms, salmoniforms and others (Grande, 1985; Arratia, 1997). Grande (1985) used this character to separate non-clupeiform clupeomorphs from more derived members of the order Clupeiformes that have parietals completely separated by the supraoccipital (lateroparietal condition).

Presence of the *recessus lateralis* is a highly diagnostic character exclusive to all extant members of the Clupeomorpha (equivalent to the order Clupeiformes). The evolutionary pattern of this character distribution within the group corresponds to the subdivision of the Clupeomorpha into two orders: Clupeiformes with a *recessus lateralis* and Ellimmichthyiformes without it. In the fossil taxa, presence of a *recessus lateralis* can be inferred from the reduced size of the dermosphenotic that does not carry the infraorbital sensory canal (Forey 1975; Grande 1985) and perforation of the pterotic with the openings for the cephalic sensory canals (Patterson 1970; Maisey 1993; Di Dario 2002). The dermosphenotic is missing in the studied specimen, but the preserved portion of the pterotic bone does not show any openings for the sensory canals; this may indicate that a *recessus lateralis* was primitively absent in the fish.

Foreyclupea loonensis also shows unfused neural spines of the abdominal vertebrae. This is a primitive condition that has been recognized in many teleost groups (Arratia 1997). Among the clupeomorphs, paired neural spines are present in the basal Early Cretaceous fossil taxa

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417 *Ranulfoichthys dorsonudum*, *Santanaclupea silvasantosi*, *Pseudoellimma gallae*, and members
418 of the Late Cretaceous genus *Armigatus*.

419 The new species is distinguished from other ellimmichthyiforms by the following
420 combination of derived characters: loss of the predorsal series of scutes, presence of at least two
421 broad postcleithra, and position of the pelvic fin anterior to the origin of the dorsal fin. Some of
422 these features also occur in *Scutatuspinosus* and *Ranulfoichthys*, basal clupeomorphs of
423 unresolved affinities. These characteristics suggest that *Foreyclupea loonensis* is a new taxon of
424 primitive clupeomorph with close affinities to the known species of the ellimmichthyiforms. This
425 conclusion is also supported by the results of the present phylogenetic analysis.

426 Based on the phylogenetic hypothesis presented here, the Clupeomorpha includes three
427 groups with unresolved phylogenetic relationships: the recent clupeiforms (*Chirocentrus dorab*,
428 *Odaxothrissa vittata*, and *Denticeps clupeoides*), Early Cretaceous putative clupeiforms
429 (*Pseudoellimma gallae* and *Santanaclupea silvasantosi*), and extinct ellimmichthyiforms
430 including *Ornategulum sardinoides*.

431 The recent clupeiforms as well as the two putative fossil clupeiform taxa, Barremian
432 *Pseudoellimma gallae* from the brackish deposits of the Coqueiro Seco Formation, Brazil, and
433 the middle/late Albian *Santanaclupea silvasantosi* from the black shales of the Santana
434 Formation, Brazil, are distinguished from the ellimmichthyiforms by the parietals completely
435 separated by the supraoccipital (2:1) and presence of the *recessus lateralis* (8:1). However, the
436 early clupeomorphs (*Pseudoellimma gallae* and *Santanaclupea silvasantosi*) also show some
437 primitive characteristics also present in the ellimmichthyiforms—*Santanaclupea* has the
438 ‘beryciform’ foramen in the anterior ceratohyal (this condition is unknown in *Pseudoellimma*
439 due to the missing ceratohyal elements); *Pseudoellimma* shares the following characters with

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ellimmichthyiforms: long and lanceolate neural spine of the first preural centrum (44:0), subrectangular scutes in the posterior part of the predorsal series (49:1). Both taxa also primitively retain hypural 1 in contact with the first ural centrum (28:0); in derived clupeiforms, hypural 1 is separated from the first ural centrum by a gap (Grande 1985; Chang and Maisey 2003).

In a strict consensus tree (Fig. 4), recent clupeiforms and fossil clupeomorphs (*Santanaclopea* + *Pseudoellimma*) form a trichotomy with a large clade of fossil non-clupeiform clupeomorphs. Members of this clade are different from the clupeiforms in having parietals contacting each other in the midline (2:0), lacking a *recessus lateralis* (8:0). This group also includes a problematic clupeomorph taxon, *Ornategulum sardinoides*; however, phylogenetic placement of this taxon requires further investigation that is beyond the scope of this study. In addition to the mentioned above characteristics (absence of the *recessus lateralis* and parietals contacting each other in the midline), fossil non-clupeiform clupeomorphs are characterized by having the anteriormost pleural ribs articulate with deep pits on the lateral side of abdominal centra and those located posteriorly articulate with well-developed parapophyses (19:1). The first two characteristics (medioparietal condition of the skull roof and absence of *recessus lateralis*) have been attributed to the ellimmichthyiforms (Grande 1985). Grande (1982, 1985) and Alvarado-Ortega et al. (2008) also recognized the presence of subrectangular predorsal scutes as a synapomorphy of the ellimmichthyiforms; however, this character was questioned by Chang and Maisey (2003) as being a reliable diagnostic feature of the order. The latter authors noted that due to the variability in the scute shape within the Ellimmichthyiformes, it is necessary to reevaluate the shape of the dorsal scutes as a single character supporting monophyly of the order. This large clade of non-clupeiform clupeomorphs includes two major groups: a clade containing

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the Neocomian (Valanginian – Barremian) *Scutatuspinosus itapagipensis* from Brazil, and the early/middle Albian *Ranulfoichthys dorsonudum* and *Foreyclupea loonensis* from Mexico and Canada respectively as a sister group to a clade of all ellimmichthyiform taxa included in the analysis: (*Ezcutuberezi carmeni* + (*Paraclupea chetungensis* + (*Ellimma branneri* + *Ellimmichthys maceoiensis* + *Triplomystus applegatei*)+ (*Ellimmichthys longicostatus* + *Ellimmichthys goodi*)).

The clade (*Scutatuspinosus* + *Ranulfoichthys* + *Foreyclupea*) includes primitive clupeomorphs of uncertain affinities. Members of this group have torpedo-shaped body with a smooth and slightly rounded anterior dorsal margin of the body (1:0), abdominal scutes with short ascending lateral ‘arms’ (58:0), and a homoplastic character — absence of a diastema between hypurals 2 and 3 (31:1, this feature also occurs in the ellimmichthyiform genera *Armigatus* and *Diplomystus*). We here adopt Scutatospinosidae (new rank, formerly subfamily Scutatospinosinae Silva Santos and Silva Correa, 1985, with type genus *Scutatospinosus*) as a name for this clade.

Unlike any other ellimmichthyiform species, *Ranulfoichthys dorsonudum* and *Foreyclupea loonensis* do not have a predorsal series of scutes; however, a complete series of predorsal scutes is present in *Scutatuspinosus*, the oldest member of the clade. This finding supports the idea that presence of a predorsal series of scutes is a primitive characteristic within the Clupeomorpha that is retained by some living members of the Clupeiformes. *Foreyclupea* and *Ranulfoichthys* share at least one more characteristic unique among the ellimmichthyiforms—presence of at least two expanded postcleithra. Grande (1985) regarded presence of two rod-shaped postcleithra as a diagnostic character for the Clupeidae; since then, long, rodlike postcleithra have been described in some ellimmichthyiforms: *Armigatus* (Forey et

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486 al. 2003), *Diplomystus* (pers.obs.UALVP 17731, 21163, 22860), *Thorectichthys* (Murray and
487 Wilson 2013), *Horseshoeichthys* (Newbrey et al. 2010), and *Tycheroichthys* (Hay et al. 2007).
488 Grande (1985) also noted that, in some clupeids, postcleithra can be moderately to broadly
489 expanded; however, this condition is not known in any ellimmichthyiform species.

490 *Foreyclupea* and *Ranulfoichthys* each share unique characteristics with *Scutatuspinosus*.
491 *Ranulfoichthys* and *Scutatuspinosus* have a unique morphology of the ascending lateral ‘arms’ of
492 the abdominal scutes — each ventral scute has very short, broad and subrectangular lateral
493 wings. This condition is different from the spine-like ascending processes of the abdominal
494 scutes observed in the extinct and Recent clupeomorphs (*Armigatus*, *Diplomystus*, *Sorbinichthys*,
495 *Thorectichthys*, *Ellimmichthys*, Clupeidae, Pristigasteridae) or the long spatula-like ascending
496 arms of abdominal scutes in ellimmichthyiform genera *Triplomystus*, *Tycheroichthys*, and
497 *Rhombichthys*.

498 For *Foreyclupea* and *Scutatuspinosus*, position of the pelvic fin anterior to the level of the
499 origin of the dorsal fin is recognized as a shared derived characteristic. This position of the
500 pelvic fin is not common among the ellimmichthyiforms or Recent clupeiforms and is considered
501 to be a derived feature among teleost fishes. Chang and Maisey (2003) also noted that the pelvic
502 fin is inserted in advance of the dorsal fin origin in *Ellimmichthys longicostatus*.

503 Another major group retrieved by the phylogenetic analysis contains all previously
504 recognized Early Cretaceous ellimmichthyiform taxa that have been included in the analysis; it
505 most closely corresponds to the family Paraclupeidae *sensu* Alvarado-Ortega et al. (2008) and
506 Murray and Wilson (2013). Grouping of these taxa in the analysis is supported by the following
507 characteristics: straight ascending dorsal margin of the body that forms a distinct angle at the
508 insertion of the dorsal fin (1:1), fused neural arches and spines of abdominal vertebrae (18:1), S-

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shaped cleithrum (22:1), and large lateral spines of the abdominal scutes (58:1). Within this group of ellimmichthyiforms, *Ezcutuberezi carmeni* from the Valanginian–Barremian of Spain appears as the most basal taxon; other ellimmichthyiform taxa were recovered in a sister group to *Ezcutuberezi* with two species of *Ellimmichthys* (*E. longicosatus* and *E. goodi*) forming a well-supported clade characterized by the broad distal end of hypural 2 (30:0), dorsal laminar expansion of the first uroneural (37:1), and increased number of predorsal scutes (54:2).

Overall, the results of the phylogenetic analysis of the Early Cretaceous clupeomorphs suggest that the clupeiforms and ellimmichthyiforms diverged in the early Early Cretaceous and formed separate lineages as early as in the Barremian (with the clupeiform *Pseudoellimma gallae* from Brazil, as well as the ellimmichthyiforms *Ezcutuberezi carmenae* from Spain, and *Scutatuspinosus itapagipensis* from Brazil). It is also worth noting that the oldest clupeomorphs, described from the Berriasian–Barremian, are known predominantly from freshwater and estuarine environments; this includes the Neocomian (Valanginian–Barremian) *Scutatuspinosus itapagipensis* from the lacustrine sediments of Reconcavo Basin, Brazil, *Ellimmichthys longicostatus* (Cope 1886) from the late Hauterivian – early Barremian estuarine deposits of the Marfim Formation, Brazil, *Ezcutuberezi carmenae* Poyato-Ariza et al., 2000, from the Valanginian–Barremian deltaic and lacustrine deposits of the Villaro Formation, Spain; and *Pseudoellimma gallae* from the Barremian brackish water deposits of the Coqueiro Seco Formation, Brazil. The evolutionary significance of this pattern is yet not clear but it may shed light on the origins of the diadromous behavior of some clupeomorphs as well as provide valuable information on the evolution of the osmoregulatory system in these fishes. It is clear that knowledge of the earliest members of the Clupeomorpha is crucial to our understanding of the complex evolutionary patterns of clupeomorph ecology and biogeography.

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Summary

The evolutionary history of the Clupeomorpha remains an unresolved issue. Major questions persist about clupeomorph origins, diversification between clupeiforms and ellimmichthyiforms, and biogeographic dynamics of these fishes. The early fossil record of clupeomorphs provides some valuable clues to these questions. *Foreyclupea loonensis*, gen. et sp. nov., is the oldest clupeomorph fossil described from Canada. Based on the primitive cranial characteristics (parietals contacting each other in the midline and absence of the *recessus lateralis*), the new species is classified as a member of the Ellimmichthyiformes. *Foreyclupea loonensis* is a remarkable taxon in showing a number of derived characteristics (absence of dorsal scutes, pelvic fin insertion anterior to the origin of the dorsal fin, and presence of at least two broad postcleithra) that distinguish it from other ellimmichthyiforms. Together with other primitive clupeomorphs from the Neocomian deposits of Brazil (*Scutatuspinosus*) and Albian of Mexico (*Ranulfoichthys*), the new species forms a clade of torpedo-bodied fishes. This clade supports Grande’s (1985) idea of the evolutionary pattern of the predorsal series of scutes in the clupeomorphs—a complete series of predorsal scutes is a primitive condition in clupeomorphs that precedes the loss of this feature in multiple lineages.

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FIGURE CAPTIONS

Figure 1. *Foreyclupea loonensis*, gen. et sp. nov.; **A**, photograph of the holotype, UALVP 17535a; **B**, line drawing of the specimen UALVP 17535a. **Abbreviations:** **abds**, abdominal scutes; **epl**, epipleural; **epn**, epineural; **pcl 1-2**, postcleithra 1-2; **pcl2 (l)**, left postcleithrum 2; **sn**, supraneural bones; **scl**, supracleithrum. Scale bars = 5 mm.

Figure 2. Reconstruction of *Foreyclupea loonensis*, gen et sp. nov. Scale bar = 5 mm.

Figure 3. *Foreyclupea loonensis*, gen. et sp. nov. **A**, photograph of the head of the holotype, UALVP 17535a; **B**, restoration of the head in right lateral view. **Abbreviations:** **br**, branchiostegal rays; **cl**, cleithrum; **cor**, coracoid; **fr**, frontal bones; **hyo**, hyomandibular; **io3**, infraorbital 3; **iop**, interopercle; **le**, lateral ethmoid; **mes**, mesethmoid; **mx**, maxilla; **op**, opercle; **pa**, parietal; **pcl 1-2**, postcleithra 1-2; **pmx**, premaxilla; **pop**, preopercula; **ps**, parasphenoid; **pto**, pterotic; **ptt**, posttemporal; **r**, rib; **scl**, supracleithrum; **soc**, supraoccipital; **sop**, subopercle; **smx 1-2**, supramaxillae 1-2. Scale bar = 5 mm

Figure 4. Results of the phylogenetic analysis of the Early Cretaceous clupeomorphs including *Foreyclupea loonensis*, gen. et sp. nov. A strict consensus of the two most-parsimonious trees (tree length = 155 steps, CI = 0.519, RI = 0.588). Bootstrap support values that are higher than 50% are shown above the branches.

TABLE 1. Counts and measurements of *Foreyclupea loonensis*, sp. et gen. nov. specimen

UALVP 17535. All measurements are in mm.

Characteristic \ UALVP	13575
Standard length (SL)	?
Head length	21
Head depth	15
Greatest body depth	19
Predorsal length	42
Prepelvic length	40
Preal length	?
Dorsal fin rays	?11
Pectoral fin rays	14
Pelvic fin rays	?6
Abdominal vertebrae	22-23
Predorsal bones	?
Abdominal scutes	?19
Pre-pelvic scutes	13
Post-pelvic scutes	6
Pre-dorsal scutes	-
Pairs of ribs	18

Figure 1. *Foreyclupea loonensis*, gen. et sp. nov.; A, photograph of the holotype, UALVP 17535a; B, line drawing of the specimen UALVP 17535a. Abbreviations: abds, abdominal scutes; epl, epipleural; epn, epineural; pcl 1-2, postcleithra 1-2; pcl2 (l), left postcleithrum 2; sn, supraneural bones; scl, supracleithrum. Scale bars = 5 mm.
1516x1729mm (72 x 72 DPI)

Reconstruction of *Foreyclupea loonensis*, gen et sp. nov. Scale bar = 5 mm.
758x273mm (72 x 72 DPI)

Draft

Foreyclupea loonensis, gen. et sp. nov. A, photograph of the head of the holotype, UALVP 17535a; B, restoration of the head in right lateral view. Abbreviations: br, branchiostegal rays; cl, cleithrum; cor, coracoid; fr, frontal bones; hyo, hyomandibular; io3, infraorbital 3; iop, interopercle; le, lateral ethmoid; mes, mesethmoid; mx, maxilla; op, opercle; pa, parietal; pcl 1-2, postcleithra 1-2; pmx, premaxilla; pop, preopercula; ps, parasphenoid; pto, pterotic; ptt, posttemporal; r, rib; scl, supracleithrum; soc, supraoccipital; sop, subopercle; smx 1-2, supramaxillae 1-2. Scale bar = 5 mm
716x1069mm (72 x 72 DPI)

Results of the phylogenetic analysis of the Early Cretaceous clupeomorphs including *Foreyclupea loonensis*, gen. et sp. nov. A strict consensus of the two most-parsimonious trees (tree length = 155 steps, CI = 0.519, RI = 0.588). Bootstrap support values that are higher than 50% are shown above the branches.

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APPENDIX 1. Character state list used in the phylogenetic analysis based on Murray and Wilson (2013):

1. Anterior dorsal margin of body: [0] rounded and convex; [1] almost straight, forming a marked angle at the dorsal fin insertion.
2. Skull roof: [0] parietal bones contacting each other in the midline; [1] supraoccipital separates parietal bones.
3. Lateral profile of skull roof: [0] a straight line from anterior tip of frontal to back of skull, with no distinct angle apparent; [1] with distinct angle between anterior and posterior parts, normally in the region of the parietal.
4. Ornamentation of skull roof bones: [0] absent; [1] present.
5. Ornamentation of skull roof bones: [0] fine, more or less parallel grooves; [1] strong grooves with numerous fine, radiating ridges.
6. Posttemporal fossa: [0] absent; [1] present.
7. Cavity in the temporal region of the skull: [0] pre-epioccipital fossa (between parietal, epioccipital and pterotic bones); [1] pre-epioccipital fenestra (between the parietal, epioccipital and supraoccipital bones); [2] absence of cavity or fenestra.
8. *Recessus lateralis*: [0] absent; [1] present.
9. Supramaxillary bones: [0] two; [1] one or none.
10. 'Basipterygoid' process of parasphenoid: [0] absent; [1] present.
11. 'Osteoglossid' tooth patch on the parasphenoid: [0] absent; [1] present.
12. Supraorbital bone: [0] absent; [1] present.
13. Antorbital bone: [0] absent; [1] present.
14. Beryciform foramen within the anterior ceratohyal: [0] absent; [1] present.
15. Foramen in posterior ceratohyal: [0] absent; [1] present.
16. Teeth on endopterygoid: [0] absent; [1] present.
17. Total number of vertebrae excluding uralcentra: [0] 30-40; [1] 41-43; [2] more than 50.

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18. Halves of the neural arches of most abdominal vertebrae: [0] separate medially; [1] fused medially.
19. Pleural ribs: [0] all ribs articulate with parapophyses along the abdominal region; [1] anteriormost ribs articulate with deep pits on the lateral side of all abdominal centra and those located posteriorly articulate with well-developed parapophyses; [2] all ribs articulate with deep pits on the lateral side of all abdominal centra.
20. Epineurals and epipleurals in the caudal region: [0] absent; [1] present.
21. Epicentrals: [0] absent; [1] present.
22. Shape of cleithrum: [0] L-like (having a single angle in the bone); [1] S-like (having two angles).
23. Dorsal process of posttemporal: [0] slender and sharp; [1] sub-rectangular; [2] broad, wider at distal tip than at midpoint of bone.
24. Number of anal fin rays: [0] eight to eleven; [1] fourteen or fifteen; [2] seventeen or eighteen; [3] twenty; [4] twenty-two to thirty-two; [5] thirty-six to forty-one.
25. Number of dorsal fin rays: [0] eight to thirteen; [1] fourteen to nineteen; [2] twenty-one to twenty-five.
26. Number of hypurals: [0] seven; [1] six; [2] five.
27. Hypural 2: [0] autogenous; [1] fused to first ural centrum (diural terminology).
28. Length of hypural 1: [0] long, reaching ural centrum 1; [1] short, not reaching ural centrum 1.
29. Proximal end of hypural 1 (was originally termed “articulation of hypural 1”): [0] massive and forming an upward process; [1] sharp; [2] massive but no upward process.
30. Shape of hypural 2: [0] Distal end distinctly broader than proximal end; [1] very thin and stick-like.
31. Diastema between second and third hypural: [0] third hypural not expanded posteriorly leaving a gap or notch between the second and third hypural; [1] third hypural expanded posteriorly, leaving no gap or notch between second and third hypural.
32. Shape of diastema between hypurals 2 and 3: [0] small triangular notch; [1] deep triangular cavity; [2] large concavity formed by hypural 3 having a concave ventral edge.

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33. Size of first ural centrum (diural terminology): [0] roughly the same size (length and depth) as the preuralcentra; [1] much smaller than the preuralcentra.
34. Number of uroneurals: [0] three; [1] two; [2] one.
35. First uroneural: [0] extends anteriorly to reach second preural centrum; [1] does not reach second preural centrum.
36. Fusion of first uroneural and first ural centrum: [0] absent; [1] present.
37. First uroneural bearing a dorsal expansion of laminar bone: [0] absent; [1] present.
38. Distal end of second uroneural: [0] reaching the distal end of the first uroneural; [1] not reaching the distal end of the first uroneural.
39. Parhypural: [0] base/arch of bone fused with preural centrum 1; [1] autogenous.
40. Fusion of hypural two and first ural centrum: [0] absent; [1] present.
41. Number of epurals: [0] three; [1] two; [2] none, or those present are weakly ossified, perhaps cartilaginous.
42. Position of epurals: [0] epurals fill the space between the neural spines of pu1 and pu2; [1] epurals are located far from the spine of pu2, leaving an open space between them.
43. Caudal scutes: [0] absent; [1] present.
44. Neural spine of first preural centrum: [0] large or lanceolate; [1] short or sub-rectangular.
45. Neural arch of first ural centrum: [0] absent; [1] present.
46. Predorsal scutes: [0] absent; [1] present.
47. Predorsal scute series: [0] incomplete (absent in anterior part); [1] complete.
48. Subrectangular scutes (i.e., scutes significantly broader than long) in anterior part of predorsal series: [0] absent; [1] present.
49. Subrectangular scutes in posterior part of predorsal series: [0] absent; [1] present.
50. Series of spines on the posterior margin of the lateral wings of the predorsal scutes: [0] absent; [1] present.
51. Prominent median strong spine on posteriormost predorsal scutes: [0] absent; [1] present.

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52. Size of scutes of predorsal series: [0] all scutes of same size; [1] irregular in size, size of scutes increasing posteriorly.
53. Surface of predorsal scutes: [0] smooth; [1] ornamented with radiating grooves.
54. Number of predorsal scutes: [0] six to fourteen; [1] sixteen to nineteen; [2] twenty to forty-one.
55. Abdominal scute series: [0] absent; [1] present.
56. Complete abdominal scute series between isthmus and anus (i.e., postpelvic scutes are present): [0] absent; [1] present.
57. Postpelvic abdominal scutes bearing very prominent and strong ventral spine: [0] absent; [1] present.
58. Size of lateral wings of abdominal scutes: [0] small; [1] large, extended upward and covering the abdominal cavity laterally for at least one quarter of the distance from ventral body edge to vertebral column.
59. Shape of lateral wing of abdominal series scutes: [0] spine-like, with large spaces between wings of scutes; [1] wide or spatula-like, with wings of adjacent scutes touching for most of their length.
60. Postdorsal scute series: [0] absent; [1] present.
61. Number of abdominal scutes (in some taxa they will not be equivalent to vertebral counts): [0] fewer than 20; [1] 22-30; [2] more than 32.
62. Number of predorsal bones: [0] 10 or more; [1] 7-9; [2] 6 or fewer.

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APPENDIX 2. Data matrix used in the phylogenetic analysis of the Early Cretaceous clupeomorphs (based on the data matrices of Murray and Wilson (2013) and Alvarado-Ortega et al. (2008)).

	000000001	111111112	222222223	333333334	444444445	555555556	66
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12
<i>Chanos chanos</i>	0100-?20?0	01?0001001	1100110111	00-1-10110	100100----	----0----0	-0
<i>Chirocentrus dorab</i>	010??10100	0110002101	1014111111	0110110011	100100----	----10-100	??
<i>Denticeps clupeoides</i>	0100?02110	0010110021	1014021020	0102101101	100110----	----110000	0?
<i>Odaxothrissa vittata</i>	0100?10110	01100111?1	1012111111	0110110011	000100----	----110100	00
<i>Ornategulum sardinoides</i>	0001100001	0111?12001	?010101121	??00001001	000100----	----0----0	?0
<i>Ellimma branneri</i>	00011???01	0??1?10?1?	?1011110?1	0100000001	0011?11110	1110111110	11
<i>Ellimmichthys goodi</i>	1??031?000	??????0110	1110111000	0?00001000	0010111110	1112111110	??
<i>Ellimmichthys longicostatus</i>	1??11?000?	0???100110	1110111000	0?00001000	0110111110	1112111110	??
<i>Ellimmichthys maceioensis</i>	1?110??0?	??????0???	?1?11?102?	1-01000101	0101111010	11101111?0	21
<i>Ez kutuberezi carmenae</i>	100?0??0?	?????00111	?1?42?1021	??0?0000?1	100101??00	111?111100	20
Foreyclupea loonensis	00010??0?	01?????011	?00?1?????	???????????	?????0----	----111000	0?
<i>Parachupea chetungensis</i>	10011??01	0??1010???	?1?1111011	0100000101	0111010-10	1111111110	21
<i>Pseudoellimma gallae</i>	11?101010?	0????00001	?0?1121001	00?0000001	???0?1??10	1?0?111000	10
<i>Ranulfoichthys dorsonudum</i>	00010??001	0111101011	?000111001	1-00000001	0011?0----	----111000	10
<i>Santanachupea silvasantosi</i>	010101010?	0??1??000?	?0?0121001	00?1000001	???100----	----111010	1?
<i>Scutatuspinosus</i>	00010??01	01?1100111	0100010021	1?01100000	0111011001	11101110-0	10
<i>itapagipensis</i>							
<i>Triplomystus applegatei</i>	10011????1	00????011?	?1121?1011	0011100101	0010111010	1110111111	22