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A phylogeny and revised classification of clupeomorph fishes (Teleostei, Otomorpha)

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ABSTRACT

The study of the Clupeomorpha Greenwood, Rosen, Weitzman & Myers, 1966 (herrings and allies) has made remarkable progress in recent years. Since the publication of the monographic work by Lance Grande "Recent and fossil clupeomorph fishes with material for revision of the subgroups of clupeoids" in 1985, a number of phylogenetic studies and new paleontological discoveries have largely expanded our understanding of the evolutionary history of clupeomorphs. However, the majority of the fossil clupeomorphs have never been included in a comprehensive morphological phylogenetic framework. As a matter of fact, despite the longstanding recognition of clupeomorph monophyly, the internal relationships of the Clupeomorpha, particularly between the extinct †Ellimmichthyiformes and extant Clupeiformes, their evolutionary history, and the biogeographic and ecological transitions that shaped their past and modern biogeography remain inadequately resolved and poorly understood. In this paper, 40 years after Grande's work, we re-evaluate the clupeomorph intrarelationships, test the monophyly of key lineages (including the new taxa Engrauloidae n. epifam., †Clupeopsidae n. fam., and †Eollimmichthyinae n. subfam.), and discuss biogeographic patterns by analysing 368 morphological characters across 124 clupeomorph taxa, including both fossil and living species. The hypothesis of relationships was used to revise the classification of the Clupeomorpha, emphasizing the importance of integrating fossil data to understand the evolutionary history of the group.

KEY WORDS
Clupeomorpha,
Clupeiformes,
†Ellimmichthyiformes,
phylogeny,
morphological
characters,
ancestral state
reconstruction,
new epifamily,
new family,
new subfamily.

RÉSUMÉ
Une phylogénie et une classification révisée des poissons clupéomorphes (Teleostei, Otomorpha).
L'étude des Clupeomorpha Greenwood, Rosen, Weitzman & Myers, 1966 (harengs et apparentés) a connu des avancées remarquables ces dernières années. Depuis la publication de l'ouvrage monographique de Lance Grande *Recent and fossil clupeomorph fishes with material for revision of the subgroups of clupeoids* en 1985, de nombreuses études phylogénétiques et découvertes paléontologiques ont considérablement enrichi notre compréhension de l'histoire évolutive des clupéomorphes. Cependant, la majorité des clupéomorphes fossiles n'a jamais été intégrée dans un cadre phylogénétique morphologique global. En réalité, malgré la reconnaissance ancienne de la monophylie des clupéomorphes, leurs relations internes, en particulier entre les †Ellimmichthyiformes fossiles et les Clupeiformes actuels, ainsi que leur histoire évolutive et les transitions biogéographiques et écologiques ayant façonné leur répartition passée et actuelle, demeurent mal résolues et peu comprises. Dans cette étude, quarante ans après le travail de Grande, nous réévaluons les relations internes des clupéomorphes, testons la monophylie de lignées clés (y compris les nouveaux taxons Engrauloidae n. epifam., †Clupeopsidae n. fam. et †Eollimmichthyinae n. subfam.) et analysons les modèles biogéographiques en examinant 368 caractères morphologiques chez 124 taxons de clupéomorphes, fossiles et actuels. L'hypothèse de relations phylogénétiques ainsi obtenue a permis de réviser la classification des Clupeomorpha, en soulignant l'importance de l'intégration des données fossiles pour comprendre l'histoire évolutive du groupe.

MOTS CLÉS
Clupeomorpha,
Clupeiformes,
†Ellimmichthyiformes,
phylogénie,
caractères morphologiques,
reconstitution des états ancestraux,
nouvelle épifamille,
nouvelle famille,
nouvelle sous-famille.

INTRODUCTION

The Otomorpha Wiley & Johnson, 2010 is one of the most distinctive and a phylogenetically well-supported subdivisions of Teleostei Müller, 1845 and includes a morphologically and ecologically diverse assemblage of fishes that inhabit both marine and freshwater environments worldwide (Arratia 2018). With about 11 000 extant species in 1500 genera and 90 families, it is one of the largest vertebrate clades, comprising more than one-quarter of all extant teleost species and representing the major components of marine and freshwater food webs (Arratia 2018). Otomorphs are united by a suite of unique anatomical traits, most notably a specialized connection between the swim bladder and inner ear via otophysic structures, a feature traditionally linked to enhanced auditory capabilities (Fink & Fink 1981; Di Dario 2004a; Lavoué *et al.* 2005; Arratia 2018). Despite this shared specialization, otomorphs are notably heterogeneous in both morphology and ecology, encompassing deep-bodied, pelagic filter feeders and elongate benthic, epipelagic forms. The clade includes three main lineages at superorder or subcohort level, depending on the studies: Clupeomorpha (/Clupei), Alepocephali Betancur-R. *et al.*, 2017 and Ostariophysi Sagemehl, 1885. The monophyly of Otomorpha has been demonstrated by studies based on morphological (Wiley & Johnson 2010; Arratia 2018) and molecular (Near *et al.* 2012; Betancur-R *et al.* 2013, 2017) evidence.

Among the three otomorph clades recognized by Wiley & Johnson (2010), the Clupeomorpha includes over 800 extant and fossil species distributed among more than 120 genera and 15 families that are traditionally grouped in two main orders: Clupeiformes and †Ellimmichthyiformes (Grande 1985; Nelson *et al.* 2016; Fricke *et al.* 2025).

The Clupeiformes (Fig. 1) include about 450 marine, freshwater, and diadromous living species arranged in about 80 genera with global distribution, including ecologically and economically important fishes such as herrings, sardines, shads and anchovies (Whitehead 1985; Whitehead *et al.* 1988; Fricke *et al.* 2025). Except for the longfin herrings (Pristigasteridae), all the main clupeiform families are well-represented in the fossil record, with at least 130 valid species dating back to the Lower Cretaceous (e.g., Figueiredo 2009a, b; Malabarba & Di Dario 2017) (Fig. 2).

The extinct order †Ellimmichthyiformes (Fig. 3), also known as double-armoured herrings, constitutes an extinct clade of clupeomorph fishes characterized by a wide palaeogeographical and palaeoenvironmental distribution in marine, estuarine and freshwater deposits of Africa, Asia, Europe, and North and South America (Grande 1982a; Chang & Maisey 2003; Forey *et al.* 2003; Murray & Wilson 2013; Marramà *et al.* 2019; Marramà & Carnevale 2023). This order currently includes about 40 species arranged in 20 genera and spanning from the Early Cretaceous to the Oligocene (Chen *et al.* 2021; Figueiredo & Gallo 2021), adding considerable morphological and ecological diversity to the clupeomorph clade, despite their relationships with the Clupeiformes remains largely unresolved (e.g., Zaragüeta Bagils 2004; Murray *et al.* 2016; Vernygora 2020).

Although these two orders have unique characters that allow to distinguish them, the internal relationships within the group, particularly those linking fossil and extant lineages, are still debated. Clupeomorphs have been traditionally perceived as a monophyletic, natural assemblage due to their shared specialized features, including the presence of one or more abdominal scutes across the ventral midline of the body, an otophysic connection formed by diverticula from the swimbladder entering the skull, and a characteristic configuration of the caudal skeleton (e.g., Greenwood *et al.* 1966; Patterson 1970; Nelson 1973; Grande 1985). The work of Grande (1985) should be regarded as the most important contribution to the systematics and taxonomy of Clupeomorpha so far, as it provided, for the first time, a systematic revision of the entire group, with descriptions of the main diagnostic features and comparative osteological data for most of the taxa above the genus level, and also listing the nominal fossil species known by that time.

As discussed above, despite the long-standing consensus on clupeomorph monophyly, the intrarelationships of the group remain unresolved. Traditional classifications based on comparative osteology and phylogenetic analyses focused on a single order have suggested that †Ellimmichthyiformes form either the sister group to Clupeiformes (Chang & Maisey 2003; Forey 2004; Marramà & Carnevale 2023), a paraphyletic grade or a clade within the Clupeiformes (Alvarado-Ortega *et al.* 2008; Vernygora 2020; Kevrekidis *et al.* 2024), or even a group that includes the Clupeiformes (Zaragüeta Bagils 2004). However, being these analyses primarily focused on only one of the two orders, they result in incomplete and limited character and taxon sampling that precludes a comprehensive assessment of their true phylogenetic affinities. Furthermore, several molecular studies have addressed the phylogenetic structure of extant Clupeiformes (Lavoué *et al.* 2007, 2013; Bloom & Egan 2018; Wang *et al.* 2022), but their exclusive focus on living taxa and lack of fossil data (except for tree calibration purposes) strongly limits the historical resolution of clupeomorph diversification.

As a result, no consensus currently exists regarding the internal structure of the Clupeomorpha, and the evolution of important clupeomorph traits, their origin, evolutionary and biogeographic history remain poorly understood. Consequently, the relationships among major clupeomorph lineages and the biogeographic and ecological transitions they underwent during their evolutionary history remain inadequately resolved.

Therefore, the goals of this study are: (1) to provide a comprehensive sampling and critical review of phenotypic data relevant to Clupeomorpha; (2) to test the monophyly of Clupeomorpha and its constituent lineages; (3) to evaluate the intrarelationships of Clupeiformes and the phylogenetic position of †Ellimmichthyiformes; and (4) to interpret the ancestral habitat preferences and biogeographic history of clupeomorph fishes based on the resulting tree topologies.

To achieve these goals, we conducted a phylogenetic analysis based on 368 morphological characters and 130 terminal taxa, including 124 clupeomorphs and six outgroup species. This sampling encompasses all extant and extinct clupeomorph families, as well as a number of fossil species of uncertain familial placement, which nonetheless represent key taxa for understanding the evolution of traits and, consequently, the lineages to which they belong.

Morphological characters primarily concern osteology, myology, and squamation. In addition to the parsimony analysis, we performed ancestral state reconstructions to explore shifts in habitat and geographic distribution across the clupeomorph tree and to detect if vicariance or dispersal played the major role in shaping the past and present distribution of the different clupeomorph lineages.

This study represents the most inclusive and comprehensive morphological analysis of the Clupeomorpha since the monographic work of Grande (1985), as it is the first to integrate most of the fossil and extant diversity of the two main lineages, the Clupeiformes and †Ellimmichthyiformes, with an explicit focus on their morphology-based relationships, historical biogeography and ecological evolution.

PREVIOUS PHYLOGENETIC HYPOTHESES

The historical hypotheses on the Clupeomorpha intrarelationships have undergone significant revisions, integrating both morphological and molecular approaches. A summary of the previous main morphological and molecular hypotheses on the phylogenetic relationships of the Clupeomorpha is depicted in Figures 4; 5.

During the 18th and 19th centuries, the Clupeomorpha classification was highly inconsistent, often grouping them with a variety of unrelated "primitive" teleosts. For example, Berg (1940), Svetovidov (1952), Jordan (1923), and Gosline (1971) included clupeomorphs in a "wastebasket" group, lumping them together with ichthyodectiforms, gonorynchiforms, salmoniforms, osteoglossomorphs, albuloids and elopoids. In particular, Berg (1940) admitted that the Clupeiformes was an "artificial assemblage", predicting future taxonomic divisions, whereas Gosline (1971) further emphasized that the order was too diverse to be diagnosed without exceptions. During this period, no clear synapomorphies uniquely defining the Clupeomorpha were recognized.

Greenwood *et al.* (1966) provided the first synapomorphy-based definition of the Clupeomorpha, eliminating many unrelated groups from this clade and identifying four main key features to define the superorder, including the peculiar inner ear-swim bladder connection, the presence of unique features in the skull (temporal foramina, pre-epioccipital fossae and auditory fenestrae), the recessus lateralis and, in the caudal skeleton, the fusion of the second hypural with the first ural centrum in all life stages. Despite some of these characters had been previously reported and discussed in the literature (e.g., Wohlfahrt 1936; Cavender 1966), they had not been formally integrated into a diagnostic framework for the group prior to Greenwood *et al.* (1966). These traits excluded many previously misclassified taxa, refining the Clupeomorpha to a more natural group.

This classification was further refined by Patterson & Rosen (1977) who added another clupeomorph synapomorphy: the presence of supratemporal commissural sensory canal passing through parietal and supraoccipital.

Nelson (1970) based on the analysis of the gill arches of the Clupeoidei, recognized four different superfamilies, each comprising only a single family: superfamily Chirocentroidea (family Chirocentridae), Engrauloidea (Engraulidae), Pristigasteroidea (Pristigasteridae) and Clupeoidea (Clupeidae), although the interrelationships among the four superfamilies were left unresolved.

After the establishment of the extinct order †Ellimmichthyiformes for the fossil double-armored herrings (Grande 1982a), Grande (1985) conducted the first extensive morphological study on Clupeomorpha, proposing that †*Armigatus*, the monophyletic orders †Ellimmichthyiformes (†*Diplomystus* and †*Ellimmichthys*) and Clupeiformes form an unresolved trichotomy, refining at the same time the synapomorphies that characterize each of these clades. Within the Clupeiformes, Grande (1985) found that the suborder Clupeoidei is a natural group distinct from the Denticipitoidei (*Denticeps* and †*Palaeodenticeps*). He recognized the monophyly of the superfamilies Engrauloidea (family Engraulidae), Pristigasteroidea (families Pristigasteridae and Pellonidae) and Clupeoidea (families Chirocentridae and Clupeidae), but found the relationships among the Clupeidae subfamilies (Alosinae, Clupeinae, Dorosomatinae, Dussumieriinae, Pellonulinae) undefined, leaving the Alosinae, Clupeinae and Dorosomatinae without substantial morphological support. The monographic study carried out by Grande (1985) became the starting point for later morphological studies on Clupeomorpha.

Sato (1994) produced the first computer-generated phylogeny for the Clupeiformes, and re-ranked some of the groups proposed by Grande (1985). He treated the Pristigasteroidea as subfamily (Pristigasterinae) by placing it within the Clupeidae, and refined the relationships among Clupeinae, Alosinae, and Dorosomatinae. Sato (1994) recognized and listed new synapomorphies for the clupeiform classification but did not resolve deeper evolutionary relationships.

Di Dario (2002) identified three synapomorphies of the vertebral column structure (presence of cartilage chevron, posteriorly directed second parapophyses, and interzygapophysal articulation) that support the sister-group relationship between the Grande's Clupeoidea and Engraulidae, with the Pristigasteroidea that was supposed to be the sister group of this clade.

Chang & Maisey (2003) performed the first computer-generated phylogeny for the whole group Clupeomorpha based on a set of 30 morphological traits, providing evidence for the first time that the †Ellimmichthyiformes (†*Armigatus*, †*Diplomystus*, †*Ellimma*, †*Ellimmichthys*, †*Paraclupea*) and Clupeiformes (*Clupea*, *Denticeps*, †*Knightia*, †*Santanaclupea*) are both monophyletic and forming a sister pair, although uncertainty involved the position of the Lower Cretaceous clupeomorph †*Santanaclupea*, being recovered as both sister to the Clupeoidei or as stem Clupeiformes.

Di Dario (2004b)'s PhD thesis mainly focused on Otomorpha, the broader group containing Clupeiformes and Ostariophysi, recovering the Clupeiformes monophyletic, in which the superfamily Engrauloidea (formed by the Pristigasteridae sister to a clade including Dussumieriidae, Chirocentridae and Engraulidae) represents the sister group to the superfamily Clupeoidea (his Pellonulidae plus the rest of clupeoids).

Forey (2004) proposed a tree topology consistent with that of Chang & Maisey (2003) in which a monophyletic †Ellimmichthyiformes is sister to a clade formed by the Lower Cretaceous clupeomorph †*Spratticeps* plus a monophyletic Clupeiformes, this latter formed by an unresolved trichotomy including *Denticeps*, †*Santanaclupea* and Clupeoidei. A number of subsequent analyses focused on the Ellimmichthyiformes and using Clupeiformes as outgroup (e.g., Murray & Wilson 2013; Marramà *et al.* 2019, 2022) agree with Chang & Maisey (2003) and Forey (2004) in detecting the two orders as sister groups.

Zaragüeta-Bagils (2004) performed the most extensive phylogenetic study of the extinct double-armored herrings, in which he rejected the monophyly of the †Ellimmichthyiformes as it was defined by previous authors, with the Clupeomorpha formed by an unresolved trichotomy that included †*Ornategulum*, the pair †*Armigatus* + †*Diplomystus*, and a clade formed by the Clupeiformes as sister to the rest of the †Ellimmichthyiformes.

Large-scale molecular studies started with the analysis by Li & Ortí (2007) who used a combination of mitochondrial (12S, 16S) and nuclear (RAG1, RAG2) markers to examine the relationships between 37 clupeiform species. Their study challenged traditional morphology-based hypotheses by finding *Denticeps* more closely related to Ostariophysi than to other clupeiforms, making Clupeiformes non-monophyletic and contradicting the previous hypotheses. Additionally, the family Chirocentridae was recovered as the sister group to the pair *Jenkinsia* + *Spratelloides*, with the Pristigasteridae being nested within the Clupeidae, making the latter as polyphyletic.

Alvarado-Ortega *et al.* (2008) performed a new cladistic parsimony analysis of the †Ellimmichthyiformes and, although they recovered a well-resolved tree topology, they still found the Clupeomorpha formed by an unresolved trichotomy that included †*Ornategulum*, the Clupeiformes and the other †Ellimmichthyiformes, with †*Armigatus* regarded as a non-†ellimmichthyiform clupeomorph; in addition, the †Ellimmichthyiformes were interpreted as formed by two families, the Sorbinichthyidae (including †*Sorbinichthys* and a non-monophyletic †*Diplomystus*) and Paraclupeidae (all the other taxa, but †*Armigatus* and †*Ornategulum*).

In a later work, Di Dario (2009) expanded the relationships within the Clupeiformes emphasizing the sister-group relationship between Chirocentridae and Engraulidae, a relationship supported by seven synapomorphies of the suspensorium, branchial arches, and infraorbital bones. This study refuted the monophyly of the Clupeoidea *sensu* Grande (1985), suggesting that the monotypic family Chirocentridae (*Chirocentrus*) was closer to Engraulidae than to Clupeidae. For this reason, Di Dario (2009) proposed the inclusion of the Chirocentridae within the superfamily Engrauloidea.

Miyashita (2010) postulated a different hypothesis in which the Engraulidae is the sister group to the other clupeoids since the pristigasterids, chirocentrids and clupeids share a unique W-shaped occipital articulation with the first vertebra.

Lavoué *et al.* (2013, 2014, 2017a) using stronger molecular evidence based on mitochondrial genomes, supported a monophyletic Clupeiformes including Denticipitoidei and Clupeoidei, contradicting Li & Ortí (2007), but the interrelationships among Clupeoidei remained largely unresolved since they recovered the Clupeidae as polyphyletic. Moreover, Lavoué *et al.* (2013, 2014, 2017a) consider the traditional Dussumieriidae (Spratelloidinae, *Etrumeus*) and Clupeidae (Clupeinae, Ehiravinae, Dorosomatinae, Alosinae) as non-monophyletic, with only Engraulidae, Chirocentridae, and Pristigasteridae representing well-supported clades.

Bloom & Egan (2018) reviewed the systematics of the Clupeiformes and explored the discordance in phylogenetic relationships and divergence times between mitochondrial and nuclear loci. Their results showed that *Denticeps* was more closely related to the Euteleostei than to the Clupeoidei and, within this latter, in the nuclear-loci-based analysis, they found that the Spratelloidinae (*Jenkinsia* and *Spratelloides*) is sister to all the other clupeoids.

Vernygora (2020), integrating morphological and molecular data, hypothesized the Clupeiformes as non-monophyletic, since she recovered the extinct double-armored herring order †Ellimmichthyiformes nested within the traditional Clupeiformes, and therefore proposed a classification of the Clupeomorpha into three orders: Denticipitiformes (*Denticeps* and †*Palaeodenticeps*), †Ellimmichthyiformes (the extinct non-clupeoid double-armored herrings), and Clupeiformes (including †*Pseudoellimma*, †*Santanaclupea* and the Clupeoidei). This study also confirms the non-monophyletic status of the Clupeidae (*sensu* Grande 1985).

Wang *et al.* (2022), using exon-capture sequencing of over 1100 nuclear loci from 66 species, provided the most resolved molecular phylogeny of the Clupeiformes to date. This study resolved the monophyly of the Clupeiformes, Chirocentridae, Engraulidae and Pristigasteridae, as well as of many clupeiform interrelationships, confirming the placement of Spratelloidinae (that they elevate at family level) as the basalmost clade within the Clupeoidei, and *Etrumeus* as sister to the pair formed by *Clupea* + *Sprattus*.

Egan *et al.* (2024) largely corroborated the results of the study by Wang *et al.* (2022) and further refined the clupeiform relationships, although the relationships among Clupeidae, Dussumieriidae, and Pristigasteridae were left unresolved, suggesting the necessity of additional taxon sampling and integration of palaeontological information.

Kevrekidis *et al.* (2024) recently provided a morphology-based cladistic analysis using 192 characters incorporating 79 extant and 37 fossil clupeomorph taxa mainly focused on the intrarelationships within the Clupeiformes, since only two †ellimmichthyiform taxa were included. This study recovered the †Ellimmichthyiformes as crown Clupeiformes or even crown Clupeoidei in the unconstrained and constrained parsimony analyses, respectively. The relationships of the rest of the fossil and living clupeiform families were interpreted with varying degrees of certainty but were left mostly unresolved, even after constraining analyses using the tree topology of Wang *et al.* (2022).

MATERIAL AND METHODS

TERMINOLOGY AND TAXONOMIC CLASSIFICATION

Taxonomic classification for higher ranks (cohort, subcohort, suborder, order) follows Wiley & Johnson (2010). However, we prefer to avoid the synonymy between Clupei Wiley & Johnson, 2010 and Clupeomorpha Greenwood *et al.*, 1966 as done in recent classifications (e.g., Wiley & Johnson 2010; Betancur-R *et al.* 2017; Wang *et al.* 2022) since they represent different taxonomic ranks (subcohort and suborder, respectively). Since Clupeomorpha is the lowest rank to be clearly defined by morphological synapomorphies, there is no reason for considering Clupeomorpha and Clupei as synonyms and we therefore keep valid both taxonomic ranks for our purposes.

After the publication of the comprehensive study by Grande (1985), molecular and morphology-based analyses never recovered the family Clupeidae as monophyletic. This has therefore prompted the elevation of the clupeid subfamilies at familial level, and therefore, to the recognition of the families Alosidae (shads), Clupeidae (herrings), Dorosomatidae (gizzard shads), Dussumieriidae (round herrings), Ehiravidae (ehiravines), and Spratelloididae (small round herrings) (Near & Thacker 2024). For this reason, the nomenclature used for lower-level taxa (families, subfamilies, etc) follows Wang *et al.* (2022), Near & Thacker (2024) and Van der Laan & Fricke (2025). In some cases, when an available taxonomic name is retained but applied to a different set of genera than in earlier classifications, this is indicated as 'new usage'; when an available name is assigned to a rank different from that previously adopted, this is indicated as 'new rank'.

All extinct taxa are marked with a dagger (†) preceding their name.

Authorships and dates of the extant and fossil suprageneric taxa and species examined in this study are provided in Table 1 and Appendix 1, respectively; taxa cited in the text but not included therein are given with their authorship and date at their first mention.

OUTGROUP CHOICE

The present study is not aimed to solve the relationships of the Otomorpha *sensu* Wiley & Johnson (2010) (Clupei + Ostariophysi) or *sensu* Betancur-R *et al.* (2017) (Clupei + (Ostariophysi + Alepocephali)) and the outgroups included herein aimed and helped primarily to test the clupeomorph intrarelationships. Consequently, our outgroup sampling prioritized those taxa that have been proposed as the most closely related to clupeomorphs by previous studies (e.g., Arratia 1999, 2018). These include the extant *Albula vulpes* (Linnaeus, 1758), *Alepocephalus rostratus* Risso, 1820, *Osmerus mordax*, *Chanos chanos* (Forsskål, 1775), *Kneria auriculata* and the Jurassic ostariophysan †*Tischlingerichthys viohli* Arratia, 1997.

MATERIAL EXAMINED

The material analysed to carry out this study includes extant and fossil specimens housed in several museums and institutions. The osteology of extant species was examined mostly using cleared and stained specimens housed in the American Natural History Museum, New York (AMNH), encompassing 52 clupeiform genera (each represented by one to three specimens) and two outgroup genera. Data for other 13 living clupeiform genera was compiled mainly from original descriptions (e.g., Phillips 1942; Whitehead 1964, 1968; Yabumoto & Uyeno 1982) and/or from datasets (e.g., Sato 1994; Di Dario 2004b). This extensive sample and the resulting dataset represent most of the currently described clupeiform genera (83; Van der Laan & Fricke 2025) covering more than 77.1% of the total known α-diversity. The fossil material examined includes 18 †ellimmichthyiform species and ten genera. Data for the other 24 †ellimmichthyiform species included in the matrix comes from original descriptions (e.g., Murray & Wilson 2013; Alvarado-Ortega *et al.* 2020) and sometimes completed with personal observation. We also examined dozens of specimens of ten fossil clupeiform genera and species, some of them already described in previous papers by us (e.g., Marramà & Carnevale 2015a, b, 2016, 2018).

See Appendix 1 for the complete list of the material examined.

Data analysis

The matrix used for the phylogenetic analyses (Appendix 2) and related time calibration, habitat and biogeographic reconstruction (Appendix 3) was compiled in Mesquite v. 4.01 (Maddison & Maddison 2025) and analysed with TNT v.1.6 (Goloboff & Morales 2023) using New Technology Search method and with the following algorithms and parameters that tend to be very effective for large datasets (Goloboff 2002; Goloboff & Catalano 2016): 10 iterations of ratchet (in order to perform frequent reweighting of the characters at each iteration), 10 cycles of tree drift (to explore nearby suboptimal trees that might connect to other tree islands and to improve the resolution of results for large matrices), 20 rounds of tree-fusing (to combine multiple best trees to yield potentially better solutions) and constrained (CSS), random (RSS) and exclusive (XXS) sectorial searches (to uncover "islands" of optimal trees), holding 20 000 trees, and collapsing trees after search. Fifteen multistate characters (see below) were treated as ordered to reflect evolutionary pathways when a natural progression exists (e.g., increase in pleural ribs/preural vertebrae ratio and in the number of gill rakers, both reflecting a shift from a piscivorous towards a zooplanktivorous diet; see, e.g., Grande 1985). Being the clupeomorphs characterized by a high degree of morphological homoplasy, particularly regarding the overall body physiognomy but also in the structure of cranium, gill arches, jaws, caudal skeleton and scute morphology (Nelson 1970; Whitehead 1985; Lavoué *et al.* 2013; Wang *et al.* 2022), we employed an implied weight analysis to reduce the influence of homoplastic characters on tree topology and to avoid that strong homoplasy might lead to an artificial topology. This approach assigns lower weights to characters with higher homoplasy, favouring characters that support more parsimonious groupings (Goloboff *et al.* 2008a). We used the "setk.run" script (Santos *et al.* 2015) to estimate the most appropriate K value through the formula suggested by Goloboff *et al.* (2008b, 2017). In our case, the script estimated a K= 29.6191. Tree length, consistency (CI), homoplasy (HI) and retention (RI) indices subsequently were calculated for the strict con*sensus* tree, using the TNT script "stats". Relative Bremer support (Goloboff & Farris 2001) for the strict con*sensus* tree retrieved by the main analysis was calculated in TNT using TBR and retaining suboptimal trees by 15 steps. These calculations totalled 1 899 607 unique suboptimal trees with ≤ 15 extra steps.

A second analysis employing only living taxa and excluding fossils has been performed to crosscheck the results of the main analysis and to see if the most recent tree topologies and relationships recovered from molecular-based analyses of Clupeiformes could be biased by the lack of data from fossil taxa. In this regard, we performed a new phylogenetic analysis based on a subset including the living 69 taxa only. The "xinact" command was used to remove 36 uninformative characters and the "setk.run" script estimated a new k value of 20.0488. The new matrix has been analysed under maximum parsimony implied weight bootstrap analysis (with 1000 replicates) using the branch-and-bound method under Traditional Search (suitable for smaller datasets) employing the tree bisection reconnection (TBR) algorithm with 1000 replicates and saving 100 trees per replication.

All tree searches were not constrained to any previous topology to ensure genuine morphological signals, to avoid limits to observed changes in morphology, and to help in revealing cases of evolutionary tendency (convergence, morphological plasticity, etc). Moreover, since fossil taxa are included to detect evolutionary signal, unconstrained analysis allows fossils to independently inform evolutionary history, rather than being forced into a molecular tree based only on extant taxa (Dávalos *et al.* 2012; Mongiardino Koch *et al.* 2021).

Time-scaled phylogenetic trees

The tree from the main analysis was scaled to geologic time to show the phylogenetic diversification of the Clupeomorpha through time using the Strap R package (Bell & Lloyd 2015) in R version 3.2.3 (R Core Team 2015). As we are focusing on macroevolutionary trends over deep time (100+ Mya), a minimum branch length of 1 million years was applied to avoid excessive short branches due to dating uncertainties. The chronostratigraphic ranges of fossil taxa (FAD, First Appearance Datum, and LAD, Last Appearance Datum) were set to the boundaries of the stratigraphic stage(s) of the deposits from which the fossils were recovered. Ten additional calibration points were selected a posteriori for divergence time estimation of some nodes based on fossil representatives that were not included in the analysis, whose taxonomic placement in a particular genus is reliable: 1) a minimum age of 132.6 Mya was applied to the ancestral node of *Chanos* and *Kneria* based on the pan-chanid †*Rubiesichthys gregalis* Wenz, 1984 from the Berriasian-Valanginian deposit of Montse, Lerida, Spain (Poyato-Ariza 1996; Near & Thacker 2024); 2) a minimum age of 124.0 Mya was applied to the node containing all the †*Armigatus* species based on †*Armigatus simonettoi* Amalfitano *et al.*, 2025 from the upper Hauterivian-lower Barremian of Vernasso, NE Italy (Amalfitano *et al.* 2025); 3) a minimum age of 97.0 Mya was applied to the node of †*Thorectichthys marocensis* Murray & Wilson, 2013 and †*T. rhadinus* Murray & Wilson, 2013 based on †*T. fideli* Than-Marchese *et al.*, 2024 from the early Cenomanian deposits of Chiapas, southeastern Mexico (Than-Marchese *et al.* 2024); 4) a minimum age of 12.7 Mya was applied to the ancestral node containing *Spratelloides* and *Jenkinsia* based on the presence of an extinct *Spratelloides* species from the Badenian deposits of St. Margarethen, Austria (pers. obs. GC); 5) a minimum age of 40.0 Mya was applied to the node containing *Etrumeus* and *Dussumieria* based on †*Etrumeus hafizi* Arambourg, 1966 from the lower Bartonian strata of the Pabdeh Formation (Arambourg 1966);

6) a minimum age of 3.60 Mya was applied to the ancestral node containing *Anchoa* and *Anchovia* based on the abundant *Anchoa* otoliths from the early Pliocene of the Onzole Formation, Ecuador (Carnevale *et al.* 2011); 7) a minimum age of 5.33 Mya was applied to the node containing *Engraulis* and *Cetengraulis* based on †*Engraulis tethensis* Grande & Nelson, 1985 from the Messinian deposits of the Mesaoria Group in Cyprus (Grande & Nelson 1985); 8) a minimum age of 61.66 Mya was applied to the node containing †*Knightia* and †*Gosiutichthys* based on †*Knightia vetusta* Grande, 1982 from the middle Paleocene Tongue River Formation, Montana (Grande 1982b); 9) a minimum age of 11.63 Mya was applied to the node containing *Alosa* and *Brevoortia* based on †*Alosa elongata* Agassiz, 1842 the Upper Tortonian of the Mediterranean area (Arambourg 1927; Gaudant & Cavallo 2008); 10) a minimum age of 5.33 Mya was applied to the node containing *Harengula* and *Herklotsichthys* based on *Harengula* sp. from the Messinian deposits of Central Italy (Carnevale & Schwarzhans 2022); 11) a minimum age of 40.0 Mya was applied to the node of the most inclusive clade containing *Opisthonema* and *Anodontostoma* based on †*Opisthonema persicum* Arambourg, 1966 from the lower Bartonian strata of the Pabdeh Formation (Arambourg 1966); finally, 12) a minimum age of 16.8 Mya was applied to the node of the most inclusive clade containing *Sardinella* and *Anodontostoma* based on †*Sardinella miyanoshitaensis* Sato & Uyeno, 1999 from the late Burdigalian of Japan (Sato & Uyeno 1999).

Ancestral habitat and origination area reconstruction

We followed Lavoué *et al.* (2013) to reconstruct the ancestral habitat preference and areas of origination of the Clupeomorpha using the maximum clade credibility tree through the "Mk1" evolutionary model ("Markov k-state 1 parameter model") of the Likelihood approach as implemented in Mesquite v. 4.01 that considers any particular change (from state 0 to 1 or state 3 to 2, for example) as equally probable (Maddison & Maddison 2025).

We assigned three states for salinity preference of living and fossil clupeomorphs: marine, euryhaline (taxa capable of living in waters of a wide range of salinities, i.e., in euhaline, brackish and freshwater condition), and freshwater.

To reconstruct the ancestral areas of origination of the living taxa, we assigned 11 biogeographical marine regions to the living marine clupeiforms, considering the water isotherm of 25°C and the intercontinental open ocean regions as frontiers to delimit these areas (see Lavoué *et al.* 2013). The modern marine regions are: West Atlantic (WA), Northwest Atlantic (NA), Northeast Atlantic (NE), East Atlantic (EA), North Pacific (NP), Ponto Caspian system (PC), Indo-West Pacific (IWP), East Pacific (EP), south South America (SS), South Africa (SA) and South Australia (AU). Following Lavoué *et al.* (2013), a multistate coding was applied to a few terminal taxa representing species groups with distributions spanning multiple regions. In this perspective, *Alosa sapidissima* belongs to a clade (*Alosa*) that includes species found in the Northeast Atlantic, Northwest Pacific, and Ponto-Caspian regions, and therefore was coded as NA+NE+PC. The genus *Brevoortia* (including our terminal taxon *B. tyrannus*) is distributed across the East Pacific, Northwest and West Atlantic realm (EP+WA+NA). The genus *Clupea* (including *C. harengus* and *C. pallasi* Valenciennes, 1847) is distributed in Northeast and Northwest Atlantic, and in the North Pacific. *Dorosoma* (including *D. petenense*) spans from the East Pacific and West Atlantic (EP+WA). *Sardinella maderensis* belongs to the subgenus *Clupeonia* Valenciennes, 1847 that has a widespread tropical distribution covering the Indo-West Pacific, East and West Atlantic regions (IWP+WA+EA). Among pristigasterids, *Pellona* is present in the Indo-West Pacific and West Atlantic regions (IWP+WA), whereas *Ilisha* has a broader range, extending also into the East Pacific (IWP+WA+EP). The warm-tropical genus *Etrumeus* is unique within Clupeoidei, as it consists of multiple allopatric species distributed worldwide (IWP+WA+EP+NP+NA). The New World anchovies *Anchoviella* and *Lycengraulis* are found in the West Atlantic and East Pacific regions (WA+EP), whereas *Engraulis* and *Sardinops* (NP+NA+NE+EP+WA+IWP) are worldwide distributed.

To infer the ancestral areas of origin of fossil taxa, we assigned the marine taxa of the †Ellimmichthyiformes and fossil Clupeiformes to one of the five palaeobiogeographic systems that were in place at the time of existence of these taxa, following the palaeogeographic framework of Scotese *et al.* (2025): Neotethys (NT), Gulf of Mexico (GU), South Atlantic Ocean (SAO), Circum Arctic Ocean (CAO), North Pacific Ocean (NPO).

Following the largely accepted scheme for the freshwater systems of Lavoué (2020), we assigned the fossil and living freshwater taxa to six biogeographical regions: Afrotropical (AF), Australian (AUS), Nearctic (NEA), Neotropical (NEO), Oriental (OR), and Palaearctic (PA).

Ecological and biogeographic data for living species were obtained from the online repository of FishBase (Froese & Pauly 2025) that were eventually implemented with information from the two volumes FAO species catalogue of "Clupeoid fishes of the World" (Whitehead 1985; Whitehead *et al.* 1988). Palaeoecological and palaeobiogeographic data for fossil taxa were instead obtained from the published literature. Ecological, palaeoecological, biogeographic and palaebiogeographic data are summarized in Appendix 3.

Institutional abbreviations

AMNH	American Museum of Natural History, New York City;
CLC	Collection Luigi Capasso, Chieti;
CMSNF	Centro Musei delle Scienze Naturali e Fisiche dell'Università degli Studi di Napoli Federico II, Napoli;
DGM	Divisão de Geologia e Mineralogia do Departamento Nacional de Produção Mineral, nowadays Museu de Ciências da Terra, Rio de Janeiro;
DNPM	Departamento Nacional de Producao Mineral (DNPM), Rio de Janeiro;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
MCSNV	Museo Civico di Storia Naturale, Verona;

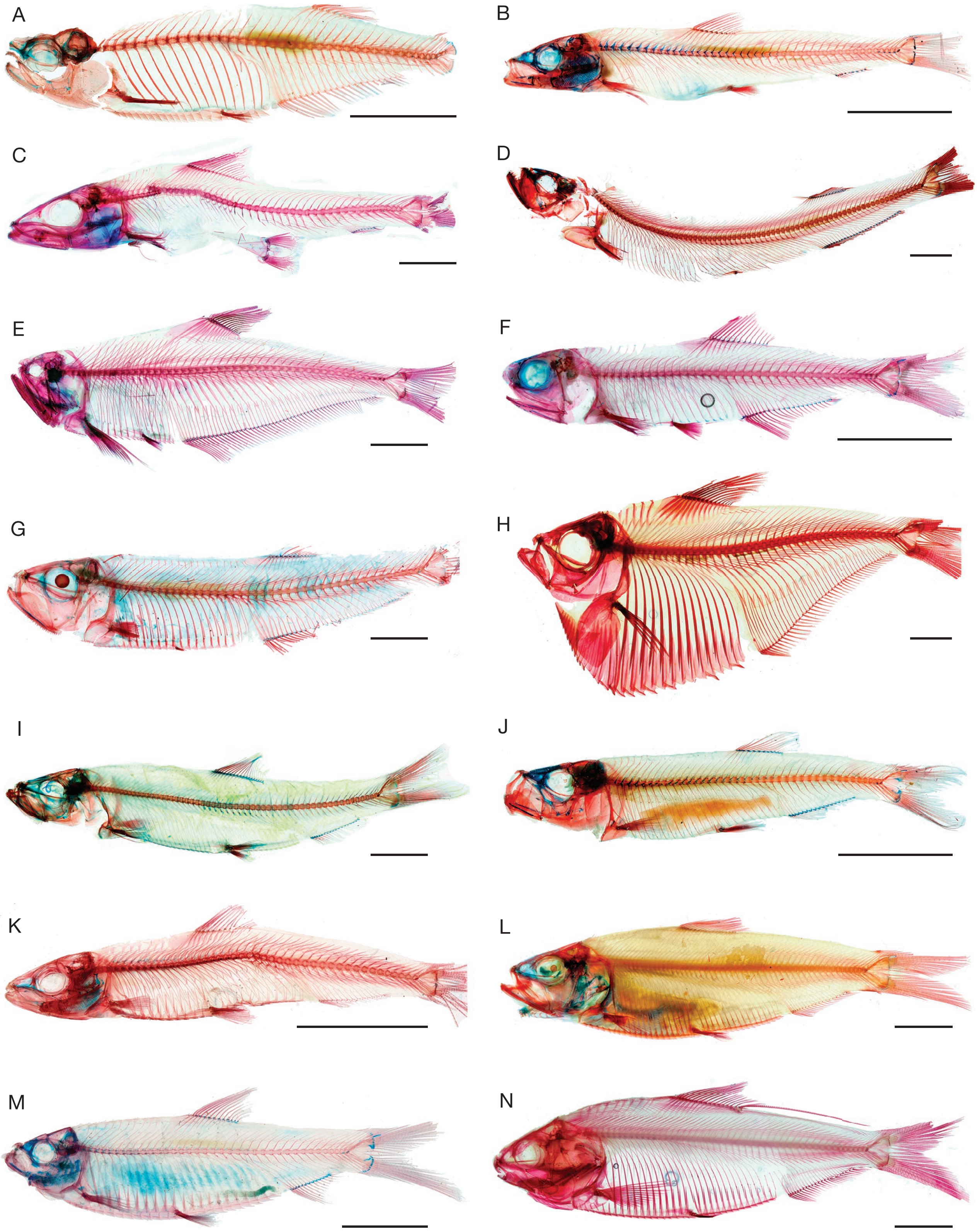

Fig. 1. — Selected representatives of the living families of the Clupeiformes represented by cleared and stained specimens: **A**, *Denticeps clupeoides* Clausen, 1959 (Denticipitidae), AMNH 53082; **B**, *Spratelloides delicatulus* (Bennett, 1832) (Spratelloididae), AMNH 54621; **C**, *Etrumeus sadina* (Mitchill, 1814) (Dussumieriidae), AMNH 736; **D**, *Chirocentrus dorab* (Forsskål, 1775) (Chirocentridae), AMNH 55306; **E**, *Setipinna tenuifilis* (Valenciennes, 1848) (Engraulidae: Coiliinae), AMNH 17551; **F**, *Anchoviella lepidentostole* (Fowler, 1911) (Engraulidae: Engraulinae); AMNH 40905; **G**, *Chirocentrodon bleekerianus* (Pristigasteridae), AMNH 10118; **H**, *Pristigaster cayana* Cuvier, 1829 (Pristigasteridae), AMNH 10186; **I**, *Clupea harengus* Linnaeus, 1758 (Clupeidae), AMNH 49397; **J**, *Gilchristella aestuaria* (Gilchrist, 1913) (Ehiravidae: Ehiravinae), AMNH 232905; **K**, *Potamothrissa obtusirostris* (Boulenger, 1909) (Ehiravidae: Pellonulinae), AMNH 5843; **L**, *Alosa sapidissima* (Wilson, 1811) (Alosidae), AMNH 32707; **M**, *Rhinosardinia amazonica* (Steindachner, 1879) (Dorosomatidae), AMNH 40923; **N**, *Clupanodon thrissa* (Linnaeus, 1758) (Dorosomatidae), AMNH 28122. Scale bars: 10 mm.

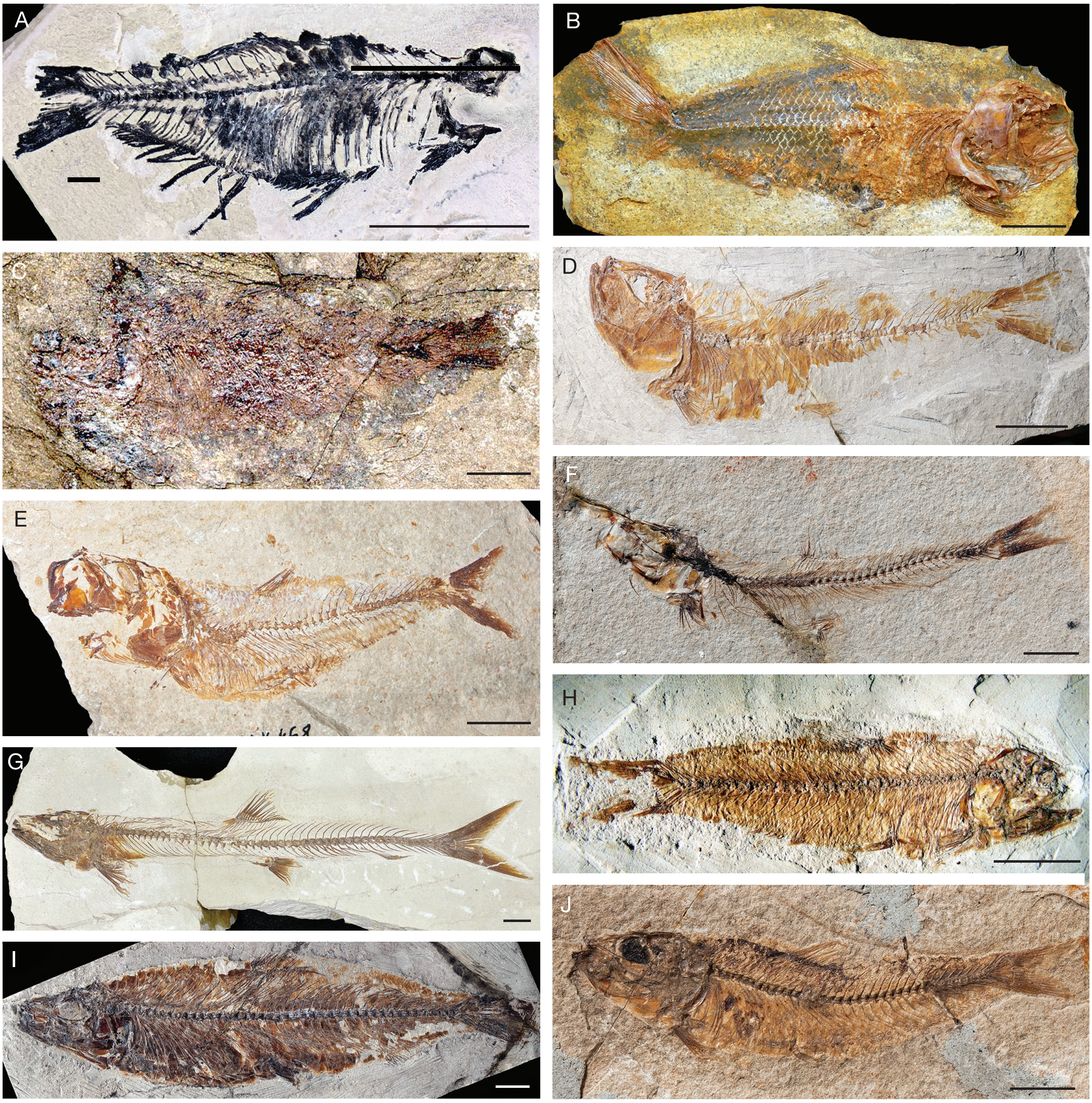

Fig. 2. — Selected representatives of the fossil Clupeiformes: **A**, †*Palaeodenticeps* sp. (Denticipitidae), Eocene, Tanzania; uncatalogued specimen from Museum für Naturkunde, Berlin (photo: courtesy of Gloria Arratia); **B**, †*Santanaclupea silvasantoi* Maisey, 1993 (†Cynoclupeidae), Lower Cretaceous, Brazil; AMNH DVP.18968 (photo: courtesy of Lorraine Meeker); **C**, †*Nolfia riachuelensis* Figueiredo, 2009 (Clupeoidei *incertae sedis*), Lower Cretaceous, Brazil; Pz. UERJ 110, holotype (photo: courtesy of Francisco Figueiredo); **D**, †*Italoclupea nolfi* Taverne, 2007 (Clupeoidei *incertae sedis*), Upper Cretaceous, Italy; MCSNV Na7, holotype; **E**, †*Scombroclupea macrophthalma* (Heckel, 1849) (Clupeoidei *incertae sedis*), Upper Cretaceous, Lebanon; MNHN F.HAK468; **F**, †*Trollichthys bolcensis* Marramà & Carnevale, 2015 (pan-Spratelloididae), Eocene, Italy; NHMUK PV OR.37227, paratype; **G**, †*Nardoclupea grandei* Taverne, 2002 (Dussumieriidae), Upper Cretaceous, Italy; MCSNV Na250, holotype; **H**, †*Eoengraulis fasoloi* (Woodward, 1901) (Engraulidae), Eocene, Italy; MCSNV T.54, holotype; **I**, †*Eoalosa janvieri* Marramà & Carnevale, 2018 (Alosidae), Eocene, Italy; MNHN F.Bol475, holotype; **J**, †*Bolcaichthys catopygopterus* (Woodward, 1901) (pan-Dorosomatidae), Eocene, Italy; NHMUK PV P.3829a, holotype. Scale bars: 10 mm.

MGPTPU	Museo di Geologia e Paleontologia del Dipartimento di Scienze della Terra, Università degli Studi di Torino, Torino;
MNHN	Muséum national d'Histoire naturelle, Paris;
MRSN	Museo Regionale di Scienze Naturali, Torino;
MSNM	Museo Civico di Storia Naturale, Milano;
NHMUK	Natural History Museum, London;
Pz UERJ	Paleontological Collection of the Departamento de Zoologia of Universidade do Estado do Rio de Janeiro.

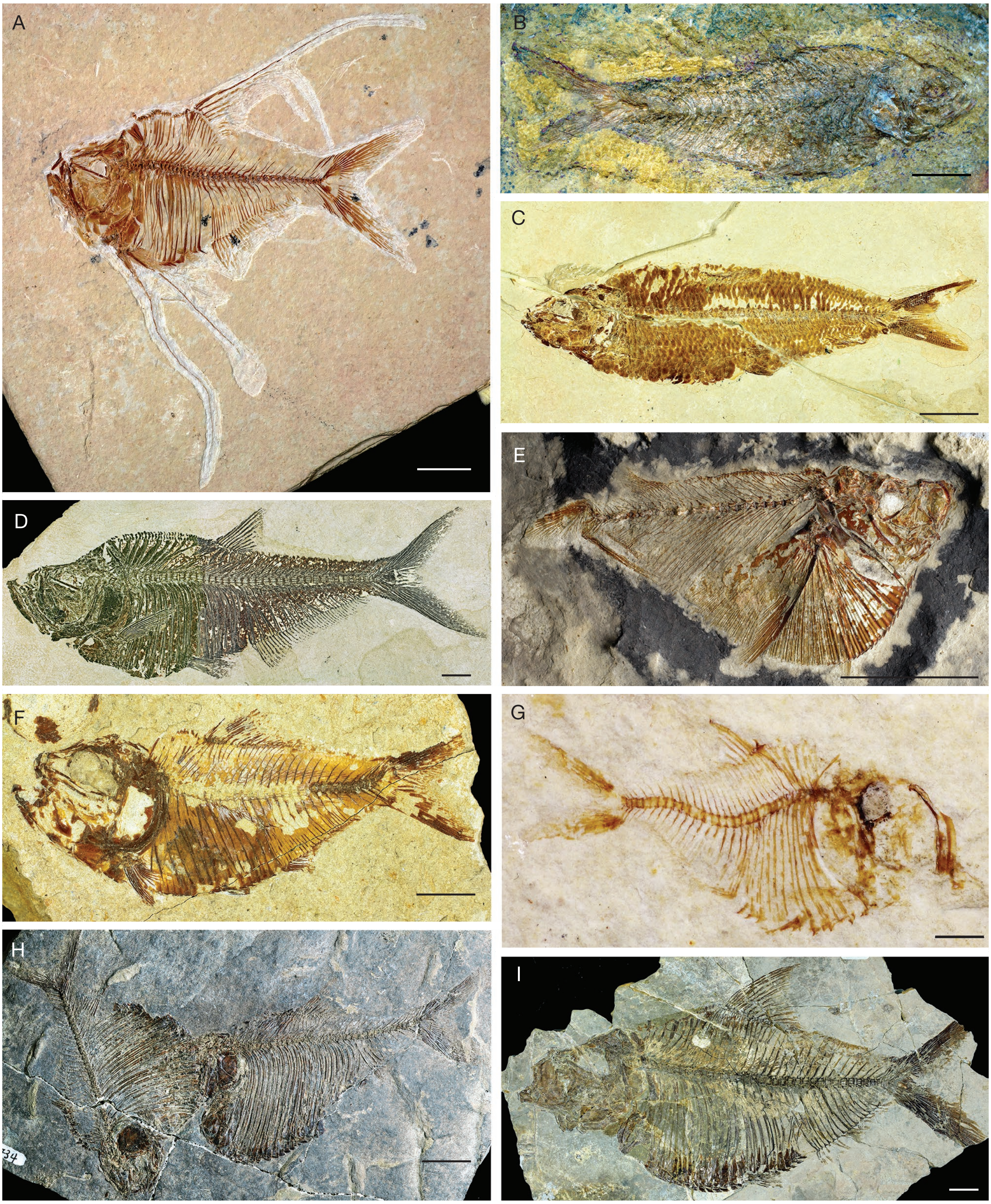

Fig. 3. — Selected representatives of the fossil families of the †Ellimmichthyiformes: **A**, †*Sorbinichthys elusivo* Bannikov & Bacchia, 2000 (†Sorbinichthyidae), Upper Cretaceous, Lebanon; CLC S-431a, holotype (photo: courtesy of Luigi Capasso); **B**, †*Codoichthys carnavalii* Santos, 1994 (†Ellimmichthyiformes *incertae sedis*), Lower Cretaceous, Brazil; DGM 435-P, holotype (photo: courtesy of Francisco Figueiredo); **C**, †*Ornategulum sardinioides* (Pictet, 1850) (†Scutatuspinosidae), Upper Cretaceous, Lebanon; NHMUK PV P.63293; **D**, †*Gasteroclupea branisai* Signeux, 1964 (†Gasteroclupeidae), Upper Cretaceous, Bolivia; MNHN F.1963.11.1, lectotype; **E**, †*Diplomystus dentatus* Cope, 1877 (†Gasteroclupeidae), Eocene, Wyoming, USA; NHMUK PV P.52501; **F**, †*Armigatus brevissimus* (Blainville, 1818) (†Armigatidae), Upper Cretaceous, Lebanon; NHMUK PV P.473/6; **G**, †*Eoellimmichthys superstes* Marramà, Bannikov, Kriwet & Carnevale, 2019 (†Paraclupeidae: †Eoellimmichthyinae n. subfam.), Eocene, Italy; MCSNV IG.23695, holotype; **H**, †*Ellimmichthys longicostatus* (Cope, 1886) (†Paraclupeidae: †Ellimmichthyinae), Lower Cretaceous, Brazil; AMNH DVP.734; **I**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Paraclupeidae: †Paraclupeinae), Upper Cretaceous, Italy; MRSN P/260.3, holotype. Scale bars: 10 mm.

CHARACTER DESCRIPTIONS

The present analysis sampled 368 morphological characters (of which 24 are used for the first time in a phylogeny of Clupeomorpha) in 130 terminal taxa at species level, including 124 clupeomorphs and six outgroup species, representing at least six orders and 23 families of teleosts (Appendices 2; 3). Quantitative (meristics and measurements) and qualitative characters were categorized based on body regions (general features, neurocranium, circumorbital series, opercular apparatus, vertebral column and intermuscular bones, paired fins and girdles, caudal skeleton and fin, dorsal and abdominal scutes, median fins, scales). Characters and states were encoded in the matrix in the same order as they are listed and described below. Missing or uncertain information was coded as "?", whereas inapplicable states resulting from anatomical absence or logical dependence on a preceding character were coded as "–". Original character definitions (author/s and original character number) used by Grande (1985) and/or for the first time in cladistic studies on clupeiforms and/or †ellimmichthyiforms were included between brackets as acronyms after each character:

AO	Alvarado-Ortega *et al.* 2008;
C	Chen *et al.* 2021;
CM	Chang & Maisey 2003;
D	Di Dario 1999;
DD	Di Dario 2004b;
DiD	Di Dario 2009;
FR	Figueiredo & Ribeiro 2016;
G	Grande 1985;
K	Kevrekidis *et al.* 2024;
M	Marramà & Carnevale 2016;
MC	Marramà & Carnevale 2017;
ME	Mertzen 2019;
MKC	Marramà *et al.* 2022;
MW	Murray & Wilson 2013;
S	Sato 1994;
V	Vernygora 2020;
Z	Zaragüeta Bagils 2004.

General features

1. Anterior dorsal margin of the body (Z56): (0) roughly parallel to the main axis of body; (1) forming a marked angle at the dorsal-fin insertion.

Description. All the outgroups and most clupeomorphs have a straight or slightly convex dorsal margin between the occiput and the insertion of the dorsal fin, which is roughly parallel to the main axis of body (Figs 1A-D, F-N; 2A-J; 3B-F). A straight or slightly concave anterior margin forming a marked angle at dorsal-fin insertion (the margin forms an acute angle with the main axis of body) is distinctive of †*Sorbinichthys*, all members of the family †Paraclupeidae (except †*Thorectichthys rhadinus*) (Fig. 3A, G-I) and, among the living clupeiforms, of *Coilia* and *Setipinna* (Fig. 1E).

2. Mouth orientation (new): (0) terminal; (1) inferior or subterminal; (2) superterminal (upward turned).

Description. In most of the taxa the mouth is terminal, opening at anterior end of head with upper and lower jaws subequal in length (Fig. 6A, B, G, H). In *Albula*, *Anodontostoma*, *Clupanodon*, *Konosirus* and *Nematalosa* the mouth is inferior or subterminal (see Whitehead 1985), i.e., positioned near or totally underside of the head (Fig. 6C). In Pristigasteroidea (except *Chirocentrodon*; Whitehead 1985), all †*Diplomystus* species, †*Gasteroclupea* and †*Guiclupea* the lower jaw is projecting, with mouth directed more or less obliquely upward (Fig. 6E, F) (see also Marramà & Carnevale 2017; Chen *et al.* 2021).

3. Denticles (odontodes) covering the dermal bones of the skull (G12): (0) absent; (1) present.

Description. *Denticeps* and †*Palaeodenticeps* are the only taxa possessing several dermal bones of the head and of part of the pectoral girdle externally covered with odontodes (Fig. 7B, C) (see Greenwood 1960, 1968).

Neurocranium

4. Parietals/supraoccipital condition (G10, CM4): (0) medioparietal; (1) lateroparietal.

Description. Most groups of lower crown teleosts (e.g., osteoglossomorphs, elopiforms, salmoniforms), †*Tischlingerichthys* and most of †ellimmichthyiforms have parietals in full contact with each other along their midline, so that the frontals do not contact the supraoccipital (medioparietal condition; Fig. 8A) (Forey 1973a, b; Grande 1985; Chang & Maisey 2003; Alvarado-Ortega *et al.* 2008). Complete separation of the parietals by the supraoccipital (lateroparietal condition; Figs 7B; 8B-D) occurs in *Alepocephalus*, *Osmerus*, Gonorynchiformes like *Chanos* (*Kneria* lacks parietals), †*Spratticeps* and all clupeiforms, including †*Cynoclupea*, †*Pseudoellimma* and †*Santanaclupea* (e.g., Rembiszewski 1964; Grande 1985; Maisey 1993; Grande & Poyato-Ariza 1999). †*Sorbinichthys elusivo* is unique among †ellimmichthyiforms in that supraoccipital separates parietals, whereas the condition in †*S. africanus* Murray & Wilson, 2011 is not clear (Bannikov & Bacchia 2000; Murray & Wilson 2011).

5. Parietal excavation (FR60): (0) absent; (1) present.

Description. The parietal excavation is a deep excavation between parietal and supraoccipital behind the level of the supratemporal commissure that has been interpreted as site of insertion of the epaxial musculature and apparently linked to the presence of a high supraoccipital crest (Forey 2004). The excavation has been originally identified by Forey (2004) in some †ellimmichthyiforms like †*Armigatus brevissimus*, †*Diplomystus dentatus*, and †*Triplomystus* (Fig. 8A), and considered absent in †*Ellimma*

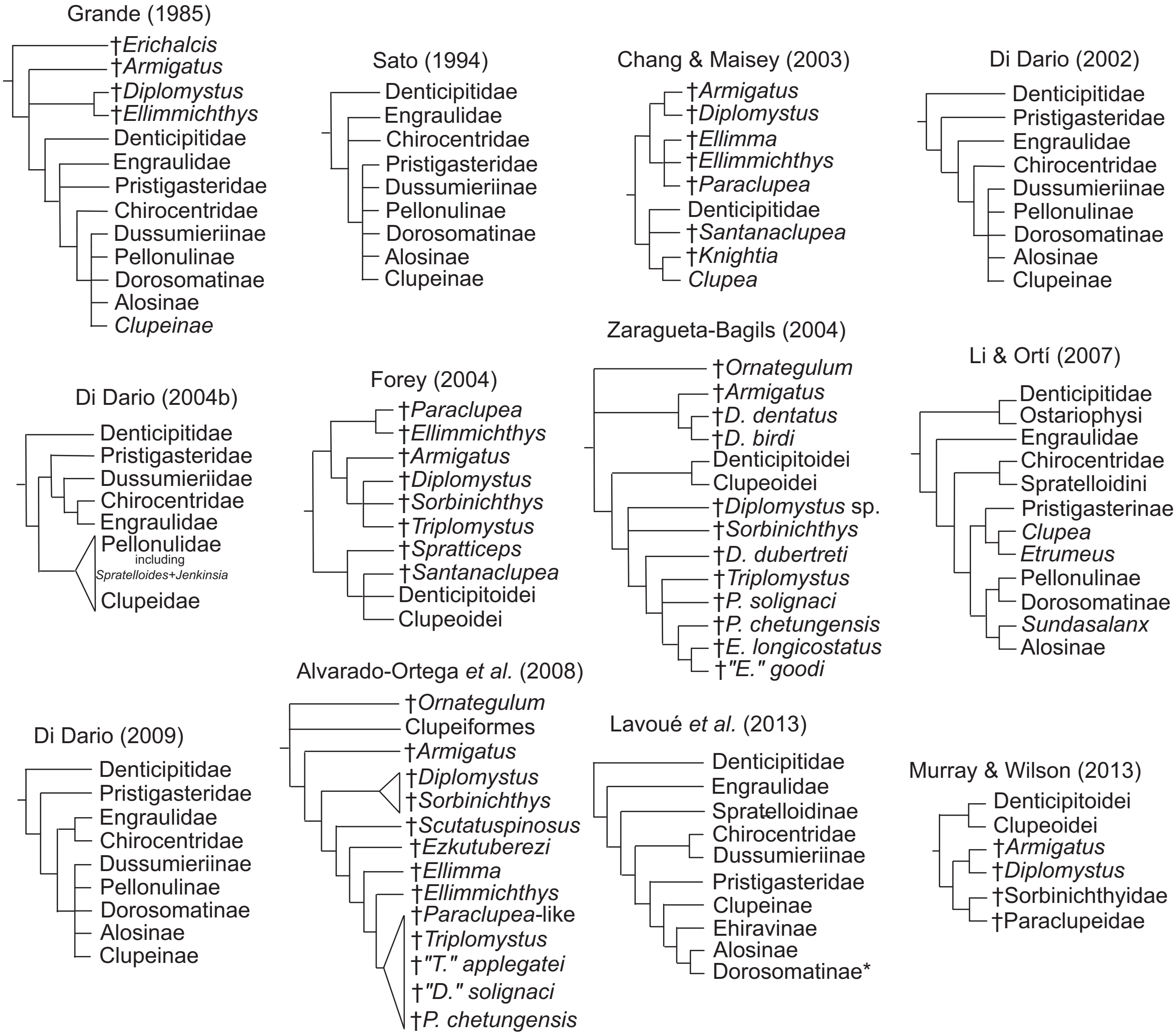

Fig. 4. — Selected morphology- and molecules-based phylogenetic hypotheses of the Clupeomorpha published from 1985 to 2013. Single asterisks (*) indicate that the Dorosomatinae include also the Grande's Pellonulini. "*D.*", *Diplomystus*; "*E.*", *Ellimmichthys*; "*P.*", *Paraclupea*; "*T.*", *Triplomystus*. Triangles represent groups with unresolved or simplified internal relationships. Some of these groups (i.e., Clupeidae, Dorosomatidae, Ehiravidae) are paraphyletic based on those analyses.

branneri, †*Ellimmichthys longicostatus*, †*Paraclupea chetungensis* and all the Clupeiformes (Fig. 8B-D). The excavation has been subsequently reported in †*Scutatuspinosus* and '†*Ellimma*' *longipectoralis* (Figueiredo & Ribeiro 2016; Polck *et al.* 2020). We agree with Figueiredo & Ribeiro (2016) that the parietal excavation should be considered absent in †*Armigatus*, also due to a low supraoccipital crest in this genus that did not allow for insertion of a robust epaxial musculature. However, contra Figueiredo & Ribeiro (2016), its presence in †*Sorbinichthys elusivo* must be considered doubtful (?) since the small supraoccipital separates the parietals in this taxon, and possibly precludes the presence of a space where a large excavation can be seen in the specimens in lateral view (Bannikov & Bacchia 2000, figs 1-5). In any case, its presence has not been reported in the original publication (Bannikov & Bacchia 2000).

6. Supratemporal commissure passing through parietals (G3, CM6): (0) absent; (1) present.

Description. We decoupled the original character statement (supratemporal commissure passing through parietals or through parietals and supraoccipital) in order to avoid the presence of two or more mutually exclusive transformational states that would fail to follow the logical bases for morphological characters in phylogenetics provided by Sereno (2007). Since Patterson (1970), several authors (e.g., Grande 1985; Sato 1994; Chang & Maisey 2003) agree that the supratemporal commissure passes exclusively through the parietals in *Chanos* and all living and fossil clupeomorphs (Fig. 7A). This is also the condition of †*Tischlingerichthys* (Arratia 1997).

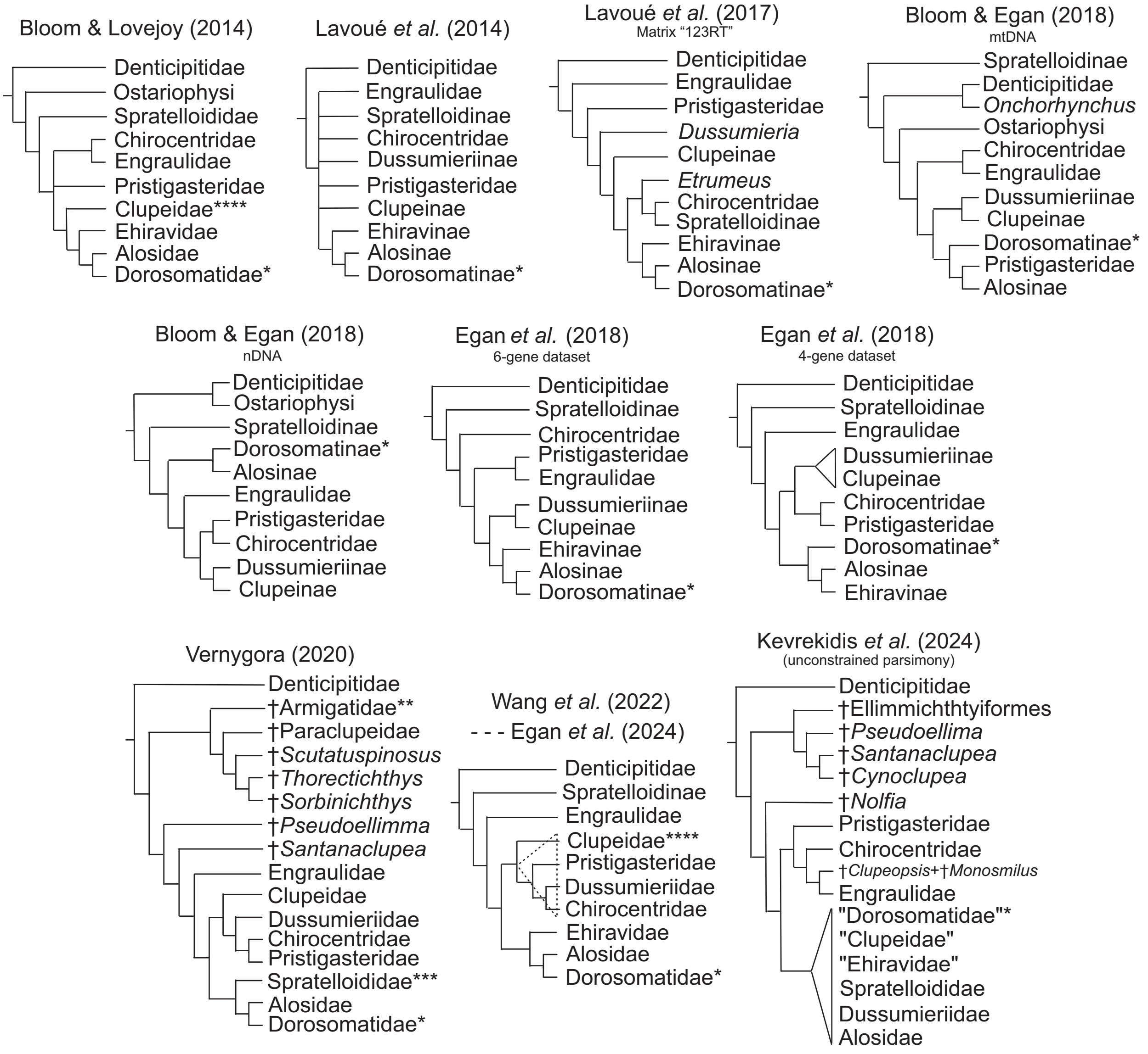

Fig. 5. — Selected morphology- and molecules-based phylogenetic hypotheses of the Clupeomorpha published from 2014 to 2024. Single asterisks (*) indicate that the Dorosomatinae/idae include also the Grande's Pellonulini. Two asterisks (**) indicate that the †Armigatidae includes †*Armigatus*, †*Codoichthys*, †*Diplomystus*, †*Foreyclupea*, †*Ranulfoichthys* and †*Kwangoclupea*. Three asterisks (***) indicate that the Spratelloididae include †*Chasmoclupea*, *Clupeichthys*, *Jenkinsia*, *Spratelloides*, *Sundasalanx* and †*Trollichthys*. Four asterisks (****) indicate that the Clupeidae include also *Etrumeus*. Suprageneric taxa within brackets (e.g., "Dorosomatidae") were recovered non-monophyletic. Triangles represent groups with unresolved or simplified internal relationships. Some of these groups (i.e., Clupeidae, Dorosomatidae, Ehiravidae) are paraphyletic based on those analyses.

7. Enclosure of the supratemporal commissure passing through parietals (S36): (0) not enclosed within a bony tube; (1) enclosed within a bony tube.

Description. In †Ellimmichthyiformes and most Clupeiformes the supratemporal commissure on parietal is normally enclosed within a bony tube in the lateral part of the parietal (Greenwood 1968; Patterson 1970; Grande 1985; Sato 1994; Mertzen 2019). However, in †*Santanaclupea*, *Spratelloides*, *Chirocentrus*, all engraulids, a few pristigasteroids (*Chirocentrodon*, *Ilisha*, *Odontognathus*, *Opisthopterus* and *Pellona*), and few other clupeoids (*Alosa*, *Gilchristella*, *Hyperlophus*, *Nannothrissa* and *Sprattus*), the supratemporal commissure is not enclosed within a bony tube but runs over the parietal freely or, like in *Chirocentrus* and *Spratelloides*, in a groove (Sato 1994; Di Dario 2004b). This condition has been also observed in *Chanos* (Grande & Poyato-Ariza 2010).

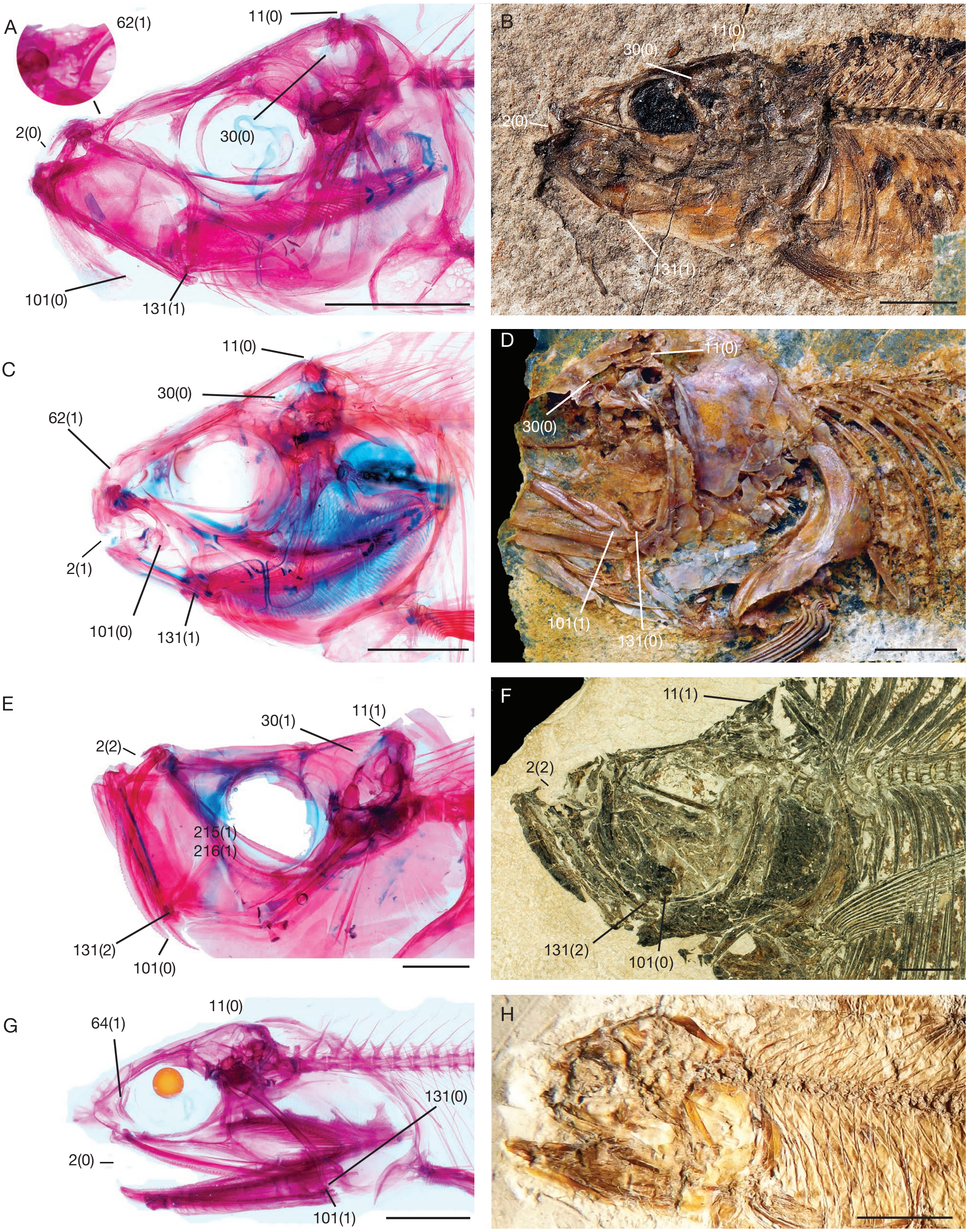

Fig. 6. — Head of selected clupeomorphs: **A**, *Sprattus sprattus* (Linnaeus, 1758) (Clupeiformes: Clupeidae), AMNH 36845 and close up of its mesethmoid showing perforations; **B**, †*Bolcaichthys catopygopterus* (Woodward, 1901) (Clupeiformes: pan-Dorosomatidae); NHMUK PV P.3829a; **C**, *Nematalosa erebi* (Gunther, 1868) (Clupeiformes: Dorosomatidae), AMNH 28097; **D**, †*Santanaclupea silvasantoi* Maisey, 1993 (Clupeiformes: †Cynoclupeidae), AMNH DVP.18968 (mirrored); **E**, *Odontognathus mucronatus* Lacépède, 1800 (Clupeiformes: Pristigasteridae), AMNH 20749; **F**, †*Diplomystus dentatus* Cope, 1877 (†Ellimmichthyiformes: †Gasteroclupeidae), NHMUK PV P.52501; **G**, *Engraulis mordax* Girard, 1854 (Clupeiformes: Engraulidae), AMNH 54600; **H**, †*Eoengraulis fasoloi* Marramà & Carnevale, 2016 (Clupeiformes: Engraulidae), MCSNV T.54. Scale bars: 5 mm. Numbers refer to characters and character states (see text).

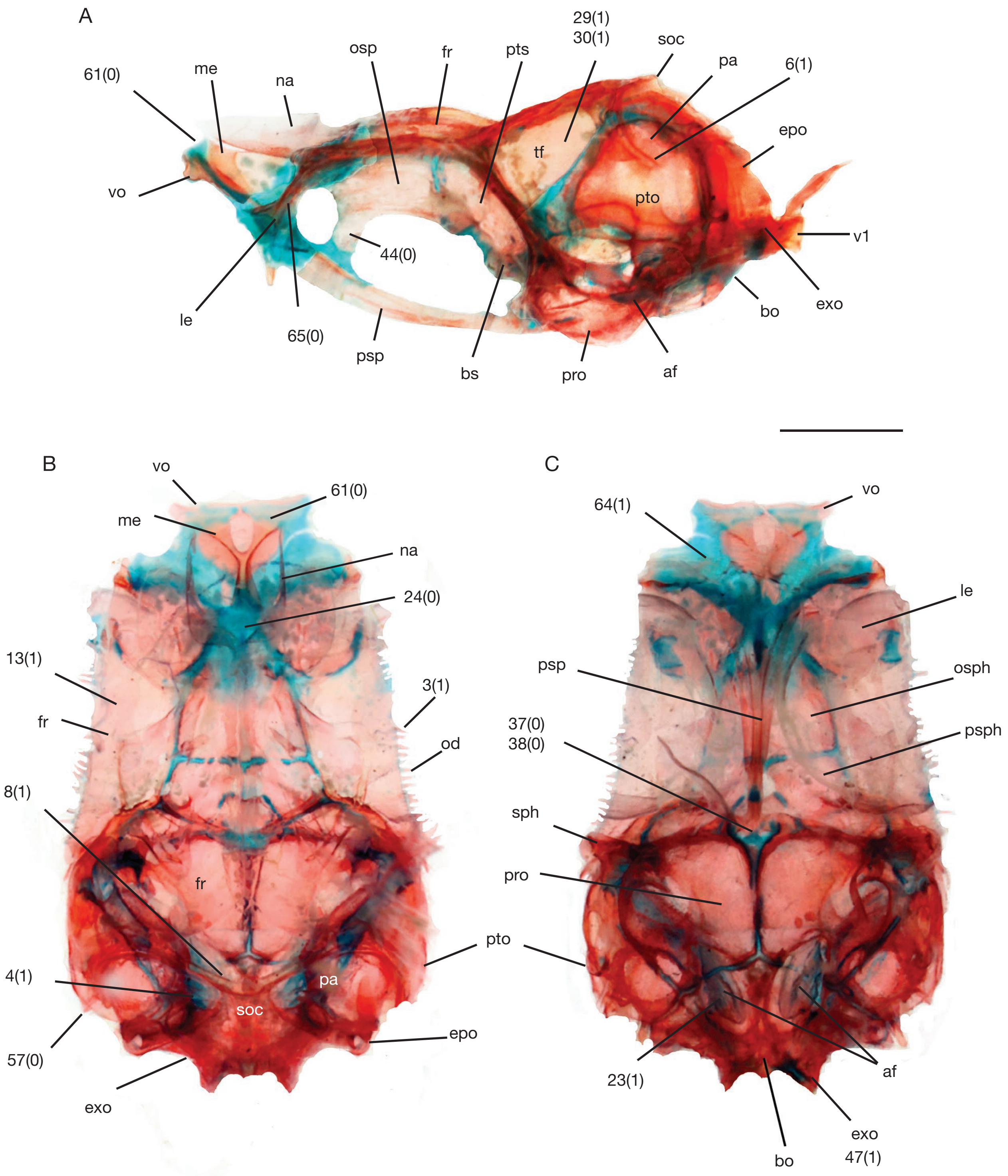

Fig. 7. — Neurocranium of *Denticeps clupeoides* Clausen, 1959 (Clupeiformes: Denticipitidae), AMNH 53082 in: **A**, left lateral, **B**, dorsal and **C**, ventral view. Scale bar: 1 mm. Abbreviations: **af**, auditory fenestra; **bo**, basioccipital; **fr**, frontal; **fro**, epo, epioccipital; **exo**, exoccipital; **le**, lateral ethmoid; **me**, mesethmoid; **na**, nasal; **od**, odontodes; **osph**, orbitosphenoid; **pa**, parietal; **pef**, pre-epioccipital fenestra; **pro**, prootic; **psp**, parasphenoid; **psph**, pterosphenoid; **pto**, pterotic; **soc**, supraoccipital; **sph**, sphenoid; **tf**, temporal foramen (unexposed); **vo**, vomer; **v1**, first vertebra. Numbers refer to characters and character states (see text)

8. Supratemporal commissure sensory canal passing through supraoccipital (CM6): (0) absent; (1) present.

Description. In †*Spratticeps* and Clupeiformes (including †*Pseudoellimma* but not †*Santanaclupea*), and in a few †ellimmichthyiforms (†*Ornategulum*, †*Ranulfoichthys* and †*Paraclupea*) the commissure runs, other than through parietals also, at least in part, through supraoccipital (Figs 7B; 8B-D), whereas this condition is absent in other †ellimmichthyiforms (Fig. 8A) (see Patterson 1970; Forey 1973a; Grande 1985; Chang & Grande 1997; Marramà & Carnevale 2023).

9. Type of head sensory-canal system (MC12): (0) walkeri condition; (1) panamensis condition.

Description. Nelson (1983) identifies two main types of head sensory-canal system in engraulid fishes, the "walkeri condition" and the "panamensis condition", which differ in the course of the sensory canals, particularly on the opercular bone. The "walkeri condition", typical of *Anchoa walkeri* Baldwin & Chang, 1970, includes extra ramifications extending posteriorly from the preopercular canal over the opercular bone and is present in most of clupeoids, including, among engraulids, the Coiliinae (*Coilia*, *Lycothrissa*, *Setipinna*, *Thryssa*), *Stolephorus*, *Anchoviella lepidentostole* and *Lycengraulis grossidens*. However, the "walkeri condition" of the engraulids might be convergent with that of the other clupeoids. Conversely, the derived "panamensis condition" features is a simpler sensory-canal pattern without additional branches, and is typical of most of the New World anchovies (*Anchoa*, *Anchovia*, *Cetengraulis*, *Pterengraulis*) plus the cosmopolitan *Engraulis* and the Indo-Pacific *Encrasicholina*; it shares, among the others features, additional ramifications of preopercular and temporal sensory canals, absent in *Stolephorus* and the coiliine engraulids, indicating that these taxa form a well-defined monophyletic group. It is not possible to detect this character in fossil clupeomorphs.

10. Expanded orbital reticulum (new): (0) absent; (1) present.

Description. Stephens (2010) evidenced the role of the expanded orbital reticulum of the cephalic lateralis system, formed by orbital, infraorbital and preoperculomandibular canal branches anostomosed over a dorsal portion of the eye, as a potential synapomorphy of the Engraulidae. Some primary and secondary canals of the engraulids were considered homologs to those of *Denticeps* (Stephens 2010). No other living clupeoids or outgroup possess the expanded orbital reticulum. It is difficult to detect this character in fossil clupeomorphs.

11. Supraoccipital crest (Z2, DD63): (0) low; (1) high.

Description. The supraoccipital crest is a medial bony protrusion originating from the dorsal aspect of the supraoccipital bone that serves as the attachment points of the epaxial muscles that generate force during suction feeding. The supraoccipital crest is usually low, restricted to a small laminar structure which barely projects dorsally, forming an angle of 180 degrees or more with the back of the skull in outgroups and the majority of clupeomorphs (Figs 6A-D, G, H; 7A). Conversely, it is very high, with its laminar structure that abruptly projected upward forming an angle of less than 180 degrees with the dorsal profile of parietal and frontal bones in *Odontognathus* and *Opisthopterus*, †*Codoichthys*, †*Diplomystus*, †*Gasteroclupea*, and †*Guiclupea* (Fig. 6E, F) (see character definition in Alvarado-Ortega *et al.* 2008).

12. Posterior dorsal opening for supraorbital canal of frontals (S30): (0) small; (1) large.

Description. In clupeiforms, the posterior dorsal opening of the supraorbital canal of frontals usually opens to a posterior depressed mid-dorsal area of frontal and leads the epiphyseal branch of supraorbital canal. In most clupeoids the posterior dorsal opening for supraorbital canal on frontal is small and directed medially. However, in *Denticeps* and all engraulids this opening is large, developed and directed dorsally (Sato 1994). The condition is difficult to detect in fossil taxa.

13. Lateral expansion of the frontal above the orbit (S25): (0) absent; (1) present.

Description. In clupeiforms and most of the outgroups the frontals are more anterodorsally expanded with no lateral expansion above the orbit (Fig. 8A, C). The orbital eaves of the frontals, however, are more expanded laterally than antero-posteriorly in *Albula* and *Osmerus*, *Denticeps*, †*Palaeodenticeps*, †*Clupeopsis*, the living engraulids, some alosids (*Alosa*, *Brevoortia*), dorosomatids (*Anodontostoma*, *Dorosoma*, *Konosirus*, *Nematalosa*, and *Tenualosa*) (Figs 7B, C; 8B, D) (Ridewood 1904a, b; Rembiszewski 1964; Sato 1994; Mertzen 2019). It is difficult to detect it in most of the fossils, unless they are three-dimensionally preserved (e.g., †*Clupeopsis*) or their skull roof is properly exposed.

14. Ridge between orbital wall and levator arcus palatini fossa on frontal and sphenotic (S27): (0) present and fully developed; (1) absent or poorly developed.

Description. In *Denticeps* and many clupeoids, a ridge extending from the frontal to the sphenotic defines the orbital wall and the levator arcus palatini fossa. The upper portion of the levator arcus palatini muscle attaches to the lateral fossa. However, in the engraulids, *Chirocentrodon*, *Clupea*, *Dussumieria*, *Hyperlophus*, *Ilisha*, *Limnothrissa*, *Odontognathus*, *Pellona*, *Potamalosa*, *Sprattus*, and *Stolothrissa*, this ridge is either absent, poorly developed, or discontinuous if present (Sato 1994).

15. Dorsal ridge on frontal (S28): (0) absent; (1) present.

Description. In some clupeoids (*Ilisha*, *Pellona*, *Odontognathus*, *Sardina* and *Sardinops*) a short or long longitudinal ridge is present, located near the medial edge of the anterior

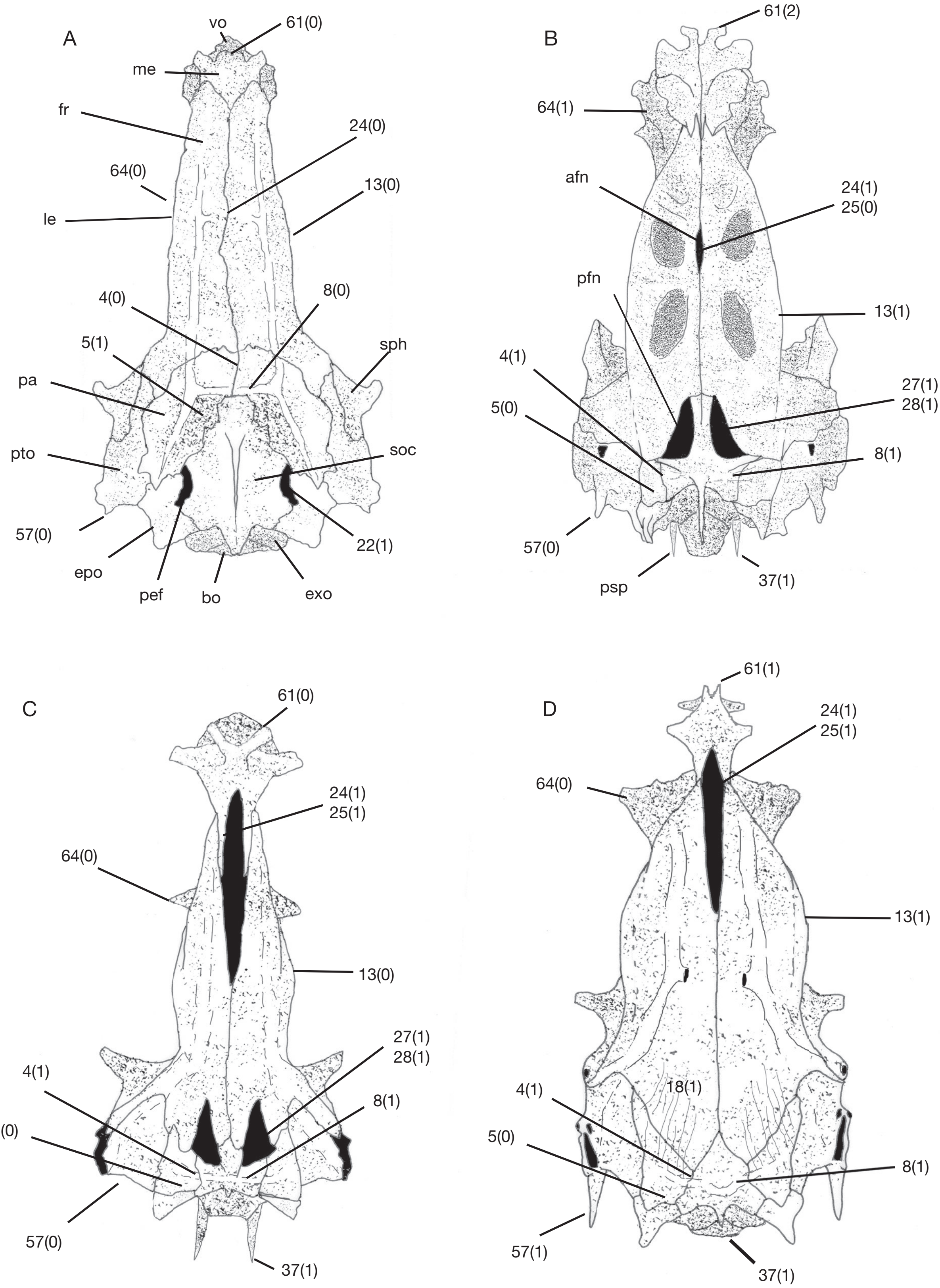

FIG. 8. — Reconstructions of the dorsal surface of skull roof of selected clupeomorphs: **A**, †*Diplomystus* sp. (†Ellimmichthyiformes: †Gasteroclupeidae) (modified after Forey 2004, figs 4, 5 and pers. obs.); **B**, *Lycothrissa crocodilus* Bleeker, 1851 (Clupeiformes: Engraulidae) (after the rendering of the specimen UMMZ 209911 depicted in Capobianco *et al.* 2020, fig. S11); **C**, *Odaxothrissa losera* Boulenger, 1899 (Clupeiformes: Ehiravidae) (modified after Grande 1985, figs 30, 32 and pers. obs.); **D**, *Dorosoma cepedianum* (Lesueur, 1818) (Clupeiformes: Dorosomatidae) (modified after Grande 1985, figs 43, 45 and pers. obs.). Abbreviations: **afn**, anterior frontal fontanelle; **bo**, basioccipital; **fr**, frontal; **epo**, epioccipital; **exo**, exoccipital; **le**, lateral ethmoid; **me**, mesethmoid; **pa**, parietal; **pef**, pre-epioccipital fenestra; **pfn**, posterior frontal fontanelle; **pto**, pterotic; **soc**, supraoccipital; **sph**, sphenoid; **vo**, vomer. Numbers refer to characters and character states (see text). Figures not to scale.

dorsal opening of the supraorbital canal and that can extend to near the fronto-parietal suture (Sato 1994). *Denticeps* and the other clupeoids lack this dorsal ridge.

16. Ornamentation of the skull roof bones (S34, Z3): (0) absent; (1) present.

Description. Contrary to the outgroups, several living and fossil clupeomorphs are characterized by more or less pronounced ornamentation in the posterior region of the frontals and the anterior region of the parietals. Among clupeiforms, in particular, frontals (and sometimes parietals) are ornamented in *Cetengraulis*, pristigasterids (except *Pristigaster*), *Potamalosa* and *Sprattus*, a few ehiravids (*Microthrissa* and *Pellonula*), all the alosids and most dorosomatids (except *Platanichthys* and *Rhinosardinia*) (e.g., Whitehead 1967, 1985; Sato 1994; Di Dario 2004b). Among the fossil clupeiforms, skull roof ornamentation is present in †*Bolcaichthys*, †*Chasmoclupea*, †*Cynoclupea*, †*Italoclupea*, †*Knightia*, †*Santanaclupea*, and †*Scombroclupea*, (e.g., Grande 1982b; Maisey 1993; Marramà & Carnevale 2015b). Most †ellimmichthyiforms have heavily ornamented skull roof, except †*Armigatus alticorpus*, †*A. dalmaticus* Murray *et al.*, 2016, †*A. oligodentatus* Vernygora & Murray, 2016, †*Diplomystus shengliensis* Zhang, Zhou & Qing, 1985, †*Guiclupea*, †*Palaeodenticeps*, †*Sorbinichthys africanus*, †*Thorectichthys rhadinus* and †*Tycheroichthys*.

17. Ornamentation pattern of the skull roof bones (S34, Z4): (0) fine, more or less parallel grooves (fronto-parietal striae); (1) strong and radiating grooves and ridges; (2) tubercles.

Description. Where the ornamentation is present, living and fossil Clupeiformes are usually characterized by the presence of fine, roughly parallel grooves in the posterior region of the frontals and the anterior region of the parietals called fronto-parietal striae or striations (see Whitehead 1985). The same condition has been described for †*Cynoclupea*, †*Pseudoellimma*, and †*Santanaclupea*, whereas †*Spratticeps* have strong and radiating grooves and ridges resembling the condition of most †Ellimmichthyiformes (except †*Codoichthys*, †*Diplomystus* and †*Scutatuspinosus*, which show fine grooves) (Patterson 1970; Zaragüeta Bagils 2004). †*Gasteroclupea* and †*Sorbinichthys elusivo* are unique in having skull roof bones ornamented with small tubercles (Bannikov & Bacchia 2000; Marramà & Carnevale 2017).

18. Number of fronto-parietal striae (DD28): (0) up to seven; (1) eight or more.

Description. The number of fronto-parietal striae is relevant for taxonomic purposes in Clupeiformes. In particular, pristigasterids, ehiravids (*Microthrissa*, *Pellonula*), *Potamalosa*, *Sprattus*, all the alosids and a few dorosomatids (*Harengula*, *Herklotsichthys*, *Tenualosa*) have a low number of fronto-parietal striae (two to seven). Conversely, the remaining dorosomatids and †*Bolcaichthys* have between 8 and 14 fronto-parietal striae (Fig. 8D). The number of fronto-parietal striae in other fossil clupeiforms remains elusive.

19. Parietal-epioccipital ridge (S37): (0) absent; (1) present.

Description. Some Clupeiformes, such as *Chirocentrus* and some pristigasterids (*Chirocentrodon*, *Ilisha*, *Pellona*, *Odontognathus*), exhibit a parietal-epioccipital ridge obliquely across from the anteromedial end of the parietal to near the posttemporal facet of the epioccipital (Sato 1994), which is absent in the other clupeomorphs and outgroups included in this analysis (see also Mertzen 2019). It is very difficult to determine its presence in fossil clupeomorphs.

20. Posttemporal fossa (Z6): (0) absent; (1) present.

Description. The posttemporal fossa is a shallow depression leading into a deep pocket extending antero-medially below the frontal, its medial wall formed by the parietal, its floor by the pterotic, sphenotic and frontal (Patterson 1970). It is present in *Albula*, *Osmerus*, Gonorynchiformes, most clupeomorphs (including †*Chasmoclupea*, †*Scombroclupea*, †*Spratticeps* and †*Pseudoellimma*) but is absent in *Alepocephalus*, *Denticeps* and †*Foreyclupea*, possibly as a consequence of their inflated braincase (Patterson 1970; Johnson & Patterson 1996; Mertzen 2019).

21. Pre-epioccipital fossa (G5, CM3): (0) reduced or obliterated; (1) well defined.

Description. The presence of a well-defined pre-epioccipital fossa was considered by Grande (1985) as a synapomorphy of the Clupeomorpha, as it was supposed to be present in †ellimmichthyiform taxa (†*Armigatus*, †*Diplomystus*), †*Spratticeps* and most clupeoids. However, the nature of this cavity in the otic region of the skull was discussed by Forey (2004), who recognized that the «pre-epioccipital fossa» of the †ellimmichthyiforms (a fenestra between the parietal, epioccipital and supraoccipital) is considerably different from the pre-epioccipital fossa of the Clupeiformes (lying between parietal, epioccipital and pterotic) suggesting that the former must be re-named as pre-epioccipital fenestra. In this perspective, the pre-epioccipital fossa is extremely reduced or sometimes obliterated because of the expansion of the pterotic bulla in †Ellimmichthyiformes, †*Spratticeps*, †*Pseudoellimma*, *Denticeps* and all engraulids (Fig. 9B, D) (Patterson 1970; Grande 1985; Sato 1994; Figueiredo 2009a). Conversely, it is large, and well defined in †*Cynoclupea*, †*Santanaclupea* and most living and fossil Clupeoidei (Fig. 9A, C, E-H) (Grande 1985; Malabarba & Di Dario 2017). It is absent in outgroups (Greenwood *et al.* 1966).

22. Pre-epioccipital fenestra (AO7): (0) absent; (1) present.

Description. The pre-epioccipital fenestra (a small fenestra between the parietal, epioccipital and supraoccipital) appears to be a failure of the dermal roofing bones to completely cover the posttemporal fossa in †Ellimmichthyiformes (Forey 2004). It is likely present in all entire group as it was reported, e.g., in †*Armigatus brevissimus*, †*A. namourensis*, †*Diplomystus* (Fig. 8A), †*Paraclupea pietrarojae* and †*Triplomystus* (Forey *et al.* 2003; Forey 2004; Marramà & Carnevale 2023).

23. Auditory fenestra (S23): (0) absent; (1) present.

Description. The auditory fenestra is a large fenestra that in *Denticeps* (Fig. 7C) and most Clupeiformes is surrounded by the prootic, exoccipital and basioccipital, whereas in *Coilia* it is small and surrounded by the prootic and exoccipital only (Ridewood 1904b; Sato 1994). This fenestra is also present in †*Cynoclupea* and †*Santanaclupea* (Maisey 1993; Malabarba & Di Dario 2017) but is absent in †*Spratticeps* and the †ellimmichthyiforms (e.g., †*Armigatus brevissimus*, †*Diplomystus dentatus*, †*Ornategulum*) likely due their heavier ossification of the skull (Patterson 1970; Forey 1973a, 2004). The auditory fenestra is absent in the outgroups considered (Ridewood 1904a, b; Greenwood *et al.* 1966).

24. Anterior frontal fontanelle (CM5, S32): (0) absent; (1) present.

Description. The anterior fontanelle is an unossified area in the dorsal region of the skull, bounded posterolaterally by the frontals and anterolaterally by the mesethmoid (e.g., Sato 1994). It is present in *Albula*, *Alepocephalus*, *Chanos* and most extant clupeoids (Fig. 8B-D), but it is absent in *Denticeps* (Fig. 7B), *Coilia*, †*Italoclupea*, and †*Nardoclupea* (Ridewood 1904b; Sato 1994; Mertzen 2019), †*Pseudoellimma* and †*Santanaclupea* (Maisey 1993; Figueiredo 2009a). It is present in fossil clupeoids (e.g., Grande 1985; Marramà & Carnevale 2015a; Capobianco *et al.* 2020) but absent in most †ellimmichthyiforms (Fig. 8A) (e.g., Forey 1973a; Alvarado-Ortega *et al.* 2020) although it was described in †*Paraclupea chetungensis* (Chang & Grande 1997).

25. Size of the anterior frontal fontanelle (S32, CM5): (0) small, narrow laterally; (1) very large.

Description. When present, the anterior fontanelle can be small with an oval shape more or less laterally compressed, like in outgroups, engraulids (Fig. 8B), *Dussumieria*, *Etrumeus*, *Jenkinsia Spratelloides* and †*Trollichthys*, the pristigasterids *Ilisha* and *Opisthopterus*, the dorosomatid *Rhinosardinia*, and the †ellimmichthyiform †*Paraclupea chetungensis* (see also, e.g., Yabumoto 1988; Sato 1994; Mertzen 2019). In all the other fossil and living clupeoids, including †*Clupeopsis* and †*Monosmilus* (Capobianco *et al.* 2020), and the other pristigasteroids and clupeoids, the anterior frontal fontanelle is large, nearly circular (Fig. 8C, D) (Sato 1994).

26. Expansion of sacculus (S24): (0) sacculus not expanded; (1) sacculus expanded.

Description. In the majority of clupeoids, the outer wall of the sacculus does not exhibit significant expansion. In contrast, in *Denticeps* and *Setipinna*, the outer wall of the sacculus, formed by the prootic and basioccipital and aligned with the perimeter of the auditory fenestra, shows substantial expansion (Sato 1994).

27. Posterior frontal fontanelles (in adult) (S33): (0) closed; (1) open.

Description. Although the posterior frontal fontanelles between the frontals and the supraoccipital are usually open in juveniles of most clupeiforms, they remain open only in adult individuals of *Chirocentrus*, *Jenkinsia* and *Spratelloides*, the Engraulidae (except *Cetengraulis* and *Coilia*), some pristigasteroids (*Chirocentrodon*, *Ilisha*, *Odontognathus*, *Opisthopterus*, *Pellona*), most ehiravids (*Clupeoides*, *Clupeonella*, *Corica*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*), the hyperlophines *Hyperlophus and Potamalosa*, and the dorosomatid *Platanichthys* (Fig. 8B, C) (Whitehead 1962, 1963, 1964, 1985; Grande 1985; Sato 1994). Posterior frontal fontanelles are absent (or are closed in adult) in the outgroups, all †ellimmichthyiforms examined and all other clupeiforms (Fig. 8A, D), including †*Clupeopsis* (Capobianco *et al.* 2020).

28. Size of posterior frontal fontanelle (DD26): (0) reduced; (1) large.

Description. The posterior frontal fontanelle is small in *Jenkinsia*, *Spratelloides*, *Chirocentrus*, some engraulids (*Anchoa*, *Anchoviella*, *Engraulis*, *Lycengraulis*), some pristigasterids (*Ilisha*, *Opisthopterus*, *Pellona*), and a few other clupeoids (*Hyperlophus*, *Herklotsichthys* and *Platanichthys*), whereas it is large in *Encrasicholina*, *Lycothrissa*, *Stolephorus* and *Thryssa*, and most ehiravids (*Clupeichthys*, *Clupeoides*, *Clupeonella*, *Gilchristella*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*) (Fig. 8B, C) (see Di Dario 2004b).

29. Temporal foramen (S35, MKC14): (0) absent; (1) present.

Description. The temporal foramen is a subcircular or ovoid cavity dorsal to the recessus lateralis in the region of articulation between frontal and parietal, where a sac-like expansion of the supraorbital canal (the sinus temporalis)

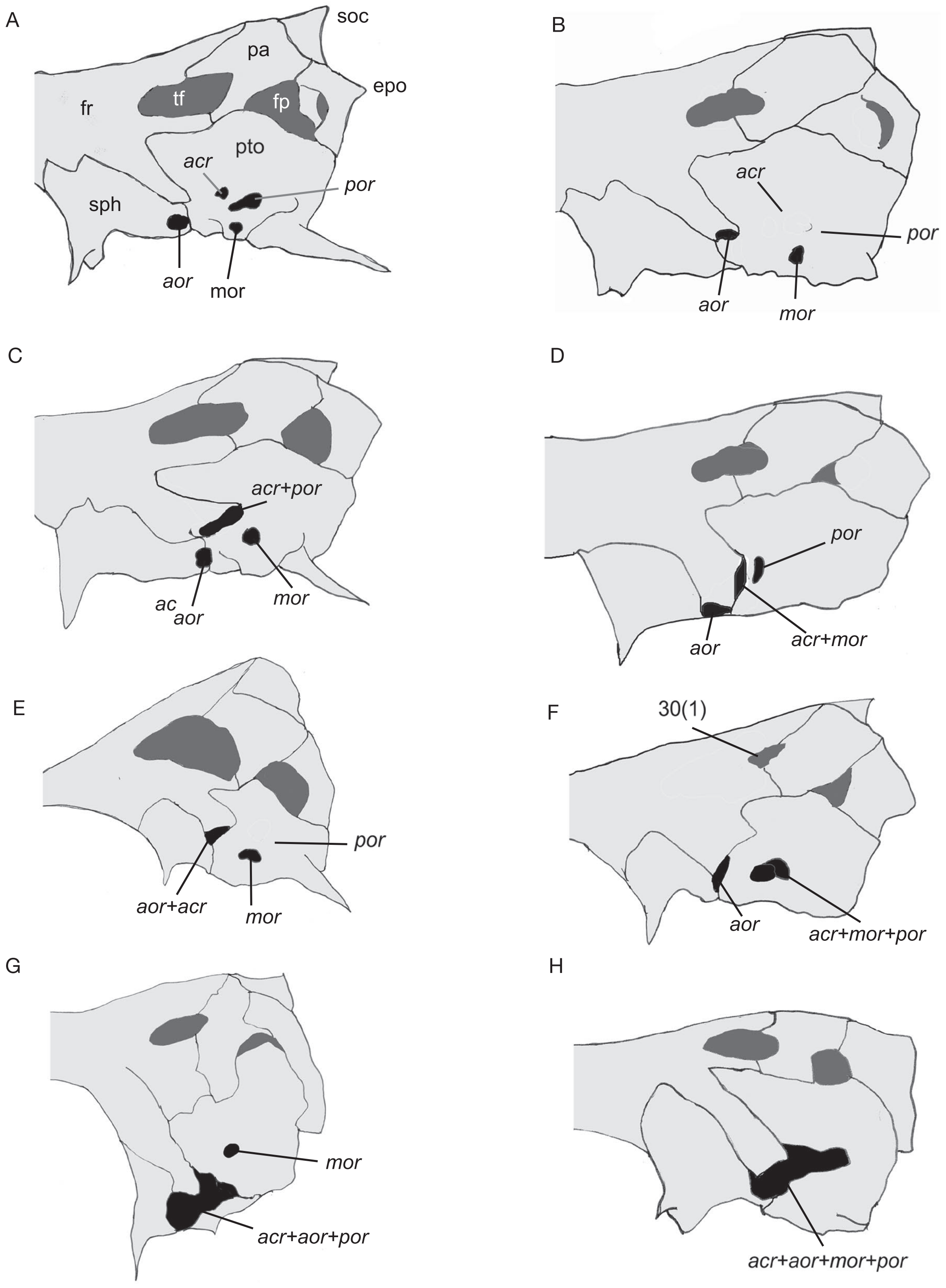

Fig. 9. — Schematic reconstructions of the otic region (anterior to the left) of selected clupeiforms, showing the openings of the recessus lateralis: **A**, *Dorosoma cepedianum* (Lesueur, 1818) (Dorosomatidae) (after Grande 1985); **B**, *Cetengraulis edentulus* (Cuvier, 1829) (Engraulidae), AMNH 37073; **C**, *Sardinella maderensis* (Lowe, 1838) (Dorosomatidae), AMNH 44448; **D**, *Anchoviella cayennensis* (Puyo, 1946) (Engraulidae) (after Agostinho *et al.* 2022); **E**, *Amblygaster leiogaster* (Valenciennes, 1847) (Dorosomatidae), AMNH 17581; **F**, *Spratelloides delicatulus* (Bennett, 1832) (Spratelloididae), AMNH 54621; **G**, *Pellona harroweri* (Fowler, 1917) (Pristigasteridae) (after Di Dario 1999); **H**, *Odaxothrissa losera* Boulenger, 1899 (Ehiravidae) (after Grande 1985). Images not to scale. Abbreviations: **acr**, accessory temporal sensory canal opening to the chamber of the recessus lateralis (for pterotic extension of sensory canal); **aor**, anterior opening to the chamber of the recessus lateralis (for infraorbital sensory canal); **epo**, epioccipital; **fp**, pre-epioccipital fossa; **fr**, frontal; **mor**, middle opening to the chamber of the recessus lateralis (for preopercular sensory canal); **pa**, parietal; **por**, posterior opening to the chamber of the recessus lateralis (for lateral extrascapular=cephalic lateralis sensory canal); **pto**, pterotic; **soc**, supraoccipital; **sph**, sphenotic; **tf**, temporal foramen.

fits. It is exclusive of †*Spratticeps* and all fossil and extant Clupeiformes (Greenwood *et al.* 1966; Patterson 1970; Sato 1994) (Figs 6A-E; 7A; 9). It is absent in all outgroups and †ellimmichthyiforms.

30. Exposition of the temporal foramen (S35): (0) fully exposed; (1) unexposed, almost completely obliterated by frontal.

Description. In most clupeiforms the temporal foramen is large and fully exposed (Figs 6A-D; 9A-E, G, H), whereas in †*Spratticeps*, denticipitids, †*Italoclupea*, *Jenkinsia*, *Spratelloides*, †*Nardoclupea* and †*Pseudoellimma*, some engraulids (*Coilia*, †*Eoengraulis*, *Setipinna*) and pristigasterids (*Odontognathus*, *Opisthopterus*, *Raconda*), the temporal foramen is exceptionally small or completely covered by the posterodorsal region of the frontal or by the parietal (Figs 6A, E; 7A; 9F) (e.g., Whitehead 1963; Patterson 1970; Sato 1994).

31. Recessus lateralis (G9, CM1): (0) absent; (1) present.

Description. The recessus lateralis is a chamber in the otic region of the head into which several lateral-line canals open that is considered one of the exclusive synapomorphies of the Clupeiformes (Grande 1985). It is also present in the basal †*Cynoclupea*, †*Pseudoellimma* and †*Santanaclupea* but not in †*Spratticeps* (Patterson 1970; Maisey 1993; Figueiredo 2009a). The recessus lateralis is absent in the outgroups and the †Ellimmichthyiformes (Grande 1985; Zaragüeta Bagils 2004). This can be also detected, mostly in fossils, because the infraorbital canal of the dermosphenotic does not merge with the preopercular canal, as it does in clupeiforms, thus indicating the absence of the recessus lateralis (Grande 1982a).

32. Pattern of openings of the recessus lateralis (G*q*, S19): (0) four discrete openings present: the opening for the infraorbital sensory canal opens between sphenotic, pterotic and sometimes frontal; all other openings open on pterotic; (1) four discrete openings present: the opening for the infraorbital sensory canal opens between sphenotic, pterotic and frontal; the preopercular sensory canal and the cephalic sensory canal open on the pterotic; the accessory temporal canal opens on the pterotic and frontal; (2) three discrete openings present: the infraorbital sensory canal opens between the sphenotic and pterotic; the cephalic and the accessory temporal canals meet in a single opening between pterotic and frontal; the preopercular sensory canal opens on the pterotic; (3) three discrete openings present: infraorbital sensory canal opens between the sphenotic, pterotic and frontal; the preopercular and the accessory temporal canals converge into a single opening between the pterotic and frontal; the cephalic sensory canal opens on the pterotic; (4) three discrete openings present: the preopercular and the cephalic sensory canals open on the pterotic; the infraorbital and the accessory temporal canals are confluent into a single opening between the sphenotic, pterotic and frontal; (5) two discrete openings present: the infraorbital sensory canal opens between the sphenotic, pterotic and frontal; the preopercular, cephalic and accessory temporal canals converge into single opening on the pterotic; (6) two discrete openings present: the infraorbital + cephalic +accessory temporal canals meet into a single open between the sphenotic, pterotic and frontal; the preopercular sensory canal opens on the pterotic; (7) all four canals confluent into a single opening between the sphenotic, pterotic and frontal; (8) all four canal confluent, with the single opening divided into two, anterior and posterior portions, united by a slight gap.

Description. In Clupeiformes, the infraorbital, preopercular, cephalic and accessory sensory canals of the recessus lateralis open in the otic region through a series of openings. However, the number of openings to the recessus and their relative position can vary, depending on species, since two, three or all the four canals can be confluent, forming common openings to the recessus chamber (Grande 1985; Sato 1994; Di Dario 2004a). In this perspective, Sato (1994) recognized several different patterns in relation to the number and position of these openings. In clupeoids with four distinct openings, two main configurations exist: in the first one (Fig. 9A), all the openings except the infraorbital open on pterotic bone; this is the most common condition and is present in *Denticeps* and most clupeoids (*Chirocentrus*, *Dussumieria*, *Etrumeus*, the alosids *Alosa*, *Brevoortia*, *Sardina*, *Sardinops*, and the dorosomatids *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Konosirus*, *Nematalosa*, *Opisthonema* and *Tenualosa*); according to Grande (1985) the "Ehiravini" (represented herein by *Clupeichthys*, *Corica* and *Gilchristella*) exhibit this plesiomorphic condition. Conversely, in *Cetengraulis*, *Engraulis*, *Setipinna* and *Stolephorus*, although being characterized by four openings, the preopercular and cephalic sensory canal openings open on the pterotic alone, while the accessory temporal canal opens between the pterotic and frontal (Fig. 9B). Among clupeoids with three openings, there are three distinct types: *Harengula*, *Herklotsichthys*, *Lile* and *Sardinella* exhibit state 2 (Fig. 9C). *Anchoviella* and *Lycengraulis* show state 3 (Fig. 9D). *Amblygaster* is unique in having state 4 (Fig. 9E). Taxa with two openings can be distinguished in two groups: state 5 is unique to *Spratelloides* (Fig. 9F), whereas *Coilia*, *Escualosa* and *Pellona* exhibit state 6 (Fig. 9G). All the other pristigasteroids (except *Odontognathus*), plus *Clupea*, *Hyperlophus*, *Platanichthys*, *Rhinosardinia*, *Sprattus*, and most of the other Grande's (1985) pellonulines (*Clupeoides*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*) have a common opening to the recessus for all the sensory canals (state 7; Fig. 9H) (Di Dario 2004a, b). Sato (1994) considered the condition of *Odontognathus* different from that of other pristigasteroids because it appears to have two openings connected by a slight gap (state 8). Among fossil clupeiforms, †*Cynoclupea*, †*Clupeopsis* and †*Pseudoellimma*

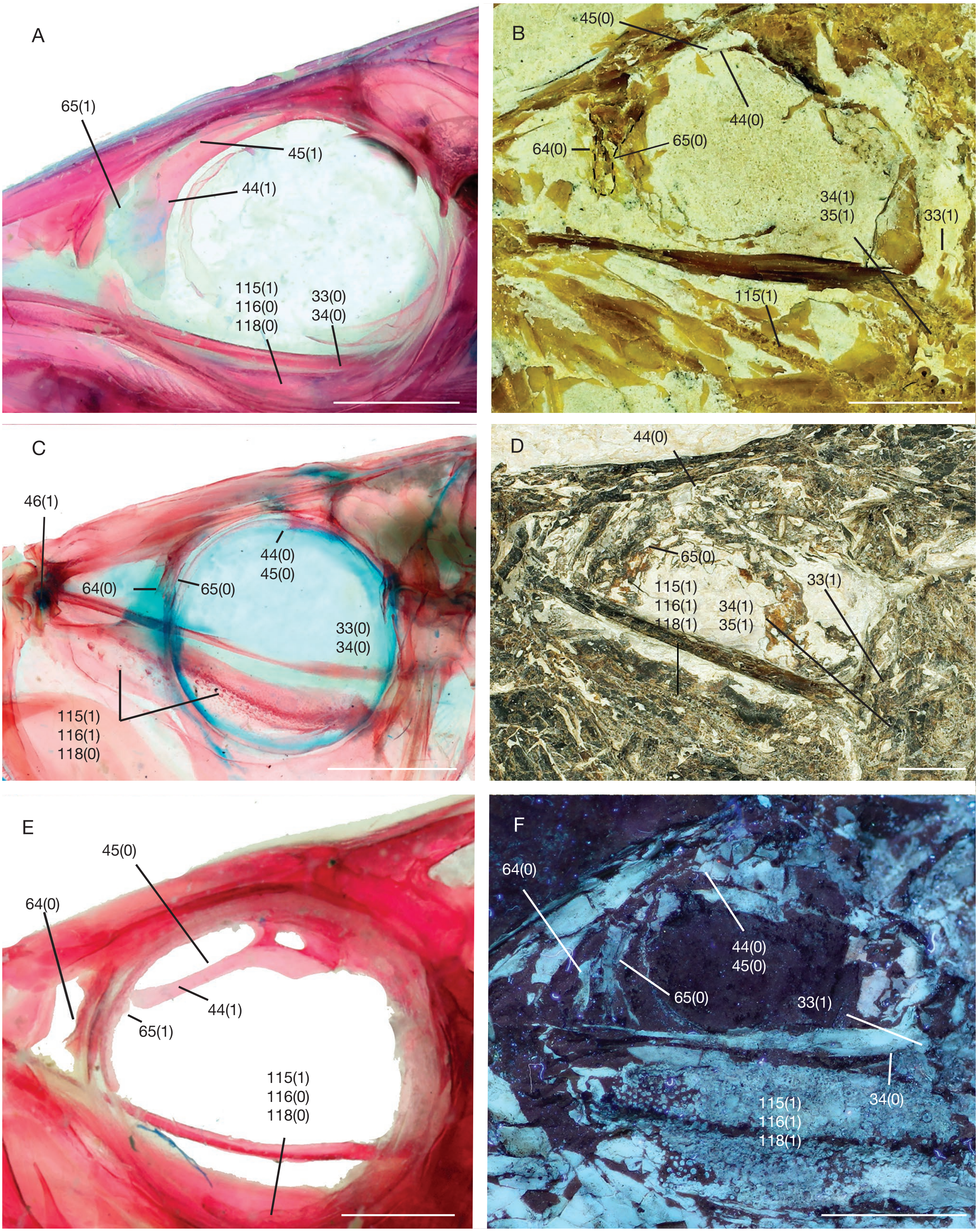

Fig. 10. — Orbital region of selected clupeomorphs: **A**, *Etrumeus sadina* (Mitchill, 1814) (Clupeiformes: Dussumieriidae), AMNH 736; **B**, †*Armigatus namourensis* Forey, Yi, Patterson & Davies, 2003 (†Ellimmichthyiformes: †Armigatidae) NHMUK PV P.62528; **C**, *Chirocentrodon bleekerianus* (Poey, 1867) (Clupeiformes: Pristigasteridae), AMNH 10118; **D**, †*Diplomystus dentatus* Cope, 1877 (†Ellimmichthyiformes: †Gasteroclupeidae), NHMUK PV P.52501; **E**, *Microthrissa royauxi* Boulenger, 1902 (Clupeiformes: Ehiravidae), AMNH 5830; **F**, †*Paraclupea solignaci* (Gaudant & Gaudant, 1971) (†Ellimmichthyiformes: †Paraclupeidae), MNHN F.PSA215 (reversed). Scale bars: 5 mm. Numbers refer to characters and character states (see text).

have four openings resembling the generalized clupeiform condition (Figueiredo 2009a; Malabarba & Di Dario 2017; Capobianco *et al.* 2020) possibly suggesting that this was the ancestral condition for Clupeiformes. †*Santanaclupea* has two large openings within the pterotic although it is not clear which branches of the sensory canal network occupied each opening (Maisey 1993). Being the recessus lateralis absent in outgroups and †Ellimmichthyiformes, this character is unapplicable for them.

33. 'Basipterygoid' processes of the parasphenoid (CM11): (0) absent; (1) present.

Description. The basipterygoid processes (ventrolateral processes of Arratia & Schultze [1991]) are two large processes lying on the posterior part of the parasphenoid and that project latero-ventrally and articulate with the suspensorium in the †Ellimmichthyiformes (Fig. 10B, D, F) (Forey 1973a, 2004; Chang & Maisey 2003) (we consider their apparent absence in †*Armigatus alticorpus* as dubious; Vernygora & Murray 2021). They are absent in all Clupeiformes (Fig. 10A, C, E) (Grande 1985; Chang & Maisey 2003), including †*Cynoclupea*, †*Leufuichthys*, †*Pseudoellimma* and †*Santanaclupea* (Maisey 1993; Figueiredo 2009a), and in all outgroups (Ridewood 1904a; Johnson & Patterson 1996; Arratia 1997; Poyato-Ariza *et al.* 2010).

34. Teeth on parasphenoid (CM10): (0) absent; (1) present.

Description. Teeth on parasphenoid have been reported in manyl teleosts, including *Albula*, †*Tischlingerichthys* and some †ellimmichthyiforms like †*Armigatus alticorpus*, †*A. brevissimus*, †*A. carrenoae*, †*A. namourensis*, †*A. elatus*, †*Diplomystus birdi*, *D. dentatus*, and †*D. shengliensis* (Fig. 10B, D) (see, e.g., also Grande 1982a; Forey *et al.* 2003a; Alvarado-Ortega *et al.* 2020). Our new observation revealed the presence of parasphenoid teeth in form of "osteoglossid-like" tooth patch also in the holotype of *A. alticorpus* (NHMUK PV P.63134) The parasphenoid is edentulous in all the Clupeiformes, Gonorynchiformes, *Osmerus* and *Alepocephalus* (Grande & Nelson 1985; Grande & Poyato-Ariza 1999; Forey 2004; Poyato-Ariza *et al.* 2010).

35. Disposition of teeth on parasphenoid (CM10): (0) present along most of its length; (1) restricted to a small posterior area ('osteoglossid-like' tooth patch *sensu* Grande 1982a).

Description. In *Albula* and †*Tischlingerichthys* the parasphenoid carries small conical teeth along most of its length (Forey 1973b; Arratia 1997). In the †ellimmichthyiforms †*Armigatus* and †*Diplomystus* these teeth are restricted in a small posterior area on parasphenoid, forming an "osteoglossid-like patch" similar to the condition of osteoglossomorph fishes (Fig. 10B, D) (see, e.g., Hilton 2001, 2003).

36. Prominent keel on posterior half of parasphenoid (S11): (0) absent; (1) present.

Description. In *Anodontostoma*, *Brevoortia*, *Dorosoma*, *Konosirus*, *Nematalosa*, and *Tenualosa* the parasphenoid bears a prominent ventral keel in its posterior half (Grande 1985; Sato 1994). The keel is absent in the outgroups and all the other fossil and extant clupeomorphs examined.

37. Posterior ramus of parasphenoid (S12): (0) not extending posteriorly to neurocranium; (1) extending posteriorly to neurocranium.

Description. In most clupeiforms the parasphenoid extends posteriorly to the neurocranium (Fig. 8B-D), whereas it is short without extending posteriorly to neurocranium in *Denticeps* (Fig. 7C), *Coilia*, and *Setipinna* (Greenwood 1968; Sato 1994). The parasphenoid of the outgroups (e.g., Ridewood 1904a; Gosline 1969) and †ellimmichthyiforms (e.g., Forey 1973a, 2004) does not extend behind the occiput (Fig. 8A).

38. Bifurcation on posterior ramus of parasphenoid (S12): (0) absent; (1) present.

Description. In *Alepocephalus*, *Chanos*, *Kneria* (Gosline 1969; Grande & Poyato-Ariza 2010) and most clupeoids the parasphenoid is bifurcated posteriorly (Fig. 8B-D), whereas in *Albula*, *Osmerus*, *Denticeps* (Fig. 7C), *Coilia* and *Setipinna* this bifurcation is absent (Sato 1994). It is difficult to detect this character in fossil clupeomorphs but in those preserving the occipital region in dorso-ventral view, bifurcation appears absent (see also Forey 1973a, 2004).

39. Supratemporal system (MKC18): (0) absent; (1) present.

Description. The supratemporal system is a complex structure formed by branched canals in the temporal region that originate from the sac-like expanded sensory canal that fills the temporal foramen (the *sinus temporalis*) (Patterson 1970; Di Dario & De Pinna 2006). It is present in all the living Clupeiformes, including *Denticeps* (Di Dario & De Pinna 2006). The supratemporal system is a delicate structure, not preserved in fossils; however, since the sinus temporalis is homologous to the parietal branch of the supraorbital canal, its absence can be inferred in fossils where that portion of the canal is unmodified, like in †*Spratticeps* and the †ellimmichthyiforms (Patterson 1970; Di Dario & De Pinna 2006). The supratemporal system is also absent in all the other known teleosts. It was likely present in the fossil clupeiforms †*Pseudoellimma*, †*Santanaclupea* and †*Scombroclupea* (Greenwood *et al.* 1966), but not in †ellimmichthyiforms or other teleosts.

40. Basisphenoid (S17, FR54): (0) present; (1) absent.

Description. The basisphenoid is present in all living clupeiforms, except *Coilia* (Sato 1994); it has been detected also in several fossil clupeiforms including the basal †*Leufuichthys* and †*Spratticeps* (Patterson 1970; Gallo *et al.* 2011). †*Ornategulum* is the only †ellimmichthyiform in which the presence of a basisphenoid has been demonstrated (Forey 1973a). Although a basisphenoid was reported in †*Armigatus carrenoae*, *E. longicostatus* and "*E.*" *spinosus* (Alvarado-Ortega *et al.* 2020; Figueiredo & Gallo 2021), we consider its presence as doubtful since the lamina that extends dorsal to the trabeculum communis lying in the postero-ventral margin of the orbit, and which was traditionally considered a basisphenoid in *Chanos*, *Clarias* or *Silurus*, has been proven to actually represents a dorsal extension of the parasphenoid rather than a separate ossification (Fink & Fink 1981). For this reason, Figueiredo & Ribeiro (2016) consider the absence of basisphenoid as a probable case of secondary loss for †Ellimmichthyiformes. Among outgroups, the basisphenoid is present in *Albula* and *Alepocephalus* (Ridewood 1904a; Johnson & Patterson 1996), but absent in *Osmerus*, †*Tischlingerichthys*, *Chanos* and *Kneria* (Fink & Fink 1981, 1996; Johnson & Patterson 1996; Arratia 1997).

41. Vertical process of the basisphenoid (S17): (0) present; (1) absent.

Description. In *Albula*, *Alepocephalus*, †*Spratticeps* and several Clupeiformes, the basisphenoid has a slender vertical process (Gosline 1969; Sato 1994). However, the vertical process is absent in *Denticeps*, *Chirocentrus*, engraulids, dussumieriids, spratelloidids, some pristigasteroids (*Chirocentrodon*, *Ilisha*, *Neoopisthopterus*, *Odontognathus*, *Pliosteostoma*), some ehiravids (*Clupeonella*, *Clupeoides*, *Clupeichthys*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Pellonula*, *Stolothrissa*), some dorosomatids (*Clupanodon*, *Escualosa*, *Konosirus Tenualosa*), *Hyperlophus* and *Sprattus* (Sato 1994; Di Dario 1999, 2004b).

42. Post-coelomic swimbladder extensions (S161): (0) absent; (1) present.

Description. The pristigasteroids *Ilisha kampeni* Weber & de Beaufort, 1913 and *Raconda* are unique among the clupeomorphs examined herein in having one or two post-coelomic tubes extending from the hind end of the swimbladder back into the muscles of the body (Whitehead 1985; Whitehead & Blaxter 1989; Di Dario 1999, 2004b . *Opisthopterus equatorialis* has not extension, although other species of the genus (not considered in this study) do. The character is impossible to detect in fossil species.

43. Orbitosphenoid (DD43): (0) present; (1) absent.

Description. The orbitosphenoid is present in all clupeomorphs, *Albula*, *Alepocephalus* and †*Tischlingerichthys*, but it is absent in Gonorynchiformes and *Osmerus* (Ridewood 1904a, b; Rembiszewski 1964; Gosline 1969; Forey 1973b; Johnson & Patterson 1996).

44. Length of the anterior arm of the orbitosphenoid (S14): (0) short, not reaching the ethmoid region; (1) long, reaching the lateral ethmoid.

Description. The orbitosphenoid usually has a robust and long anterior arm that reaches the lateral ethmoid, as is typical of *Albula*, *Alepocephalus*, †*Tischlingerichthys* and most of the clupeoids (Fig. 10A, E), including the fossil taxa †*Clupeopsis* and †*Monosmilus* (Capobianco *et al.* 2020). However, in *Denticeps*, †*Santanaclupea*, *Chirocentrus*, †*Nardoclupea*, Engraulidae, Pristigasteroidea, and the other outgroups the anterior arm of the orbitosphenoid is short, not reaching the ethmoid region (Figs 7A; 10C) (Sato 1994; Di Dario 2004b). Most †ellimmichthyiforms preserving the orbitosphenoid have a short projection not reaching the ethmoid region (Fig. 10B, D, F), except †*Ornategulum* and †*Sorbinichthys* that have a long anterior arm (Forey 1973a; Taverne & Capasso 2022).

45. Dorsal medial lamella on orbitosphenoid: (DD47): (0) absent; (1) present.

Description. In *Dussumieria* and *Etrumeus* a medial lamella extends dorsally along the anterior projection of the orbitosphenoid and articulates with the frontal bone for most of its length, leaving almost no gap between these two bones (Fig. 10A). Conversely, in outgroups and most clupeomorphs, this lamella is absent, and the gap located between the skull roof and the anterior arm of the orbitosphenoid is therefore large, with the orbitosphenoid anterior arm that resembles a narrow tube (Fig. 10B-F).

46. Ethmopalatine cartilage (DD3): (0) absent; (1) present.

Description. The ethmopalatine cartilage is a globular structure located between the distal end of the palatine and the maxilla in *Albula* and *Chanos* and, among clupeiforms, in *Amblygaster*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Ilisha*, *Opisthopterus*, *Pellona*, and *Sprattus* (Di Dario 2004b). We observed its presence also in *Chirocentrodon* and *Odontognathus* (Fig. 10C). It is not possible to detect the presence of this cartilage in fossil taxa.

47. Exoccipitals (S40): (0) not expanded, not reaching posteriorly to the level of the basioccipital; (1) expanded, extending posteriorly beyond the level of the basioccipital.

Description. In the majority of the outgroups and clupeomorphs, the exoccipitals do not reach posteriorly the level of the basioccipital (Fig. 8). However, *Chanos*, and *Coilia* are unique in having exoccipitals expanded posteriorly, extending beyond the level of the basioccipital (Sato 1994; Arratia 1997; Grande & Poyato-Ariza 1999). Contra Sato (1994) we observe that also in denticipitids the exoccipitals slightly extend beyond the level of basioccipital, articulating to the first vertebra along with the basioccipital, a condition unseen in the Clupeoidei where only the basioccipital builds this articulation (Fig. 7A, C) (Greenwood 1968; Mertzen 2019). Exoccipitals are not expanded either in †*Diplomystus* (Poyato-Ariza *et al.* 2010) nor in the other fossil clupeomorphs.

48. Otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase (G2, CM2): (0) absent; (1) present.

Description. This character is unique to the Clupeomorpha and, together with the presence of one or more abdominal scutes, is considered as one of the most easily recognizable synapomorphies of their skeleton (Grande 1985). In fossil clupeiforms (e.g., †*Cynoclupea*, †*Clupeopsis*, †*Italoclupea*, †*Spratticeps*, †*Pseudoellimma*, †*Santanaclupea*) and †ellimmichthyiforms (e.g., †*Armigatus*, †*Diplomystus*, †*Ellimmichthys*, †*Ornategulum*, †*Paraclupea*) the otophysic connection penetrating the exoccipital and extending into the prootic can be inferred by the presence of the “strawberry appearance” of the surface of the prootic or because of the presence of an inflated area of thin bone which resembles the fusiform bullae of clupeoids (Grande 1985: 253).

49. Peritoneal tunic covering the swim bladder (DD455): (0) non-silvered; (1) silvered.

Description. Fink & Fink (1996) suggested that the presence of a silvery peritoneal tunic covering the swim bladder might be a synapomorphy uniting Ostariophysi and Clupeomorpha. A silverly peritoneal tunic is present in fact in *Chanos* and *Kneria* and, among clupeiforms, in *Denticeps*, *Dussumieria*, some engraulids (*Coilia* and *Thryssa*, *Anchoviella*, *Encrasicholina*, *Lycothrissa*, *Lycengraulis* and *Stolephorus*), pristigasteroids (*Chirocentrodon*, *Ilisha*, *Opisthopterus*, *Odontognathus*, *Pellona*), and a few other clupeoids (*Brevoortia*, *Clupea*, *Lile*, *Sardina*, *Sardinella*, *Sardinops*, *Sprattus*). Conversely, the peritoneal tunic is non-silvered in *Chirocentrus*, *Etrumeus*, *Spratelloides*, *Jenkinsia*, *Pristigaster*, some engraulids (*Anchoa*, *Cetengraulis*, *Engraulis*, *Pterengraulis*, *Setipinna*), ehiravids (*Clupeoides*, *Limnothrissa*, *Odaxothrissa*, *Pellonula*), *Hyperlophus*, *Potamalosa*, the alosid *Alosa*, and most dorosomatids (*Amblygaster*, *Anodontostoma*, *Dorosoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Konosirus*, *Nematalosa*, *Opisthonema*, *Tenualosa*) (Whitehead & Blaxter 1989; Di Dario 2004b). This character cannot be checked in fossils.

50. Prootic bullae (Z9, DD55): (0) absent; (1) present.

Description. Prootic bullae characterize all the extant and fossil clupeomorphs (Grande 1985). Their presence in fossil taxa can be inferred because of the “strawberry appearance” of the surface of the prootic or because of the presence of an inflated area of thin bone which resembles the fusiform bullae of clupeoids (Grande 1985 and pers. obs.). †*Ranulfoichthys* is the only clupeomorph which apparently lacks prootic bullae (Alvarado-Ortega 2014).

51. Size of prootic bulla (Z9, DD55): (0) small; (1) large.

Description. The prootic bulla is larger in *Denticeps* and *Coilia* than in the other clupeiforms, resulting in a shorter parasphenoid (Greenwood 1968; Mertzen 2019). As the same condition has been reported in †*Spratticeps* (Patterson 1970) and †*Santanaclupea* (Maisey 1993), it is possible to hypothesize that a large prootic bulla is the ancestral condition in clupeomorphs.

52. Posterior process of prootic (S21): (0) absent; (1) present.

Description. The prootic of *Lycengraulis* and *Cetengraulis* has a long process that extends posteriorly from the anterodorsal margin of the auditory fenestra (Sato 1994). This process has been reported also in the Gonorynchiformes (Poyato-Ariza *et al.* 2010) but not in other teleosts (e.g., Forey 1973b; Hilton 2003). The recognition of this process is often problematic in fossils.

53. Extension of the posterior myodome (DD35): (0) extending widely into the prootic and basioccipital; (1) restricted to the prootic.

Description. The posterior myodome is a space in the orbitotemporal and otic regions that occurs in the skull of many teleosts and that accomodates the posterior portion of the recti muscles of the eye (De Pinna 1996). It extends widely into the prootic and basioccipital in all outgroups, living clupeiforms, and †*Spratticeps* (Patterson 1970), but is restricted to the prootic in *Coilia* and *Denticeps* (Ridewood 1904a, b; Di Dario 2004b). It is difficult to determine this character in most of the fossil taxa.

54. Posterior medial opening that communicates with the posterior myodome (S13): (0) absent or vestigial; (1) large.

Description. The ventral region of the posterior myodome is usually open between the rami of the parasphenoid. In outgroups, *Denticeps*, *Setipinna* and *Coilia* (Sato 1994; Di Dario 2004b) the posterior area between the parasphenoid and basioccipital is closed, or only a discrete opening is present, whereas in all the other living clupeomorphs, a large opening is present in the posterior region of the parasphenoid that communicates with the posterior myodome. It is often difficult to determine the presence of this character in fossil taxa.

55. Pterotic bulla (G2, S20): (0) absent; (1) present.

Description. The pterotic is a paired complex bone that forms most of the wall of the recessus lateralis of the Clupeiformes that in most taxa (including the fossil †*Bolcaichthys*, †*Clupeopsis*, †*Cynoclupea*, †*Nardoclupea*, †*Pseudoellimma*, †*Santanaclupea*, †*Scombroclupea*) includes an intracranial bulla, called pterotic bulla associated with the otophysic connection (Patterson 1970; Sato 1994). However, contrary to the prootic bullae, the pterotic bullae are absent in *Clupeonella*, *Sprattus* and †*Spratticeps*, although it is likely that the absence in †*Spratti*ceps represents the ancestral condition in clupeiforms, whereas the absence in *Clupeonella* and *Sprattus* might be a secondary loss (Patterson 1970; Grande 1985). Being the pterotic bullae recovered as absent in †*Armigatus brevissimus*, †*Diplomystus dentatus*, †*Ornategulum* and †*Ranulfoichthys* (e.g., Alvarado-Ortega 2014), it is likely that this is the condition of all the other †ellimmichthyiforms (Grande 1985), and therefore, their presence should be considered as an autapomorphy of the Clupeiformes.

56. Relative size of pterotic bulla (DD76): (0) bulla not dorsally expanded or with a very small dorsal expansion; (1) bulla greatly expanded dorsally, obliterating the pre-epioccipital fossa.

Description. When present, the pterotic bulla is usually small, not dorsally expanded or with a very weak dorsal expansion. In *Denticeps* and all the engraulids the pterotic bulla is large, its expansion causing the reduction or obliteration of the pre-epioccipital fossa (Grande 1985; Sato 1994). This latter condition has been also reported in †*Pseudoellimma* and †*Santanaclupea* (Maisey 1993; Gallo *et al.* 2011).

57. Posterior pterotic spine (DD61): (0) absent or rudimentary; (1) developed or well-developed.

Description. The pterotic of the alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*) and most dorosomatids (*Anodontostoma*, *Dorosoma*, *Clupanodon*, *Escualosa*, *Hilsa*, *Konosirus*, *Nematalosa*, *Opisthonema*, *Sardinella*, and *Tenualosa*) has a long posterior process or spine (Fig. 8D), whereas it is absent or rudimentary in the other clupeiforms (Fig. 8A-C) (see also Svetovidov 1964; Di Dario 2004b; Carnevale *et al.* 2026). This process has been reported, among clupeiforms, also in †*Pseudoellimma*, †*Santanaclupea* and †*Scombroclupea*, and in the ellimmichthyiform †*Ornategulum* (Forey 1973a; Maisey 1993; Giersch *et al.* 2011) but not in other lower teleosts, except *Chanos* (e.g., Ridewood 1904a, b; Forey 1973b; Hilton 2003). It seems that the pterotic spine is absent or vestigial in the other †Ellimmichthyiformes (Grande 1982a; Alvarado-Ortega & Melgarejo-Damián 2017).

58. Participation of the pterotic in forming the sub-epioccipital fossa (S38): (0) pterotic not participating in sub-epioccipital fossa: (1) pterotic participating in sub-epioccipital fossa.

Description. The subepioccipital fossa is a concave region on the posterior surface of the occiput that provides additional surface for attachment of epaxial muscles and that is bordered by epioccipital, supraoccipital, and exoccipital, with a posterior extension of the pterotic bone that may or may not contribute to the formation of the fossa (Phillips 1942). In *Denticeps* and most clupeoids, the pterotic participates in the formation of the subepioccipital fossa. However, in *Alosa*, *Anchoviella*, *Clupea*, *Hyperlophus* and *Sprattus*, the pterotic does not contribute to the fossa (Sato 1994). Among fossil forms, this character can be checked only in three-dimensionally preserved specimens, like in †*Spratticeps* and †*Diplomystus*, where the pterotic contributes to the formation of the subepioccipital fossa (Patterson 1970; Forey 2004). Among the outgroups, *Albula* and *Chanos* show the plesiomorphic clupeoid condition (Forey 1973b; Buri 1979) but this is unknown in other taxa.

59. Posterodorsal region of the lateral aspect of the skull (D24): (0) sinuous or slightly triangular; (1) high and truncated.

Description. The postero-dorsal region of the skull of fossil and living clupeomorphs is formed by the articulation between epioccipitals and parietals. In most of the taxa this margin is sinuous or slightly triangular but always more or less inclined backward toward the main axis of the body or at least perpendicular to it. However, in *Albula vulpes* (Forey 1973b) and the pristigasteroids *Ilisha*, *Odontognathus* (Fig. 6E), *Opisthopterus*, *Pellona*, *Pliosteostoma*, and *Raconda* the postero-dorsal region of the skull is elevated and truncated (Di Dario 1999).

60. Relationship between extrascapular and parietal (new): (0) unfused; (1) ankylosed or fused.

Description. When the supratemporal commissure canal passes through the parietals it is supposed that extrascapular and parietal are fused (Lecointre & Nelson 1996; Arratia 1999). For this reason, all the authors agree that all clupeomorphs and *Chanos* share the fusion or anchylosis between extrascapulars and parietals (Arratia 1999).

61. Dorsal process of mesethmoid (G19, S3) - ordered: (0) not projecting beyond the vomer; (1) at the same level of the anterior tip of vomer; (2) projecting beyond the vomer.

Description. Most of outgroups and clupeomorphs have the anterior tip of the dorsal process of mesethmoid (= 'median ethmoid' of Greenwood [1968], 'ethmoid' of Sato [1994] located posteriorly to the tip of the vomer (Fig. 7; 8A, C). In *Anodontostoma*, *Dorosoma*, *Nematalosa*, *Konosirus* and *Tenualosa* the anterior tip of mesethmoid lies roughly at the same level of the anterior tip of vomer (Sato 1994) (Figs 6C; 8D). Conversely, in *Albula* and all the engraulids, the dorsal process of the mesethmoid is well expanded and projects well beyond the tip of the vomer (Figs 6G; 8B) (see e.g., Grande 1985; Grande & Nelson 1985; Sato 1994).

62. Anterior region of the mesethmoid keel (DD11): (0) unperforated; (1) perforated.

Description. The anterior region of the mesethmoid keel is pierced by one or more holes in *Albula* (Ridewood 1904a), and in *Alosa*, *Brevoortia*, *Clupanodon*, *Clupea*, *Dorosoma*, *Sardinops*, and *Tenualosa* among the clupeiforms (Fig. 6C) (see Grande 1985; Di Dario 2004b). Our observations show that this region is perforated also in *Sprattus* (Fig. 6A) whereas it is unperforated in the other clupeoids (see, e.g., *Odaxothrissa* in Grande 1985, fig. 31), †ellimmichthyiforms (e.g., †*Armigatus*, †*Diplomystus*, †*Paraclupea*), and also in *Denticeps* (Mertzen 2019).

63. Anterior lateral process of mesethmoid for articulation of palatine (S1): (0) absent or vestigial; (1) present, well developed.

Description. In Clupeiformes two paired lateral processes of the mesethmoid can be present: the lower anterior ones and the posterior ones. The anterior lateral processes of most clupeiforms are well developed, located near the anterior tip of the mesethmoid, and serve as articulation to the palatine (Sato 1994). However, in *Denticeps*, all the Engraulidae, *Chirocentrus*, *Dussumieria*, and †*Nardoclupea* the anterior processes are considerably reduced or totally absent (Sato 1994; Mertzen 2019). Among fossil clupeomorphs, these processes are absent in †*Cynoclupea*, †*Clupeopsis* and †*Eoengraulis* (Marramà & Carnevale 2016; Capobianco *et al.* 2020) but have been detected in several other fossil clupeiforms and †ellimmichthyiforms (e.g., Forey 1973a; Forey *et al.* 2003; Figueiredo 2009a; Figueiredo & Ribeiro 2016; Alvarado-Ortega & Melgarejo-Damián 2017). These processes are absent or vestigial also in *Albula*, †*Tischlingerichthys*, Gonorynchiformes and *Osmerus* (Ridewood 1904a; Arratia 1997; Hilton 2003) but present in *Alepocephalus* (Mertzen 2019).

64. Position of the anterior margin of the lateral ethmoid (S4): (0) far back from the anterior portion of the mesethmoid; (1) close (contacting or articulating) to the anterior portion of the mesethmoid.

Description. The lateral ethmoid is usually located far back posterior to the anterior portion of the mesethmoid in all the outgroups and most clupeomorphs (Figs 6A-C, 7C, D; 8A, C, D) (Ridewood 1904a, b; Sato 1994). However, in *Chirocentrus* and all the Engraulidae (including †*Eoengraulis*) the anterior margin of the lateral ethmoid is close to the anterior portion of the mesethmoid, contacting or articulating with it (Figs 6G; 8B) (see e.g., Greenwood 1968; Sato 1994). Contra Sato (1994) we did not detect this feature in *Escualosa*. Interestingly, †*Santanaclupea* seems to show the engraulid condition (Maisey 1993), whereas the stem engraulids †*Clupeopsis* and †*Monosmilus* do not show this condition, being their lateral ethmoid far back posterior to the anterior portion of the mesethmoid (Capobianco *et al.* 2020). All the †Ellimmichthyiformes show that anterior part of the lateral ethmoid being located far back posterior to the anterior portion of the mesethmoid (Figs 6F; 8A).

65. Posterior process of lateral ethmoid (S5): (0) absent; (1) present.

Description. The lateral ethmoid usually bears two lateral processes, the anterior, which is present in all the taxa considered herein, and the posterior. The posterior process of the lateral ethmoid is a projection located approximately in the medial region of each lateral ethmoid, facing posteriorly towards the orbitosphenoid and articulating with its anterior margin. For this reason, the presence of the posterior process of the lateral ethmoid appears to be strongly correlated to the length of the orbitosphenoid. The posterior process is present in most of the Clupeoidea (Fig. 10A E), but absent in *Denticeps*, extant engraulids (but not in the stem †*Clupeopsis*; Capobianco *et al* 2020), *Chirocentrus*, †*Nardoclupea* and Pristigasteroidea, and, likely, †*Trollichthys* (Figs 7A; 10B, C, D, F) (Sato 1994; Di Dario 2004b; Marramà & Carnevale 2015a). Contra Sato (1994) we observed this process also in *Etrumeus*. This process is also absent in the †ellimmichthyiforms (except †*Ornategulum* and †*Sorbinichthys elusivo*; Forey 1973a; Taverne & Capasso 2022) and the outgroups examined in this study (Gosline 1969; Marramà *et al.* 2022; Marramà & Carnevale 2023).

66. Olfactory nerve foramen of the lateral ethmoid (S6): (0) passing dorsally outside the lateral ethmoid; (1) piercing the lateral ethmoid only; (2) surrounded by lateral ethmoid and mesethmoid.

Description. According to Sato (1994), *Dussumieria* is unique among clupeiforms in that the olfactory nerve does not pass through the lateral ethmoid. Conversely, in *Coilia*, *Setipinna* and most clupeoids, the olfactory foramen pierces only the body of lateral ethmoid, and the nerve passes only through this bone (Sato 1994), similar to the condition found in *Osmerus* (Rembiszewski 1964) and †*Ornategulum* (Forey 1973a). In

Denticeps, as well as in some engraulids (*Anchoviella*, *Cetengraulis*, *Engraulis*, *Lycengraulis* and *Stolephorus*) and in some non-engraulid clupeoids (*Anodontostoma*, *Clupea*, *Nematalosa* and *Sprattus*), the olfactory nerve passes through a foramen that is bordered dorsally by mesethmoid and ventrally by the lateral ethmoid. This latter condition has been also observed in *Alepocephalus* (Gosline 1969). This condition is difficult to detect in fossils.

67. Length to width of the vomer (S8): (0) vomer wider than long; (1) vomer longer than wide.

Description. The vomer is long and narrow, with its length more than twice its width in most outgroups, most Clupeiformes (including †*Cynoclupea*) and all the †Ellimmichthyiformes where this bone is preserved (e.g., †*Armigatus brevissimus*, †*Guiclupea*, †*Ornategulum*, etc). In contrast, in *Osmerus*, *Chirocentrus*, *Coilia*, *Denticeps* and *Setipinna* the vomer is shorter and wider, its length being less than twice of its width (Rembiszewski 1964; Sato 1994; Mertzen 2019).

68. Bony medial lamina on the vomer (DD23): (0) absent; (1) present.

Description. The anterior end of the vomer is usually swollen or projects ventrally for most of its length. According to Di Dario (2004b), in *Clupeonella*, *Escualosa*, *Herklotsichthys* and *Sprattus* a medial lamina is present ventrally along the mid-anterior region of the vomer. This character is difficult to detect in fossil material.

69. Vomerine teeth (S10): (0) absent; (1) present.

Description. Teeth on vomer are present in *Albula*, *Osmerus* and †*Tischlingerichthys* (e.g., Ridewood 1904a; Rembiszewski 1964), all the engraulids (except *Cetengraulis*), †*Clupeopsis* and †*Monosmilus* (Capobianco *et al.* 2020), *Chirocentrus*, *Dussumieria*, *Etrumeus*, *Jenkinsia* and a few other clupeoids (*Alosa*, *Clupea*, *Sprattus*) (Ridewood 1904b; Sato 1994; Di Dario 2004b). Among †ellimmichthyiforms, vomerine teeth were reported in †*Ornategulum* (Forey 1973a). They are absent in *Alepocephalus* (Markle 1976), Gonorynchiformes (Johnson & Patterson 1996) and the other clupeiforms and †ellimmichthyiforms.

70. Size of vomerine teeth (K3): (0) small or minute; (1) massive, fang-like.

Description. Massive fang-like vomerine teeth are only present in †*Clupeopsis* and †*Monosmilus* (Capobianco *et al.* 2020), and *Osmerus* (Rembiszewski 1964), whereas the other taxa show minute teeth on vomer.

71. Distribution of teeth on vomer (DD22): (0) grouped into two well-defined groups, each at anterolateral end of the vomer; (1) forming a narrow straight line in the medial region of the vomer; (2) diffusely clustered in the anterior region of the vomer; (3) grouped in a row along the entire anterior margin of the vomer.

Description. According to Di Dario (2004b), in *Anchoa*, *Anchoviella*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Setipinna*, *Stolephorus*, and *Thryssa* the vomer has two lateral projections in its anterior region, each bearing posteroventrally directed caniniform teeth; similar pattern can be interpreted for the fang-like teeth of †C*lupeopsis* and †*Monosmilus* (Capobianco *et al.* 2020). In *Alosa*, *Chirocentrus*, and *Jenkinsia* the teeth are aligned along the medial region of the vomer; the same pattern has been described in *Dussumieria* and †*Ornategulum* (Ridewood 1904b; Forey 1973a). In *Clupea* and *Etrumeus* the teeth are arranged in a different way compared to those described above, generally forming one or two dense blocks in the anterior region of the vomer. In *Albula*, teeth are present along the entire anterior margin of the vomer.

72. Ossification of the anterodorsal portion of vomer (S9): (0) ossified; (1) not ossified.

Description. In most clupeoids, the anterodorsal section of the vomer is thoroughly ossified, allowing it to directly connect with the mesethmoid. However, in *Denticeps* and the ehiravids *Limnothrissa* and *Stolothrissa* this portion remains unossified, resulting in cartilage serving as the intermediary between the vomer and the mesethmoid (Sato 1994).

Circumorbital series

73. Nasal (S42): (0) small, bearing a bony tube for the anterior continuation of the supraorbital canal; (1) small, bearing a bony flange to form a narrow groove for supraorbital canal opening posteriorly; (2) small, bearing a bony flange to form a broad groove for supraorbital canal opening anteriorly; (3) large and almost flattened, with no bony tube or flange.

Description. The nasal of the †Ellimmichthyiformes and most clupeoids is usually small and bears (or is entirely formed by) a bony tube for the anterior continuation of the supraorbital canal (Fig. 11A, B) (Forey 1973a; Sato 1994; Vernygora & Murray 2016; Marramà & Carnevale 2023). In some taxa, such as *Hyperlophus*, *Spratelloides*, and pristigasterids *Ilisha*, *Odontognathus*, *Pellona*, and *Chirocentrodon* this tube is incomplete and the nasal bears a bony flange forming a narrow groove opening posteriorly (Sato 1994). In the Engraulidae there is no bony tube but the nasal bears a bony flange to form a broad groove for supraorbital canal that opens anteriorly (Fig. 11C, D) (Sato 1994). *Denticeps* is unique among Clupeiformes in which the nasal is very large compared to the neurocranium and almost flattened, with no bony tube or flange (Grande 1985; Sato 1994). Among the fossil clupeomorphs, †*Cynoclupea* shows the most generalized features, with a bony tube for the anterior continuation of the supraorbital canal, whereas in *Kneria* the nasal is flat with no bony tube or flange for the supraorbital sensory canal. Among the outgroups, *Albula*, *Alepocephalus*, and *Chanos* show the most generalized condition, with a bony tube for the anterior continuation of the supraorbital canal, whereas in *Kneria* the nasal is flat with no bony tube or flange for the supraorbital sensory canal (Gosline 1969; Forey 1973b; Davis *et al.* 2013).

74. Antorbital (S44, Z16): (0) crescent or oval, with no bony constituent for sensory canal; (1) crescent or oval, with bony constituent (flange or tube) for sensory canal; (2) complex morphology.

Description. The antorbital of *Denticeps* and most clupeoids is usually small and crescent or oval-shaped, with no bony constituent for sensory canal (Fig. 11A, B) (Nelson 1969; Sato 1994). The same condition is characteristic of *Alepocephalus*, Gonorynchiformes and the †ellimmichthyiforms, like †*Armigatus*, †*Leufuichthys*, †*Ornategulum*, †*Paraclupea*, †*Ranulfoichthys*, †*Scutatuspinosus* in which the antorbital is small and does not carry the infraorbital sensory canal (Nelson 1969; Forey 1973a; Gallo *et al.* 2011; Alvarado-Ortega 2014). However, in *Ilisha*, *Pellona* and *Odontognathus* the antorbital carries a bony flange or tube for the sensory canal (Sato 1994; Di Dario 2004b). The same condition is also shared by *Albula* and *Osmerus* where the antorbital encloses the anterior part of the suborbital canal (Rembiszewski 1964; Forey 1973b). Conversely, in all the engraulids, the antorbital has an irregular shape with an anteromedial cup to accommodate the olfactory organs and a lateral process for the articulation with the lachrymal (Fig. 11C, D) (Sato 1994; Di Dario 2004b).

75. Number of infraorbitals (G*l*, S46): (0) six; (1) five, resulting from absence of the sixth infraorbital; (2) five or less, resulting from fusion of some infraorbitals.

Description. Most outgroups and clupeomorphs have six infraorbital bones (including the dermosphenotic, excluding the antorbital) (Fig. 11) (Nelson 1969; Grande 1985). However, some taxa exhibit five infraorbitals, due to the fusion of two or more of them, or the absence of one infraorbital. Among the Clupeiformes only *Jenkinsia* and *Spratelloides* and sometimes *Hyperlophus* and *Potamalosa* have five infraorbitals (Yabumoto & Uyeno 1981; Grande 1985; Sato 1994). However, the reduction in *Jenkinsia*, *Spratelloides* and †*Trollichthys* is the result of the true absence of the sixth infraorbital (=dermosphenotic) (Grande 1985; Sato 1994; Marramà & Carnevale 2015a), whereas in *Potamalosa* and *Hyperlophus* this condition is the result of a fusion between infraorbitals 3+4. However, this latter condition is not always present, as specimens of *Potamalosa* and *Hyperlophus* have sometimes six infraorbitals (Grande 1985; Sato 1994). For this reason, we coded these two taxa as polymorphic (0/2). It is not clear if the lack of dermosphenotic in †*Pseudoellimma* (Figueiredo 2009a) is the result of taphonomic loss or a genuine feature (?). †Ellimmichthyiformes usually have six infraorbitals, as can be observed in some †*Armigatus*, †*Diplomystus* and †*Triplomystus* species, and †*Ranulfoichthys* (Grande 1982a; Forey *et al.* 2003; Alvarado-Ortega 2014). Among the outgroups, *Chanos*, *Kneria* and †*Tischlingerichthys* are characterized by a fusion of some infraorbitals (Arratia 1997; Poyato-Ariza *et al.* 2010).

76. Posterior process of lachrymal (infraorbital 1) (D7): (0) absent; (1) present.

Description. The lachrymal of most clupeoids bears a small or large process in its posterior margin that projects underneath and is partially covered by the ventral margin of the anterior region of infraorbital 2 (Fig. 11) (Di Dario 2009). However, this process is absent in *Denticeps* (Greenwood 1968; Mertzen 2019), *Dussumieria*, *Etrumeus*, †*Nardoclupea* and †*Trollichthys* (Di Dario (2009): 373; Marramà & Carnevale 2015a). This process has been recognized also in some fossil clupeoids like †*Clupeopsis* and †*Eoengraulis*, but it appears to be absent also in outgroups and the †ellimmichthyiforms preserving the lachrymal, like †*Armigatus*, †*Codoichthys*, †*Ornategulum*, †*Paraclupea*, †*Ranulfoichthys*, †*Scutatuspinosus* and †*Triplomystus* (Patterson 1967; Forey 1973a; Figueiredo & Ribeiro 2016), whereas it is present in †*Diplomystus dentatus* and †*Guiclupea* (Grande 1985, fig. 4; Chen *et al.* 2021).

77. Posterior process of the lachrymal (infraorbital 1) (S45): (0) small, not postero-ventrally expanded; (1) large, postero-ventrally expanded.

Description. In clupeoids and †ellimmichthyiforms having the posterior process on the lachrymal, this is usually small (Fig. 11A, B). However, in *Chirocentrus*, the stem engraulid †*Clupeopsis* and all engraulids (including †*Eoengraulis*) this process is strongly developed, posteroventrally expanded, well-developed and extending along the ventral margin of infraorbital 2 (Fig. 11C, D) (Sato 1994; Di Dario (2009); Marramà & Carnevale 2016; Capobianco *et al.* 2020).

78. Posterior process of the lachrymal (infraorbital 1) (S45): (0) not reaching the infraorbital 3; (1) articulates with the greatly elongate posterior process of infraorbital 3.

Description. In clupeoids showing the posterior process on the lachrymal this process usually articulates with the anterior margin of the infraorbital 2 never reaching the infraorbital 3 (Fig. 11A, B) (Sato 1994; Di Dario 2009). However, in all extant and fossil engraulids (including †*Eoengraulis*) this

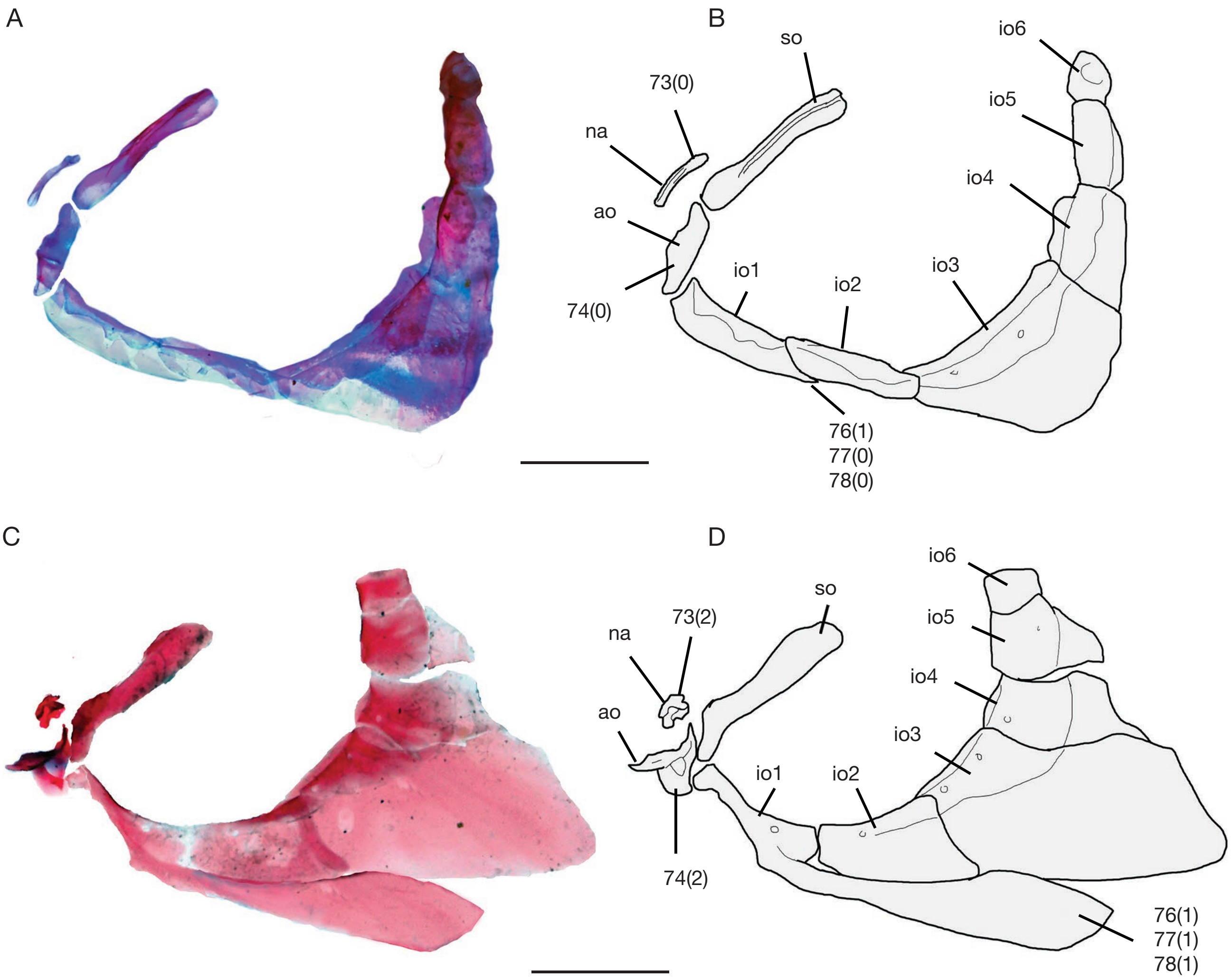

Fig. 11. — Left circumorbital series of selected clupeiforms: **A**, **B**, *Gudusia variegata* (Day, 1870) (Dorosomatidae), AMNH 8355; with interpretative reconstruction (**B**); **C**, **D**, *Thryssa hamiltonii* Gray, 1835 (Engraulidae), AMNH 38188; with interpretative reconstruction (**D**). Scale bars: 5 mm. Abbreviations: **ao**, antorbital; **io**, infraorbital; **na**, nasal; **so**, supraorbital. Numbers refer to characters and character states (see text).

process, which is strongly developed, extends posteriorly to reach the infraorbital 3 (Fig. 11C, D) (Sato 1994; Di Dario (2009); Marramà & Carnevale 2016). Although *Chirocentrus* has a well-developed posterior process of the lachrymal, it does not reach the anterior margin of infraorbital 3 (Sato 1994; Di Dario 2009).

79. Anterior border of the infraorbital 3 (D13): (0) convex or straight; (1) concave.

Description. The anterior margin of the laminar ventral expansion of infraorbital 3 is convex or straight in most clupeoids (Fig. 11) (Wongratana 1980; Di Dario 1999, 2009) and outgroups (Ridewood 1904a; Rembiszewski 1964; Nelson 1969), as well as in the †ellimmichthyiforms preserving this bone (Forey 1973a). However, in the pristigasteroids *Ilisha*, *Neoopisthopterus* and *Pellona* (Di Dario 1999), but also in *Alosa*, *Brevoortia*, *Sardina* and *Sardinops* (Wongratana 1980; Segura & De Astarloa 2004), the distal end of the ventral expansion of infraorbital 3 is concave anteriorly.

80. Sclerotic bones (S47): (0) absent; (1) present.

Description. The periphery of the eyeball in most extant and fossil outgroups and clupeiforms is surrounded by a series of sclerotic bones forming a sclerotic ring (Sato 1994; Kubicek *et al.* 2022). Complete sclerotic bones or their traces have been found also in a few †ellimmichthyiforms, including species of †*Armigatus*, †*Diplomystus* and †*Paraclupea*, †*Codoichthys*, †*Ellimma*, etc. (e.g., Figueiredo & Ribeiro 2016; Marramà & Carnevale 2023). Sclerotic bones are completely absent in *Alepocephalus* and *Coilia* (Sato 1994; Mok & Liu 2012).

81. Number of sclerotic bones (S47): (0) one; (1) two; (2) three.

Description. In most of clupeiforms and outgroups, the sclerotic ring is formed by two semicircular sclerotic bones, as well as that of †ellimmichthyiforms (when present). However, *Denticeps* and *Albula* have three sclerotic bones, whereas *Setipinna* has only one (Sato 1994; Kubicek *et al.* 2022).

82. Total size of sclerotic bones (S47): (0) small to medium size, their total length is half or less of the circumference of the orbit; (1) large, their total length is almost the entire circumference of the orbit.

Description. In most clupeiforms and the outgroups, the sclerotic ring is small or medium sized, since the total length formed by the sum of the length of the sclerotic bones forming it is half or less of the orbital circumference. Conversely, in Pristigasteroidea the sum of the length of the sclerotic bones forming the sclerotic ring is almost equivalent to the entire circumference of orbit, leaving small gaps between the bones (Fig. 10C) (Sato 1994; Mok & Liu 2012; Kubicek *et al.* 2022).

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83. Anterior supramaxilla (G*m*, CM8): (0) absent; (1) present.

Description. Clupeiforms and †ellimmichthyiforms usually have two supramaxillae (Fig. 12B, C, E). However, several lineages of clupeiforms have lost independently the anterior supramaxilla, including *Denticeps*, *Etrumeus*, *Jenkinsia* and †*Nardoclupea*, the engraulids *Lycothrissa* and *Setipinna*, some dorosomatids (*Anodontostoma*, *Clupanodon*, *Konosirus*, *Nematalosa*), several ehiravids (*Clupeichthys*, *Clupeoides*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*), plus *Hyperlophus* and *Potamalosa* (Fig. 12A, D, F), and, among fossils, †*Knightia* and †*Palaeodenticeps* (Grande 1982b, 1985; Sato 1994; Di Dario 2004b). The anterior supramaxilla is also absent in *Albula*, Ostariophysi and *Osmerus*, whereas it is present in *Alepocephalus* (Ridewood 1904a, b; Rembiszewski 1964; Fink & Fink 1981).

84. Posterior supramaxilla (CM8, S66): (0) absent; (1) present.

Description. All the clupeomorphs have the posterior supramaxilla, except *Denticeps* (Fig. 12A) and †*Palaeodenticeps* (Greenwood 1960; Sato 1994). It is also absent in Ostariophysi, including †*Tischlingerichthys* (Fink & Fink 1981; Arratia 1997).

85. Angle between anterior and posterior region of the posterior supramaxilla (DD110): (0) about 180°; (1) lower than 180°.

Description. The posterior supramaxilla of clupeomorphs usually has a narrow and tubular anterior region, whereas the posterior region is more or less large and paddle shaped (Whitehead 1985). In the majority of the clupeomorphs, the antero-posterior axis of the posterior supramaxilla is approximately equal to 180°. However, in *Dussumieria* and *Chirocentrus* the anterior region of the posterior supramaxilla is displaced more dorsally, so that a pronounced ventrally directed concavity is present in its medial region (Fig. 12B) (see Whitehead 1985; Di Dario 2004b). This latter condition has been also observed in †*Santanaclupea* (Maisey 1993) and *Alepocephalus* (Diogo *et al.* 2008).

86. Portion of anterior supramaxilla that overlaps laterally the posterior supramaxilla (DD111): (0) ≤50% of the anterior supramaxilla overlaps the posterior supramaxilla; (1) >50% of the anterior supramaxilla overlaps the posterior supramaxilla.

Description. In most clupeomorphs, a little portion of the anterior supramaxilla (usually less than half) overlaps the posterior supramaxilla. However, in *Dussumieria* and *Chirocentrus* more than half of the anterior supramaxilla overlaps the posterior supramaxilla (Fig. 12B) (see Di Dario 2004b).

87. Ornamentation of the supramaxillae (MKC24): (0) absent; (1) present.

Description. Supramaxillae are smooth and unornamented in all the fossil and living clupeiforms and, among the †ellimmichthyiforms, in †*Armigatus brevissimus*, †*A. elatus*, †*A. namourensis*, †*Guiclupea*, †*Diplomystus dentatus*, †*D. shengliensis*, †*Gasteroclupea*, †*Ellimmichthys longicostatus*, †"*E.*" *spinosus*, and †*Triplomystus* (Grande 1982a; Figueiredo 2009a; Chen *et al.* 2021; Marramà & Carnevale 2023). Supramaxillary sculpturing consisting of simple or branched ridges has been described in †*Armigatus carrenoae*, †*A. felixi*, †*E. branneri*, †*Foreyclupea*, †*Ornategulum*, †*Ranulfoichthys*, †*Rhombichthys*, †*Tunisiaclupea*, and all †*Paraclupea* species (Forey 1973a; Chang & Maisey 2003; Alvarado-Ortega 2014; Alvarado-Ortega *et al.* 2020).

88. Maxillo-premaxillary gap (G*a*): (0) present; (1) absent.

Description. Most outgroups and clupeomorphs have a distinct gap between the hind tip of the premaxilla and the anterior border of maxilla (Figs 12D-F; 13B, C). However, in *Osmerus*, *Chirocentrus*, engraulids, dussumieriids and spratelloidids, †*Nardoclupea* and †*Santanaclupea* there is no large free area between the posterior region of the premaxilla and maxilla, so that the posterior end of the premaxilla articulates

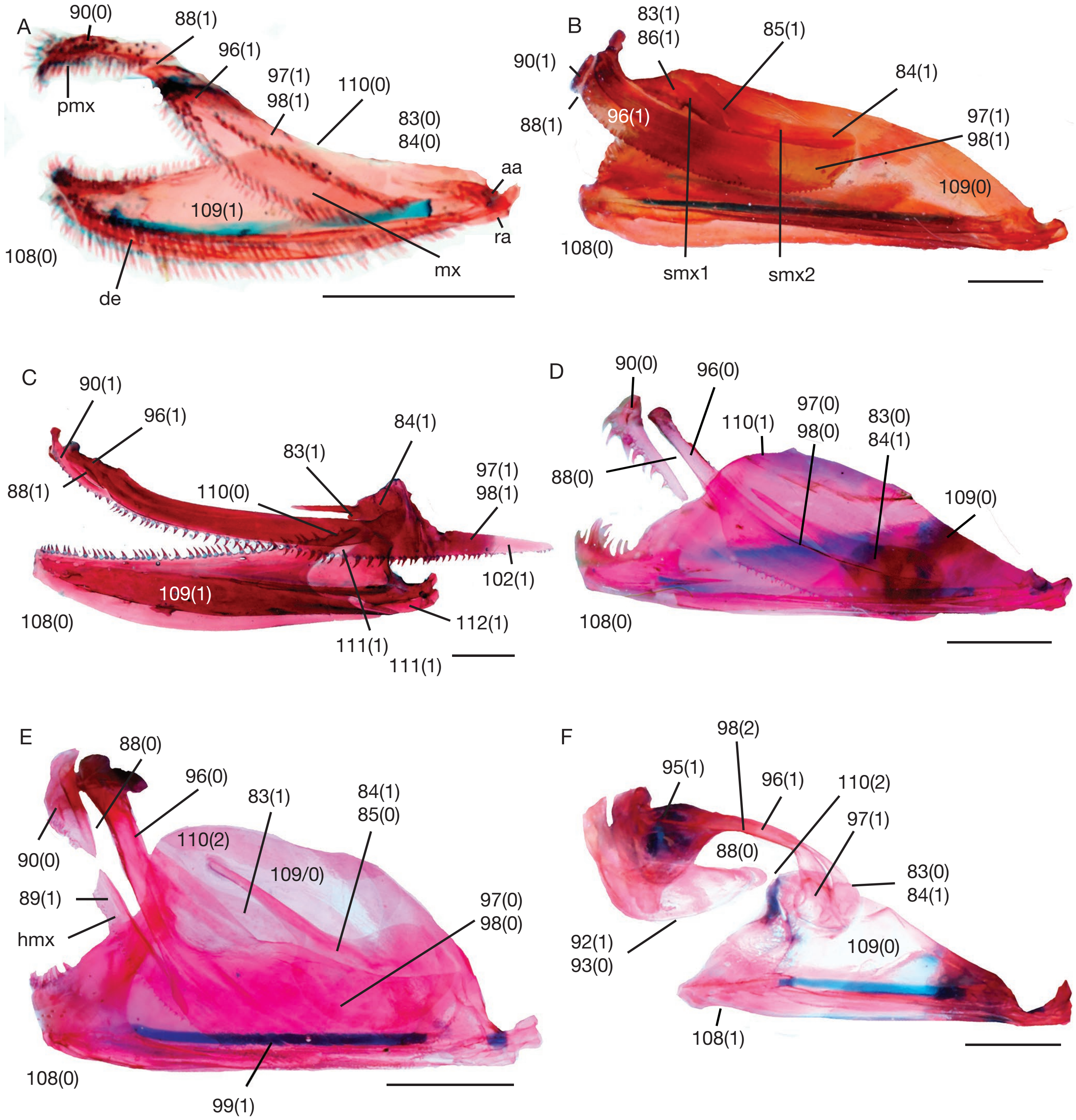

FIG. 12. — Upper and lower jaws of selected cleared and stained clupeiforms: **A**, *Denticeps clupeoides* Clausen, 1959 (Denticipitidae), AMNH 53082; **B**, *Dussumieria acuta* Valenciennes, 1847 (Dussumieriidae), AMNH 17555; **C**, *Thryssa hamiltonii* Gray, 1835 (Engraulidae), AMNH 38188; **D**, *Odaxothrissa losera* Boulenger, 1899 (Ehiravidae), AMNH 236933; **E**, *Harengula jaguana* Poey, 1865 (Dorosomatidae), AMNH 28283; **F**, *Nematalosa erebi* (Gunther, 1868) (Dorosomatidae), AMNH 28097. Scale bars: 3 mm. Abbreviations: **aa**, anguloarticular; **de**, dentary; **hmx**, hypomaxilla; **mx**, maxilla; **pmx**, premaxilla; **ra**, retroarticular; **smx1**, anterior supramaxilla; **smx2**, posterior supramaxilla. Numbers refer to characters and character states (see text).

directly with the maxilla and the ventral margin of the premaxilla is continuous with the ventral margin of the maxilla, which usually does not have an expanded area forming an attachment surface for a ligament developed between the premaxilla and the maxilla (Fig. 12B, C; 14) (Grande 1985; Maisey 1993; Di Dario 2004b). *Denticeps* and †*Palaeodenticeps* can be considered as having no gap (Fig. 12A), being the movement of maxilla and premaxilla considered as a single functional unit with no distinct gap in between (Greenwood 1960; Mertzen 2019). Gap is absent also in *Chirocentrodon*, *Neoopisthopterus* and *Limnothrissa*, being these taxa characterized by an extension of the anterior tip of maxilla (possibly, at least in pristigasterids, representing a hypomaxilla fused onto the maxilla) that occludes the maxillo-premaxillary gap (Grande 1985; Whitehead 1985).

89. Gap covered by a hypomaxilla (S68): (0) absent; (1) present.

Description. The maxillo-premaxillary gap of *Pellona*, *Pliosteostoma* and *Harengula* is covered by a small, toothed bone called hypomaxilla (Fig. 12E) (Grande 1985; Sato 1994). Grande (1985) stated that *Chirocentrodon* and *Neoopisthopterus* might have the maxillo-premaxillary gap covered by an extension of the maxilla, which is possibly a hypomaxilla fused onto the maxilla, but such a fusion has never been seen ontogenetically nor this fusion demonstrated.

90. Shape of premaxillae (DD90, K35): (0) subtriangular; (1) subrectangular.

Description. In most clupeomorphs the premaxilla is subtriangular, whereas in *Dussumieria*, *Etrumeus* and †*Nardoclupea* it is subrectangular (Fig. 12B) (Whitehead 1985; Taverne 2002). The same condition is present in †*Santanaclupea* (Maisey 1993) and most engraulids (Fig. 12C) (except *Coilia*), where it is subrectangular but more slender, almost rodlike and slightly bent.

91. Distinct median notch or cleft between premaxillae when seen from front (DD89): (0) absent; (1) present.

Description. The presence of a median "cleft" or "notch" between the two contralateral premaxillae into which the symphysis of the lower jaw fits is a diagnostic feature of the Alosinae of Whitehead (1985), including *Alosa*, *Brevoortia*, *Hilsa* and *Tenualosa*. This notch is difficult to detect in fossils since, being their body laterally compressed, they are mostly preserved in lateral view. However, this notch is clearly absent in 3D fossils like †*Clupeopsis* and †*Monosmilus* (Capobianco *et al.* 2020), and stated as absent in †*Gosiutichthys* and †*Knightia* (Grande 1982b).

92. Relative length of premaxilla (S62): (0) premaxilla short, less than 50% of the maxillary length; (1) premaxilla long 50% or more of the maxillary length.

Description. Most of clupeomorphs have a small premaxilla which is usually less than 50% of the length of the maxilla (Fig. 12A-E). However, the premaxilla is long at least 50% of the maxillary length in *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Konosirus*, and *Nematalosa* (Fig. 12F) (Sato 1994; Di Dario 2004b), but also in *Albula*, *Chanos* and *Kneria* (Forey 1973b; Grande & Poyato-Ariza 2010) and, among †ellimmichthyiforms, in †*Sorbinichthys africanus* and †*Thorectichthys* (Murray & Wilson 2011, 2013).

93. Premaxillary teeth (S63): (0) absent; (1) present.

Description. Premaxillary teeth are present in most clupeomorph taxa (Fig. 12B-E), including *Denticeps* and †*Palaeodenticeps* (Fig. 12A), as the odontodes (present on their jaws) are regarded as homologous to oral teeth of teleosts (Sire *et al.* 1998). Among living clupeiforms, premaxillary teeth are absent in *Cetengraulis*, *Hyperlophus*, alosids (but present in *Alosa*), dorosomatids (Fig. 12F) (but present in *Lile*, *Platanichthys*, *Harengula* and *Herklotsichthys*), and some ehiravids (*Clupeonella*, *Clupeoides*, *Corica*) (Sato 1994; Di Dario 2004b). Among fossil clupeiforms, they are absent in †*Bolcaichthys*, †*Eoalosa*, †*Leufuichthys*, †*Scombroclupea* and †*Trollichthys* (Marramà & Carnevale 2015a, b, 2018). A few †ellimmichthyiform taxa lack premaxillary teeth, including †*Codoichthys*, †"*Ellimma*" *longipectoralis*, †"*Ellimmichthys*" *spinosus*, †*Gasteroclupea*, †*Ornategulum*, †*Paraclupea seilacheri* Alvarado-Ortega & Melgarejo-Damián, 2017, †*Rhombichthys*, †*Scutatoclupea* and †*Triplomystus* (e.g., Forey 1973a; Khalloufi *et al.* 2010; Gallo *et al.* 2011; Figueiredo & Ribeiro 2016). Among outgroups, only *Chanos* and *Kneria* lack premaxillary teeth (Ridewood 1904a; Di Dario 2004b).

94. Size of premaxillary teeth (S63): (0) minute or small; (1) large, canine-like or fang-like.

Description. The majority of clupeomorphs bear small or minute premaxillary teeth. However, in *Chirocentrodon*, *Chirocentrus*, *Clupeichthys*, and *Odaxothrissa* premaxillary teeth are large or fang-like (Fig. 12D) (Grande 1985; Whitehead 1985; Sato 1994).

95. Width of anterior head of the maxilla (S64): (0) about equal or narrower than the maxillary central shaft; (1) far wider than the maxillary central shaft.

Description. The anterior (proximal) head of the maxilla is equal or narrower than the central shaft of maxilla in most living and fossil clupeomorphs, except *Anodontostoma*, *Konosirus* and *Nematalosa* (Fig. 12F) in which it is far wider than the central shaft (Sato 1994). Among outgroups *Chanos* and *Kneria* exhibit the same condition (Grande 1994, fig. 16-17; Grande & Poyato-Ariza 1999, fig. 7).

96. Length of the central shaft of the maxilla (S64): (0) long, greater than the length of the articular head; (1) short, almost equal or shorter than the length of the articular head.

Description. The central shaft of the maxilla is longer than the articular head length in most clupeomorphs (Fig. 12D, E). However, it is almost equal or shorter than the length of the articular head in *Denticeps*, *Chirocentrus*, engraulids (including the stem †*Clupeopsis*), *Dussumieria*, *Etrumeus*, †*Nardoclupea*, the clupeoideans *Anodontostoma*, *Limnothrissa*, *Nematalosa*, and the pristigasteroids *Chirocentrodon*, and *Odontognathus* (Fig. 12A-C, F) (Sato 1994), and among fossils also in †*Santanaclupea* and †*Scutatuspinosus* (Maisey 1993; Figueiredo & Ribeiro 2017). Among outgroups, *Albula* is the only taxon that shows a long central shaft (Tercerie *et al.* 2025).

97. Width of the posterior blade of maxilla (S64): (0) broad, much wider than the central shaft; (1) roughly the same size or slender than the central shaft.

Description. The posterior (distal) blade of the maxilla is broader than its central shaft in most clupeomorphs (Fig. 12D, E), but is approximately the same size or even slender than the central shaft in *Denticeps* and †*Palaeodenticeps*, *Chirocentrus*, *Dussumieria*, *Etrumeus*, †*Nardoclupea*, fossil and living engraulids, *Chirocentrodon*, *Anodontostoma*, *Dorosoma*, *Konosirus*, *Nematalosa* (Fig. 12A-C, F) (Greenwood 1960; Sato 1994); this is also the condition of basal clupeiforms †*Cynoclupea* and †*Santanaclupea* and, among †ellimmichthyiforms, †*Ornategulum*, †*Scutatuspinosus* and †*Sorbinichthys* (Forey 1973a; Maisey 1993; Bannikov & Bacchia 2000; Malabarba & Di Dario 2017). The posterior blade of maxilla is broader than its central shaft in *Albula*, *Alepocephalus* and *Chanos*, whereas in *Kneria*, *Osmerus* and †*Tischlingerichthys* it is approximately of the same size as the central shaft.

98. Dorsal and ventral profiles of the maxilla (S64): (0) dorsal margin concave or nearly straight, ventral margin convex; (1) both nearly straight; (2) dorsal margin convex, ventral margin concave.

Description. Most outgroups and clupeomorphs have the maxilla with dorsal margin concave or nearly straight, and ventral margin convex (Fig. 12D, E) (see Whitehead 1985; Sato 1994). Nearly straight dorsal and ventral margins are typical of *Denticeps* and †*Palaeodenticeps* (Greenwood 1960, 1968), fossil and extant engraulids, *Dussumieria*, *Etrumeus* and †*Nardoclupea* (Fig. 12A-C) (see Whitehead 1985; Di Dario 2004b), †*Santanaclupea*, †*Scutatuspinosus* and †*Sorbinichthys africanus* (Murray & Wilson 2011; Figueiredo & Ribeiro 2017) and, among outgroups, *Alepocephalus*, †*Tischlingerichthys* and *Osmerus* (Rembiszewski 1964; Gosline 1969). A maxilla with convex dorsal margin and concave ventral margin is typical only of *Anodontostoma* and *Nematalosa* (Fig. 12F) (see Whitehead 1985; Sato 1994).

99. Striations on the lateral surface of the maxilla (DD104): (0) absent; (1) present.

Description. According to Di Dario (2004b), *Alosa*, *Brevoortia*, *Harengula*, *Hilsa* and *Rhinosardinia* possess striations on the lateral surface of the maxilla, although in *Alosa*, *Harengula* and *Rhinosardinia* these ridges are not conspicuous and do not extend along the entire bone. Maxillary ornamentation is not present or has never been reported in other extant or fossil clupeomorphs, nor in outgroups.

100. Posterior border of the maxilla (to preopercle) (D2) - ordered: (0) does not reach the preopercle; (1) reaching backward the preopercle but not beyond its posterior margin; (2) extending backward beyond the posterior margin of the preopercle.

Description. In outgroups and most clupeomorphs, the posterior border of the maxilla does not reach the anterior border of the preopercle. In some engraulids (*Anchoa*, *Anchovia*, *Engraulis*, *Lycengraulis*, *Setipinna*, *Stolephorus*) and the pristigasterid *Chirocentrodon*, the posterior border of the maxilla extends posteriorly to reach the preopercle but not beyond its posterior margin (Whitehead *et al.* 1988). In other engraulids (*Coilia* and *Thryssa*) and the pristigasteroid *Odontognathus* the posterior border of the maxilla extends posteriorly beyond the posterior margin of the preopercle (Whitehead *et al.* 1988; Di Dario 1999).

101. Posterior border of the maxilla (to the orbit) (K47): (0) does not reach the posterior margin of the orbit; (1) extends posteriorly beyond the orbit.

Description. In outgroups and most clupeomorphs, the posterior border of the maxilla usually does not reach the anterior margin of the orbit (Fig. 6A-C, E, F). Conversely, in *Chirocentrus*, all engraulids, the stem engraulid †*Clupeopsis*, and the fossil clupeoid †*Santanaclupea*, the posterior border of the maxilla extends posteriorly beyond the orbit (Fig. 6D, G, H) (see Whitehead 1985; Whitehead *et al.* 1988; Maisey 1993).

102. Posterior border of the maxilla (S67): (0) not projecting beyond posterior tip of the posterior supramaxilla; (1) projecting well beyond the posterior tip of the posterior supramaxilla.

Description. Some engraulids (*Anchoa*, *Anchovia*, *Coilia*, *Encrasicholina*, *Lycengraulis*, *Pterengraulis*, *Stolephorus* and *Thryssa*), *Odontognathus*, *Raconda*, and †*Santanaclupea* have the posterior tip of maxilla projecting well beyond the posterior tip of the posterior supramaxilla (Fig. 12C) (Whitehead 1985; Whitehead *et al.* 1988; Maisey 1993; Sato 1994). In outgroup taxa possessing the supramaxilla and all the other clupeomorphs the posterior border of the maxilla does not project beyond the posterior tip of the posterior supramaxilla.

103. Maxillary teeth (S65): (0) absent; (1) present.

Description. Maxillary teeth are present in denticipidoids and most clupeoids (Fig. 12A-E) but they are absent in zooplanktivorous feeders like *Amblygaster*, *Anodontostoma*, *Brevoortia*, *Clupanodon*, *Clupeoides*, *Dorosoma*, *Escualosa*, *Hilsa*, *Konosirus*, *Nematalosa*, *Potamalosa*, *Spratelloides* and *Tenualosa* (Fig. 12F), whereas they can be present or not in *Corica* and *Sprattus* (0/1) (Whitehead 1985; Sato 1994; Di Dario 2004b). Among fossil clupeiforms, maxillary teeth are absent in †*Bolcaichthys*, †*Chasmoclupea*, †*Clupeopsis*, †*Eoalosa*, †*Monosmilus*, †*Nolfia*, †*Pseudoellimma*, †*Trollichthys*, and †ellimmichthyiforms †*Codoichthys*, †*Ellimmichthys*, †*Gasteroclupea*, †*Ornategulum*, †*Rhombichthys* and †*Triplomystus* (e.g., Forey 1973a; Figueiredo 2009a; Marramà & Carnevale 2015a; Capobianco *et al.* 2020). They are absent in *Albula*, *Alepocephalus*, *Chanos* and *Kneria*, but they are present in *Osmerus* and †*Tischlingerichthys* (e.g., Rembiszewski 1964; Gosline 1969; Fink & Fink 1981, 1996).

104. Dentary teeth (S70): (0) absent; (1) present.

Description. Dentary teeth are present in *Denticeps* and †*Palaeodenticeps*, all engraulids (except *Cetengraulis*), and most clupeoids (Fig. 12A-E). However, they are absent in spratelloidids, *Clupeonella*, *Corica*, all alosids, and some dorosomatids (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Hilsa*, *Konosirus*, *Nematalosa*, *Rhinosardinia* and *Tenualosa*; Fig. 12F; see also Whitehead 1985; Sato 1994; Di Dario 2004b). Among fossils, dentary teeth are absent in some clupeiforms (†*Bolcaichthys*, †*Eoalosa*, †*Leufuichthys*, †*Nolfia*, †*Pseudoellimma*, †*Trollichthys*), as well as in a few ellimmichthyiforms (†*Ellimmichthys longicostatus*, †*Gasteroclupea*, †*Ornategulum*, †*Rhombichthys*, †*Triplomystus*) (e.g., Forey 1973a; Figueiredo 2009a, b; Marramà & Carnevale 2015a; Capobianco *et al.* 2020). Dentary teeth are absent in *Chanos* and *Kneria*, but present in *Albula*, *Alepocephalus*, *Osmerus* and †*Tischlingerichthys* (e.g., Rembiszewski 1964; Gosline 1969; Fink & Fink 1981, 1996; Arratia 1997).

105. Size of dentary teeth (S70): (0) minute or small; (1) large, canine-like or fang-like.

Description. When present, dentary teeth are usually small in both the outgroups and clupeomorphs. However, they are large, often canine- or fang-like in *Chirocentrus*, the pristigasterid *Chirocentrodon*, the engraulid *Lycothrissa*, the ehiravids *Clupeichthys* and *Odaxothrissa* (Fig. 12D) (Grande 1985; Sato 1994; Di Dario 2004b) and, among fossils, in †*Cynoclupea*, †*Clupeopsis* and †*Monosmilus* (Malabarba & Di Dario 2017; Capobianco *et al.* 2020).

106. Distribution of dentary teeth (S70): (0) restricted to the region near the mandibular symphysis; (1) extending back to the border of the coronoid process.

Description. In most clupeomorphs dentary teeth are restricted to a small region of the dentary near the symphysis, without reaching posteriorly the coronoid process (Fig. 12D, E). However, *Denticeps*, *Chirocentrus*, all the fossil and extant engraulids, *Dussumieria* and *Etrumeus*, the non-engraulid clupeoids *Clupeichthys*, *Limnothrissa*, *Microthrissa*, and the pristigasterids *Chirocentrodon* and *Neoopisthopterus* have the dentary teeth extending back to the coronoid process (Fig. 12A-C) (Sato 1994; Di Dario 2004b). This latter condition is also reported in the fossil †*Clupeopsis*, †*Codoichthys*, †*Cynoclupea*, †*Palaeodenticeps*, †*Ranulfoichthys*, †*Santanaclupea*, †*Scutatuspinosus*, and †*Sorbinichthys* (e.g., Maisey 1993; Alvarado-Ortega 2014), but also in *Albula*, *Alepocephalus*, *Osmerus* and †*Tischlingerichthys* (e.g., Rembiszewski 1964; Fink & Fink 1981).

107. Gap in the tooth row of the dentary (DD92): (0) absent; (1) present.

Description. A gap in the tooth row of the dentary is a synapomorphy uniting certain engraulids, including *Stolephorus*, *Encrasicholina*, *Engraulis* and the New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Pterengraulis*) (Grande & Nelson 1985). This gap has not been detected in the Coiliinae, †*Eoengraulis* nor in the stem engraulids †*Clupeopsis* and †*Monosmilus* (Marramà & Carnevale 2016; Capobianco *et al.* 2020), neither in other clupeomorphs.

108. Ventral margin of the dentary at the symphysis (S69): (0) straight; (1) concave.

Description. In most clupeomorphs the ventral margin of the dentary near the symphysis is nearly straight (Fig. 12A-E). However, in *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Konosirus*, *Nematalosa*, and *Tenualosa* the ventral margin of the dentary at the symphysis is concave, making the tip of dentary projecting ventrally (Fig. 12F) (Whitehead 1985; Sato 1994; Di Dario 2004b). The same condition can be referred to the dentary of †"*Ellimmichthys*" *spinosus* and †*Pseudoellimma* (Figueiredo 2009a; Figueiredo & Gallo 2021). Among outgroups, also *Albula*, *Chanos* and *Kneria* exhibit a concave ventral margin of the dentary (Ridewood 1904a, b; Fink & Fink 1981; Arratia & Schultze 1990).

109. Length of the lower jaw (DD112): (0) short, its length less than three times its depth (=high coronoid process); (1) long, its length three or more times its depth (=low coronoid process).

Description. In most clupeomorphs, the lower jaw (functionally, the lengths of dentary and anguloarticular combined) is short, with its length being approximately twice or slightly less than three times its depth (Fig. 12D-F); in these taxa the coronoid process is therefore well developed, and the horizontal axis of the dentary is therefore reduced (Wongratana 1980; Di Dario 2004b). Conversely, in *Denticeps*, *Chirocentrus*, *Dussumieria*, *Etrumeus*, and all engraulids the coronoid process is low and the lower jaw extends anteriorly, so that the general shape of the dentary is comparatively longer and thinner, with its length being approximately three or more times its depth (Fig. 12A-C) (see also Wongratana 1980; Di Dario 2004b); this latter condition is also detectable in fossil clupeomorphs like †*Clupeopsis*, †*Cynoclupea*, †*Eoengraulis*, †*Monosmilus*, †*Palaeodenticeps*, †*Santanaclupea*, †*Sorbinichthys*, †*Scutatuspinosus* and, among outgroups, in †*Tischlingerichthys* and *Osmerus* (Rembiszewski 1964; Maisey 1993; Marramà & Carnevale 2016; Capobianco *et al.* 2020), but not in other outgroups and †ellimmichthyiforms.

110. Position of the coronoid process on dentary (S69) - ordered: (0) displaced in the posterior half of the lower jaw; (1) located from midlength to the anterior third of the lower jaw; (2) located very close to the anterior end of the dentary.

Description. In basal teleosts, including outgroups analysed herein, the coronoid process is usually displaced in the posterior third of the lower jaw (e.g., Ridewood 1904a; Rembiszewski 1964; Fink & Fink 1981). This is also the condition of some basal clupeiforms like *Denticeps*, †*Palaeodenticeps*, *Chirocentrus*, all engraulids, †*Clupeopsis*, †*Cynoclupea*, †*Nolfia*, †*Pseudoellimma*, †*Santanaclupea* (Fig. 12A, C) (see e.g., Maisey 1993; Sato 1994; Di Dario 2004b) and, among the †ellimmichthyiforms, †*Ornategulum*, †*Ranulfoichthys*, †*Scutatuspinosus* and †*Sorbinichthys africanus* (e.g., Forey 1973a; Alvarado-Ortega 2014; Figueiredo & Ribeiro 2017). In most clupeomorphs, however, the coronoid process is displaced more anteriorly, with its dorsal end located from the midlength to the anterior third of the lower jaw (Fig. 12B, D). Conversely, in *Hyperlophus*, *Sprattus*, and some dorosomatids (*Amblygaster*, *Anodontostoma*, *Dorosoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Lile*, *Nematalosa*, *Opisthonema*, *Platanichthys*, *Rhinosardinia*, *Sardinella*) the coronoid process occupies an even more anterior position in the dentary, making the lower jaws rising very steeply (Fig. 12E, F). The latter condition is also characteristic of †*Bolcaichthys* (Marramà & Carnevale 2015b).

111. Dorsal gap between the coronoid processes of the dentary and the anguloarticular (S71): (0) absent; (1) present.

Description. In *Denticeps* and most of clupeoids the dentary and the anguloarticular are tightly associated and overlap significantly, with their dorsal margin being continuous and with no gap between these two bones. Conversely, in *Spratelloides* and some engraulids (*Cetengraulis*, *Coilia*, *Setipinna*) a distinct gap (also referred to as “dorsal separation”) is present between the coronoid processes of the dentary and the anguloarticular, with these two bones being less associated (Sato 1994). We found this gap also in *Thryssa* (Fig. 12C). This region is often obliterated by the upper jaw in fossil specimens, so we did not code the characters for fossil clupeiforms and ellimmichthyiforms.

112. Retroarticular and anguloarticular (S73): (0) unfused; (1) fused.

Description. In *Denticeps* and most clupeoids, the retroarticular is a discrete bone articulated but unfused to the anguloarticular (Fig. 12A, B, D-F). In *Spratelloides* and all the engraulids however, the retroarticular is fused to the anguloarticular (Fig. 12C) (Sato 1994). A discrete, unfused retroarticular has bee also reported in †ellimmichthyiforms (†*Armigatus*, †*Guiclupea*, †*Ornategulum*, †*Paraclupea*, †*Scutatuspinosus*, †*Triplomystus*) (Forey 1973a; Grande 1982a; Alvarado-Ortega *et al.* 2020) and most outgroups (Diogo & Doadrio 2008; Grande & Poyato-Ariza 2010); the retroarticular is fused with the anguloarticular in *Albula* (Forey 1973b; Di Dario 2004b).

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113. Palatine condition (new): (0) autopalatine and dermopalatine separated; (1) autopalatine and dermopalatine fused; (2) palatine formed by the autopalatine only (dermopalatine absent).

Description. The palatine of Teleostei is generally formed by a chondral portion (autopalatine) and a dermal portion (dermopalatine) (Forey 1973b; Hilton 2003). These two portions can be independent as in *Albula*, *Alepocephalus* and *Osmerus* (Gosline 1969; Forey 1973b; Hilton 2003) or fused to each other as in †*Tischlingerichthys* and all clupeomorphs (Arratia & Schultze 1991; Arratia 1997). Although dermopalatine fused with autopalatine is characteristic of clupeocephalan (Arratia & Schultze 1991; Arratia 2010), in *Chanos* and *Kneria* the palatine is formed by the autopalatine only, whereas the dermopalatine is absent (Fink & Fink 1981, 1996).

114. Palatine teeth (S48): (0) absent or inconspicuous; (1) present.

Description. Palatine teeth characterize most outgroups (*Albula*, *Alepocephalus*, *Osmerus* and †*Tischlingerichthys*) and the clupeiforms *Denticeps*, †*Cynoclupea*, †*Clupeopsis*, *Chirocentrus*, *Dussumieria*, *Etrumeus*, †*Nardoclupea*, all pristigasteroids, most engraulids (except *Anchovia*, *Anchoviella* and *Cetengraulis*) and a few other clupeoids (*Clupeichthys*, *Harengula*, *Lile*, *Microthrissa*, *Odaxothrissa*, *Pellonula*, *Platanichthys* and *Stolothrissa*) (Whitehead 1973; Sato 1994; Di Dario 2004b; Capobianco *et al.* 2020). Conversely, the other clupeoids do not possess palatine teeth, showing a palatine condition similar to that of gonorynchiforms *Chanos* and *Kneria* (Fink & Fink 1981). Teeth are present also in the palatine of †ellimmichthyiforms †*Ornategulum*, †*Paraclupea*, and †*Triplomystus* (Forey 1973a; Malabarba & Di Dario 2017; Marramà & Carnevale 2023). Palatine teeth are absent in †*Ranulfoichthys*, †*Scutatuspinosus* and †*Ellimma longipectoralis* (Figueiredo & Ribeiro 2017; Polck *et al.* 2020).

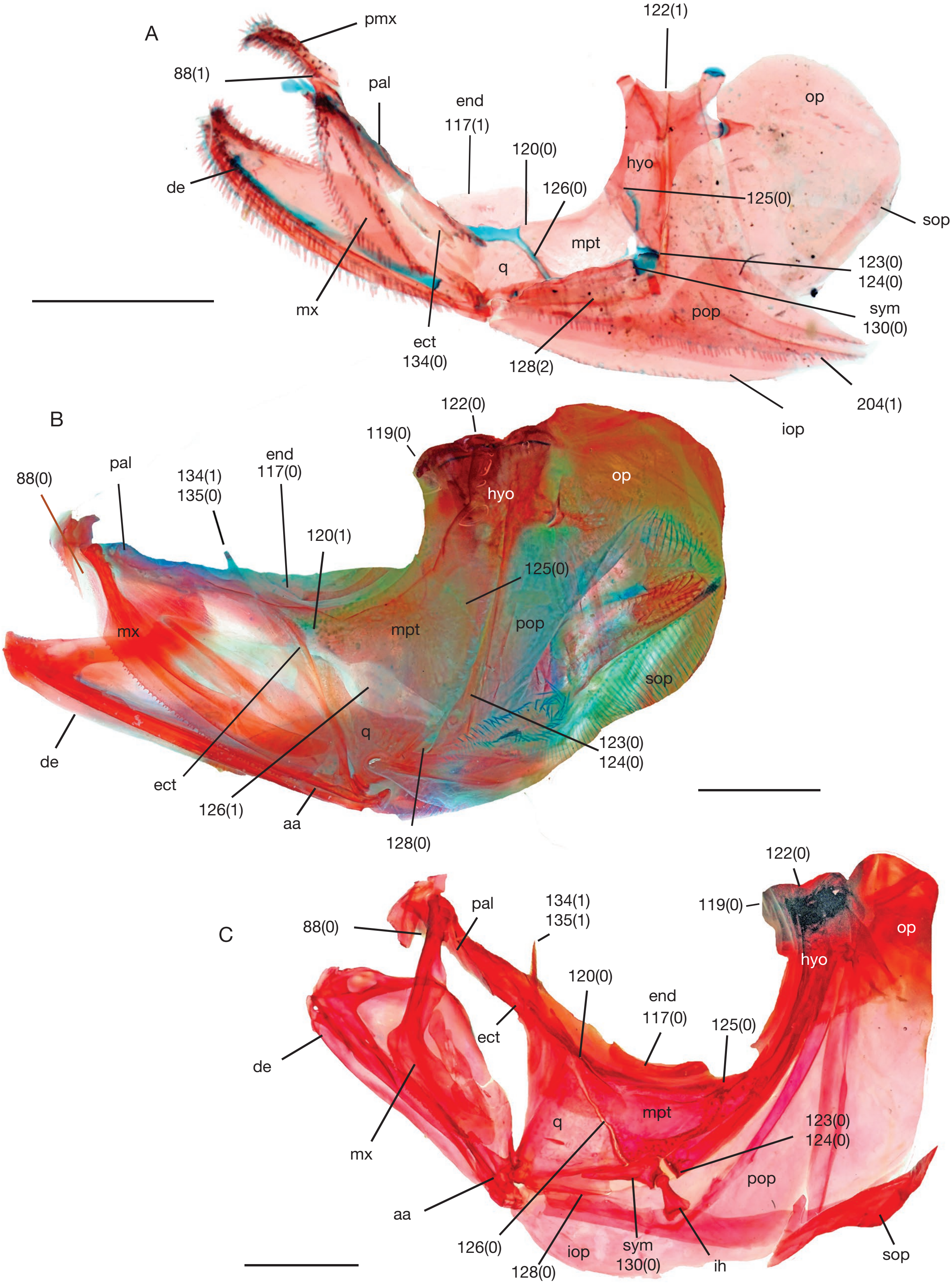

Fig. 13. — Suspensorium and opercular apparatus of selected cleared and stained clupeiforms: **A**, *Denticeps clupeoides* Clausen, 1959 (Denticipitidae), AMNH 53082; **B**, *Alosa sapidissima* (Wilson, 1811) (Alosidae), AMNH 32707; **C**, *Pristigaster cayana* Cuvier, 1829 (Pristigasteridae), AMNH 10186. Scale bars: 3 mm. Abbreviations: **aa**, anguloarticular; **de**, dentary; **ect**, ectopterygoid; **end**, endopterygoid; **hyo**, hyomandibula; **ih**, interhyal; **iop**, interopercle; **mpt**, metapterygoid; **mx**, maxilla; **op**, opercle; **pal**, palatine; **pmx**, premaxilla; **pop**, preopercle; **q**, quadrate; **sop**, subopercle; **sym**, symplectic. Numbers refer to characters and character states (see text).

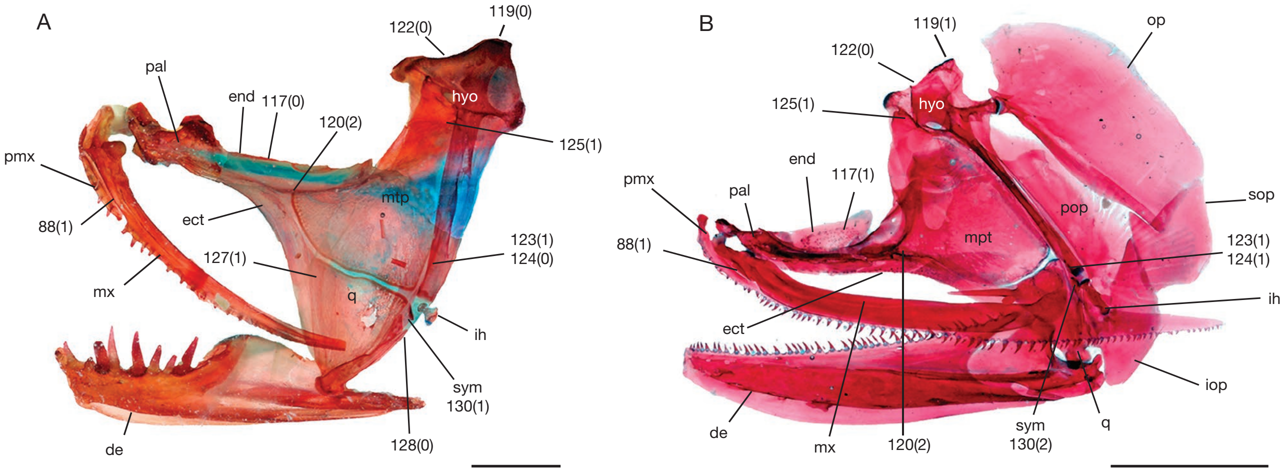

FIG. 14. — Suspensorium and opercular apparatus of selected cleared and stained clupeiforms: **A**, *Chirocentrus dorab* (Forsskål, 1775) (Chirocentridae), AMNH 55306; **B**, *Thryssa hamiltonii* Gray, 1835 (Engraulidae), AMNH 38188. Scale bars: 3 mm. Abbreviations: **aa**, anguloarticular; **de**, dentary; **ect**, ectopterygoid; **end**, endopterygoid; **hyo**, hyomandibula; **ih**, interhyal; **iop**, interopercle; **mpt**, metapterygoid; **mx**, maxilla; **op**, opercle; **pal**, palatine; **pmx**, premaxilla; **pop**, preopercle; **q**, quadrate; **sop**, subopercle; **sym**, symplectic. Numbers refer to characters and character states (see text).

115. Endopterygoid teeth (CM9, S52): (0) absent; (1) present.

Description. Teeth on endopterygoid are present in several clupeiform taxa including *Chirocentrus*, *Denticeps*, *Dussumieria*, *Etrumeus*, all engraulids (except *Coilia*), pristigasteroids, some ehiravids (*Clupeichthys*, *Clupeoides*, *Clupeonella*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*), dorosomatids (*Amblygaster*, *Escualosa*, *Harengula*, *Lile*, *Platanichthys*, *Rhinosardinia*) and a clupeid (*Sprattus*) (Figs 10; 13A, C; 14), but they are absent in most of the other clupeoids (Fig. 13B) (Whitehead 1973; Sato 1994; Di Dario 2004b). Endopterygoid teeth were reported as absent in †*Clupeopsis*, †*Monosmilus*, †*Cynoclupea*, and †*Pseudoellimma* (Figueiredo 2009a; Malabarba & Di Dario 2017; Capobianco *et al.* 2020). Most †ellimmichthyiforms bear endopterygoid teeth, except †*Armigatus oligodentatus*, †*Codoichthys*, †*"Ellimma" longipectoralis*, †*"Ellimmichthys" spinosus*, †*Ranulfoichthys* and †*Scutatuspinosus* (e.g., Figueiredo & Ribeiro 2016, 2017; Vernygora & Murray 2016; Figueiredo & Gallo 2021). Among outgroups, *Albula*, *Osmerus* and †*Tischlingerichthys* have endopterygoid teeth (Rembiszewski 1964; Forey 1973b; Arratia 1997).

116. Distribution of endopterygoid teeth (DD157): (0) limited to a small area of endopterygoid; (1) widely distributed on most of the endopterygoid surface.

Description. Among clupeiforms teeth are limited to a small area of the endopterygoid in *Amblygaster*, *Clupeichthys*, *Clupeoides*, *Clupeonella*, *Denticeps*, *Engraulis*, *Escualosa*, *Lile*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Platanichthys*, *Potamothrissa*, *Rhinosardinia*, and *Sprattus* (Figs 10E; 13A) (Whitehead 1967, 1973; Di Dario 2004b). Teeth are distributed on most of the endopterygoid surface in †Ellimmichthyiformes, *Anchoa*, *Anchoviella*, *Chirocentrodon*, *Chirocentrus*, *Dussumieria*, *Encrasicholina*, *Etrumeus*, *Harengula*, *Ilisha*, *Lycengraulis*, *Lycothrissa*, *Neoopisthopterus*, *Odontognathus*, *Opisthopterus*, *Pellona*, *Setipinna*, *Stolephorus*, and *Thryssa* (Figs 10A-D, F; 14) (Di Dario 2004b), as well as in *Albula*, *Osmerus* and †*Tischlingerichthys* (Ridewood 1904a, b; Rembiszewski 1964; Arratia 1997).

117. Length of the endopterygoid (with respect to the palatine) (S51): (0) longer than palatine; (1) subequal or shorter than palatine.

Description. In all the †ellimmichthyiforms and all non-engraulid clupeoids, the endopterygoid is a plate-like bone moderately larger than the palatine (Figs 13B; 14A). However, in *Denticeps* and engraulids the endopterygoid is roughly equal or shorter than palatine (Figs 13A; 14B) (Sato 1994). This condition is also characteristic of *Alepocephalus*, *Osmerus*, *Chanos* and *Kneria* (e.g., Gosline 1969; Grande & Poyato-Ariza 2010).

118. Size of endopterygoid teeth (CM9, DD158): (0) small; (1) strongly developed.

Description. Endopterygoid teeth are strongly developed in *Albula*, *Osmerus* and all the †Ellimmichthyiformes with teeth on this bone (Fig. 10B, D, F) (e.g., Ridewood 1904b; Rembiszewski 1964; Forey 1973a, 2004; Grande 1982a; Chang & Maisey 2003; Zaragüeta Bagils 2004; Alvarado-Ortega *et al.* 2008).

119. Inclination of the suspensorium (G18, S58): (0) inclined obliquely forward or vertical; (1) inclined obliquely backward.

Description. A suspensorium obliquely inclined backward is traditionally considered one of the most peculiar synapomorphies of the living engraulids (Fig. 14B) (Grande 1985; Grande & Nelson 1985) but characterizes also the fossils †*Clupeopsis*, †*Eoengraulis* and †*Monosmilus* (Marramà & Carnevale 2016; Capobianco *et al.* 2020). A similar condition characterizes also the basal clupeiforms †*Cynoclupea* and †*Santanaclupea* (Fig. 15) (Maisey 1993; Malabarba & Di Dario 2017), whereas all the other clupeomorphs and outgroups have a suspensorium vertical or anteriorly inclined (Figs 13, 14A).

120. Anterior margin of the metapterygoid (DiD1) - ordered: (0) located posterior to the anterior margin of the quadrate; (1) located at same level as the quadrate; (2) located anterior to the anterior margin of the quadrate.

Description. The metapterygoid is a trapezoid bone that lies postero-dorsally to the quadrate in clupeomorphs. In *Denticeps* and most clupeoids, the anterior margin of the metapterygoid is located posterior to the anterior border of the quadrate, which, in turn, articulates with the ectopterygoid (Fig. 13A, C) (see Di Dario (2009)). Conversely, since in *Chirocentrus* and extant Engraulidae the quadrate is displaced to a more posterior position in the suspensorium, a substantial portion of the anterior margin of the metapterygoid is located anterior to the quadrate in these taxa (Fig. 14) (see Di Dario (2009)); this condition is also seen in †*Eoengraulis*, in stem engraulids †*Clupeopsis* and †*Monosmilus* (Marramà & Carnevale 2016; Capobianco *et al.* 2020) and likely in †*Cynoclupea* (Malabarba & Di Dario 2017). In *Alosa*, *Brevoortia*, *Hilsa* and *Tenualosa* the metapterygoid is located in a more anterior position in the suspensorium relative to other clupeoids, but the anterior margin of the metapterygoid is located at same level as the anterior margin of the quadrate without projecting in advance to the anterior border of the quadrate (Fig. 13B) (Di Dario (2009)); this condition can be also detected in †*Pseudoellimma* and †*Santanaclupea* (Fig. 15) (Maisey 1993; Figueiredo 2009a).

121. Anterior margin of the non-laminar area of the tubular branch of the hyomandibula (DD183): (0) continuous and on the same plane as the adjacent laminar area; (1) with a crescent-shaped concavity along most of its length.

Description. In teleosts, the medio-ventral region of the hyomandibula, ventral to its articulation with the opercle, is formed by a solid, tubular ventral branch and an adjacent anterior laminar bone region. In outgroups and most clupeomorphs, the outer surface of the vertical branch and the laminar region are continuous and lie on the same plane, with no significant concavity between them. In *Chirocentrus*, *Dussumieria*, *Etrumeus* and all the engraulids, the anterior margin of the vertical branch, which connects to the symplectic and interhyal, is deeply excavated, forming a pronounced concavity. As a result, the laminar region and the articulating margin of the metapterygoid are located more medially than the outer surface of the branch (Di Dario 2004b).

122. Cranial facet of the hyomandibula (S59, CM7): (0) single, undivided; (1) divided in two distinct articulatory facets.

Description. All the †Ellimmichthyiformes and the majority of Clupeiformes have the proximal part of the hyomandibula that articulates to both the sphenotic and pterotic through a single, undivided articulatory facet (most Clupeoidei; Figs 13B, C; 14) or with its articulatory site confined to the sphenotic only (like in *Coilia*) (Sato 1994; Chang & Maisey 2003). Conversely, *Denticeps* and †*Santanaclupea* (Figs 13A; 15), all the fossil and extant engraulids (except *Coilia* and *Thryssa*; Fig. 14B), dussumieriids and spratelloidids, *Alosa*, *Tenualosa*, and the pristigasterid *Odontognathus* have the proximal head of the hyomandibula divided in two distinct articulatory facets, the anterior articulating with sphenotic, the posterior with pterotic, resembling the condition of *Chanos* and *Kneria* (Sato 1994; Poyato-Ariza *et al.* 2010), but not that of the other outgroups (Rembiszewski 1964; Grande 1994).

123. Ventral limb of the hyomandibula (DiD2): (0) not meeting the posterior margin of the quadrate (completely separated by the metapterygoid); (1) meeting the posterior margin of the quadrate (not separated by the metapterygoid).

Description. In *Denticeps* and most clupeoids, the ventral limb of the hyomandibula and the posterodorsal margin of the quadrate are separated by the metapterygoid, keeping these two bones separated (Fig. 13) (see Di Dario (2009)). This is also the condition of the outgroups considered herein and all †Ellimmichthyiformes. In *Chirocentrus* and engraulids, however, as a consequence of the relative inclination of these bones in the suspensorium, the ventral limb of the hyomandibula meets the posterodorsal margin of the quadrate, since these two bones are not separated by the metapterygoid (Fig. 14) (see Di Dario (2009)). Among fossil clupeiforms, this condition can be detected also in †*Clupeopsis* and †*Eoengraulis*, but difficult to detect in †*Monosmilus* (?) (Marramà & Carnevale 2016; Capobianco *et al.* 2020).

124. Articulation between the ventral limb of the hyomandibula and the quadrate (DiD2): (0) absent; (1) present.

Description. In †*Clupeopsis* and Engraulidae (including †*Eoengraulis*) (Marramà & Carnevale 2016; Capobianco *et al.* 2020) the ventral limb of the hyomandibula and the quadrate are articulated to each other due to the backward inclination of the suspensorium (Fig. 14B), whereas in other Clupeiformes, including *Chirocentrus*, the vertical limb of the

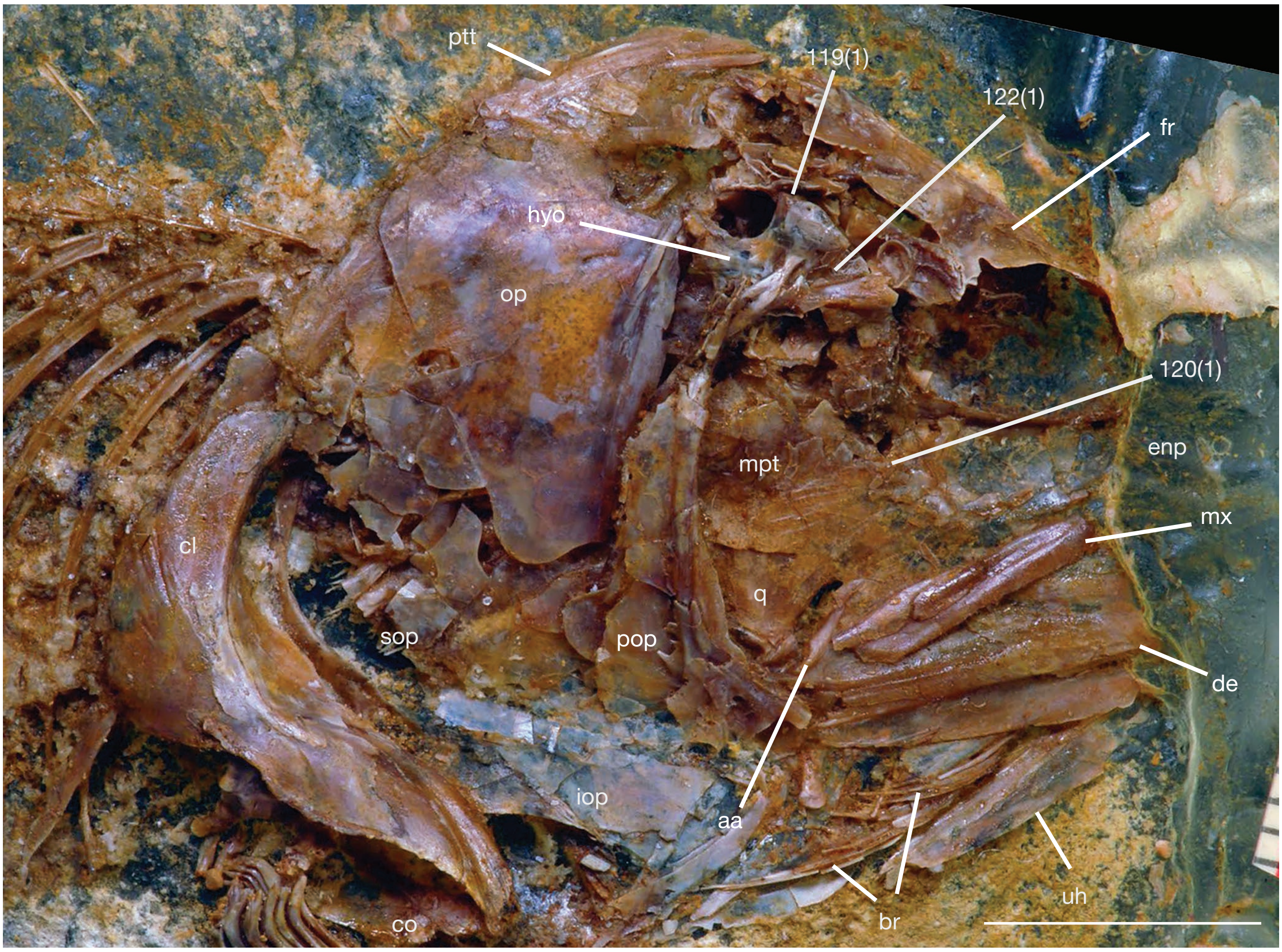

Fig. 15. — Head region of †*Santanaclupea silvasantoi* Maisey, 1993 (Clupeiformes: †Cynoclupeidae), Lower Cretaceous, Brazil; AMNH DVP.18968 (photo: courtesy of Lorraine Meeker). Scale bar: 10 mm. Abbreviations: **aa**, anguloarticular; **br**, branchiostegal rays; **cl**, cleithrum; **co**, coracoid; **de**, dentary; **end**, endopterygoid; **fr**, frontal; **hyo**, hyomandibula; **iop**, interopercle; **mpt**, metapterygoid; **mx**, maxilla; **op**, opercle; **pop**, preopercle; **ptt**, posttemporal; **q**, quadrate; **sop**, subopercle; **uh**, urohyal. Numbers refer to characters and character states (see text).

hyomandibula articulates exclusively with the metapterygoid but not with the quadrate (Figs 13; 14A) (Di Dario (2009). This latter condition is also exhibited by the outgroups and †Ellimmichthyiformes.

125. Posterodorsal margin of the metapterygoid: (DiD3): (0) ventral to the condyle of articulation of the hyomandibula with the opercle; (1) in line with the condyle of articulation of the hyomandibula with the opercle.

Description. The posterodorsal margin of the metapterygoid of *Denticeps* and most clupeoids extends to a region located approximately halfway between the dorsal and ventral margins of the hyomandibula (Fig. 13). *Chirocentrus* and the Engraulidae are unique within the Clupeiformes in having the posterodorsal margin of the metapterygoid that reaches a relatively more dorsal position in the suspensorium, in line with the condyle of articulation of the hyomandibula with the opercle (Fig. 14) (Di Dario (2009)). This derived condition is also seen in †*Clupeopsis*, †*Eoengraulis* and †*Monosmilus* (Marramà & Carnevale 2016; Capobianco *et al.* 2020), but not in the †ellimmichthyiforms and outgroups.

126. Quadrate-metapterygoid fenestra (S56): (0) absent; (1) present.

Description. A peculiar feature of the hyopalatine arch of certain teleost lineages (e.g., Cypriniformes, Characiformes) is the presence of a conspicuous opening between the metapterygoid and the quadrate, the so-called quadrate-metapterygoid fenestra, resulting from a marked concavity or embayment in the dorsal and ventral margins of the quadrate and metapterygoid, respectively (Britz *et al.* 2023). In Clupeiformes, a distinct fenestra can be seen in *Jenkinsia* and *Spratelloides*, as well as in *Alosa*, *Brevoortia*, and *Sardinops* (Fig. 13B) (Ridewood 1904b; Phillips 1942; Gosline 1975; Arratia & Schultze 1991; Sato 1994; Britz *et al.* 2023). It appears also present in †*Eoalosa* (Marramà & Carnevale 2018, fig. 2). It is absent in outgroups, other fossil clupeiforms and all †ellimmichthyiforms.

127. Laminar outgrowth on the anterior margin of quadrate (DiD4): (0) absent; (1) present.

Description. The anterior margin of the quadrate of *Chirocentrus* and Engraulidae is unique within Clupeiformes in having a laminar outgrowth that projects anterodorsally beyond the cartilage that borders the dorsal margin of the bone (Fig. 14) (Di Dario (2009)). This laminar outgrowth has been also detected in †*Clupeopsis* and †*Eoengraulis* (Marramà & Carnevale 2016; Capobianco *et al.* 2020) and, interestingly, in †*Cynoclupea* (Malabarba & Di Dario 2017), whereas its presence is unclear in †*Monosmilus*.

128. Extension of the ventral process of the quadrate (DD149) – ordered: (0) short; (1) moderately developed; (2) well-developed.

Description. The quadrate of teleosts usually has a laminar process in its ventral region, where the symplectic inserts. In most extant clupeiforms, this process is short, with its distal end not reaching the posterior margin of the main body of the quadrate (Fig. 13B, C). In *Etrumeus*, Spratelloididae, a few pristigasterids (e.g., *Ilisha*, *Pellona*), *Hyperlophus*, *Potamalosa*, most ehiravids (*Clupeoides*, *Gilchristella*, *Microthrissa*, *Nannothrissa*, *Pellonula*, *Odaxothrissa*, *Potamothrissa*, *Stolothrissa*; see also Grande 1985, fig. 28), *Sardina* and a few dorosomatids (*Dorosoma*, *Escualosa*, *Lile*, *Nematalosa*, *Platanichthys*, *Rhinosardinia*) the process extends posteriorly to align with or project slightly beyond the posterior margin of the quadrate, resembling the condition of *Alepocephalus* and *Osmerus*, among outgroups. Conversely, in *Denticeps*, the process is more extensively developed, with its posterior margin projecting beyond the posterior margin of the quadrate by a distance equivalent to one or more times the distance between the quadrate condyle articulating with the lower jaw and the posterior margin of the main body of the quadrate (Fig. 13A), resembling the condition of *Chanos*, *Kneria* and *Albula*. It is difficult to determine this condition in fossils since this part of the quadrate is usually covered by the opercular bones, although †*Italoclupea* seems to show the condition (1).

129. Shape of quadrate (DiD5): (0) as equilateral triangle; (1) as isosceles triangle.

Description. The quadrate of teleosts, including most Clupeiformes and all †Ellimmichthyiformes, is usually well developed and equilateral triangular in shape (Figs 13; 15) (Arratia & Schultze 1991; Di Dario 2009). Conversely, in *Chirocentrus* and Engraulidae the shape of the endochondral portion of the quadrate is similar to that of an isosceles triangle (Fig. 14) (see Di Dario (2009)). This latter condition is also typical of †*Clupeopsis* and †*Eoengraulis*, and unknown in †*Monosmilus* (Marramà & Carnevale 2016; Capobianco *et al.* 2020).

130. Dorsal tip of the symplectic (new) - ordered: (0) dorsal to the proximal margin of quadrate; (1) in line with the proximal margin of the quadrate; (2) ventral to the proximal margin of quadrate.

Description. In many teleost (including the outgroups, most clupeiforms and all †ellimmichthyiforms) the dorsal tip of the symplectic is usually located dorsal to the proximal margin of the quadrate (Fig. 13). However, in *Chirocentrus* the dorsal tip of the symplectic is in line with the proximal margin of the quadrate (Fig. 14A); interestingly, this condition has been also observed in †*Cynoclupea* (Malabarba & Di Dario 2017). In †*Clupeopsis* and Engraulidae, because of the pronounced shift to a more dorsal position of the quadrate and metapterygoid, the dorsal tip of the symplectic lies in a position ventral to the proximal margin of the quadrate (Fig. 14B) (see Di Dario (2009); Capobianco *et al.* 2020).

131. Quadrate-mandibular articulation (G18): (0) posterior to orbit; (1) below the orbit; (2) anterior to orbit.

Description. Most clupeiforms, including denticipitids, *Chirocentrus* and †*Pseudoellimma*, have the quadrate-mandibular articulation directly below the orbit (Fig. 6A-C). However, in stem (†*Clupeopsis* and †*Monosmilus*) and crown engraulids (including †*Eoengraulis*) and the fossil clupeiforms †*Cynoclupea* and †*Santanaclupea* the lower jaw articulation lies well posterior to the orbit (Figs 6D, G, H; 15). All pristigasteroids (except *Chirocentrodon* and *Neoopisthopterus* whose condition is similar to that of most clupeiforms) have the anguloarticular-quadrate articulation anterior to the orbit (Fig. 6E) (see Grande 1985); the same condition is characteristics of †*Diplomystus*, †*Gasteroclupea* and †*Guiclupea* (Fig. 6F) (see Marramà & Carnevale 2017; Chen *et al.* 2021) and, among outgroups, *Chanos* and *Kneria* (Arratia 1999).

132. Ectopterygoid teeth (S50): (0) absent; (1) present.

Description. Teeth on the ventral surface of the anterior arm of the ectopterygoid are present in †*Nardoclupea*, *Chirocentrus*, *Dussumieria*, *Etrumeus*, pristigasteroids (except *Odontognathus* and *Pristigaster*) and engraulids (except *Cetengraulis* and †*Monosmilus*) but also in *Amblygaster*, *Clupeichthys*, *Harengula*, *Herklotsichthys*, *Lile*, *Opisthonema*, *Platanichthys*, *Potamalosa*, and *Sardinella* (Fig. 14) (Whitehead 1973; Sato 1994; Di Dario 2004b). No teeth are reported in the ectopterygoid of *Chanos*, *Kneria* and *Osmerus* (Rembiszewski 1964; Fink & Fink 1981), but they are present in *Albula*, †*Tischlingerichthys* (Ridewood 1904a; Arratia 1997) and some individuals of *Alepocephalus rostratus* (0/1) (Johnson & Patterson 1996). Alvarado-Ortega *et al.* (2020) reported ectopterygoid teeth in †*Armigatus carrenoae* but we consider this interpretation as doubtful since no other authors ever reported ectopterygoid teeth in †Ellimmichthyiformes.

133. Ectopterygoid and metapterygoid (S54): (0) unfused; (1) fused.

Description. In most clupeomorphs the ectopterygoid is a boomerang-shaped autogenous bone, with the posterior, vertical arm that generally is free or articulates dorsally with the anterior margin of metapterygoid (Figs 13; 14). However, in *Stolephorus*, *Encrasicholina*, *Engraulis* and the New World anchovies the ectopterygoid is fused with the metapterygoid (Grande & Nelson 1985; Sato 1994). This fusion has been also observed in the engraulid †*Eoengraulis* but not in †*Clupeopsis*, †*Monosmilus* (Marramà & Carnevale 2016; Capobianco *et al.* 2020), the outgroups and the †Ellimmichthyiformes.

134. Dorsal process of ectopterygoid (S49): (0) absent; (1) present.

Description. In most of the advanced Clupeiformes the ectopterygoid bears a more or less long process on its dorsal margin that serves as articulation to the lateral ethmoid (Fig. 13B, C) (Sato 1994). However, the basal clupeiforms like *Denticeps*, *Chirocentrus* and the Engraulidae lack this process (Figs 13A; 14) (Sato 1994; Mertzen 2019). The process is also absent in all the outgroups (e.g., Rembiszewski 1964; Gosline 1969; Grande 1994) and the basal clupeiform †*Pseudoellimma* (Figueiredo 2009a). The dorsal process that seems to be present in the ectopterygoid of *Albula* actually is the lateral ethmoid process of the autopalatine (Forey 1973b). In †ellimmichthyiforms preserving the ectopterygoid (e.g., some †*Armigatus* species, †*Ellimma branneri*, †*Eoellimmichthys*, †*Ornategulum*, †*Ranulfoichthys*, etc) the dorsal process appears to be absent (Forey 1973a; Alvarado-Ortega 2014; Marramà *et al.* 2019).

135. Shape of the dorsal process of ectopterygoid (S49): (0) short and blunt; (1) elongated and slender.

Description. Among clupeoids showing the dorsal process of the ectopterygoid, only pristigasteroids have an elongated and slender process (Fig. 13C), whereas all the others non-engraulid clupeoids have a short and blunt process (Fig. 13B) (Sato 1994; Di Dario 2004b).

136. Lateral horizontal lamina of the ectopterygoid (K65): (0) absent; (1) present.

Description. The fossil stem engraulids †*Clupeopsis* and †*Monosmilus* are unique among clupeiforms in having a lateral horizontal lamina on the ectopterygoid that underlies the orbit and overlies dorsally the maxilla (Capobianco *et al.* 2020). The presence of this lamina has never been reported in other extant or fossil clupeomorphs, or in the outgroups.

137. Bony walls on the anterior aspect of the hyomandibula (DD195): (0) absent; (1) present.

Description. In all the Clupeoidei the anterior region of the hyomandibula has two laminar, vertical and approximately parallel bony walls, one mesial and the other external, running at level of the articular condyle with the sphenotic and extending towards the metapterygoid, whereas *Denticeps* and all outgroups are devoid of these walls (Di Dario 1999, 2004b). It is difficult to detect their presence in fossil taxa (except in †*Clupeopsis*, where they seem to be present), so we preferred to code this state as indeterminate (?).

138. External wall of the hyomandibula (DD196): (0) gradually decreasing towards the base of the hyomandibula; (1) projecting anteriorly and with a pronounced concavity in its ventral region.

Description. In most clupeoids, the anterior margin of the outer wall of the hyomandibula gradually coalesces ventrally toward the anterior margin of the tubular body of the hyomandibula (Fig. 13) (Di Dario 2004b). However, in *Chirocentrus*, *Dussumieria*, *Etrumeus*, †*Clupeopsis* and engraulids, the outer wall of the hyomandibular projects anteriorly toward the metapterygoid, and its ventral margin is deeply concave (Di Dario 2004b).

139. Ventral process on inner wall of the hyomandibula (DD191): (0) absent; (1) present.

Description. The inner wall of the hyomandibula of *Chanos* and clupeoids has a ventral process that extends towards the medioposterior, crescent-shaped process of the metapterygoid (Di Dario 1999, 2004b). This process is absent in *Denticeps* and all the outgroups (e.g., Di Dario 1999, 2004b). It is difficult to detect this process in the fossils.

BRANCHIAL ARCHES

140. Foramen on the anterior ceratohyal produced by the overlap between lateral and medial foramina of the hyoid arterial duct (CM12, S77): (0) absent; (1) present.

Description. Although several clupeoids present a perforation on medial side of anterior ceratohyal, it usually does not penetrate completely also its lateral wall, thereby not resulting in a true foramen (Fig. 16A, B). However, lateral and medial foramina overlap forming a small foramen in *Clupea*, *Hyperlophus*, *Sprattus* and some alosids (*Alosa*, *Brevoortia*, *Sardinops*) (Sato 1994; Segura & De Astarloa 2004) or a large one, the so called "beryciform foramen" of McAllister (1968), in †*Italoclupea*, †*Santanaclupea* and †*Scombroclupea* (Fig. 16C) (e.g., Maisey 1993; Than-Marchese *et al.* 2020). A large foramen on the anterior ceratohyal produced by the overlap between lateral and medial foramina of hyoid arterial duct is typically present in all †ellimmichthyiforms (Fig. 16D) (e.g., Grande 1985; Chang & Maisey 2003; Forey 2004; Zaragüeta Bagils 2004). Bannikov & Bacchia (2000) stated that "the anterior ceratohyal is not clearly visible in any specimen [of †*Sorbinichthys elusivo*], but it seems to be without a beryciform foramen". However, being the "beryciform foramen" likely present in †*Sorbinichthys africanus* (Murray & Wilson 2011), we prefer to consider its absence in *S. elusivo* as doubtful. A foramen is absent in all the outgroups and the other clupeiforms here considered.

141. Size of the foramen on the anterior ceratohyal (G11, S77, CM12): (0) small, less than one third of the length of anterior ceratohyal; (1) large, one third or more of the length of anterior ceratohyal (beryciform foramen).

Description. The "beryciform foramen" is a large perforation formed by the overlap between the lateral and medial foramina of hyoid arterial duct in anterior ceratohyal (McAllister 1968) that has been considered a "primitive" feature of several groups of teleosts, including some elopomorphs, osteoglossomorphs, paracanthopterygians and beryciforms (Rosen & Patterson 1969). A large "beryciform foramen", covering a third or more of the length of anterior ceratohyal, is only typical of †ellimmichthyiforms but also of the basal clupeiforms †*Italoclupea*, †*Santanaclupea*, and †*Scombroclupea* (Fig. 16C, D), whereas the foramen of †*Gasteroclupea* and the clupeiforms *Alosa*, *Brevoortia*, *Clupea*, *Hyperlophus*, *Sardinops* and *Sprattus* is typically small or extremely reduced, covering less than one third of the anterior ceratohyal length (e.g., Grande 1985; Maisey 1993; Chang & Maisey 2003).

142. Ventral margin of the anterior ceratohyal (DD223): (0) smooth; (1) with notches or holes where branchiostegal rays are inserted.

Description. All outgroups, *Denticeps* and †ellimmichthyiforms have a smooth ventral margin of the anterior ceratohyal (Fig. 16D) (e.g., Di Dario 2004b; Mertzen 2019; Marramà & Carnevale 2023). Conversely, most fossil and living clupeiforms (including *Italoclupea*, *Nardoclupea*, and *Scombroclupea*, unknown in other fossils) bear notches or holes on anterior ceratohyal where branchiostegal rays are inserted (Fig. 16A-C) (Di Dario 1999, 2004b).

143. Ventral margin of the anterior ceratohyal (DD223): (0) with grooves or notch; (1) with holes where branchiostegal rays are inserted.

Description. The ventral border of the anterior ceratohyal is notched in †*Italoclupea*, †*Scombroclupea*, †*Nardoclupea*, *Etrumeus*, *Spratelloides*, all the engraulid genera, Pristigasteroidea (except *Pliosteostoma*), and a few other clupeoids (*Clupeoides*, *Gilchristella*, *Hyperlophus*, *Pellonula*) (Fig. 16A, C). Conversely, a few ehiravids (*Clupeichthys*, *Corica*, *Konosirus*, *Odaxothrissa*) and the rest of clupeoids have complete holes where branchiostegal rays insert (Fig. 16B) (e.g., Di Dario 1999, 2004b).

144. Length to depth of the anterior ceratohyal (S74): (0) <5; (1) 5 or more.

Description. In *Denticeps*, all non-engraulid clupeoids and †ellimmichthyiforms the anterior ceratohyal is short, not elongate, its length being less than five times of its depth (Fig. 16B-D). Conversely, in all engraulids (but not in the stem †*Clupeopsis*) the length of the anterior ceratohyal is five or more times than its depth (Whitehead 1973; Sato 1994) (Fig. 16A). This latter condition is also typical of *Albula*, *Alepocephalus* and *Chanos* (Ridewood 1904a; Gosline 1969; Fink & Fink 1981), but not of *Osmerus* (Rembiszewski 1964) and unknown in †*Tischlingerichthys*.

145. Length of the anterior ceratohyal in relation to the posterior ceratohyal (DD229): (0) up to 2.5 times the length of the posterior ceratohyal; (1) more than 2.5 times the length of the posterior ceratohyal.

Description. The anterior ceratohyal of the outgroups and most clupeomorphs has a length up to 2.5 times the length of the posterior ceratohyal (Fig. 16B-D). However, in †*Clupeopsis*, all engraulids (including †*Eoengraulis*), *Chirocentrus*, *Dussumieria* and *Etrumeus* the anterior ceratohyal has a length that is more than 2.5 times the length of the posterior ceratohyal (Fig. 16A) (Di Dario 1999, 2004b).

146. Foramen in the posterior ceratohyal (S80, Z15): (0) absent; (1) present.

Description. A distinct perforation on the medial side of the hyoid arterial duct in the posterior ceratohyal occurs in some clupeoids (*Alosa*, *Anodontostoma*, *Brevoortia*, *Clupanodon*, *Dorosoma*, *Hilsa*, *Hyperlophus*, *Konosirus*, *Nematalosa*, *Rhinosardinia*, *Sardinops*, *Tenualosa*) (Fig. 16B) (Sato 1994; Di Dario 2004b) and in some †ellimmichthyiforms like †*Armigatus carrenoae*, †*A. felixi*, †*Paraclupea pietrarojae*, †*P. seilacheri*, and †*Ranulfoichthys* (Fig. 16D) (Alvarado-Ortega 2014; Alvarado-Ortega *et al.* 2020; Marramà & Carnevale 2023), whereas it is absent in outgroups, *Denticeps* and the other clupeoids (Fig. 16A, C) (Sato 1994; Di Dario 2004b) and, among the †ellimmichthyiforms in †*Armigatus namourensis*, †*A. oligodentatus*, †*Diplomystus dentatus*, †*Guiclupea*, †*Scutatuspinosus*, and †*Thorectichthys* (e.g., Forey *et al.* 2003a; Murray & Wilson 2013; Chen *et al.* 2021).

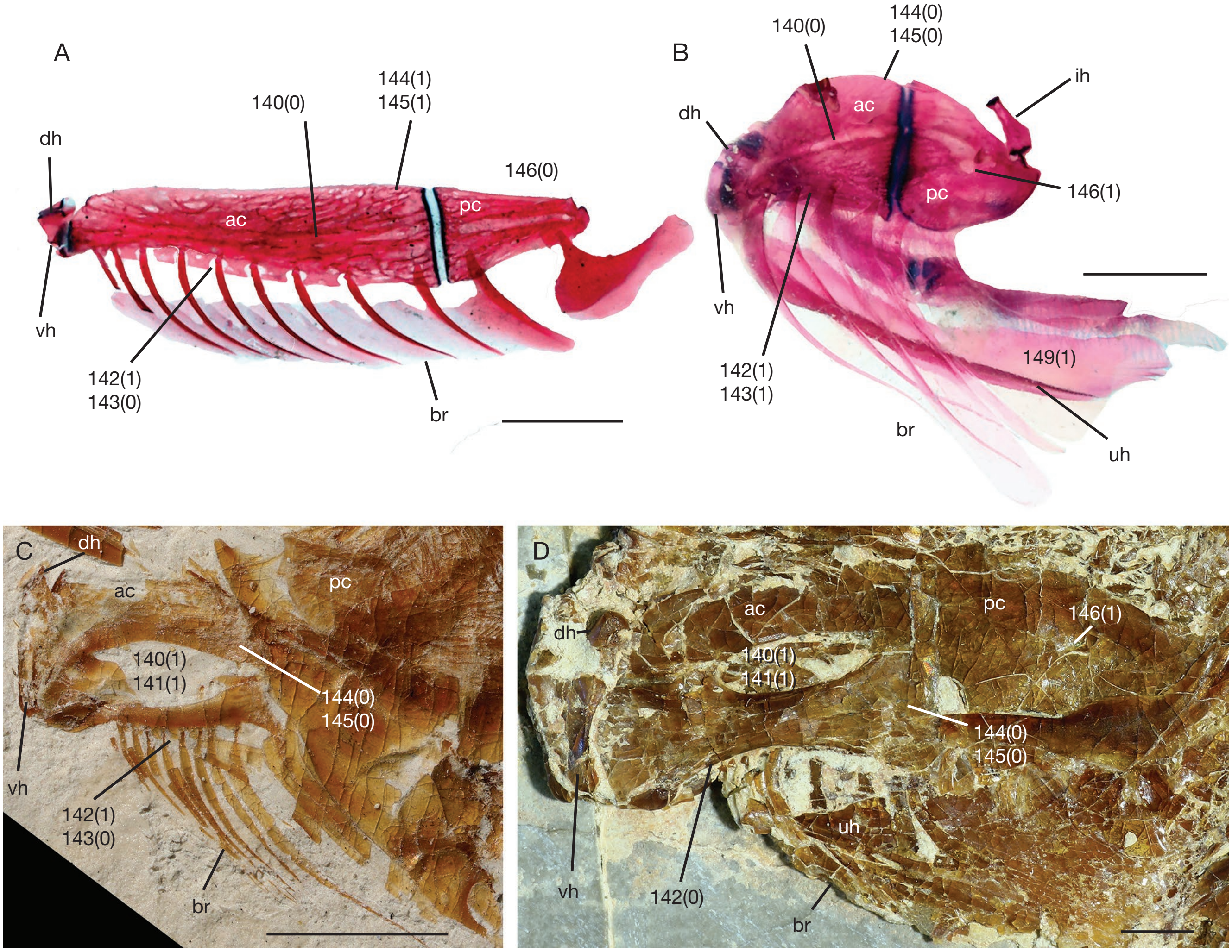

FIG. 16. — Part of the hyoid apparatus of selected clupeomorphs: **A**, *Thryssa hamiltonii* Gray, 1835 (Clupeiformes: Engraulidae), AMNH 38188; **B**, *Hilsa kelee* (Cuvier, 1829) (Clupeiformes: Dorosomatidae), AMNH 32828, **C**, †*Italoclupea nolfi* Taverne, 2007 (Clupeiformes: Clupeoidei *incertae sedis*), MCSNV Na530; **D**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Ellimmichthyiformes: †Paraclupeidae), MRSN P/260.2 (reversed). Scale bars: 2 mm. Abbreviations: **ac**, anterior ceratohyal; **br**, branchiostegal rays; **dh**, dorsal hypohyal; **gha**, groove for the afferent hyoidean artery; **ih**, interhyal; **pc**, posterior ceratohyal; **uh**, urohyal; **vh**, ventral hypohyal. Numbers refer to characters and character states (see text).

147. Dorsal process of posterior ceratohyal (S78): (0) small or indefinite; (1) definite and large.

Description. The dorsal process of the posterior ceratohyal serves as the articulation site for the interhyal and is present in outgroups and all clupeomorphs. This process is small or indefinite in outgroups (Johnson & Patterson 1996; Poyato-Ariza *et al.* 2010), most clupeiforms and †ellimmichthyiforms, but it is well definite and large in all the pristigasteroids (Sato 1994; see also Di Dario 1999, fig. 7).

148. Hyoid arterial duct in posterior ceratohyal (S79): (0) completely exposed; (1) covered, at least partially, by bony wall.

Description. In most clupeoids and †ellimmichthyiforms, the hyoid arterial duct in the posterior ceratohyal is completely grooved and exposed (sometime allowing to observe the foramen). However, in *Denticeps*, and the engraulids *Coilia* and *Setipinna* the duct is partially or completely covered by a bony wall (Sato 1994). Among outgroups, the hyoid arterial duct on posterior ceratohyal is grooved and exposed in *Albula*, *Chanos* and *Osmerus* (unknown in †*Tischlingerichthys*), but the groove is covered by bone in *Alepocephalus* (see Johnson & Patterson 1996).

149. Dorsal blade of the urohyal (S83): (0) absent or inconspicuous; (1) present and well developed.

Description. Character 83 of Sato (1994), regarding the shape of the urohyal, was a mix of neomorphic and transformational character statements that has been split herein in four separate characters (149 to 152) following the logical basis for morphological characters in phylogenetic analyses provided by Sereno (2007). In this perspective, clupeiforms with well-developed process (blade) on the dorsal aspect of the urohyal are: *Chirocentrus*, †*Nardoclupea*, all pristigasteroids, all dorosomatids (*Amblygaster*, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Lile*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Konosirus*, *Nematalosa*, *Opisthonema*, *Platanichthys*, *Rhinosardinia*, *Sardinella*, and *Tenualosa*), and some ehiravids (*Clupeonella*, *Clupeichthys*, *Clupeoides*, *Microthrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*) (Fig. 16B) (Wongratana 1980; Sato 1994; Di Dario 2004b). Some †ellimmichthyiforms with preserved urohyal (†*Armigatus carrenoae*, †*A. namourensis*, †*Diplomystus dentatus*, †*Ellimma branneri*, †*Guiclupea*, †*Paraclupea pietrarojae*, †*Ranulfoichthys*, †*Rhombichthys*, †*Tunisiaclupea*) exhibit a robust dorsal blade as well (e.g., Chang & Maisey 2003; Alvarado-Ortega *et al.* 2020; Chen *et al.* 2021). Among outgroups, the dorsal blade of the urohyal is present in *Alepocephalus* and *Chanos* (Di Dario 2004b).

150. Ventral blade of the urohyal (S83): (0) absent or inconspicuous; (1) present and well developed.

Description. Clupeiforms with a well-developed vertical process (blade) on the ventral aspect of the urohyal include all the engraulids, *Pellona*, alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*), *Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus* and some ehiravids (*Clupeichthys*, *Clupeoides*, *Clupeonella* and *Gilchristella*) (Wongratana 1980; Sato 1994; Di Dario 2004b). The †ellimmichthyiforms in which the urohyal is preserved (†*Armigatus carrenoae*, †*Diplomystus dentatus*, †*Ellimma branneri*, †*Guiclupea*, †*Paraclupea pietrarojae*, †*Ranulfoichthys*, †*Rhombichthys*, †*Tunisiaclupea*; see Forey 2004) and outgroups (*Alepocephalus* and *Chanos*) do not possess the ventral blade on the urohyal.

151. Lateral wings of the urohyal (S83): (0) absent; (1) present.

Description. The urohyal of clupeomorphs (including †*Diplomystus*; see Forey 2004) usually possess more or less developed lateral wings, which are absent in *Denticeps*, *Chirocentrus*, the pristigasteroids *Chirocentrodon*, *Ilisha*, *Odontognathus* and *Opisthopterus*, and the ehiravids *Clupeichthys*, *Clupeoides*, *Corica* and *Gilchristella* (Wongratana 1980; Sato 1994; Di Dario 2004b; see also Grande 1985, figs 34, 47). Lateral wings are present in all extant outgroups and unknown in †*Tischlingerichthys* (Gosline 1969; Fink & Fink 1981; Di Dario 2004b).

152. Shape of the lateral wings of the urohyal (S83): (0) weakly developed and uniformly narrow; (1) well-developed, triangle-shaped profile in dorsal or ventral view.

Description. The lateral wings of the urohyal of *Chanos* and clupeomorphs are usually narrow and weakly developed, whereas they are well-developed and triangular in *Alepocephalus* (Gosline 1969), *Anodontostoma*, *Brevoortia*, *Clupanodon*, *Dorosoma*, *Dussumieria*, *Etrumeus*, *Jenkinsia*, *Konosirus*, *Limnothrissa*, *Microthrissa*, *Nematalosa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Spratelloides* and *Stolothrissa* (Sato 1994; see also Wongratana 1980; Grande 1985, figs 34, 47).

153. Maximum number of branchiostegal rays (Gg, S81) - ordered: (0) less than six; (1) 6-10; (2) more than 10.

Description. Most clupeomorphs have between six and ten branchiostegal rays (Fig. 16B, D). However, *Denticeps* and †*Palaeodenticeps*, clupeoids like *Anodontostoma*, *Clupeoides*, *Escualosa*, *Harengula* and *Hyperlophus* (Greenwood 1960; Grande 1985), but also †*Cynoclupea*, †*Pseudoellimma* and the †ellimmichthyiform †*Sorbinichthys africanus* have five or less branchiostegals (Figueiredo 2009a; Murray & Wilson 2011; Malabarba & Di Dario 2017). Conversely, all engraulids (except *Cetengraulis*), *Dussumieria*, *Etrumeus*, †*Italoclupea*, †*Nardoclupea*, †*Scombroclupea* and the †ellimmichthyiforms †*Armigatus* (except †*A. alticorpus* and †*A. oligodentatus*), †*Diplomystus*, †*Ezkutuberezi*, †*Ornategulum*, and †*Ranulfoichthys*, have 11 or more branchiostegal rays (Fig. 16A, C) (Forey 1973a; Grande 1985; Alvarado-Ortega 2014). Among the outgroups, *Chanos*, *Kneria*, †*Tischlingerichthys* and *Osmerus* have five or less branchiostegals, *Alepocephalus* has 6 to 10 rays, and *Albula* has more than ten branchiostegal rays (Ridewood 1904a; Rembiszewski 1964; Johnson & Patterson 1996).

154. Number of branchiostegal rays articulating with the anterior ceratohyal (excluding those rays on the distinct posteroventral process, if present) (new) - ordered: (0) one; (1) two; (2) three; (3) four to nine; (4) ten or more.

Description. The distribution of branchiostegal rays among the anterior and posterior ceratohyal in clupeomorphs is highly variable. We follow Nelson (1970) for accounting on the ray distribution of clupeomorphs, integrating with data from Wongratana (1980). Teleosts usually have the branchiostegal rays distributed between the anterior and the posterior ceratohyal, but some taxa have the anterior ceratohyal with a distinct posteroventral process supporting one or two rays. *Denticeps* is the only taxon with a single ray on the anterior ceratohyal. Some ehiravids (*Clupeoides*, *Corica*, *Microthrissa*), dorosomatids (*Anodontostoma*, *Escualosa*, *Platanichthys*, *Rhinosardinia*) and *Hyperlophus*, other than *Chanos*, have two rays on the anterior ceratohyal. Most clupeiforms (*Jenkinsia*, *Clupeonella*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, all pristigasteroids and all the other dorosomatids) plus *Alepocephalus* have three branchiostegal rays on the anterior ceratohyal, whereas *Cetengraulis*, *Chirocentrus*, *Spratelloides*, all alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*), *Clupea*, *Potamalosa*, *Sprattus*, the other ehiravids and *Osmerus* have four to six rays. Conversely, *Dussumieria*, *Etrumeus* and all engraulids (except *Cetengraulis*) plus *Albula* have more than 10 rays on the anterior ceratohyal. It is difficult to detect precisely the distribution of branchiostegal rays in fossils because inadequate preservation may prevent the correct evaluation. However, according to Nelson (1970) †*Armigatus brevissimus* and †*Scombroclupea* have five and eleven rays on the anterior ceratohyal, respectively.

155. Number of branchiostegal rays on the distinct posteroventral process of the anterior ceratohyal (if present) (new) - ordered: (0) none; (1) one; (2) two.

Description. Most clupeiforms have a distinct posteroventral process of the anterior ceratohyal supporting a single branchiostegal ray, whereas some dorosomatids (*Anodontostoma*, *Clupanodon*, *Nematalosa* and *Rhinosardinia*) have two rays on this process. Conversely, *Denticeps*, *Dussumieria*, *Etrumeus*, *Jenkinsia*, *Spratelloides*, and all the engraulids have no distinct posterior process (and rays) on the anterior ceratohyal.

156. Number of branchiostegal rays on the posterior ceratohyal (new) - ordered: (0) one; (1) two; (2) three; (3) four or more.

Description. Most clupeiforms have two branchiostegal rays articulated to the posterior ceratohyal, resembling the condition of the outgroups *Albula* and *Chanos*. Conversely, *Hyperlophus* and some dorosomatids (*Anodontostoma*, *Clupanodon*, *Nematalosa*, *Rhinosardinia*) have a single ray on the posterior ceratohyal. Three rays are typical of *Jenkinsia*, *Spratelloides*, *Chirocentrus* and some engraulids (*Stolephorus* and *Setipinna*) and *Potamalosa*, plus †*Armigatus brevissimus*, *Alepocephalus*, and *Osmerus*, whereas four or more rays are articulated to the posterior ceratohyal of *Denticeps*, *Dussumieria* and *Etrumeus*.

157. Teeth or tooth plates on ceratobranchial 1 (S116): (0) absent; (1) present.

Description. *Albula* and most clupeiforms have teeth on the first ceratobranchial forming sometimes (as in *Chirocentrus* and some engraulids) autogenous, narrow, equally sized and rectangular tooth plates (Figs 17B-E; 18C) (Sato 1994; Di Dario 2004b, 2009). Conversely, *Denticeps*, *Clupea*, some dorosomatids (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Konosirus*, *Nematalosa*, *Opisthonema* and *Tenualosa*), and some ehiravids (*Clupeonella*, *Clupeoides*, *Gilchristella*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*) do not possess teeth or tooth plates on the first ceratobranchial (Figs 17A; 18A, B, D), similar to the condition of most outgroups (Gosline 1969; Johnson & Patterson 1996). In *Hyperlophus* both conditions have been reported (0/1). The presence of teeth or autogenous tooth plates on ceratobranchials 1 of most fossil clupeiforms is difficult to detect (?), but these were supposed to be absent in †*Cynoclupea* (Malabarba & Di Dario 2017). In †ellimmichthyiforms teeth or tooth plates on the first ceratobranchials seem to be absent, as observed and/or figured at least for †*Paraclupea seilacheri* and †*Ranulfoichthys* (Alvarado-Ortega 2014; Alvarado-Ortega & Melgarejo-Damián 2017).

158. Development of teeth or tooth plates on ceratobranchial 1 (S116): (0) well developed; (1) small.

Description. Well-developed teeth overlying the first ceratobranchial are typically present in *Chirocentrus*, *Dussumieria*, most engraulids and the pristigasteroids *Ilisha*, *Opisthopterus*, *Pellona*, showing a condition similar to that of *Albula*, among outgroups. Conversely, the first ceratobranchial possesses small teeth in *Etrumeus*, *Jenkinsia*, *Spratelloides*, *Potamalosa*, *Hyperlophus*, *Sprattus*, the engraulids *Encrasicholina* and *Engraulis*, the ehiravid *Clupeichthys*, alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*) and some dorosomatids (*Amblygaster*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Lile*, *Platanichthys*, *Rhinosardinia*, *Sardinella*).

159. Teeth or tooth plates on ceratobranchials 2 and 3 (S117-118): (0) absent; (1) present.

Description. The presence of teeth on second and third ceratobranchials in outgroups and clupeiforms is similar to that concerning the first ceratobranchial (Figs 17; 18), with the only difference that *Escualosa* and *Sardinella* (bearing small teeth on the first element) do not possess teeth on the second and third ceratobranchials (Sato 1994; Di Dario 2004b, 2009).

160. Development of teeth or tooth plates on ceratobranchials 2 and 3 (S117-118): (0) well developed; (1) small.

Description. The development of teeth on the second and third ceratobranchials in outgroups and clupeiforms resembles that of the teeth of the first ceratobranchial (Sato 1994; Di Dario 2004b, 2009).

161. Cartilage process of the anterior margin of the fourth ceratobranchial directed medially, forming a bridge over the ventral surface of the fourth basibranchial (DD249): (0) absent; (1) present.

Description. In *Denticeps*, *Chirocentrus*, Dussumieriidae, Spratelloididae, pristigasterids, some engraulids (*Anchoviella*, *Cetengraulis*, *Pterengraulis*, *Setipinna*), and a few other clupeoids (*Clupea*, *Clupeichthys*, *Potamothrissa*, *Rhinosardinia*) the anterior margin of the fourth ceratobranchial does not possess any cartilage process (Di Dario 2004b). However, in all the other clupeoids the anterior margin of the fourth ceratobranchial has a relatively developed process directed medially from the anterior region of the ventral surface of this cartilage. Among outgroups, this cartilage process is found only in *Albula* (Di Dario 2004b). The occurrence of this cartilage cannot be determined in fossil taxa.

162. First epibranchial fused to a tooth plate (MC13): (0) absent; (1) present.

Description. Nelson (1970) provided osteological evidence indicating that the New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*) plus the cosmopolitan *Engraulis* and the Indo-Pacific *Encrasicholina* form a well-defined monophyletic group because, among the other features, they are characterized by a tooth plate on the first epibranchial that is fused with this bone (Fig. 19D), a trait that is absent in Coiliinae, *Stolephorus* and other clupeoids. This character is very difficult to detect in fossil taxa.

163. Foramen for the efferent artery in the fourth epibranchial (S95): (0) absent; (1) present.

Description. Among clupeoid fishes, the morphology of the fourth epibranchial is remarkably heterogenous. According to Nelson (1967a, b, 1970) the fourth epibranchial is pierced by the foramen for the efferent artery in *Etrumeus*, *Jenkinsia*, *Spratelloides*, *Clupea*, *Sprattus* and *Potamalosa* (Fig. 19C, F). It is difficult to detect this character in fossil clupeomorphs but it can be considered absent in †*Ranulfoichthys* (Alvarado-Ortega 2014).

164. Surface of the fourth epibranchial (DD315): (0) not perforated; (1) widely perforated.

Description. In most clupeiforms, the fourth epibranchial is not perforated, except occasionally for the foramen for the efferent artery in a few taxa. However, in *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Hilsa*, *Opisthonema* and *Sardinella*, the bony surface of the fourth epibranchial has a series of subcircular perforations (Fig. 19I) (Nelson 1967a; Di Dario 2004b).

165. Anterior facet of the fourth epibranchial (S96): projected anteriorly; (1) not projected anteriorly.

Description. The anterior facet of the fourth epibranchial functions as the articulation point for the fourth infrapharyngobranchial. In *Denticeps* and most clupeoids, this facet extends prominently forward, accompanied by an embayment along the anterior margin of the bone. Conversely, in some dorosomatids (*Anodontostoma*, *Dorosoma*, *Hilsa*, *Konosirus*, *Nematalosa*, *Tenualosa*), the anterior facet is recessed, and the bone exhibits a remarkable enlargement (Fig. 19I) (Nelson 1967a; Sato 1994). This state cannot be checked in fossil taxa and has not been reported in outgroups.

166. Posterior concavity of the fourth epibranchial (S97): (0) present; (1) absent.

Description. In *Chanos* and most clupeoids, the posterior margin of the fourth epibranchial is concave, forming a foramen for the fifth efferent artery of the branchial arches between this bone and its posterior cartilage (Fig. 19A, D, E, G-I). However, in *Alepocephalus* and some clupeoids, such as *Chirocentrus*, *Clupea*, *Clupeonella*, *Etrumeus* and *Sprattus*, this concavity is absent and the foramen for the fifth efferent artery is located within the posterior cartilage attached to the bone (Fig. 19B, C, F) (Nelson 1967a, b; Sato 1994). This state is impossible to check in fossil taxa and unknown in other outgroups.

167. Posterior cartilage of the fourth epibranchial (S98): (0) formed by three discrete elements: upper, middle, and lower; (1) formed by two portions: upper+middle fused in a single element, and lower autogenous element; (2) formed by two portions: upper, and middle+lower elements; (3) all three cartilaginous elements fused into one; no any prominent outgrowths present; (4) all three cartilaginous elements fused into one; posterior process well developed, but neither anterior process nor medial expansion developed; (5) all three cartilaginous elements fused into one; anterior and posterior processes well developed, but medial expansion not developed; (6) all three cartilaginous elements fused into one; medial expansion well developed, but anterior and posterior processes indefinite; (7) all three cartilaginous elements fused into one; anterior process and medial expansion well developed, but posterior process indefinite.

Description. The posterior cartilage of the fourth epibranchial comprises three main elements: upper, middle, and lower. The upper element connects to the dorsal process of the bone, while the lower element attaches to the posterior process. The middle element, identified by Nelson (1967a, b) as the fifth epibranchial cartilage, lies between the other two elements. In *Chirocentrodon* and most examined engraulids, except *Coilia*, these three cartilaginous elements are separate or distinctly segmented. In some clupeoids, partial fusion may occur in *Sprattus*, the upper and middle elements are fused, leaving the lower element separate. In *Odontognathus*, the middle and lower elements are fused, while the upper remains distinct. The most common condition in clupeoids (observed in *Chirocentrus*, *Clupea*, *Coilia*, *Escualosa*, *Etrumeus*, *Hyperlophus*, *Ilisha*, *Limnothrissa*, *Lycengraulis*, *Pellona*, *Potamalosa*, *Spratelloides*, *Stolothrissa*) is the fusion of all the three elements into a single cartilaginous block without prominent outgrowths, aside from small, knob-like projections. *Alosa*, *Sardina*, and *Sardinops* show a complete fusion of all these three elements with a well-developed posterior process. *Amblygaster*, *Harengula*, *Herklotsichthys*, *Opisthonema*, and *Sardinella* also show complete fusion of all the three elements but features both posterior and anterior cartilaginous outgrowths. *Anodontostoma*, *Konosirus*, and *Nematalosa* show complete fusion of all the three elements with medial expansion well developed, but anterior and posterior processes indefinite. The state of *Tenualosa* is similar to state 6 but with a unique long, coiled anterior process. This state is impossible to check in fossil taxa nor has been reported in outgroups.

168. Posterior process of the fifth epibranchial (DD312): (0) absent or inconspicuous; (1) short; (2) well developed.

Description. In some engraulids (*Anchoa*, *Anchoviella*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Stolephorus*), dussumieriids, spratelloidids, *Sardina*, *Sprattus*, some ehiravids (*Clupeoides*, *Clupeonella*, *Gilchristella*, *Nannothrissa*), and dorosomatids (*Escualosa*, *Platanichthys*, *Rhinosardinia*) the fifth epibranchial bears a short and roughly triangular cartilaginous process in its posterior region (Nelson 1967a; Di Dario 2004b). In some alosids (*Alosa*, *Brevoortia*, *Sardinops*) and dorosomatids (*Amblygaster*, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Nematalosa*, *Opisthonema*, *Sardinella*, *Tenualosa*) the projection is significantly more developed and extends posteroventrally, sometimes articulating with the fifth ceratobranchial (Fig. 19H, I), resembling the condition of *Chanos* (Nelson 1967a; Di Dario 2004b). Conversely, in *Chirocentrus*, *Clupea*, *Clupeichthys*, *Coilia*, *Denticeps*, *Ilisha*, *Lile*, *Lycothrissa*, *Microthrissa*, *Opisthopterus*, *Pellona*, *Pellonula*, *Potamalosa*, *Potamothrissa*, *Setipinna*, *Stolothrissa* and *Thryssa*, there is no posteriorly directed projection at the dorsal end of the fifth epibranchial, resembling the condition of most outgroups. This feature is impossible to check in fossil taxa due to the cartilaginous nature of the fifth epibranchial.

169. Tooth patch on the dorsal surface of the dorsal hypohyal (S75): (0) absent; (1) present.

Description. Teeth in form of a fused tooth patch on the dorsal hypohyal are unique of the pristigasteroids *Chirocentrodon* and *Odontognathus* (Sato 1994). Di Dario (1999) found this tooth patch also in *Neoopisthopterus*. No outgroups or other clupeiforms have teeth on dorsal hypohyal, nor those †ellimmichthyiforms in which the dorsal hypohyal is preserved (e.g., †*Armigatus*, †*Diplomystus*, †*Ornategulum*, †*Ranulfoichthys*, †*Paraclupea*, †*Scutatuspinosus*, etc.; e.g., Forey 1973a; Alvarado-Ortega 2014; Marramà & Carnevale 2023).

170. Basihyal (S100): (0) absent or inconspicuous; (1) large.

Description. Most outgroups and clupeiforms have a large and well-developed basihyal which is sometimes toothed (Figs 17A-C, E; 18). Conversely, the basihyal of the Engraulidae is inconspicuous (Fig. 17D), often absent like in *Coilia*, *Setipinna*, and in the stem-engraulids †*Clupeopsis* and †*Monosmilus* (Sato 1994; Mertzen 2019; Capobianco *et al.* 2020). It is difficult to detect the basihyal in fossil clupeomorphs although its presence been reported in †*Gosiutichthys*, †*Nardoclupea*, †*Armigatus carrenoae*, †*A. namourensis* and †*Diplomystus* (e.g., Forey *et al.* 2003b; Alvarado-Ortega *et al.* 2020).

171. Basihyal teeth (S101): (0) absent; (1) present.

Description. The basihyal of clupeomorphs is usually well ossified and bears a patch of teeth forming well-developed tooth plates in *Chirocentrus*, *Dussumieria* and *Etrumeus*, the engraulids *Anchoviella*, *Engraulis*, *Lycengraulis* and *Stolephorus*, all pristigasteroids, *Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*, some ehiravids (*Clupeichthys*, *Clupeoides*, *Gilchristella*, *Limnothrissa*, *Odaxothrissa*, *Pellonula*), some alosids (*Alosa*, *Sardina*) and dorosomatids (*Amblygaster*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Lile*, *Platanichthys* and *Sardinella*) (Figs 17B-E; 18A-C) (Nelson 1970; Whitehead 1968; Sato 1994). Among outgroups, basihyal teeth are present in *Osmerus*, but absent in *Albula*, *Alepocephalus* and the Gonorynchiformes (Forey 1973b; Fink & Fink 1981; Begle 1992; Johnson & Patterson 1996). It is difficult to detect the presence of basihyal teeth in fossil clupeomorphs although the presence of a toothed basihyal has been reported in †*Gosiutichthys*, †*Armigatus* and †*Diplomystus* (Grande 1982b; Forey *et al.* 2003).

172. Number of basihyal cartilages (S102): (0) one (1) two or more.

Descriptions. In the outgroups and most clupeoids, the basihyal is single, undivided. However, in *Potamalosa*, alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*; Fig. 18C) and numerous dorosomatids (*Amblygaster*, *Anodontostoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Lile*, *Opisthonema*, *Platanichthys*, *Rhinosardinia*, *Sardinella*, *Tenualosa*), the basihyal is formed by two cartilages, whereas *Denticeps* can have two or even three or four basihyal cartilages (Fig. 17A) (Sato 1994; De Pinna & Di Dario 2010).

173. Teeth or tooth plate on basibranchial 1 (S104): (0) absent; (1) present.

Description. Most clupeomorphs usually possess teeth over one, two, three or all four basibranchials with their increasing presence that is thought to be directly related, together with those on the basihyal, to a more predatory feeding strategy (Nelson 1967a, b; Forey *et al.* 2003). Data for extant clupeoids follow Nelson (1970), completed with data from Sato (1994) and Di Dario (2004b). Teeth or tooth plates over the first basibranchial are present in dussumieriids and all engraulids (Fig. 18C, D), whereas the other clupeoids and *Denticeps* have no teeth or tooth plates on the first basibranchial (De Pinna & Di Dario 2010). Among fossils, †*Clupeopsis* and †*Monosmilus* have teeth on the first three basibranchials (Capobianco *et al.* 2020). This might be also the condition for the order †Ellimmichthyiformes, as observed in †*Armigatus brevissimus*, †*A. namourensis*, †*Diplomystus dentatus*,

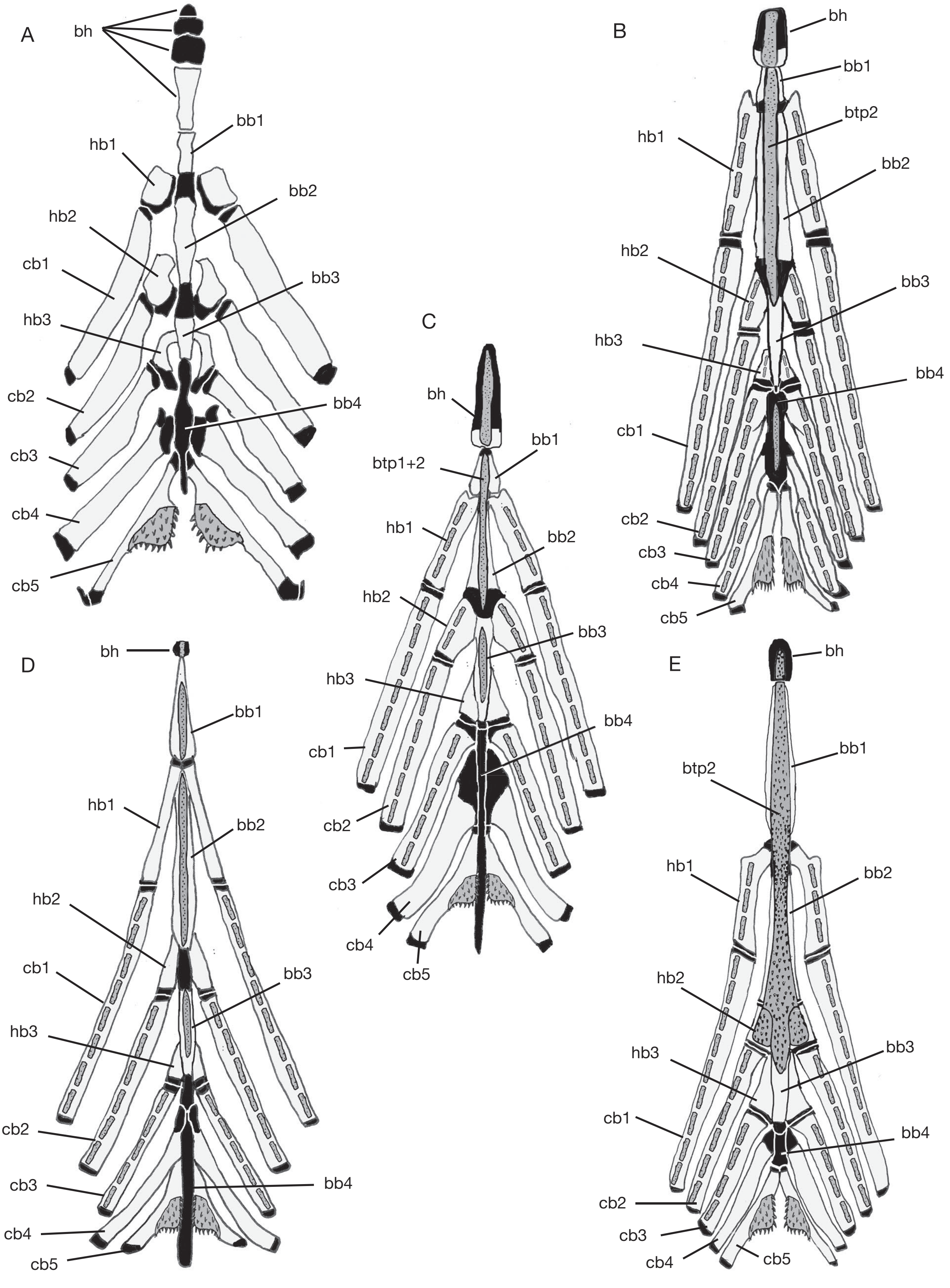

FIG. 17. — Interpretative reconstructions of the lower gill arches of selected clupeiforms in dorsal view based on Grande (1985), Nelson (1967a, b, 1970), Di Dario (2009) and De Pinna & Di Dario (2010): **A**, *Denticeps clupeoides* Clausen, 1959 (Denticipitidae); **B**, *Chirocentrus dorab* (Forsskål, 1775) (Chirocentridae); **C**, *Etrumeus sadina* (Mitchill, 1814) (Dussumieriidae); **D**, *Engraulis mordax* Girard, 1854 (Engraulidae); **E**, *Chirocentrodon bleekerianus* (Poey, 1867) (Pristigasteridae). Gill rakers omitted. Images not to scale. Tooth patches and tooth plates in **grey**; cartilage in **solid black**. Abbreviations: **bb**, basibranchial; **bh**, basihyal; **btp**, basibranchial tooth plate; **cb**, ceratobranchial; **hb**, hypobranchial. Numbers refer to characters and character states (see text).

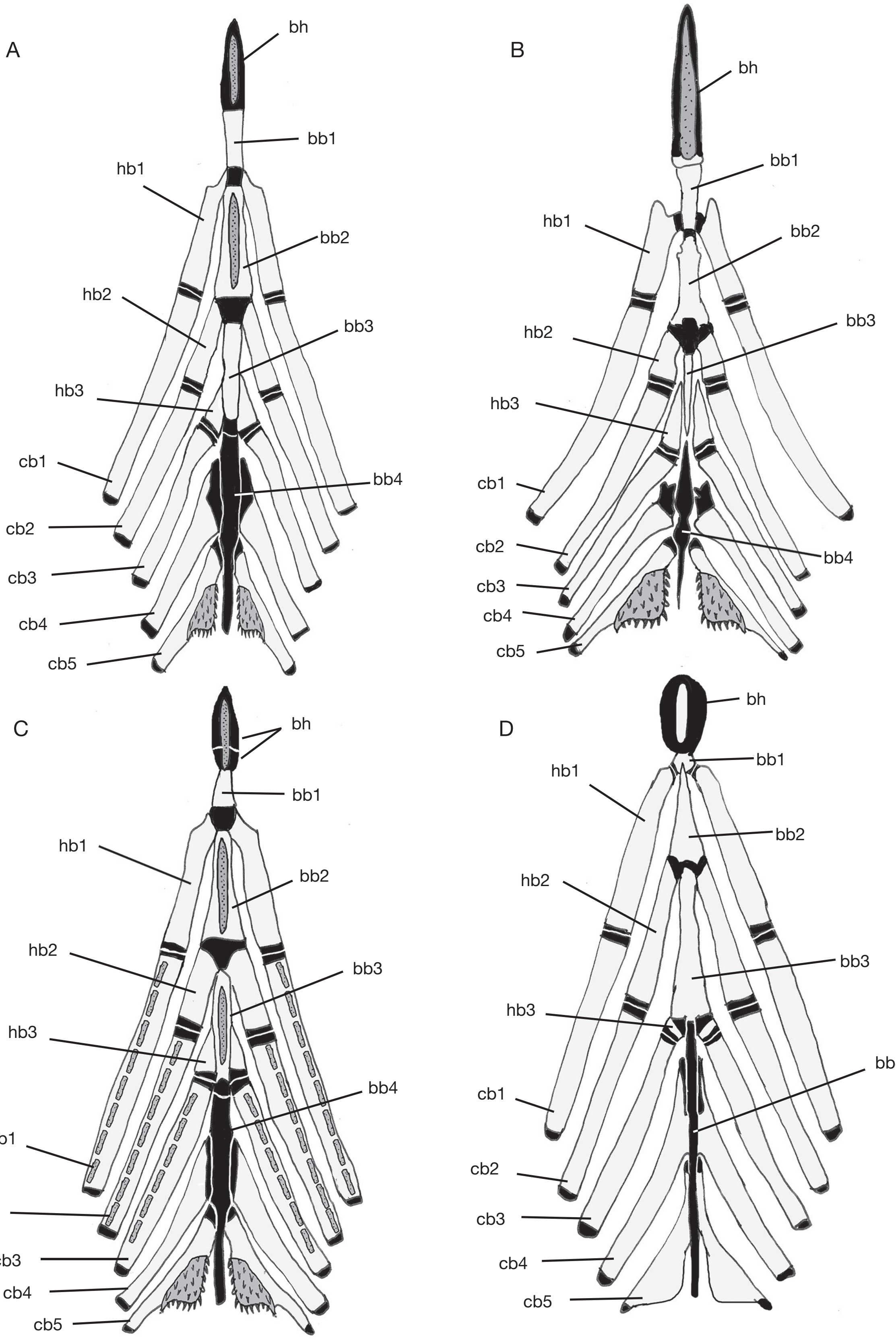

Fig. 18. — Interpretative reconstructions of the lower gill arches of selected clupeiforms in dorsal view based on Grande (1985), Nelson (1967a, b, 1970) and Di Dario (2009). **A**, *Clupea harengus* (Clupeidae); **B**, *Odaxothrissa vittata* (Ehiravidae); **C**, *Alosa chrysochloris* (Alosidae); **D**, *Dorosoma cepedianum* (Dorosomatidae). Gill rakers omitted. Images not to scale. Tooth patches and tooth plates in **grey**; cartilage in **solid black**. Abbreviations: **bb**, basibranchial; **bh**, basihyal; **btp**, basibranchial tooth plate; **cb**, ceratobranchial; **hb**, hypobranchial. Numbers refer to characters and character states (see text).

†*D. shengliensis* and †*Rhombichthys*, where robust basibranchial tooth plates overlie at least three basibranchials (Chang & Maisey 2003; Forey *et al.* 2003; Forey 2004; Khalloufi *et al.* 2010). Among outgroups, *Alepocephalus*, *Chanos* and *Kneria* have no teeth or tooth plates on the basibranchials, whereas *Albula* and *Osmerus* have teeth on all four basibranchials (Rembiszewski 1964; Nelson 1967a; Forey 1973b; Markle 1976).

174. Teeth or tooth plate on basibranchial 2 (S108): (0) absent; (1) present.

Description. Among Clupeiformes, teeth on the second basibranchial are present in *Chirocentrus*, dussumieriids, all engraulids and pristigasterids, *Alosa*, *Clupeoides*, some dorosomatids (*Escualosa*, *Harengula*, *Herklotsichthys*, *Lile*, *Opisthonema*, *Rhinosardinia*, *Sardinella*), *Clupea*, *Hyperlophus*, and *Potamalosa* (Figs 17B-E; 18A, C).

175. Teeth or tooth plate on basibranchial 3 (S110): (0) absent; (1) present.

Description. Teeth or tooth plate on the third basibranchial are present in dussumieriids, *Alosa*, and some engraulids (*Coilia*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Pterengraulis*, *Setipinna*, *Stolephorus*, *Thryssa*) (Figs 17C, D; 18C).

176. Teeth or tooth plate on basibranchial 4 (S112): (0) absent; (1) present.

Description. Teeth on the fourth basibranchial are only present in *Chirocentrus*, *Pellona*, and few engraulids (*Lycothrissa*, *Pterengraulis*, *Setipinna*, *Thryssa*) (Fig. 17B) (Nelson 1970; Sato 1994).

177. Posterior process of the second basibranchial (S107): (0) not reaching the third basibranchial; (1) reaching the third basibranchial.

Description. In most clupeoids, the dermal process of the second basibranchial extends backward and connects with the third basibranchial. However, in engraulids (except *Engraulis* and *Setipinna*), as well as in *Denticeps* and *Alosa*, *Dussumieria*, *Lile*, *Limnothrissa*, *Sardinops*, *Spratelloides* and *Tenualosa*, this process does not extend far enough to contact the third basibranchial (Sato 1994). This cannot be checked in fossil taxa nor has been reported in outgroups.

178. Ventral processes on the second basibranchial (S109): (0) not developed; (1) well developed.

Description. In *Denticeps* and most clupeoids, the second basibranchial has a semicircular cross-section, creating a distinctly separated double ventral margin. However, in some clupeoids, such as *Cetengraulis*, *Chirocentrodon*, *Ilisha*, *Odontognathus*, and *Pellona*, the ventral margins are extended and either come close to or touch each other (Sato 1994). This state is impossible to check in fossil taxa nor has been reported in outgroups.

179. Teeth on the first hypobranchial (S113): (0) absent; (1) present.

Description. In Clupeiformes, the first hypobranchial is usually edentulous. However, minute teeth on the first hypobranchial are present in the engraulids (except *Cetengraulis* and *Engraulis*; Fig. 17D), *Chirocentrodon*, *Chirocentrus*, *Dussumieria*, *Etrumeus*, *Ilisha*, *Odontognathus*, *Opisthopterus* and *Pellona* (Fig. 17B, C, E) (Sato 1994; Di Dario 2004b). Teeth on the first hypobranchial are absent in outgroups, except in *Albula* (Di Dario 2004b; Mertzen 2019).

180. Teeth on the second hypobranchial (S114): (0) absent; (1) present.

Description. In Clupeiformes, the second hypobranchial is usually edentulous. However, in some engraulids (*Anchoa*, *Anchoviella*, *Coilia*, *Encrasicholina*, *Lycengraulis*, *Lycothrissa*, *Setipinna*, *Thryssa*), *Chirocentrus*, *Dussumieria*, *Etrumeus*, and pristigasterids (*Chirocentrodon*, *Ilisha*, *Odontognathus*, *Opisthopterus* and *Pellona*), the second hypobranchial bears minute teeth (Fig. 17B, C, E) (Sato 1994; Di Dario 2004b). Teeth on second hypobranchial are absent in outgroups, except in *Albula* (Di Dario 2004b; Mertzen 2019).

181. Teeth on the third hypobranchial (S115): (0) absent; (1) present.

Description. In Clupeiformes, the third hypobranchial is usually edentulous. However, in *Chirocentrus* (Fig. 17B) and some engraulids (*Coilia*, *Lycengraulis*, *Lycothrissa*, *Setipinna*, *Thryssa*), the third hypobranchial bears minute teeth (Sato 1994; Di Dario 2004b). Teeth on the third hypobranchial are absent in outgroups, except in *Albula* (Di Dario 2004b; Mertzen 2019).

182. Basibranchial tooth plates 1-3 fused with the second basibranchial (new): (0) absent; (1) present.

Description. The members of the Pristigasteroidea are unique in having a prominent basibranchial dentition, including a single basibranchial tooth plate (formed by the fusion of basibranchial plates 1 to 3) fused with the second basibranchial, other than with one or more pairs of hypobranchials (Fig. 17E) (Nelson 1967b; McAllister 1970).

183. Shape of the fifth ceratobranchial (S120): (0) narrow; (1) wide.

Description. In Clupeiformes, the fifth ceratobranchial is usually narrow, its length being more than three times that of the width. In *Anodontostoma*, *Konosirus*, and *Nematalosa*, however, this bone is more expanded and spoon-like, its length being less than two times that of the width (Sato 1994). The fifth ceratobranchial is wide also in *Chanos* (Fink & Fink 1981).

184. Tooth plates overlying the fifth ceratobranchial (S121): (0) absent; (1) present.

Description. In most clupeomorphs the fifth ceratobranchials possess developed tooth plates or patches that are fused to the bones (Figs 17; 18A-C). However, teeth overlying the fifth ceratobranchial are absent in *Cetengraulis*, *Brevoortia*, and the dorosomatids *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Konosirus*, *Nematalosa*, and *Tenualosa* (Fig. 18D) (Nelson 1970; Sato 1994; De Pinna & Di Dario 2010). In fossil clupeiforms, tooth plates over the fifth ceratobranchials were detected in †*Nardoclupea* and †*Ranulfoichthys*. Among outgroups they are present in *Albula*, *Alepocephalus* and *Osmerus*, but absent in gonorynchiforms (e.g., Grande & Poyato-Ariza 2010).

185. Distance between the contralateral paired infrapharyngobranchials (new): (0) widely separated each other; (1) close to each other.

Description. Nelson (1967b, 1970) first observed that the dorsal gill arches elements, particularly the infrapharyngobranchials, of most of clupeoids are characterized by a close proximity of the contralateral elements across the midline, almost contacting each other anteriorly (Fig. 19C, D, F, H, I). Conversely, *Denticeps*, *Chirocentrus*, the basalmost engraulids (*Coilia*, *Lycothrissa*, *Setipinna*, *Thryssa*, *Stolephorus* and *Encrasicholina*), the pristigasterid *Chirocentrodon* and the ehiravid *Odaxothrissa* differ in having the paired dorsal gill arch elements well separated at the midline (Fig. 19A, B, E, G), similar to the condition of the lower teleosts (Nelson 1967b, 1970; De Pinna & Di Dario 2010).

186. Teeth or tooth plate over the infrapharyngobranchial 1 (new): (0) absent; (1) present.

Description. Like for data on basibranchial, information on the presence of teeth or tooth plates overlying infrapharyngobranchials follows Nelson (1970), and with data from Sato (1994) and Cione *et al.* (1998). Teeth or tooth plates overlying the first infrapharyngobranchial are present only in *Alepocephalus* and most engraulids (*Anchoa*, *Anchoviella*, *Coilia*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Pterengraulis*, *Thryssa*; Fig. 19D). The presence of upper pharyngeal tooth plates is almost impossible to detect in fossil material.

187. Teeth or tooth plate over the infrapharyngobranchial 2 (S85): (0) absent; (1) present.

Description. Teeth or tooth plates overlying the second infrapharyngobranchial are present in *Albula*, *Alepocephalus*, dussumieriids, *Jenkinsia*, most engraulids (*Anchoa*, *Anchoviella*, *Cetengraulis*, *Coilia*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Pterengraulis*, *Setipinna*, *Stolephorus*, *Thryssa*) and pristigasterids (*Ilisha*, *Odontognathus*, *Opisthopterus*, *Pellona*, *Pliosteostoma*, *Pristigaster*, *Raconda*), *Clupea* and few ehiravids (*Clupeichthys*, *Corica*) (Fig. 19C, D, F).

188. Teeth or tooth plate over the infrapharyngobranchial 3 (S86): (0) absent; (1) present.

Description. Teeth or tooth plates overlying the third infrapharyngobranchial are present in *Albula*, *Alepocephalus*, *Osmerus*, dussumieriids, *Jenkinsia*, most engraulids (*Anchoa*, *Anchoviella*, *Cetengraulis*, *Coilia*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Pterengraulis*, *Setipinna*, *Stolephorus*, *Thryssa*) and pristigasterids (*Ilisha*, *Odontognathus*, *Opisthopterus*, *Pellona*, *Pliosteostoma*, *Pristigaster*, *Raconda*), *Clupea*, *Potamalosa*, few ehiravids (*Clupeonella*, *Clupeichthys*, *Corica*) and dorosomatids (*Amblygaster*, *Herklotsichthys*) (Fig. 19C, D, F).

189. Teeth or tooth plate over the infrapharyngobranchial 4 (S89): (0) absent; (1) present.

Description. Teeth or tooth plates overlying the fourth infrapharyngobranchial are present in *Albula*, dussumieriids, spratelloidids, *Chirocentrus*, most engraulids (*Anchoa*, *Anchovia*, *Anchoviella*, *Coilia*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Pterengraulis*, *Setipinna*, *Stolephorus*, *Thryssa*) and pristigasterids (*Ilisha*, *Pellona*, *Raconda*), *Alosa*, *Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*, few ehiravids (*Clupeonella*, *Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*) and dorosomatids (*Amblygaster*, *Herklotsichthys*, *Lile*, *Platanichthys*) (Fig. 19B-F, H). *Denticeps* has a single tooth plate supported, at least in part, by the fourth infrapharyngobranchial (Fig. 19A) (De Pinna & Di Dario 2010).

190. Teeth or tooth plate over the infrapharyngobranchial 5 (S90): (0) absent; (1) present.

Description. Teeth or tooth plates overlying the fifth infrapharyngobranchial are present in dussumieriids, spratelloidids, *Chirocentrus*, most engraulids (*Anchoa*, *Anchovia*, *Anchoviella*, *Coilia*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Lycothrissa*, *Pterengraulis*, *Setipinna*, *Stolephorus*, *Thryssa*) and pristigasterids (*Chirocentrodon*, *Ilisha*, *Odontognathus*, *Opisthopterus*, *Pellona*, *Pliosteostoma*, *Pristigaster*, *Raconda*), *Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*, some alosids (*Alosa*, *Sardina*, *Sardinops*), few ehiravids (*Clupeonella*, *Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*,) and dorosomatids (*Escualosa*, *Harengula*, *Herklotsichthys*, *Lile*, *Opisthonema*, *Rhinosardinia*, *Sardinella*) (Fig. 19B-H).

191. Posteriorly facing process on the infrapharyngobranchial 1 (D34): (0) absent; (1) present.

Description. The ventral margin of the first infrapharyngobranchial of *Alosa* and *Brevoortia*, and some pristigasteroids (*Ilisha*, *Pellona*, and *Pliosteostoma*) has a posteriorly facing process that, when highly developed, partially overlaps the infrapharyngobranchial 2 (Di Dario 1999). In all the other clupeiforms, †ellimmichthyiforms (e.g., †*Ranulfoichthys*) and outgroups this process is absent and the first infrapharyngobranchial generally has an approximate "spatula" shape (Di Dario 1999).

192. First mediopharyngobranchial cartilage (S84): (0) absent; (1) present.

Description. The mediopharyngobranchial cartilages are cartilaginous elements located in the anterior tip of the first three pairs of epibranchials and, among vertebrates, are uniquely present in some clupeoids and they serve as support for some gill rakers (Nelson 1967b, 1970). The first mediopharyngobranchial cartilages articulate with the first epibranchials and are usually medially united to form a V structure with the apex directed anteriorly that is only present in alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*) and most dorosomatids (*Amblygaster*, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Konosirus*, *Lile*, *Nematalosa*, *Opisthonema*, *Platanichthys*, *Rhinosardinia*, *Sardinella*, *Tenualosa*) (Fig. 19 H, I) (Nelson 1967b, 1970; Sato 1994). Rudimentary first mediopharyngobranchial cartilages are also present in a few engraulids (*Anchoviella*, *Coilia*, *Lycothrissa*, *Thryssa*) and ehiravids (*Clupeonella*, *Gilchristella*, *Pellonula*, *Stolothrissa*) (Nelson 1967b; Di Dario 2004b). Possible homologous elements to the first mediopharyngobranchial cartilages of clupeoids have been reported also in *Chanos* and *Kneria* (Johnson & Patterson 1996; Springer & Johnson 2004). The presence of mediopharyngobranchial cartilages is impossible to observe in fossils.

193. Second mediopharyngobranchial cartilage (DD279): (0) absent; (1) present.

Description. The mediopharyngobranchial cartilages on the anterior tip of the second pairs of epibranchials are only present in some dorosomatids (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Hilsa*, *Nematalosa*, *Opisthonema*, *Rhinosardinia*, *Sardinella*, *Tenualosa*; Fig. 19I) (Di Dario 2004b).

194. Third mediopharyngobranchial cartilage (DD280): (0) absent; (1) present.

Description. Description. The mediopharyngobranchial cartilages on the anterior tip of the third pairs of epibranchials are only present in some dorosomatids (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Nematalosa*, *Rhinosardinia*, *Tenualosa*; Fig. 19I) (Di Dario 2004b).

195. Epibranchial organs (new): (0) absent; (1) present.

Description. Epibranchial organs, which consist of paired pharyngeal pouches, are found in certain teleost groups, including osteoglossiforms, cypriniforms, gonorynchiforms, and clupeiforms. These organs appear to have evolved independently in each of these lineages and are part of a set of digestive system adaptations linked to microphagy (Nelson 1967a, 1970). According to Nelson (1970) this is one of the characters that define the Clupeoidae (= Clupeidae *sensu* Grande 1985). Among clupeiforms, these are uniquely present in some engraulids (*Anchovia*, *Engraulis*, *Cetengraulis*), *Hyperlophus*, some ehiravids (*Gilchristella*, *Stolothrissa*), alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*) and numerous dorosomatids (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Konosirus*, *Nematalosa*, *Opisthonema*, *Rhinosardinia*, *Sardinella*). They are also present in *Chanos* and *Kneria* but not in other outgroups (Nelson 1967a, 1970; Greenwood & Rosen 1971). The condition in fossil taxa is unknown.

196. Size of epibranchial organs (new): (0) small; (1) large.

Description. Epibranchial organs, if present, were subjectively classified by Nelson (1967a) as small or large, depending on the degree of differentiation of a definite pharyngeal diverticulum. They were classified as small in kneriids, in the engraulids *Anchovia* and *Engraulis*, in the ehiravids *Gilchristella* and *Stolothrissa*, in *Hyperlophus*, and also in *Alosa*, *Harengula* and *Herklotsichthys*; conversely, they are large, supported by enlarged fourth epibranchials, in *Chanos* and in zooplanktivorous clupeoids (*Anodontostoma*, *Brevoortia*, *Clupanodon*, *Dorosoma*, *Hilsa*, *Konosirus*, *Nematalosa*, *Opisthonema*, *Rhinosardinia*, *Sardina*, *Sardinella*, *Sardinops*), as well as and in the engraulid *Cetengraulis*.

197. Relation of fifth upper pharyngeal to fourth epibranchial (S91): (0) fifth upper pharyngeal free from fourth epibranchial; (1) fifth upper pharyngeal connected to the fourth epibranchial.

Description. In *Denticeps* and most clupeoids, the dermal plate of the fifth upper pharyngeal remains separate from the fourth epibranchial. However, in *Anodontostoma*, *Dorosoma*, *Hilsa*, *Konosirus*, *Nematalosa*, and *Tenualosa*, the dermal plate is closely connected to the ventromedial margin of the fourth

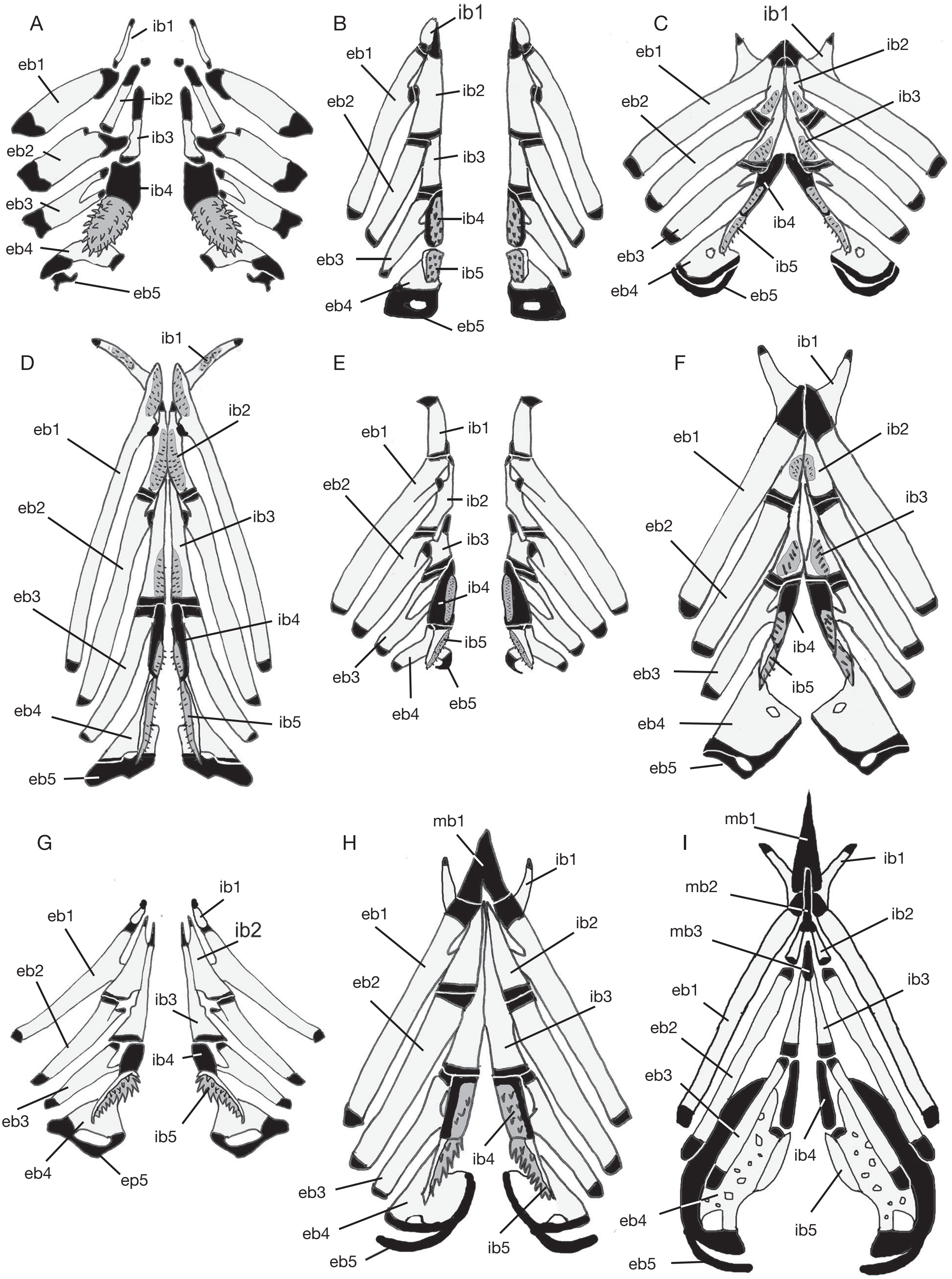

Fig. 19. – Interpretative reconstructions of the upper gill arches of selected clupeiforms in ventral view based on Grande (1985), Nelson (1967a, b, 1970), Di Dario (2009) and Di Dario & De Pinna (2010 . **A**, *Denticeps clupeoides* (Denticipitidae); **B**, *Chirocentrus dorab* (Chirocentridae); **C**, *Etrumeus teres* (Dussumieriidae); **D**, *Engraulis mordax* (Engraulidae); **E**, *Chirocentrodon bleekerianus* (Pristigasteridae); **F**, *Clupea harengus* (Clupeidae); **G**, *Odaxothrissa vittata* (Ehiravidae); **H**, *Alosa chrysochloris* (Alosidae); **I**, *Dorosoma cepedianum* (Dorosomatidae). Gill rakers omitted. Images not to scale. Tooth patches and tooth plates in **grey**; cartilage in **solid black**. Abbreviations: **eb**, epibranchial; **ib**, infrapharyngobranchial; **mb**, mediopharyngobranchial cartilage. Numbers refer to characters and character states (see text).

epibranchial (Fig. 19I) (Nelson 1967a; Sato 1994). This state is impossible to check in fossil taxa.

198. Maximum number of lower gill rakers (new): (0) up to 165; (1) over 165.

Description. The high number of gills rakers enhances cross-flow filtering and is generally highly related to planktivorous feeding behaviour. In clupeiforms, the number of lower gill rakers (those articulating with the ceratobranchials) are much easier to count than the upper gill rakers articulating to the epibranchial (Whitehead 1985). The maximum number of lower gill rakers is generally low (up to 165) in *Denticeps* and most clupeoids (Whitehead 1973, 1985; McGowan & Berry 1984; Whitehead *et al.* 1988). However, *Clupanodon*, *Dorosoma*, *Hilsa*, *Konosirus*, *Nematalosa*, *Sardinella* and *Tenualosa* have more than 165 gill rakers on the ceratobranchials (Whitehead 1973, 1985; McGowan & Berry 1984). All outgroups have less than 165 gill rakers. Because of the inadequate preservation of the gill raker region in fossil taxa, this character is unknown in †Ellimmichthyiformes and fossil clupeiforms.

199. Overlap of the upper and lower gill rakers (new): (0) absent; (1) present.

Description. Regan (1917) first noticed that in some clupeoids (*Alosa*, *Brevoortia*, *Ethmidium*) the upper gill rakers near the angle of the first epibranchial, folding downwards, overlap the lower gill rakers (on first ceratobranchial), whereas the upper gill rakers of *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Hilsa*, and *Nematalosa* do not overlap the lower ones. Overlap of the upper and lower gill rakers at the angle between epibranchial and ceratobranchial of the first arch also characterizes *Clupea*, *Clupeonella*, *Harengula*, *Sardina*, *Sardinops* and *Sprattus*, whereas *Herklotsichthys*, *Sardinella* and *Opisthonema*, are characterized by the non-overlap (Whitehead 1964, 1985; Nelson 1967a, 1970). The non-overlap of the gill rakers was considered a synapomorphy of the Dorosomatinae in the sense of Nelson (1970), although the non-overlap appears to be the plesiomorphic condition in clupeiforms, since most of the other clupeoids do not show gill raker overlap. Because of the inadequate preservation of the gill rakers region in fossil taxa, this character is unknown in †Ellimmichthyiformes and fossil clupeiforms.

OPERCULAR APPARATUS

200. Bony flange on the outer surface of the opercle close to the joint area with the hyomandibula (DD199): (0) absent; (1) present.

Description. In most clupeomorphs the external surface of the opercle near the area of articulation with the hyomandibula is smooth or has a sinuous and slightly pronounced callosity (Fig. 20B, D, F). Conversely, in *Chirocentrus*, *Dussumieria*, *Etrumeus*, *Jenkinsia*, *Spratelloides*, the Coiliinae, pristigasteroids, *Clupea*, *Hyperlophus*, *Nematalosa*, and *Sprattus*, the opercle shows in this area a noticeable bony fold or flange (Fig. 20A, C) (Whitehead 1973; Di Dario 1999, 2004b). This character has not been recognized in outgroups or in fossil clupeomorphs in which the opercle is preserved, except in *Knightia* (Grande 1982b).

201. Radial striations on the ventral part of the opercle (S61, FR58): (0) absent; (1) present.

Description. In Clupeiformes bony radiating striations on the ventral part of the opercle appear to be uniquely present in the Alosidae (*Alosa*, *Brevoortia*, *Sardina* and *Sardinops*; Fig. 20B) (see Sato 1994; Segura & de Astarloa 2004). The re-examination of the holotype of †*Eoalosa janvieri* allowed the recognition of faint striations on the ventral part of its opercle. Opercular striations have been also recovered in several †ellimmichthyiforms, including †*Armigatus brevissimus*, †*A. carrenoae*, †*A. felixi*, †*A. namourensis* (Fig. 20F), †*Codoichthys*, †*Ellimma branneri*, †*Ellimmichthys longicostatus*, †*Foreyclupea*, †*Paraclupea* (except †*P. chetungensis*), †*Ranulfoichthys*, †*Rhombichthys*, †*Scutatuspinosus*, †*Sorbinichthys*, †*Thorectichthys rhadinus*, †*Tunisiaclupea* and †*Tycheroichthys* (e.g., Chang & Grande 1997; Bannikov & Bacchia 2000; Forey *et al.* 2003a; Boukhalfa *et al.* 2018). All the other clupeomorphs and outgroups have smooth outer surface of the opercle.

202. Angle between the dorsal and ventral parts of the lateral line canal of the preopercle (K78): (0) <130°; (1) ≥130°.

Description. In †ellimmichthyiforms and most clupeiforms the angle between the dorsal and ventral branches of the preopercular lateral line canal is lower than 130°, making the distinction between dorsal and ventral arms very clear (Fig. 20A-C, E, F). However, due to the peculiar arrangement of the suspensorium and opercular apparatus, this angle is equal or higher than 130°, with almost no clear distinction between dorsal and ventral limbs in *Chirocentrus*, engraulids, including †*Eoengraulis* (unknown in †*Clupeopsis* and †*Monosmilus*) and †*Santanaclupea* (Fig. 20D). All outgroups have an angle lower than 130°.

203. Number of canals branching from the preopercular sensory canal (S60, FR57): (0) one to three; (1) more than three.

Description. In most clupeomorphs the preopercular sensory canal passes in a groove with bony flanges or in a tube in the dorsal shaft, and branches in the horizontal arm through extensive openings. Clupeiformes with branched preopercular canal have generally a few (one to three) canals branching off

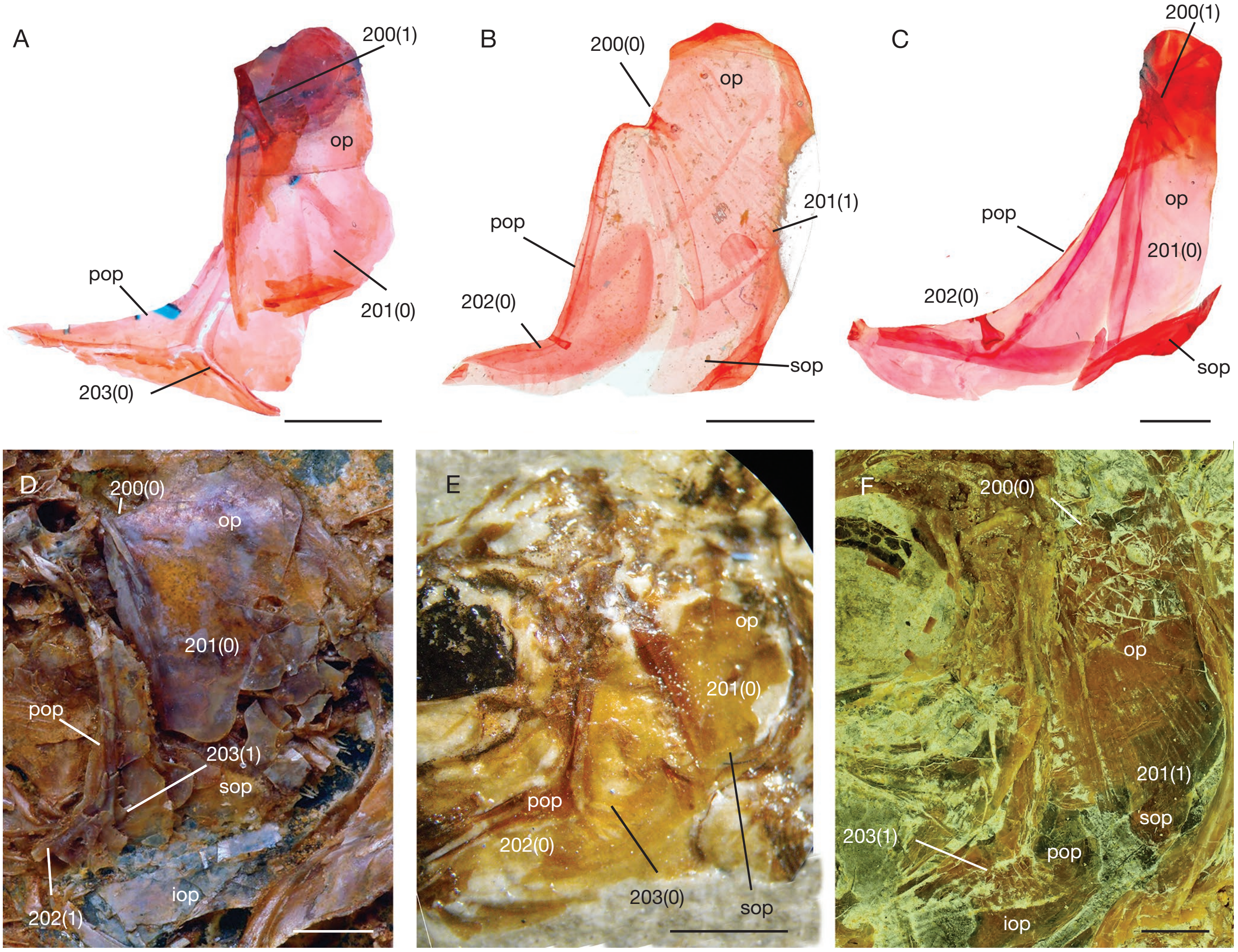

Fig. 20. — Opercular apparatus of selected clupeomorphs: **A**, *Dussumieria acuta* Valenciennes, 1847 (Dussumieriidae), AMNH 17555; **B**, *Brevoortia tyrannus* (Latrobe, 1802) (Clupeiformes: Alosidae), AMNH 27686; **C**, *Pristigaster cayana* Cuvier, 1829 (Clupeiformes: Pristigasteridae), AMNH 10186; **D**, †*Santanaclupea silvasantoi* Maisey, 1993 (Clupeiformes: †Cynoclupeidae), Lower Cretaceous, Brazil; AMNH DVP.18968 (photo: courtesy of Lorraine Meeker); **E**, †*Bolcaichthys catopygopterus* (Woodward, 1901) (Clupeiformes: pan-Dorosomatidae); MCSNV IG.37584; **F**, †*Armigatus namourensis* Forey, Yi, Patterson & Davies, 2003 (†Ellimmichthyiformes: †Armigatidae), NHMUK PV P.62529. Scale bars: 2 mm. Abbreviations: **iop**, interopercle; **op**, opercle; **pop**, preopercle; sop, subopercle. Numbers refer to characters and character states (see text).

from the main lateral line canal at the angle of the preopercle (e.g., *Chirocentrus*, *Denticeps*, *Dussumieria*, *Etrumeus*, †*Nardoclupea*, *Limnothrissa*, *Odaxothrissa Microthrissa*, *Pellonula*, *Potamothrissa*, *Potamalosa* and *Stolothrissa* and the fossils †*Bolcaichthys*, †*Eoalosa*, †*Italoclupea*, †*Palaeodenticeps*, †*Pseudoellimma* and †*Scombroclupea*; Fig. 20A, E) (see Bardack 1965; Grande 1985; Sato 1994). Among †ellimmichthyiforms, the presence of up to three branches is exclusive of †*Codoichthys*, †*Ranulfoichthys* and †*Ellimmichthys longicostatus* (Figueiredo & Ribeiro 2016; Figueiredo & Gallo 2021). Conversely, in the clupeiform †*Santanaclupea* and in all the other †ellimmichthyiforms there are more than three branches of the preopercular canal, mostly in the horizontal arm (Fig. 20D, F) (Forey 1973a; Grande 1982a, 1985; Maisey 1993). This latter condition is also typical of *Alepocephalus*, *Chanos* and *Kneria* (Gosline 1969; Fink & Fink 1996). Taxa with no branching (Spratelloididae, Engraulidae, Pristigasteroidea and most Clupeoidea; Fig. 20B, C) were coded as inapplicable (-).

204. Posterior arm of the preopercle (S60): (0) absent; (1) present.

Description. The preopercle of *Denticeps* is unique among clupeomorphs in having a posterior protrusion at the angle between the vertical and horizontal arms (Greenwood 1968; Sato 1994), giving to this bone an inverted T-shape (Fig. 13A) (Mertzen 2019). This condition is present also in †*Palaeodenticeps* (Greenwood 1960).

Vertebral column and intermuscular bones

205. Accessory neural arch (S41): (0) absent; (1) present.

Description. The accessory neural arch (= "pre-neural arch" of Sato 1994) is a paired endochondral ossified structure that lies between the occiput (exoccipital) and the neural arch of the first vertebra lacking neural spine (Thieme & Moritz 2022), which has been interpreted as a remnant of vertebral neural arches (Rosen 1985). It is present in most clupeiforms, being absent in *Denticeps*, Dussumieriidae and Spratelloididae, most ehiravids (*Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, and *Stolothrissa*), *Hyperlophus*, *Potamalosa* and *Escualosa* (Sato 1994; Patterson & Johnson 1995; De Pinna & Grande 2003; Di Dario 2004b; Thieme & Moritz 2022). The accessory neural arch is also present in *Alepocephalus* and *Osmerus* but absent in *Albula* and the Gonorynchiformes (Gosline 1969; Patterson & Johnson 1995; Thieme & Moritz 2022). It is difficult to detect its presence in the fossil material.

206. Unique W-shaped occipital articulation with the first vertebra (new): (0) absent; (1) present.

Description. Like in other non-euteleosts, in clupeomorphs the occipital-first vertebra articulation is formed by the basioccipital only. Miyashita (2010) found that in the Pristigasteroidea and Clupeoidea in the sense of Grande (1985) (*Chirocentrus*, Alosinae, Clupeinae, Dussumieriinae, Dorosomatinae and Pellonulinae) the posterior dorsal margin of the basioccipital possess a W-shaped flange covering the neural arch bases of the first vertebra, that is interpreted as being the result of the anterior extension of the neural arch base of the first vertebra. In the pristigasteroids *Neoopisthopterus*, *Odontognathus*, and *Pliosteostoma*, despite being characterized by a W-shape condyle, the articulation has a small triangular projection or condyle at the anterior dorsal margin of the centrum with which the neural arches were fused (Miyashita 2010). The W-shaped occipital articulation is also absent in *Denticeps* and the Engraulidae, where the anterior surface of the first vertebral centrum is convex and therefore articulates with a concave posterior surface of the basioccipital, showing a pattern that is regarded to be unique in chirocentrids, pristigasterids and the Grande's (1985) clupeids (Miyashita 2010). It is difficult to detect the condition of the occipital condyle-first vertebra in fossils, but the occipital condyle preserved in three-dimensional neurocranium of †*Spratticeps* (Patterson 1970) shows that the W-shape occipital articulation is absent in this pan-Clupeiformes.

207. Unique W-shaped articulation between first and second vertebrae (new): (0) absent; (1) present.

Description. A W-shaped articulation is also present between the first and the second vertebrae in most of the taxa showing the W-shaped articulation between the basioccipital and the first vertebra, except in *Jenkinsia* and *Spratelloides*, all pristigasteroids, *Hyperlophus*, and the ehiravids *Clupeoides* and *Gilchristella* (Miyashita 2010).

208. Number of supraneurals (G*d*, S134, MW62): (0) 20 or more; (1) 10-19; (2) 7-9; (3) 6 or fewer.

Description. The number of supraneurals (=predorsal bones) in Clupeiformes is highly variable but most of the taxa have between 10 and 19 supraneurals (Grande 1985). However, *Jenkinsia* and *Spratelloides*, the engraulids †*Eoengraulis*, *Setipinna*, *Stolephorus* and *Thryssa*, the pristigasterid *Pellona*, and the clupeoids *Amblygaster*, *Anodontostoma*, †*Bolcaichthys*, *Clupanodon*, †*Cynoclupea*, *Dorosoma*, †*Gosiutichthys*, *Herklotsichthys*, *Hilsa*, †*Italoclupea*, †*Knightia*, *Lile*, *Microthrissa*, *Nannothrissa*, *Nematalosa*, *Opisthonema*, †*Pseudoellimma*, †*Santanaclupea*, *Sardinella*, and *Tenualosa* have between seven and nine supraneurals. Conversely, *Chirocentrus*, †*Trollichthys*, *Coilia*, and *Pristigaster* have six or less supraneurals, whereas *Dussumieria* and all the other pristigasteroids have 20 or more supraneurals. Among †ellimmichthyiforms, most of the taxa have between 7 and 9 supraneurals; conversely, most of the †*Armigatus* species, †*Eoellimmichthys*, †*Scutatoclupea applegatei* (Alvarado-Ortega & Ovalles-Damián, 2008), †*Thorectichthys* and †*Triplomystus* have 6 or less supraneurals, whereas †*Ezkutuberezi*, †*Gasteroclupea*, †*Guiclupea*, †*Ornategulum*, †*Ranulfoichthys*, †*Scutatuspinosus*, and †*Sorbinichthys* have between 10 and 19 supraneurals. Among outgroups, *Albula*, *Chanos* and *Osmerus* have between 10 and 19 bones, whereas *Alepocephalus* and *Kneria* have six or fewer supraneurals.

209. Arrangement of the supraneurals (G20, S136, MC62): (0) posteriorly inclined; (1) oriented vertically or inclined forward; (2) showing a fan-shaped arrangement.

Description. The supraneurals of most clupeiforms are subparallel and inclined posterodorsally, i.e., with their distal (dorsal) tip posterior to their proximal (ventral) tip (Grande 1985) (Fig. 21A, B, E, F). Pristigasteroidea, however, are unique in having supraneurals that are oriented vertically or inclined forward, i.e., with their distal (dorsal) tip anterior to their proximal (ventral) tip (Fig. 21C) (see Grande 1985). Also most †ellimmichthyiforms have the supraneurals oriented posteriorly, but the supraneurals in †*Diplomystus* and †*Guiclupea* have a fan-like arrangement (Murray *et al.* 2016; Chen *et al.* 2021) (Fig. 21D). Supraneurals of all outgroups are oriented posteriorly but *Kneria* does not possess autogenous supraneurals (-) (Grande 1994).

210. Proximal region of supraneurals (D37): (0) small or not expanded; (1) greatly expanded near the tip; (2) with an antero-posterior laminar expansion that covers most of the bone length.

Description. In clupeomorphs the proximal region of supraneurals is usually needle or pin-shaped, never expanded (Fig. 22A, B, E). However, in the pristigasteroids *Ilisha*, *Odontognathus*, *Opisthopterus*, *Pliosteostoma* and *Raconda* the supraneurals are broadly expanded proximally (Fig. 22C). In the clupeiform

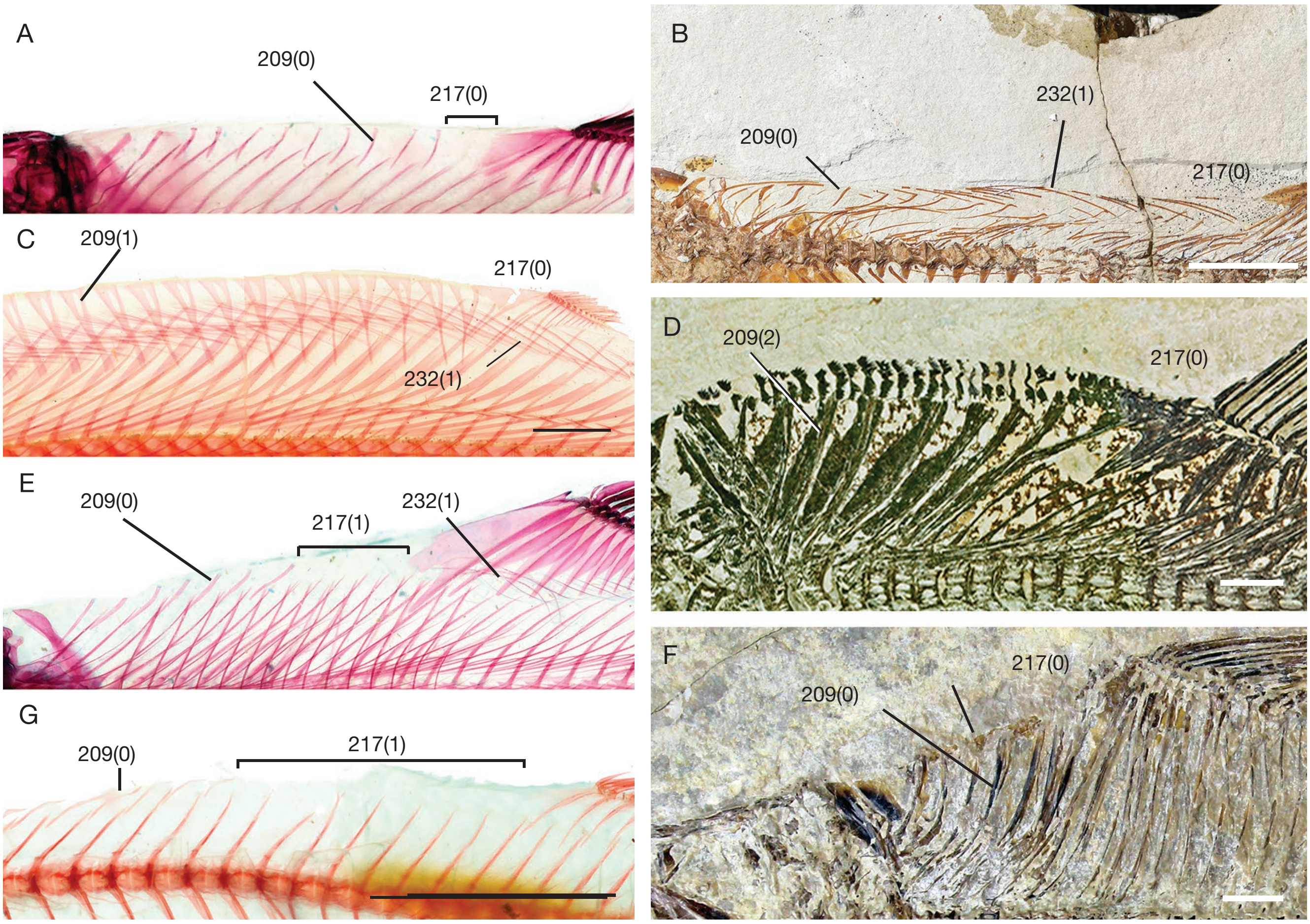

Fig. 21. — Anterior dorsal margin of the body of selected clupeomorphs: **A**, *Corica soborna* Hamilton, 1822 (Clupeiformes: Ehiravidae), AMNH 55343; **B**, †*Nardoclupea grandei* Taverne, 2002 (Clupeiformes: Dussumieriidae), MCSNV Na250; **C**, *Opisthopterus equatorialis* Hildebrand, 1946 (Clupeiformes: Pristigasteridae), AMNH 10188; **D**, †*Diplomystus dentatus* Cope, 1877 (†Ellimmichthyiformes: †Gasteroclupeidae), NHMUK PV P.52501; **E**, *Setipinna tenuifilis* (Valenciennes, 1848) (Clupeiformes: Engraulidae), AMNH 17551; **F**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Ellimmichthyiformes: †Paraclupeidae), CMSNF M.19283; **G**, *Denticeps clupeoides* Clausen, 1959 (Clupeiformes: Denticipitidae), AMNH 53082. Scale bars: 5 mm. Numbers refer to characters and character states (see text).

†*Cynoclupea* (Malabarba & Di Dario 2017, figs 2, 3) and in the †ellimmichthyiforms †*Guiclupea*, †*Diplomystus*, †armigatids and †paraclupeids the proximal part of supraneurals bears an antero-posterior laminar expansion that covers most of the length of the bone, except the distalmost part (Fig. 22D, F).

211. Distal region of most supraneurals (D38): (0) very little or not expanded; (1) expanded or greatly expanded.

Description. Most clupeomorphs usually have the distal portion of their supraneurals not expanded or slightly larger than the proximal part, giving these bones a stick or cone shape (Fig. 22A, B, D, E, F). Conversely, in *Potamalosa*, pristigasteroids (except *Ilisha*, *Pristigaster* and *Pellona*), all dorosomatids (*Amblygaster*, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Konosirus*, *Nematalosa*, *Opisthonema*, *Platanichthys*, *Rhinosardinia*, *Sardinella* and *Tenualosa*), and some ehiravids (*Clupeoides*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*) the distal region of the supraneurals is greatly expanded due to the presence of an antero-posterior laminar expansion in the distal half of the bone (Fig. 22C, E) (see also Wongratana 1980, pls 324-325). Most of the Engraulidae do not have the distal edges of supraneurals expanded, but some engraulids have the first two supraneurals with their distal portions expanded, and the same occurs in *Jenkinsia* and *Spratelloides*. However, because this condition is restricted to only a few supraneurals, the state in these taxa was considered as (0). In fossil clupeiforms, †Ellimmichthyiformes and outgroups the supraneurals are distally not expanded.

212. Perforation of the distal laminar membrane of the supraneurals (D38): (0) absent; (1) present.

Description. Among pristigasteroids with supraneurals distally expanded, *Odontognathus*, *Opisthopterus*, and *Pliosteostoma* are unique in having the distal laminar membrane of each distal expansion perforated in the middle by an oval or subcircular hollow (Fig. 22C) (see also Di Dario 1999). No other clupeomorphs and the outgroups exhibit this condition.

213. Relationship between the proximal portion of the supraneurals and the immediately posterior neural spine (D39): (0) supraneurals not extending beyond their posterior neural spine; (1) supraneurals extending beyond their posterior neural spine.

Description. In teleosts each supraneural is usually located in the interneural space (between two neural spines) and its proximal tip does not extend beyond the immediate posterior neural spine. In *Odontognathus*, *Opisthopterus* and *Pliosteostoma*, however, the proximal portion of several supraneurals extends beyond their immediately posterior neural spines (Fig. 22C) (see also Di Dario 1999).

214. Relationship between the medio-distal portion of each supraneural and the neural spines (D40): (0) mid-distal portion reaching at most one neural spine; (1) mid-distal portion reaching two neural spines.

Description. In teleosts each supraneural is located between two neural spines and being usually posteriorly inclined, its mid-distal tip does not reach the preceding neural spine or at least, reaches at most one neural spine. In the pristigasterids *Odontognathus*, *Opisthopterus* and *Raconda*, however, due to extreme anterior inclination of the supraneurals, their distal tip reaches two neural spines (Fig. 22C) (see also Di Dario 1999).

215. Anteriormost two supraneurals (M10): (0) as equally distant as the posterior ones; (1) in close proximity.

Description. The supraneurals of clupeomorphs are usually evenly spaced to each other (Fig. 23A-C). However, in *Stolephorus*, *Encrasicholina*, *Engraulis* and the New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*) the first two supraneurals are in close proximity (Fig. 23G) therefore representing another synapomorphy of the Engraulidae *sensu* Grande & Nelson (1985). This feature has not been observed in the fossil engraulid †*Eoengraulis*, suggesting that this Eocene genus might represent the sister-taxon of the taxa mentioned above (Marramà & Carnevale 2016). Interestingly, this feature has been observed herein for the first time here also in *Etrumeus*, *Jenkinsia*, *Spratelloides* and †*Trollichthys* (Fig. 23E).

216. Anteriormost two supraneurals (M10): (0) having the same shape as the other ones; (1) having different shape.

Description. The supraneurals of clupeomorphs have usually all the same shape, being rod-like, cone- or T-shaped in most taxa, hourglass-shaped in several pristigasteroids, or larger proximally in most †ellimmichthyiforms (Fig. 23A-C). However, in *Stolephorus*, *Encrasicholina*, *Engraulis*, and the New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*) the first two supraneurals have a different shape with respect to the others, since their distal region is greatly expanded due to the presence of an antero-posterior laminar expansion in the distal half of the bone (Fig. 23G). Interestingly, this feature is reported for the first time herein also in *Etrumeus*, *Jenkinsia*, *Spratelloides*, and †*Trollichthys* (Fig. 23E). All supraneurals have the same shape in outgroups and in †Ellimmichthyiformes (Fig. 23F, H).

217. Gap between the posteriormost supraneural and the first dorsal-fin pterygiophore (S135): (0) absent; (1) present.

Description. In most clupeomorphs each supraneural inserts in all the interneural spaces from the occiput to the first dorsal-fin pterygiophore (Fig. 21A-D, F). In *Denticeps*, †*Palaeodenticeps* and all the engraulids (except *Coilia*), however, there are no supraneurals in two or more interneural spaces in front of the first dorsal-fin pterygiophore, therefore leaving a gap (Fig. 21E, G) (Sato 1994). We observe that also *Jenkinsia*, †*Trollichthys* and *Spratelloides* have at least two interneural spaces without supraneurals, whereas *Chirocentrus* has a single supraneural just behind the occiput, so it is possible to consider this taxon as having the gap.

218. Maximum number of preural vertebrae (i.e., ural centra excluded) (AO17): (0) more than 65 (1); 50-65; (2) 41-50; (3) 30-40.

Description. In Clupeiformes most of the taxa exhibit between 41 and 50 preural vertebrae (see also McGowan & Berry 1984; Grande 1985); however, denticipitids, *Clupeichthys*, *Corica*, *Escualosa*, *Jenkinsia*, †*Knightia*, *Nannothrissa*, *Pristigaster*, *Rhinosardinia*, and the fossils †*Eoengraulis*, †*Gosiutichthys*, †*Italoclupea*, †*Nolfia*, †*Pseudoellimma* and †*Santanaclupea* have 40 or less preural vertebrae. Conversely, *Alosa*, *Clupea*, *Dussumieria*, *Etrumeus*, *Ilisha*, *Odontognathus*, *Raconda*, *Sardina* and *Sardinops*, plus †*Nardoclupea* and †*Scombroclupea* have between 50 and 65 vertebrae; finally, *Chirocentrus* and *Coilia* have the highest number of vertebrae (more than 65). Contrary to most clupeiforms, the †Ellimmichthyiformes generally have less than 40 preural vertebrae (e.g., †*Armigatus*, †*Ellimma*, †*Paraclupea*, etc.); the only taxa with higher count are †*Diplomystus dentatus*, †*D. shengliensis*, †*Guiclupea*, †*Ranulfoichthys*, †*Scutatoclupea* (41-50 preural vertebrae), and †*Ornategulum* (51). Among outgroups, *Kneria* has the lowest count (less than 40), followed by *Chanos* (41-50), whereas *Albula*, *Alepocephalus* and *Osmerus* have more than 65 vertebrae (e.g., Rembiszewski 1964; Gosline 1969; Forey 1973b).

219. Neural arches of most abdominal vertebrae (Z17): (0) with separate, unfused halves; (1) with fused halves forming a median neural spine.

Description. Clupeiformes usually have the neural arches of numerous abdominal vertebrae with the two halves fused for most of their length to form a single median neural spine (Fig. 22A, C, E) (Arratia 1997, 1999; Zaragüeta Bagils 2004). However, the basal †*Cynoclupea*, †*Nolfia*, †*Pseudoellimma*, †*Santanaclupea* and the more advanced †*Italoclupea* (Fig. 22B), †*Nardoclupea* and †*Scombroclupea* possess unfused neural arches (e.g., Arratia 1997; Figueiredo 2009a, b; Malabarba & Di Dario 2017). Most †Ellimmichthyiformes like †*Diplomystus* and the †Paraclupeidae, possess most of the vertebrae with the two neural arches fused to form a single median neural spine (Fig. 22F) (see Zaragüeta Bagils 2004; Murray & Wilson 2013; Marramà & Carnevale 2023); however, †*Armigatus*, †*Ellimmichthys longicostatus* and the basal †*Foreyclupea*, †*Ornategulum*, †*Scutatuspinosus*, †*Sorbinichthys*, and †*Tunisiaclupea* exhibit unfused neural arches (Fig. 22D) (Forey 1973a; Murray & Wilson 2011; Alvarado-Ortega 2014). The neural arches fused into a median neural spine are characteristic of *Chanos*, *Kneria* and †*Tischlingerichthys*, but not of other outgroups (Arratia 1997, 1999).

220. Pleural ribs (Z18): (0) all the ribs articulate with parapophyses; (1) anteriormost ribs articulate with pits on centra, followed by ribs articulating with parapophyses; (2) all ribs articulate with deep pits on the lateral side of the abdominal centra.

Description. In most Clupeiformes, including the basal †*Pseudoellimma* and †*Santanaclupea*, all the pleural ribs articulate with small parapophyses, except the last one or two articulated with the parapophyses of the anterior caudal vertebrae and sometimes interpreted as 'floating ribs' (Fig. 22A-D) (Phillips 1942; Yabumoto & Uyeno 1982; Whitehead & Teugels 1985; Maisey 1993), whereas in *Denticeps* and *Chirocentrus* all the ribs articulate with deep pits on the lateral side of the abdominal centra, and none articulate with parapophyses (Bardack 1965; Greenwood 1968). Most †Ellimmichthyiformes like the basal †*Codoichthys*, †*Foreyclupea*, †*Ranulfoichthys*, some †*Armigatus* species, and all †paraclupeids show the anteriormost ribs articulating with pits on the lateral side of vertebrae, followed by ribs articulating with long parapophyses (Forey *et al.* 2003; Vernygora & Murray 2016; Marramà & Carnevale 2023); conversely †*Armigatus alticorpus*, †*A. brevissimus*, †*A. namourensis*, and †*Ornategulum* shows the common clupeiform condition, with all the ribs articulated with the parapophyses (Fig. 22E) (Forey 1973a; Forey *et al.* 2003); †*Diplomystus*, †*Guiclupea*, and †*Ellimmichthys longicostatus*, have all the ribs articulated with deep pits on the lateral side of the abdominal centra (Grande 1982a; Newbrey *et al.* 2010; Chen *et al.* 2021). All the outgroups have the ribs articulating with small parapophyses (Forey 1973b; Fink & Fink 1981, 1996), except †*Tischlingerichthys* whose ribs articulate directly in pits on the lateral side of the vertebral centra (Arratia 1997).

221. Spoon-like expansion of rib head (S160): (0) absent; (1) present.

Description. In several teleosts, including most clupeomorphs, the proximal part of the pleural ribs does not show remarkable expansion. However, in *Chirocentrodon*, *Neoopisthopterus*, *Odontognathus* and *Opisthopterus* the proximal part of the posteriormost pleural ribs has a spoon-like expansion that forms a pocket that houses the diverticulum of the swim bladder (Fig. 22B) (Whitehead & Blaxter 1989; Sato 1994).

222. Epipleurals in the abdominal region (DD342): (0) absent in most vertebrae; (1) present in most vertebrae.

Description. In most Clupeiformes the epipleurals are present with the majority of the abdominal vertebrae, starting from the first or at the latest at the 5th vertebra and continuing in the caudal region (Fig. 22A, B, D) (Bardack 1965; Patterson & Johnson 1995); epipleurals are also present in the first abdominal vertebrae of the basal †*Cynoclupea* (Malabarba & Di Dario 2017); however, in *Denticeps*, *Hyperlophus* and *Potamalosa* most of the abdominal vertebrae (the anteriormost ones) lack epipleurals (Fig. 22C) (Yabumoto & Uyeno 1981, 1982; Di Dario 2004b); this is also the condition of the basal clupeiforms †*Italoclupea*, †*Leufuichthys*, †*Palaeodenticeps*, and †*Pseudoellimma* (Figueiredo 2009a; Gallo *et al.* 2011), whereas the condition in †*Santanaclupea* is unknown. All the †Ellimmichthyiformes, instead, show the same condition of *Albula*, *Osmerus*, and the Ostariophysi in which most of the abdominal vertebrae do not support epipleurals (Fig. 24E), whereas epipleurals are present since the first abdominal vertebrae in *Alepocephalus* (Patterson & Johnson 1995). The "modified epipleural" along most of abdominal vertebrae initially described for *Kneria* by Grande (1994), actually represent epicentrals according to Grande & Young (1997).

223. Extension of the abdominal epipleurals (distally) (DD343): (0) long, extending ventrally; (1) short.

Description. In clupeiforms in which the epipleurals are present in most of the abdominal vertebrae, these intermuscular bones are usually long and extend ventrally at least to the midlength between the vertebrae and the ventral margin of the body (Fig. 24A, D). In *Denticeps*, the basal clupeiforms †*Italoclupea*, †*Leufuichthys*, †*Pseudoellimma*, pristigasteroids (except in *Pellona*), *Hyperlophus*, *Potamalosa*, and all the †Ellimmichthyiformes the abdominal epipleurals are short and do not reach the halfway between the vertebrae and the ventral margin of the body (Fig. 24B, C, E) (Di Dario 1999, 2004b).

224. Number of divisions (forks) at the proximal region of the abdominal epipleurals (D46) - ordered: (0) undivided; (1) bifurcated; (2) trifurcated.

Description. In most clupeomorphs the proximal region of the abdominal epipleurals is undivided, articulating at ribs with a single head (Fig. 24C, D, E). In some clupeoids, in-

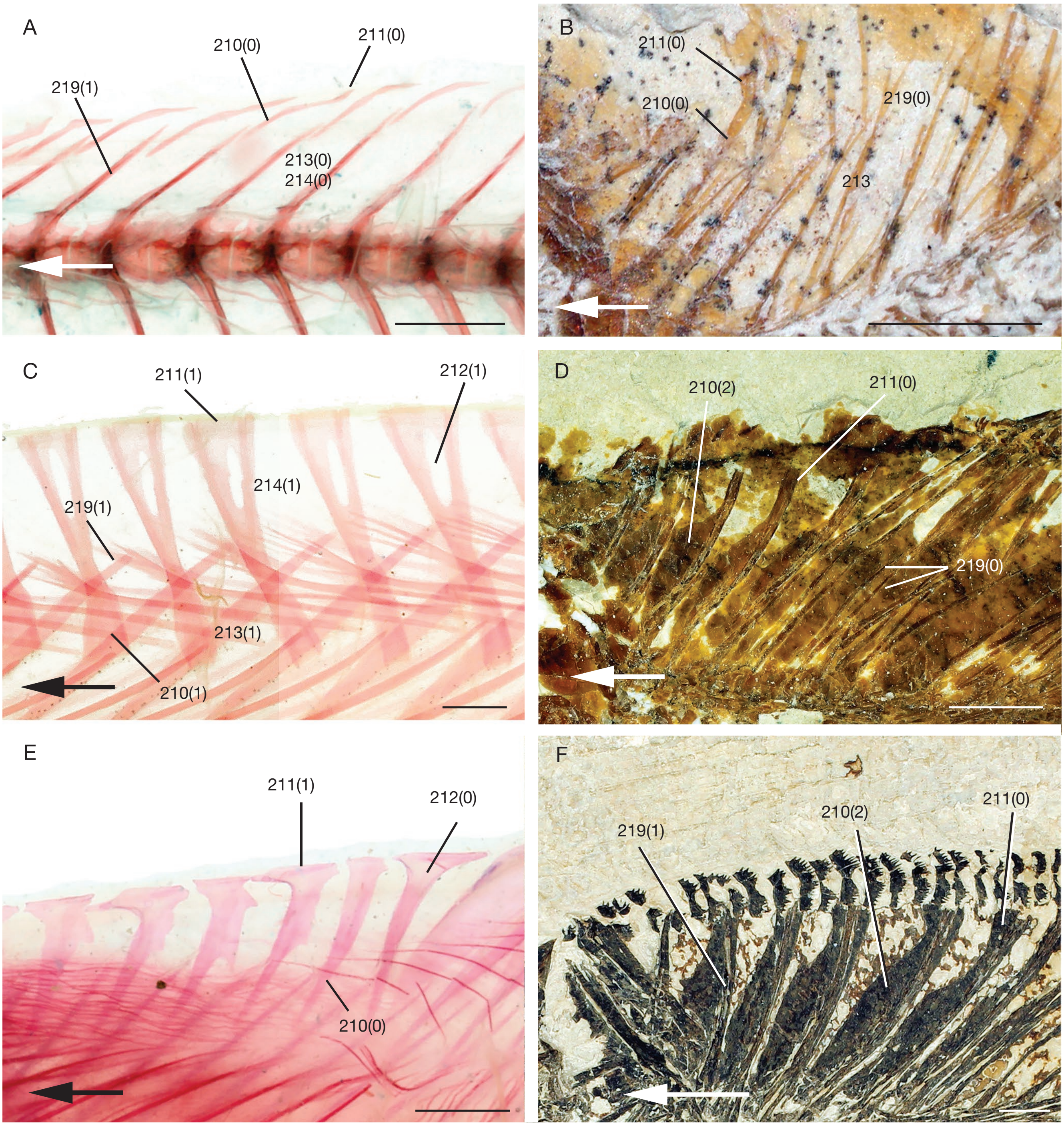

Fig. 22. — Supraneurals and neural arches of selected clupeomorphs: **A**, *Denticeps clupeoides* Clausen, 1959 (Clupeiformes: Denticipitidae), AMNH 53082; **B**, †*Italoclupea nolfi* Taverne, 2007 (Clupeiformes: Clupeoidei *incertae sedis*), MCSNV Na85; **C**, *Opisthopterus equatorialis* Hildebrand, 1946 (Clupeiformes: Pristigasteridae), AMNH 10188; **D**, †*Armigatus namourensis* Forey, Yi, Patterson & Davies, 2003 (†Ellimmichthyiformes: †Armigatidae), NHMUK PV P.63135 (mirrored); **E**, *Hilsa kelee* (Cuvier, 1829) (Clupeiformes: Dorosomatidae), AMNH 32828; **F**, †*Diplomystus dentatus* Cope, 1877 (†Ellimmichthyiformes: †Gasteroclupeidae), NHMUK PV P.52501. **Arrows** indicate anterior direction. Scale bars: 2 mm. Numbers refer to characters and character states (see text).

cluding *Dussumieria*, *Jenkinsia*, all engraulids (except *Coilia*), few pristigasterids (*Ilisha* and *Pristigaster*), some ehiravids (*Gilchristella*, *Odaxothrissa*, *Pellonula*, *Microthrissa*, *Nannothrissa*, *Limnothrissa*, *Stolothrissa*) and also *Lile*, *Platanichthys* and *Rhinosardinia*, the abdominal epipleurals are proximally bifurcated (Fig. 24A), whereas in most pristigasterids (*Chirocentrodon*, *Neoopisthopterus*, *Odontognathus*, *Opisthopterus*, *Pliosteostoma* and *Raconda*) the abdominal epipleurals are trifurcated, forming at least three branches (Fig. 24B) (Chapman 1944; Patterson & Johnson 1995; Di Dario 1999).

225. Dorsal fork (if abdominal epipleurals forked proximally) (DD349): (0) not projecting dorsally beyond the level of epicentrals; (1) projecting dorsally beyond the level of epicentrals.

Description. In some clupeoids, the dorsal fork of the abdominal epipleurals projects markedly dorsally beyond the level of epicentrals (e.g., Chapman 1944). This is the case of *Jenkinsia*, all the Engraulidae (except *Coilia*), some ehiravids (*Gilchristella*, *Odaxothrissa*, *Pellonula*, *Microthrissa*, *Nannothrissa*, *Limnothrissa*, *Stolothrissa*) and *Lile*, *Platanichthys* and *Rhinosardinia* (Fig. 24A). No other clupeomorphs or outgroups have such an arrangement of the abdominal epipleurals.

226. Number of divisions (forks) at the distal region of the abdominal epipleurals (DD344) - ordered: (0) undivided; (1) bi- or trifurcated; (2) multifurcated.

Description. The distal region of the abdominal epipleurals is usually undivided in clupeomorphs. However, in some pristigasteroids (*Ilisha*, *Pristigaster*) epipleurals are distally bi- or trifurcated, whereas epipleurals have four or more divisions in *Odontognathus*, *Opisthopterus*, *Pliosteostoma* and *Raconda* (Fig. 24B) (Di Dario 1999, 2004b).

227. Epipleurals in the caudal region (Z19): (0) absent in most vertebrae; (1) present in most vertebrae.

Description. In Clupeiformes (including *Denticeps*) the epipleurals are present in all caudal vertebrae (Fig. 24C-E) (Bardack 1965; Patterson & Johnson 1995), except in †*Santanaclupea* and †*Pseudoellimma* where they are confined to the first caudal vertebrae only (Fig. 23A) (Maisey 1993; Figueiredo 2009a). In the †Ellimmichthyiformes like †*Armigatus* (state unknown in †*A. dalmaticus*), †*Diplomystus*, †*Gasteroclupea*, †*Guiclupea*, †*Sorbinichthys*, and the †paraclupeids †*Thorectichthys* and †*Triplomystus oligoscutatus* Forey *et al.*, 2003 epipleurals are present up to the last caudal vertebrae (Fig. 24E), whereas in †*A. dalmaticus*, †*A. oligodentatus*, the other †Paraclupeidae, and the basal †*Codoichthys*, †*Foreyclupea*, †*Ornategulum* and †*Ranulfoichthys* the epipleurals are present only in the first caudal vertebrae (Fig. 23F) (Forey 1973a; Bannikov & Bacchia 2000; Forey *et al.* 2003; Murray & Wilson 2013; Marramà *et al.* 2022). Epipleurals are present in most caudal vertebrae of *Albula*, *Osmerus* and the Ostariophysi, but not in *Alepocephalus* (Gosline 1969; Forey 1973b; Patterson & Johnson 1995).

228. Epicentrals (Z20, DD347): (0) cartilaginous (=not recognizable in fossils); (1) ossified.

Description. In the Ostariophysi and Clupeiformes the epicentrals are mostly ossified, and therefore easily recognizable sometimes also in fossils like †*Bolcaichthys*, †*Cynoclupea*, †*Eoengraulis*, †*Italoclupea* and †*Palaeodenticeps*. In †Ellimmichthyiformes epicentrals were reported as absent in most taxa (likely because they were cartilaginous in origin) (Zaragüeta Bagils 2004; Alvarado-Ortega *et al.* 2008), although they have been reported (since they are ossified) in basal taxa like †*Ornategulum* and in the †paraclupeid †*Triplomystus* (Forey 1973a; Forey *et al.* 2003). In *Albula*, *Alepocephalus* and *Osmerus* the epicentrals are ligamentous (Patterson & Johnson 1995).

229. Cartilage chevron at the distal tip of the epicentrals (DD348): (0) absent; (1) present.

Description. Cartilage chevrons at the distal tips of the epicentrals have been identified in several clupeoid and engraulid taxa (Fig. 24A, D), and their presence is considered as a synapomorphy supporting their sister-group relationship (Di Dario 2002). We agree with Di Dario (2002) that epicentrals are absent in *Denticeps*, *Chirocentrus*, *Dussumieria*, all Pristigasteroidea and, among the engraulids, in *Coilia*, *Lycothrissa* and *Setipinna* but, contra Di Dario (2002), we were not able to find these structures in *Etrumeus* or in the other engraulids (except *Anchoa* and *Anchoviella*) although the alcian blue was able to stain other cartilages in our specimens, whereas we observed these cartilaginous structures in *Clupea* and *Herklotsichthys*. Cartilage chevrons are absent in other teleost groups (Patterson & Johnson 1995) and being cartilaginous, it is not possible to observe them in fossil clupeomorphs. The status was considered indeterminate (?) in *Corica*, *Hyperlophus* and *Opisthonema* as the cartilages were not properly stained in the examined specimens.

230. Epicentrals and anterior ribs (DiD9): (0) unfused; (1) fused.

Description. Fusion of the epicentrals with the proximal part of the anterior ribs is uniquely recorded in Clupeiformes (Patterson & Johnson 1995). This fusion occurs in *Chirocentrus*, dussumieriids, spratelloidids, and in all members of the Clupeoidea. This fusion does not occur in *Denticeps*, pristigasteroids or in engraulids (except in *Coilia*), *Chanos* and *Kneria* (Patterson & Johnson 1995; Di Dario 2009).

231. Pleural ribs/preural vertebrae ratio (G22) - ordered: (0) 0.20-0.40; (1) 0.41-0.46; (2) ≥0.47.

Description. In his comprehensive analysis of clupeomorph systematics, Grande (1985) highlighted a general trend of increasing relative abdominal cavity size among clupeomorphs that might be related to a shift from a piscivorous towards a zooplanktivorous diet (low ratio is regarded as the basal condition), which can be calculated as the ratio between the number of pleural ribs and the number of preural vertebrae. Among clupeiforms, this ratio reaches its minimum values (0.20-0.40) in *Denticeps*, the engraulids *Coilia*, *Lycothrissa*,

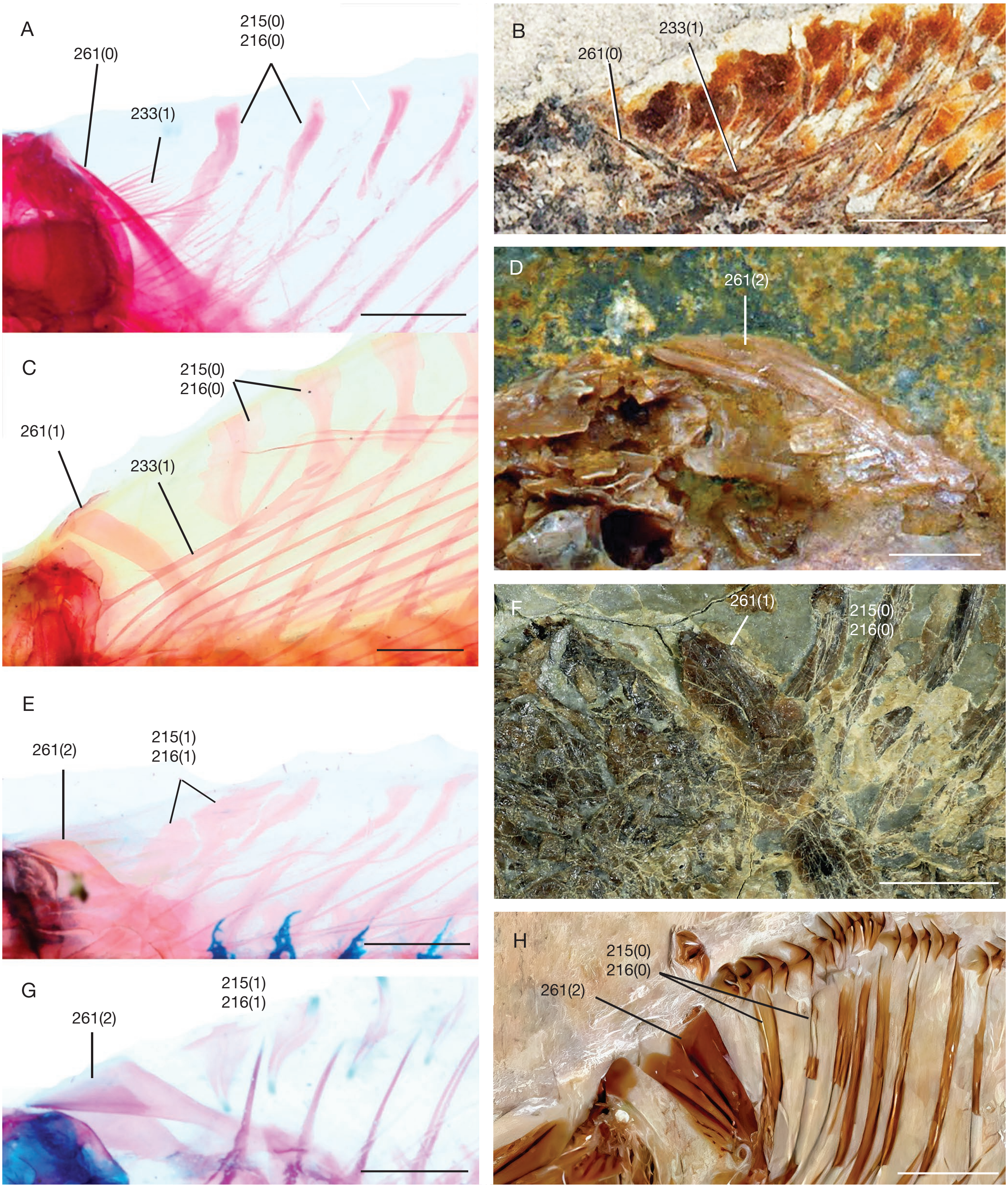

Fig. 23. — Posttemporal and supraneurals of selected clupeomorphs: **A**, *Lile stolifera* (Jordan & Gilbert, 1882) (Clupeiformes: Dorosomatidae), AMNH 7100; **B**, †*Eoalosa janvieri* Marramà & Carnevale, 2018 (Clupeiformes: Alosidae), MNHN F.Bol475; **C**, *Opisthopterus equatorialis* Hildebrand, 1946 (Clupeiformes: Pristigasteridae), AMNH 10188; **D**, †*Santanaclupea silvasantoi* Maisey, 1993 (Clupeiformes: †Cynoclupeidae), AMNH DVP.18968 (mirrored); **E**, *Spratelloides delicatulus* (Bennett, 1832) (Spratelloididae), AMNH 54621; **F**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Ellimmichthyiformes: †Paraclupeidae), MRSN P/260.3; **G**, *Anchovia clupeoides* (Swainson, 1839) (Clupeiformes: Engraulidae), AMNH 224937; **H**, †*Sorbinichthys elusivo* Bannikov & Bacchia, 2000 (†Ellimmichthyiformes: †Sorbinichthyidae), CLC S-431a. Scale bars: 2 mm. Numbers refer to characters and character states (see text).

Setipinna and *Anchovia*, and in most pristigasteroids (except *Chirocentrodon* and *Ilisha*). A mid-value ratio (0.41-0.46) is typical of †*Palaeodenticeps* and †*Santanaclupea*, the engraulids *Anchoa*, *Cetengraulis*, †*Eoengraulis*, *Lycengraulis*, *Pterengraulis*, *Stolephorus*, *Thryssa*, and the pristigasteroids *Chirocentrodon* and *Ilisha*. A further increase in the size of the abdominal cavity (≥0.47) characterizes the most derived engraulids (*Anchoviella*, *Encrasicholina* and *Engraulis*) including *Chirocentrus*, Dussumieriidae, Spratelloididae, and all the Clupeoidea. This general trend towards a higher ratio can be also recognized among the †ellimmichthyiforms. †*A. alticorpus*, †*A. plinii*, all †*Diplomystus* species, †*Eoellimmichthys*, †*Ezkutuberezi* and †*Sorbinichthys* exhibit the lowest values (0.20-0.40), whereas the ratio is moderately higher in †*A. brevissimus*, †*A. dalmaticus*, †*A. felixi*, †*Gasteroclupea*, †*Guiclupea*, and the †paraclupeids †*Thorectichthys marocensis* and †*Triplomystus oligoscutatus* (0.41-0.46), and it is the highest (≥0.47) in †*Codoichthys*, †*Ornategulum*, †*Ranulfoichthys*, and all the remaining †paraclupeids. In outgroups this ratio is very high (≥0.47), except in *Alepocephalus* where it is very low (0.20-0.40).

232. Dorsal myorhabdoi (DD351): (0) absent; (1) present.

Description. Some clupeiforms are characterized by two or more additional series of tiny, autogenous intermuscular bones in the dorsal and ventral forward flexures of the myoseptum called myorhabdoi (Chapman 1944). Dorsal myorhabdoi occur just below the dorsal margin of the body, starting just anterior to the dorsal fin and continuing backward until the caudal region. We observed these intermuscular bones in *Dussumieria*, engraulids (*Anchoa*, *Anchoviella*, *Cetengraulis*, *Coilia*, *Engraulis*, *Lycengraulis*, *Pterengraulis*, *Setipinna*, *Stolephorus*, *Thryssa*), some dorosomatids (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Harengula*, *Hilsa*, *Nematalosa* and *Sardinella*), and pristigasteroids (*Neoopisthopterus*, *Odontognathus*, *Opisthopterus*) and *Pliosteostoma*, *Pristigaster* and *Raconda* (Figs 21C, E; 24A, B, D). The autogenous intermusculars of †*Nardoclupea* called "epicentrals" by Taverne (2002) actually resemble the dorsal myorhabdoi in morphology and arrangement (Fig. 21B). These bones have not been reported in other fossil taxa.

233. Ossified occipital epineurals (DD334): (0) absent; (1) present.

Description. Epineurals are generally associated with neural arches. However, some epineurals can insert directly on the occiput (Patterson & Johnson 1995). They are present in *Dussumieria* and *Etrumeus*, in some pristigasteroids (*Ilisha*, *Odontognathus*, *Opisthopterus*, *Pliosteostoma*, *Raconda*), some ehiravids (*Clupeoides*, *Clupeonella*, *Corica*, *Gilchristella*, *Pellonula*), all alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*) and dorosomatids (*Amblygaster*, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Lile*, *Nematalosa*, *Opisthonema*, *Rhinosardinia*, *Sardinella*, *Tenualosa*) (Figs 23A, C; 24B, D) (see also Patterson & Johnson 1995; Di Dario 2004b). Ossified occipital epineurals are present in *Albula*, *Chanos* and *Kneria*, whereas in *Osmerus* these are cartilaginous. In fossils, they are present in †*Bolcaichthys* and †*Eoalosa* (Fig. 23B) (unknown or absent in other clupeiform taxa) but never reported in †Ellimmichthyiformes (Fig. 23F, H).

234. Baudelot's ligament (DD331): (0) present; (1) absent.

Description. The Baudelot's ligament is a stout ligament that originates on the ventrolateral aspect of an anterior vertebra (usually the first) or the occiput (usually the basioccipital) and inserts on the supracleithrum distally, usually after looping around the upper part of the cleithrum (Patterson & Johnson 1995). It is present in several teleost groups, including all extant Clupeiformes, *Albula*, *Alepocephalus* and *Osmerus*, whereas its absence is considered a synapomorphy of the Gonorynchiformes (Fink & Fink 1981; Patterson & Johnson 1995), including *Chanos* and *Kneria*. The occurrence and nature of the Baudelot's ligament is impossible to determine in fossil clupeomorphs.

235. Origin of Baudelot's ligament (DD333): (0) at cranium; (1) at first vertebra; (2) at both first and second vertebra; (3) at second vertebra.

Description. In most clupeiforms, the Baudelot's ligament originates on the parapophysis of the first vertebra. In *Clupanodon*, *Opisthonema*, the pristigasteroids *Ilisha*, *Opisthopterus* and *Pellona*, and engraulids *Lycothrissa* and *Thryssa* the ligament originates at first vertebra but it is elongate and articulates also at the distal tip of the parapophysis of the second vertebra; in *Chirocentrus*, *Coilia* and *Setipinna* the Baudelot's ligament originates only on the second vertebra, whereas the ehiravids *Clupeichthys*, *Microthrissa*, *Nannothrissa*, and *Potamothrissa* are unique in having this ligament originating directly at the posterior margin of the basioccipital (Patterson & Johnson 1995; Di Dario 1999, 2004b). In *Albula*, *Alepocephalus* and *Osmerus* the Baudelot's ligament originates on the first vertebra.

236. Nature of the Baudelot's ligament (DD332): (0) not ossified; (1) ossified.

Description. The Baudelot's ligament is usually not ossified in clupeiforms. However, it is ossified in *Chirocentrus*, *Dussumieria* and *Etrumeus*, and the Engraulinae (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, and *Stolephorus*), but not in the Coiliinae; it seems to be ossified also in dorosomatids *Anodontostoma*, *Clupanodon*, *Dorosoma* and *Nematalosa* (Patterson & Johnson 1995; Di Dario 1999, 2004b).

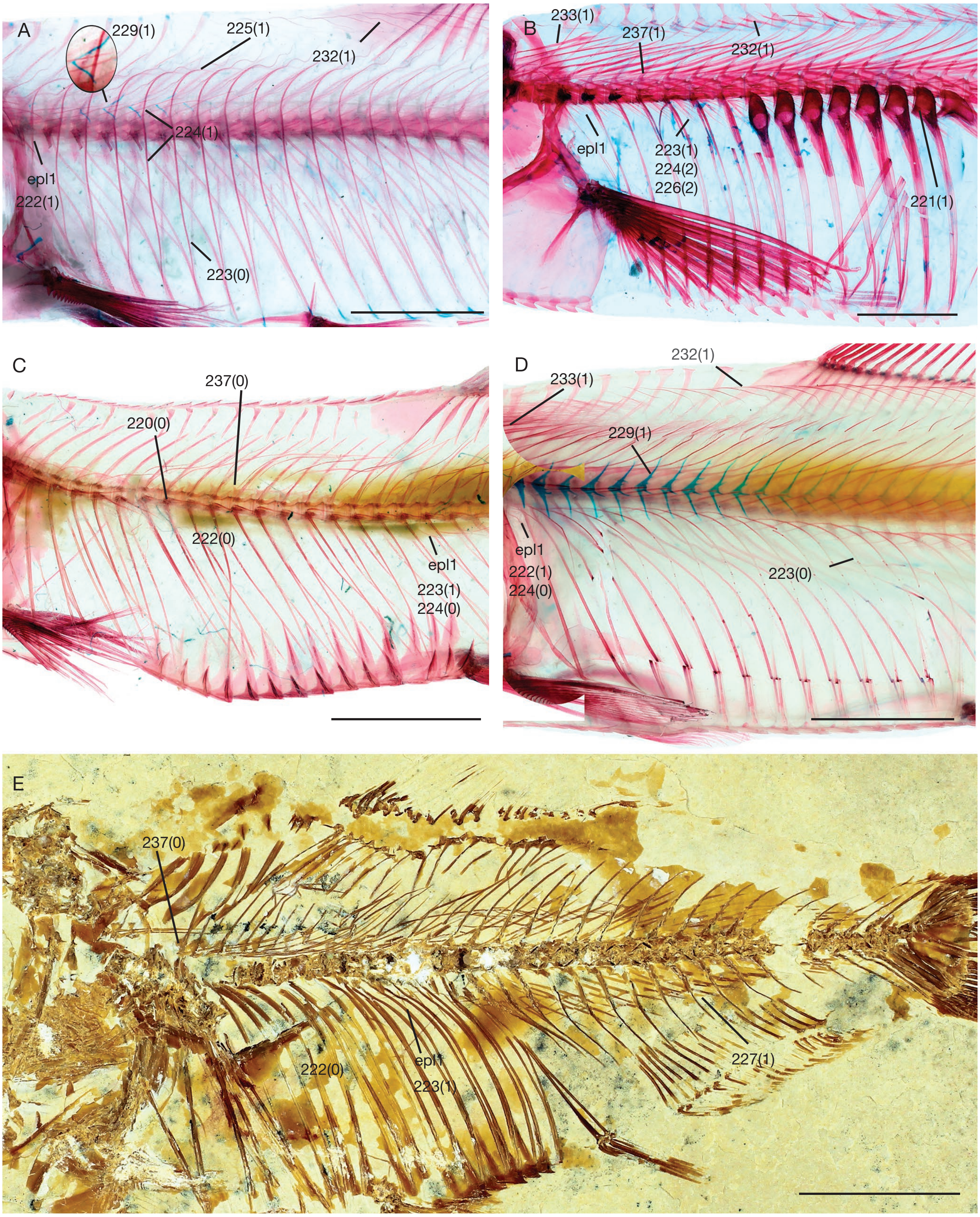

FIG. 24. — Abdominal region of selected clupeomorphs with focus on intermuscular bones (anterior to the left): **A**, *Anchoviella lepidentostole* (Fowler, 1911) (Clupeiformes: Engraulidae), AMNH 40905; **B**, *Odontognathus mucronatus* Lacépède, 1800 (Clupeiformes: Pristigasteridae), AMNH 20749; **C**, *Hyperlophus vittatus* (Castelnau, 1875) (Clupeiformes: Hyperlophidae), AMNH 3050; **D**, *Sardinella maderensis* (Lowe, 1838) (Clupeiformes: Dorosomatidae), AMNH 44448; **E**, †*Armigatus namourensis* Forey, Yi, Patterson & Davies, 2003 (†Ellimmichthyiformes: †Armigatidae), NHMUK PV P.63151. Scale bars: 10 mm. Abbreviations: **epl1**, anteriormost epipleural. Numbers refer to characters and character states (see text).

237. Anteriorly facing bony expansions at the base of the neural arches of the first abdominal vertebrae (D50): (0) present; (1) absent.

Description. In outgroups and most clupeiforms (including fossils like †*Cynoclupea* and †*Santanaclupea*) the bases of each neural arch of the anteriormost vertebrae have a bony and anteriorly directed laminar expansion (Fig. 24C). The bases of the neural arches in all the pristigasteroids (except *Ilisha* and *Pellona*) have a columnar shape and the anterior edge is contiguous with the neural spine, without anteriorly directed bony expansion (Fig. 24B) (Di Dario 1999). The bony process on the anteriormost abdominal vertebrae appears to be evident also in several †ellimmichthyiforms (Fig. 24E) (e.g., Forey *et al.* 2003a; Alvarado-Ortega & Melgarejo-Damián 2017; Boukhalfa *et al.* 2018; Alvarado-Ortega *et al.* 2020).

238. Parapophyses on the first vertebra (DD353): (0) absent; (1) present.

Description. Parapophyses associated to the first vertebra are present in several basal teleosts including the outgroups and most clupeoids (Forey 1973b; Fink & Fink 1981; Grande 1994); however, these lateral processes on the first vertebra are absent on the first centrum of *Denticeps*, *Chirocentrus*, all engraulids, *Dussumieria* and †*Nardoclupea*, and some ehiravids (*Clupeichthys*, *Clupeoides*) (e.g., Di Dario 2002, 2004b; Mertzen 2019). It is difficult to reveal the presence of parapophyses on the first centrum of fossil taxa because this region is usually hidden by bones of the opercular apparatus and pectoral girdle; however, parapophyses on the first vertebra have been recognized in the clupeiform †*Nolfia* and the †ellimmichthyiform †*Diplomystus dentatus* (e.g., Newbrey *et al.* 2010).

239. Size of the parapophyses of the second vertebra (DD354): (0) reduced, poorly developed; (1) conspicuous, well developed.

Description. The parapophyses of the second vertebra are usually small and poorly developed in most clupeiforms but they are very conspicuous in *Denticeps*, *Coilia*, *Pellonula* and all the pristigasteroids (except *Pliosteostoma* and *Pristigaster*) (Greenwood 1968; Di Dario 1999, 2002, 2004b). *Kneria* is the only outgroup taxon with well-developed parapophyses on the second vertebra (Grande 1994).

240. Orientation of the parapophysal axis of the second vertebra (DD362): (0) posteriorly directed; (1) anteriorly directed; (2) perpendicularly directed.

Description. The parapophyses of the second vertebra of most Clupeoidea and Engraulidae (except *Coilia*) are posteriorly directed, leading Di Dario (2002) to consider the posteriorly directed parapophysis of the second vertebra as a synapomorphy uniting the Clupeoidea *sensu* Grande (1985) and the Engraulidae. Conversely, the parapophysal axis of the second vertebra in *Denticeps* and some pristigasteroids (i.e., *Chirocentrodon*, *Ilisha*, *Pristigaster* and *Raconda*) are directed anteriorly, whereas *Coilia* and *Etrumeus* are the only genera in which the parapophyses of the second vertebra are nearly perpendicular to the main axis of the vertebrae (Greenwood 1968; Di Dario 1999, 2002).

241. Size of the parapophysis of the third vertebra (DD364): (0) large; (1) reduced.

Description. In basal clupeiforms, including *Denticeps*, *Dussumieria*, *Etrumeus*, Engraulidae (including †*Eoengraulis*) and Pristigasteroidea, the parapophyses of the third vertebra are moderately to remarkably large, being the length of their anterior margin approximately equal or larger than the diameter at their base. The same condition can be observed in †*Cynoclupea* (Malabarba & Di Dario 2017, fig. 8), †*Italoclupea* and †*Nardoclupea*, all the †ellimmichthyiforms (e.g., †*Armigatus*, †*Diplomystus*, †*Paraclupea*, etc.) and in the outgroups *Alepocephalus* and *Chanos*. Conversely, in *Chirocentrus*, †*Trollichthys*, Spratelloididae and all the fossil and extant Clupeoidea, including †*Bolcaichthys* and †*Eoalosa*) the parapophyses are short or extremely reduced, since the length of their anterior margin is shorter than the diameter of their base. This is also the condition of *Albula* and *Osmerus*.

242. Shape of the distal tip of the parapophysis of the third vertebra (DD368): (0) rounded, truncated or irregular; (1) triangular, pointed distally.

Description. In basal clupeiforms, including *Denticeps*, †*Cynoclupea* (Malabarba & Di Dario 2017, fig. 8), †*Italoclupea* and †*Nardoclupea*, *Dussumieria*, *Etrumeus*, Engraulidae (including †*Eoengraulis*), Pristigasteroidea and, among the Clupeoidea, *Clupeoides* and *Escualosa*, the distal region of the parapophyses of the third vertebra gradually tapers from its midpoint ending into a point, giving the parapophysis a triangular shape. The same condition can be observed in *Chanos* and all the †ellimmichthyiforms (e.g., †*Armigatus*, †*Diplomystus*, †*Paraclupea*, etc.). Conversely, in *Chirocentrus*, Spratelloididae and all the other fossil and extant Clupeoidea (including †*Bolcaichthys*, †*Eoalosa*, and †*Trollichthys*) the distal region of the parapophysis of the third vertebra is rounded or truncated or characterized by an irregular shape for the articulation with the first rib. This condition is also shared with *Albula* and *Osmerus*.

243. Interzygapophysal articulation (new): (0) absent; (1) present.

Description. The interzygapophysal articulation has been defined by Di Dario (2002) as the tight association between the highly expanded neural and haemal prezygapophyses,

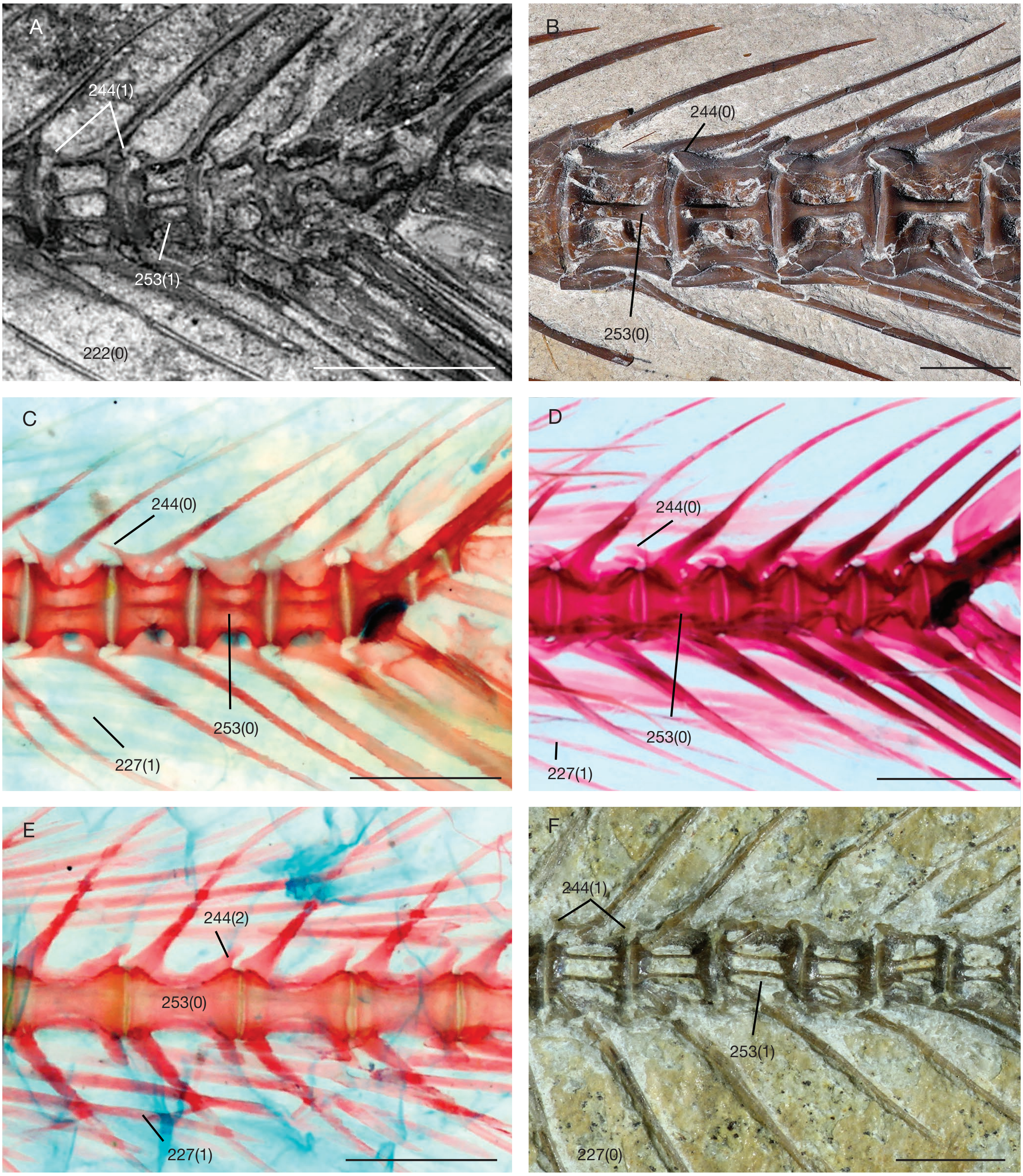

Fig. 25. — Posteriormost caudal vertebrae of selected clupeomorphs (anterior to the left): **A**, †*Santanaclupea silvasantoi* Maisey, 1993 (Clupeiformes: †Cynoclupeidae), DNPM DGM 1338-P (photo: courtesy of Lorraine Meeker); **B**, †*Nardoclupea grandei* Taverne, 2002 (Clupeiformes: Dussumieriidae), MCSNV Na221; **C**, *Clupea harengus* Linnaeus, 1758 (Clupeiformes: Clupeidae), AMNH 49397; **D**, *Lile stolifera* (Jordan & Gilbert, 1882) (Clupeiformes: Dorosomatidae), AMNH 7100; **E**, *Chirocentrodon bleekerianus* (Poey, 1867) (Clupeiformes: Pristigasteridae), AMNH 10118; **F**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Ellimmichthyiformes: †Paraclupeidae), MRSN P/260.11. Scale bars: 2 mm. Numbers refer to characters and character states (see text).

the mesially displaced neural and haemal postzygapophyses and the haemal and neural arches of the caudal vertebrae. It is present in most extant clupeiforms (Fig. 25B-D), except *Denticeps* and the Pristigasteroidea (Fig. 25E), leading Di Dario (2002) to consider its presence as a synapomorphy uniting the Clupeoidea and Engraulidae. The interzygapophysal articulation can be detected also in several fossil clupeoids (including †*Scombroclupea* and †*Italoclupea*) but it appears to be absent in the basal clupeiforms †*Leufuichthys*, †*Nolfia*, †*Palaeodenticeps*, †*Pseudoellimma* and †*Santanaclupea* (Fig. 25A) (Maisey 1993; Figueiredo 2009a). In the outgroups and the †ellimmichthyiforms, pre- and postzygapophyses are extremely reduced or not developed at all (Fig. 25F), suggesting that the interzygapophysal articulation is absent outside the Clupeiformes.

244. Asymmetry in the size of the zygapophyses of the caudal vertebrae (V152): (0) prezygapophyses more developed than postzygapophyses; (1) pre- and postzygapophyses almost equally developed; (2) postzygapophyses more developed than prezygapophyses.

Description. In most clupeiforms the prezygapophyses of the caudal vertebrae are usually more developed than the postzygapophyses (Fig. 25B-D). The pre- and postzygapophyses are almost equally developed in *Denticeps*, †*Pseudoellimma*, †*Palaeodenticeps*, †*Santanaclupea*, and in all the †Ellimmichthyiformes (Fig. 25A, F). In the pristigasteroids, the postzygapophyses are longer than the prezygapophyses (Fig. 25E). In outgroups pre- and postzygapophyses are almost equally developed.

245. Anterior bony expansion in the parapophyses of the third vertebra (D57): (0) absent; (1) present.

Description. An anterior bony expansion or process in the parapophyses of the third vertebra is characteristic of the Pristigasteroidea and has never been reported in other clupeomorphs or teleosts (Di Dario 1999, 2004b).

246. Parapophyses of the caudal vertebrae (DD383): (0) absent; (1) present.

Description. In outgroups and most of clupeomorphs, the parapophyses are absent on caudal vertebrae. However, in *Chirocentrus*, *Dussumieria*, †*Nardoclupea* and in all the pristigasteroids the caudal vertebrae bear more or less developed parapophyses (Di Dario 1999, 2004b). Similar processes called transverse processes by Forey *et al.* (2003b) or horizontal laminae by Giersch *et al.* (2011) appear to be present in †*Scombroclupea*.

247. Degree of development of the parapophyses of the caudal vertebrae (DD383): (0) reduced; (1) well developed.

Description. Among clupeoids characterized by parapophyses on the caudal vertebrae, these lateral processes are poorly developed in *Chirocentrus*, *Dussumieria*, and the pristigasteroids *Chirocentrodon*, *Neoopisthopterus*, *Odontognathus*, *Opisthopterus* and *Raconda* (0), whereas parapophyses are well-developed in *Ilisha*, *Pellona*, *Pliosteostoma* and *Pristigaster* (Di Dario 1999, 2004b).

248. Bony process on the first pleural rib (G*b*, S159): (0) absent; (1) present.

Description. The presence of a more or less developed bony process on the first pleural rib is typically present in all the pristigasteroids but not in other clupeomorphs or teleosts (Grande 1985; Sato 1994).

249. Articulation between the first pleural rib and cleithrum (G*b*): (0) absent; (1) present.

Description. The presence of a bony process on the first pleural rib that articulates with the cleithrum has been recognized by Grande (1985) to align *Ilisha africana* (Bloch, 1795), *Odontognathus*, *Opisthopterus*, *Pristigaster* and *Raconda* (=the Pristigasteridae *sensu* Grande 1985). Although other pristigasteroids (e.g., *Chirocentrodon*) have a small expansion near the top of the first pleural rib, it does not articulate with the cleithrum (Grande 1985). This articulation has never been reported in other clupeomorphs.

250. Rib length of vertebra 3 (D63): (0) equal to or close to subsequent ribs; (1) much smaller than that of subsequent ribs.

Description. Among clupeomorphs, the length of the pleural rib of the third vertebra (the first rib) is equal to or close to that of the subsequent ribs, almost reaching the ventral margin of the body in most of the taxa. The pristigasteroids *Odontognathus*, *Opisthopterus* and *Pliosteostoma*, however, are unique in having a very short first pair of ribs, not reaching the ventral margin of the body (Di Dario 1999) (e.g., Fig. 24B).

251. Laminar expansion at the base of the haemal spine of the first caudal vertebra (D68, DD384): (0) absent; (1) present.

Description. In most clupeomorphs (including the †Ellimmichthyiformes) the anterior margins of the haemal arches and spine of the first caudal vertebra are continuous with no anteriorly directed expansion. In *Ilisha*, *Pristigaster* and *Raconda* there is a conspicuous anteriorly directed laminar bony expansion at the base of the first haemal spine. Contrary to Di Dario (1999, 2004b), we did not observe the presence of this laminar expansion in the first caudal vertebra of *Denticeps*.

252. Haemal arches and centra anterior to preural vertebra 2 (new): (0) unfused; (1) fused.

Description. Fink & Fink (1996) and Lecointre & Nelson (1996) firstly reported that the Ostariophysi (represented in this study by *Chanos*, *Kneria* and †*Tischlingerichthys*) and all clupeomorphs have the haemal spines fused to their respective centra anterior to preural centrum 2 (Fig. 25), suggesting close relationships between these two groups. In *Alepocephalus* the haemal arches of the preural vertebrae 1 and 2 are autogenous, but those farther forwards are not (Gosline 1969), therefore this feature can be considered as a synapomorphy of the Otomorpha (= Otocephala or Ostarioclupeomorpha), including the alepocephaliforms (Arratia 2018). In our matrix, only *Albula* and *Osmerus* have autogenous haemal spines in first preural vertebrae.

253. Number of ridges and pits on the lateral side of the caudal vertebrae (V153): (0) one ridge and two pits; (1) at least two ridges and three pits or more.

Description. The lateral surface of the caudal vertebrae of *Chanos*, *Kneria* and most extant and fossil Clupeiformes bear an antero-posteriorly directed ridge between two shallow ovoid pits (one dorsal and one ventral to the ridge) (Fig. 25B-E). Conversely, in all the †Ellimmichthyiformes (Fig. 25F), and in the basal clupeiforms †*Palaeodenticeps*, †*Pseudoellimma* and †*Santanaclupea* caudal vertebrae bear at least two ridges and three pits or more (Fig. 25A), similarly to *Albula*, *Alepocephalus* and *Osmerus*.

Paired fins and girdles

254. Number of pectoral-fin proximal radials (S129): (0) four; (1) three or less.

Description. *Albula*, *Alepocephalus*, *Chanos*, *Osmerus*, and most of clupeiforms have four proximal radials in the pectoral fin. However, *Etrumeus* and some engraulids (*Anchoviella*, *Coilia*, *Lycengraulis*, *Setipinna*, *Stolephorus*) have three proximal radials, possibly resulting from obliteration or fusion of two radials, whereas *Denticeps* has only two proximal radials (Sato 1994; Mertzen 2019). The †ellimmichthyiforms in which this region is well preserved (†*Armigatus felixi*, †*Ornategulum*, †*Paraclupea seilacheri*, †*Ranulfoichthys*, †*Scutatuspinosus*) show the basal condition in having four proximal radials (Forey 1973a; Figueiredo & Ribeiro 2017; Than-Marchese & Alvarado-Ortega 2022).

255. Number of pectoral-fin distal radials (S130) – ordered: (0) seven or more; (1) six; (2) five or less.

Description. The number of pectoral-fin distal radials differs in the basal Teleostei but at least seven or more are present in *Albula* and *Alepocephalus* (Markle 1976). Most clupeiforms have six distal radials, whereas *Denticeps*, *Etrumeus*, all engraulids (except *Coilia*) and *Clupea* have five or less distal radials, which is the result of the fusion of two or more radials (Sato 1994). *Coilia* has no distal radials. It is difficult to recognize their presence in fossil clupeomorphs, although five distal radials have been reported, e.g., in †*Ornategulum* (Forey 1973a).

256. Upper fin ray(s) of the pectoral fin (K99): (0) not elongated; (1) extremely elongated.

Description. In most teleosts, the pectoral-fin rays are approximately of the same size or, at least, with the rays decreasing gradually in size from the first (uppermost) to the last (lowermost). Among clupeiforms, however, *Coilia* and *Setipinna* are unique in having the upper fin rays of the pectoral fin extremely elongated (=filamentous first pectoral finrays of Whitehead *et al.* 1988). Among the †Ellimmichthyiformes, this feature is clearly present in †*Gasteroclupea* and both the species of †*Sorbinichthys* (Bannikov & Bacchia 2000; Murray & Wilson 2011; Marramà & Carnevale 2017).

257. Shape of the cleithrum (AO22): (0) L-like, with a single angle; (1) S-like, with two angles.

Description. In most teleosts, including all the Clupeiformes, the cleithrum has the typically L shape, characterized by a single “angle” in the ventral part of the bone, with the concavity toward the head (Figs 26; 27A-C). Among the †Ellimmichthyiformes, however, †*Armigatus*, †*Diplomystus*, †*Gasteroclupea*, †*Guiclupea* and all the †Paraclupeidae possess a S-like cleithrum (Fig. 27D-F), thereby representing a synapomorphy for the clade comprising these taxa (Alvarado-Ortega *et al.* 2008; Marramà *et al.* 2022); conversely, in the basal †ellimmichthyiforms †*Codoichthys*, †*Foreyclupea*, †*Ornategulum*, †*Ranulfoichthys* and †*Sorbinichthys* the cleithrum is L-shaped (e.g., Forey 1973a; Figueiredo & Ribeiro 2016; Vernygora *et al.* 2016).

258. Medial process of the cleithrum (S125): (0) absent; (1) present.

Description. The anteroventral margin of the cleithrum of *Stolothrissa*, alosids (*Alosa*, *Brevoortia*, *Sardina*, *Sardinops*), *Clupea*, †*Gosiutichthys*, *Potamalosa*, *Sprattus*, dorosomatids (*Amblygaster*, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Escualosa*, *Harengula*, *Herklotsichthys*, *Hilsa*, *Konosirus*, *Lile*, *Nematalosa*, *Opisthonema*, *Platanichthys*, *Rhinosardinia*, *Sardinella*, and *Tenualosa*) bears a medial process (Fig. 26E, F) that delimits laterally the entry into the esophagous of this bone (Sato 1994; Di Dario 2004b). This process is absent in *Denticeps*, *Chirocentrus*, *Jenkinsia*, *Spratelloides*, *Dussumieria*, *Etrumeus*, engraulids, pristigasterids, ehiravids and *Hyperlophus* (Fig. 26A-D) (see also Sato 1994; Di Dario 2004b). It is also absent in †*Bolcaichthys*, †*Eoalosa*, †*Italoclupea* and †*Scombroclupea*, other than in all the outgroups and the †ellimmichthyiforms showing this part of the bone (e.g., †*Ornategulum*, and some †*Armigatus*, †*Diplomystus*, and †*Paraclupea* species).

259. Size of the medial process of the cleithrum (S125): (0) small, not reaching the dorsal arm of the cleithrum; (1) large, reaching or almost reaching the anterior margin of the dorsal arm of the cleithrum.

Description. The median process of the cleithrum is small not reaching the dorsal arm of the cleithrum in *Stolothrissa*, *Clupea*, *Sprattus*, *Hyperlophus*, *Potamalosa* and the Alosidae (Fig. 26E), and some dorosomatids (*Escualosa*, *Lile*, *Platanichthys*, *Rhinosardinia*), whereas it is very large, with its tip extending beyond the anterior border of the dorsal arm of the cleithrum in all the other dorosomatids (Fig. 26F).

260. Lateral flange of the cleithrum (S126): (0) absent; (1) present.

Description. In most clupeoids the cleithrum bears a very thin, fan-shaped lateral flange with an elongated perforation or a deep medial notch. However, *Denticeps*, the engraulids, *Dussumieria*, *Spratelloides*, some pristigasterids (*Chirocentrodon*, *Ilisha*, *Odontognathus*, *Pellona*), *Escualosa*, *Hyperlophus* and *Potamalosa* lack this lateral flange. A lateral flange of the cleithrum is absent also in the outgroups (Forey 1973b; Markle 1976; Fink & Fink 1981).

261. Dorsal process of posttemporal (Z22, DD85): (0) subtriangular, sharp distally; (1) sub-rectangular and plate-like; (2) subtriangular, wider at distal tip than at its midlength.

Description. The dorsal process of the posttemporal in most clupeiforms is subtriangular and sharp distally, decreasing gradually in thickness from its base to the distal tip (Figs 23A, B; 26A, B; 27A, C-F). However, in *Chirocentrus*, *Jenkinsia*, *Spratelloides*, all the engraulids (except *Coilia*, *Lycothrissa* and *Stolephorus*) and †*Santanaclupea*, the dorsal process is subtriangular, but wider at distal tip than at its midlength (Figs 23D, E, G; 26B; 27B). A thick and robust sub-rectangular dorsal process of the posttemporal, as almost wide at distal tip as at its midlength, is characteristic of †*Cynoclupea*, *Odontognathus*, *Opisthopterus*, and some †Ellimmichthyiformes, including †*Ellimma*, †*Ellimmichthys*, †*Guiclupea*, †*Paraclupea*, †*Scutatoclupea*, †*Scutatuspinosus* and †*Triplomystus* (Figs 23C, F; 26C) (see Zaragüeta Bagils 2004; Marramà *et al.* 2022), whereas †*Sorbinichthys* has a dorsal process of the posttemporal that is reminiscent of that of most engraulids, being subtriangular, wider at distal tip than at its midlength (Fig. 23H) (see also Bannikov & Bacchia 2000; Murray & Wilson 2011); all the other †ellimmichthyiforms (e.g., †*Armigatus*, †*Diplomystus*, etc) have a triangular dorsal process, sharp at its distal tip).

262. First postcleithrum (S124): (0) absent; (1) present.

Description. Teleosts are primitively characterized by the presence of three postcleithra (first=dorsal; second=middle; third=ventral) (Sato 1994; Johnson & Patterson 1996). The first postcleithrum (corresponding to the “third, scale-shaped cleithrum” of Grande 1985) is usually laminar or scale-like and articulated between cleithrum and supracleithrum. It is present in most extant Clupeiformes, except *Chirocentrus*, *Jenkinsia*, some engraulids (*Anchoviella*, *Cetengraulis*, *Encrasicholina*, *Lycengraulis*, *Lycothrissa*), some ehiravids (*Clupeoides*, *Clupeichthys*, *Corica*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa* and *Stolothrissa*), *Hyperlophus*, and the pristigasterid *Opisthopterus* (Grande 1985; Sato 1994; Di Dario 2004b). Although Sato (1994) reported the first postcleithrum in *Spratelloides*, we agree with Grande (1985) and Di Dario (2004b) in observing no first postcleithrum in this taxon. In fossil clupeiforms, the first scale-like or laminar postcleithrum has been observed in †*Cynoclupea*, †*Eoengraulis*, †*Leufuichthys*, †*Nolfia*, and †*Pseudoellimma* (Figueiredo 2009a, b; Malabarba & Di Dario 2017). The first postcleithrum is present in most of the †Ellimmichthyiformes (Fig. 27D, F) although no postcleithra were reported for †*Ellimma longipectoralis* and †“*Ellimmichthys*” *spinosus* (Polck *et al.* 2020; Figueiredo & Gallo 2021). Postcleithra (including the first one) are absent in *Alepocephalus*, the Gonorynchiformes, and *Osmerus*, whereas *Albula* and likely †*Tischlingerichthys* have all the three postcleithra (Gosline 1969; Forey 1973b; Fink & Fink 1981; Johnson & Patterson 1996), although in this late Jurassic ostariophysan only the third one has been recognized (Arratia 1997).

263. Second postcleithrum (G23, S124): (0) absent; (1) present.

Description. The second postcleithrum is articulated to the medial side of the first postcleithrum (or sometimes to the ventral margin of supracleithrum) and its shape varies from scale/laminar-like to rod-like (at least at its distal tip) (Grande 1985; Sato 1994). It is present in most clupeiforms, including the fossil †*Bolcaichthys*, †*Cynoclupea*, †*Eoalosa*, †*Gosiutichthys*, †*Italoclupea*, †*Knightia*, †*Leufuichthys*, †*Nardoclupea*, †*Nolfia*, †*Pseudoellimma*, †*Scombroclupea* and †*Trollichthys* (Figs 26D-F, 27C) but it is absent in *Denticeps*, *Chirocentrus*, *Dussumieria*, *Jenkinsia* and *Spratelloides*, *Clupeoides*, and all the Engraulidae and Pristigasteroidea (Fig. 26A-C), (Grande 1985; Sato 1994; Di Dario 2004b). Except for †*Ellimma longipectoralis* and †“*Ellimmichthys*” *spinosus*, the second postcleithrum has been observed in several †ellimmichthyiforms (Fig. 27D).

264. Third postcleithrum (G23): (0) absent; (1) present.

Description. The third postcleithrum, when present, is articulated proximally to the second postcleithrum, whereas its distal tip is free and directed posteroventrally, with its shape being almost always rodlike (at least at its distal tip) and sometimes bifurcating distally (Sato 1994). Like the second one, the third postcleithrum is present in most clupeiforms, including the fossil †*Bolcaichthys*, †*Eoalosa*, †*Gosiutichthys*, †*Italoclupea*, †*Knightia*, †*Nardoclupea*, †*Nolfia*, †*Scombroclupea* and †*Trollichthys* (Figs 26D- F; 27C) but not in *Denticeps*, *Chirocentrus*, *Dussumieria*, *Jenkinsia* and *Spratelloides*, all the Engraulidae and Pristigasteroidea, and *Clupeoides* (Fig. 26A-C) (Grande 1985; Sato 1994; Di Dario 2004b). The third postcleithrum has not been observed in the †Ellimmichthyiformes.

265. Shape of the second postcleithrum (G23): (0) scale- or spatula-like; (1) rod-like (at least distally).

Description. In the majority of the Clupeiformes having the second postcleithrum this is always rod-like, at least distally (Figs 26D-F; 27C). In *Albula*, the basal clupeiforms †*Cynoclupea*, †*Leufuichthys* and †*Pseudoellimma* and all the †ellimmichthyiforms the second postcleithrum is scale or spatula-like, whereas †*Sorbinichthys elusivo* is the only †ellimmichthyiform whose postcleithra have been described as rod-like (Bannikov & Bacchia 2000; Gallo *et al.* 2011; Malabarba & Di Dario 2017; Marramà & Carnevale 2023).

266. Shape of the third postcleithrum (G23): (0) scale- or spatula-like; (1) rod-like.

Description. In clupeiforms having the third postcleithrum this is always rod-like (Figs 26D-F; 27C) (Grande 1985; Sato 1994, Di Dario 2004b), including those fossil taxa in which they have been recognized (e.g., Marramà & Carnevale 2015a, b). In *Albula* and †*Tischlingerichthys* this bone is scale- or spatula-like (Forey 1973b; Arratia 1997).

267. Anterior (proximal) margin of the second rod-like postcleithrum (G23): (0) not expanded; (1) moderately or broadly expanded in a laminar bone.

Description. In clupeoid taxa having the second postcleithrum rod-like, Grande (1985) distinguishes two main shapes based on the aspect of its anterior margin (articulated to the first postcleithrum or directly to the supracleithrum). In some ehiravids (*Clupeichthys*, *Corica*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa* and *Stolothrissa*) the anterior margin is not expanded, being rod-like, similarly to its distal tip, making the entire bone rod-like (Fig. 26D). In all the other taxa with the second rod-like postcleithrum, its anterior margin is moderately or broadly expanded forming a laminar bone (Fig. 26E, F).

268. Articulation of the first rod-like postcleithrum (=second postcleithrum) with supracleithrum (G*p*, S123): (0) either overlapping or at least close against the cleithrum; (1) well behind the cleithrum.

Description. Some ehiravids (*Clupeichthys*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*) are unique among clupeiforms in having the articulation between the anterior end of the first rod-like postcleithrum (=second postcleithrum) and the posterior end of the supracleithrum well behind the cleithrum (Fig. 26D), whereas in all the other clupeomorph taxa with two rod-like postcleithra, the first one is either overlapping or at least close against the cleithrum (Figs 26E, F; 27C) (see Grande 1985).

269. Mesocoracoid (S128): (0) present; (1) absent.

Description. The mesocoracoid is a small, dorso-ventrally elongate bone, located in the mesial side of the pectoral girdle, articulating to the scapula and to coracoid. It is present in all the outgroups and clupeiforms, except in the pristigasteroids *Chirocentrodon* and *Neoopisthopterus* (Sato 1994; Johnson & Patterson 1996; Di Dario 1999). Being very small and usually obscured by the overlying larger bones, it has never been observed in fossil taxa, except in †*Armigatus simonettoi* (Amalfitano *et al.* 2025) and in a three-dimensionally preserved specimen of †*Diplomystus* (Forey 2004).

270. Posteriorly directed process on the posteroventral margin of the coracoid (D85): (0) present; (1) absent.

Description. The posteroventral margin of the coracoid bears a posteriorly directed process in most clupeiforms (Fig. 26B, D-F) (including the fossil †*Cynoclupea* and †*Pseudoellimma*). However, this process is absent in *Denticeps*, the engraulids *Anchoa*, *Anchovia*, *Coilia*, *Pterengraulis*, *Setipinna* and *Thryssa* (unknown in *Anchoviella*), and the pristigasteroids (but present in *Pellona* and *Ilisha*). However, it is absent in most †Ellimmichthyiformes, except †*Gasteroclupea* (Fig. 27E), †*Ornategulum* and †*Ranulfoichthys* (Forey 1973a; Alvarado-Ortega 2014). This process is present in all the outgroups (Forey 1973b; Diogo *et al.* 2008).

271. Size of the coracoid (S127): (0) small, its depth less than 1/3 of the body depth; (1) large, its depth at least 1/3 (or more) the body depth.

Description. In teleosts (including our outgroups and the clupeomorphs) the coracoid is usually small in relation to the body depth and, consequently, the ratio between its depth and the body depth is less than 0.3. However, in some pristigasteroids (*Ilisha*, *Odontognathus*, *Opisthopterus*, *Pristigaster* and *Raconda*; Fig. 26C) and †*Gasteroclupea* (Fig. 27E) the coracoid is deep and the coracoid depth/body depth ratio is therefore equal to or greater than 0.3 (Di Dario 1999; Marramà & Carnevale 2017).

272. Holes in the surface of the coracoid (K110): (0) absent; (1) present.

Description. In teleosts, including all †ellimmichthyiforms and most of clupeiforms, the surface of the coracoid is usually smooth and unperforated (Fig. 26A-D). In the clupeids *Clupea* and *Sprattus*, and the dorosomatids *Clupanodon*, *Dorosoma*, *Nematalosa*, the surface of the coracoid is pierced by subcircular holes for the passage of nerves and blood vessels (Fig. 24E, F).

273. Distribution of the holes on the surface of the coracoid (K110): (0) mostly covering its posterior part; (1) covering most of coracoid surface, including the anteroventral part.

Description. In *Clupanodon*, *Dorosoma*, and *Nematalosa* the coracoid is usually only perforated in its posterior part (Fig. 26F), whereas the coracoid of *Clupea* and *Sprattus* can be also pierced by holes covering most of the coracoid surface, including its anteroventral part (Fig. 26E).

274. Cleithrum-coracoid fenestra (DD430): (0) present; (1) absent.

Description. The cleithrum-coracoid fenestra is a gap or opening between the posteroventral margin of the cleithrum and the antero-dorsal margin of the coracoid that allows for the passage of muscles, nerves, or blood vessels between the cleithrum and coracoid, aiding in the movement and control of the pectoral fins. It is present in outgroups (unknown in †*Tischlingerichthys*) (Gosline 1969; Forey 1973b; Di Dario 2004b) and in all the †Ellimmichthyiformes (Fig. 25D-F). Among the Clupeiformes, the cleithrum-coracoid fenestra is present only in *Denticeps*, *Chirocentrus* (Fig. 26B), *Dussumieria*, *Etrumeus*, *Jenkinsia*, the basal engraulids *Coilia*, *Lycothrissa*, *Setipinna*, and *Thryssa*, and in the fossil clupeiforms †*Italoclupea*, †*Nolfia*, †*Pseudoellimma*, †*Santanaclupea* and †*Scombroclupea* (Fig. 27B, C) (unknown in †*Cynoclupea* and †*Leufuichthys*); it is absent in all the other clupeiforms (Di Dario 2004b).

275. Size of cleithrum-coracoid fenestra (DD430): (0) reduced; (1) large.

Description. The cleithrum-coracoid fenestra is small, reduced to a fissure in *Albula*, *Kneria*, and the clupeiforms *Denticeps*, *Chirocentrus* (Fig. 26B), *Coilia*, *Lycothrissa*, *Setipinna* and *Thryssa*, whereas it is large and ovoid in *Chanos*, *Osmerus*, the clupeiforms *Dussumieria*, *Etrumeus*, *Jenkinsia* (Di Dario 2004b), the fossil clupeiforms †*Italoclupea*, †*Pseudoellimma*, †*Santanaclupea* and †*Scombroclupea*, and all the †Ellimmichthyiformes (Fig. 27B-F).

276. Pelvic fins (G*c*): (0) present; (1) absent.

Description. Pelvic fins are typically present in most teleost (e.g., Yamanoue *et al.* 2010). However, in some pristigasteroids, including *Neoopisthopterus*, *Odontognathus*, *Opisthopterus*, *Pliosteostoma*, *Pristigaster* and *Raconda* (Fig. 1H), the pelvic fins are absent (e.g., Grande 1985). Among †ellimmichthyiforms, †*Gasteroclupea* (Fig. 3E) is the only taxon that lacks the pelvic fins (Marramà & Carnevale 2017).

277. Number of pelvic-fin rays (K115): (0) six or less; (1) seven; (2) eight; (3) nine; (4) ten or more.

Description. Although the number of pelvic-fin rays is moderately variable in clupeiforms, it is often diagnostic at family level (Whitehead 1985). A pelvic fin containing six or less rays is typical of *Denticeps* (Mertzen 2019) and *Chirocentrodon*. All the engraulids plus *Chirocentrus*, *Brevoortia*, †*Chasmoclupea*, *Escualosa*, *Pellona* and *Platanichthys* have seven pelvic-fin rays. Nine fin rays in the pelvic fins are only present in *Alosa*, *Clupea* and *Sardinella*. Multistate characters have been coded for *Ilisha* (6 or 7 rays) and *Sprattus* (7 or 8), whereas all the other clupeoids have eight pelvic-fin rays (Whitehead 1985). Ten or more pelvic-fin rays are present in *Albula* and *Chanos*, whereas *Kneria* and *Osmerus* possess eight rays, and *Alepocephalus* can have seven or eight rays (Froese & Pauly 2025). We preferred to not provide coding for fossil taxa since their pelvic-fin count can be easily biased by taphonomy and/or the overlap of the two contralateral pelvic fins. A preliminary analysis including also this coding for fossil taxa, produced a tree with lower statistical support and a higher number of steps. Moreover, as the number of pelvic-fin rays might be diagnostic at family level (Whitehead 1985), our choice will avoid wrong taxonomic placement due to taphonomic biases.

278. Basipterygium (G*c*): (0) present; (1) absent.

Description. The basipterygium is typically present in the majority of teleosts (see, e.g., Yamanoue *et al.* 2010). However, in some pristigasteroids, including *Neoopisthopterus*, *Odontognathus*, *Opisthopterus*, *Pliosteostoma*, *Pristigaster* and *Raconda* the pelvic girdle is absent (e.g., Grande 1985). Among †ellimmichthyiforms, †*Gasteroclupea* is the only taxon that lacks the basipterygium (Marramà & Carnevale 2017).

279. Anterior notch (and bifurcation) of the basipterygium (S132): (0) absent; (1) present.

Description. The basipterygium is usually slender and anteroposteriorly elongated in teleosts, characterized by a single anterior tip. In the engraulids *Coilia*, *Setipinna* and *Thryssa*, and in the pristigasteroids *Ilisha* and *Pellona* the anterior portion of the basipterygium bears an indentation that separates two small and rodlike anterior processes (Sato 1994; Di Dario

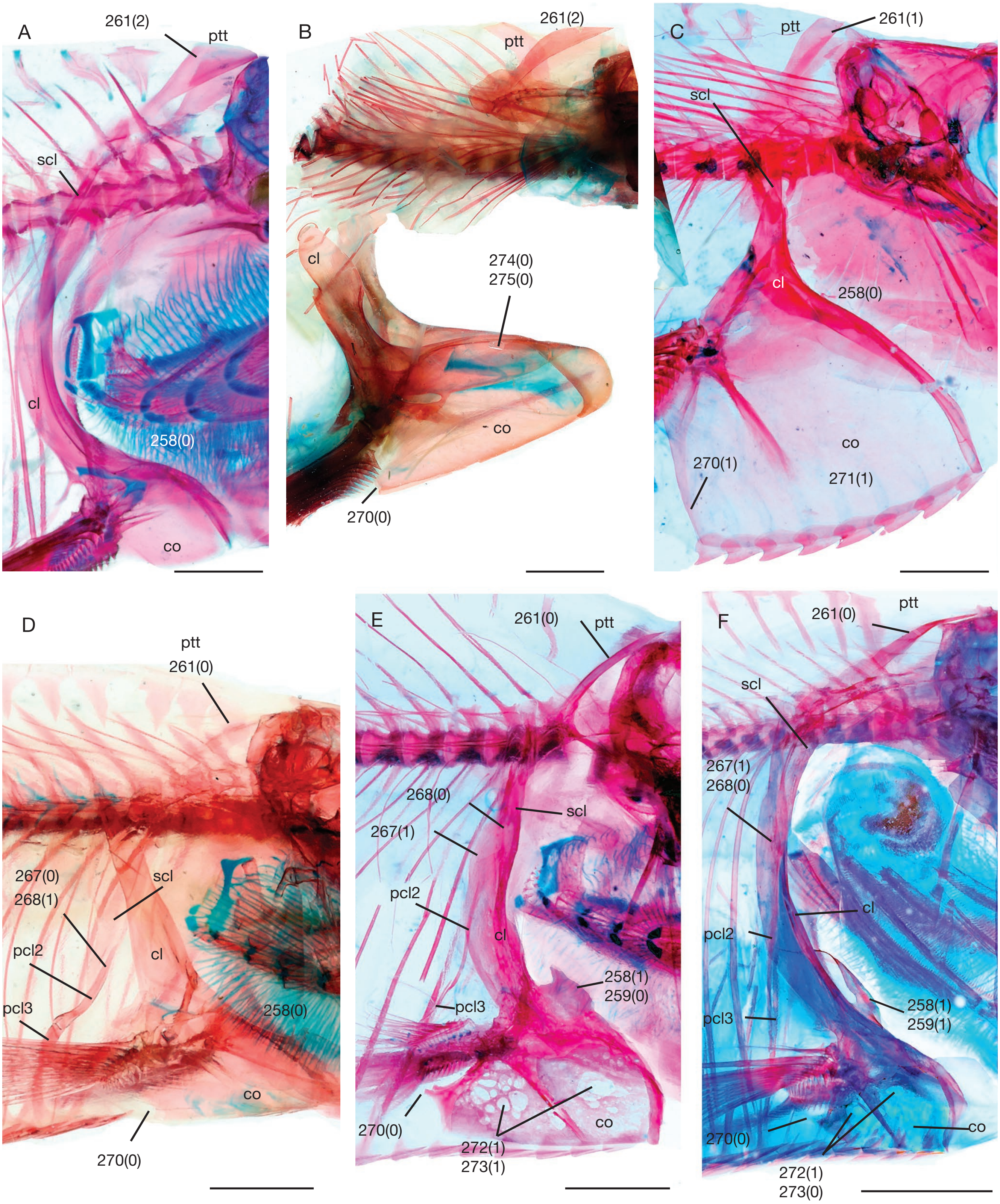

FIG. 26. — Pectoral girdle of selected clupeiforms: **A**, *Anchovia clupeoides* (Swainson, 1839) (Engraulidae), AMNH 224937; **B**, *Chirocentrus dorab* (Forsskål, 1775) (Chirocentridae), AMNH 55306; **C**, *Odontognathus mucronatus* Lacépède, 1800 (Pristigasteridae), AMNH 20749; **D**, *Potamothrissa obtusirostris* (Boulenger, 1909) (Ehiravidae), AMNH 5843; **E**, *Sprattus sprattus* (Linnaeus, 1758) (Clupeidae), AMNH 36845; **F**, *Dorosoma petenense* (Gunther, 1867) (Dorosomatidae), AMNH 54607. Scale bars: 2 mm. Abbreviations: **cl**, cleithrum; **co**, coracoid; **pcl2**, second postcleithrum; **pcl3**, third postcleithrum; **ptt**, posttemporal; **scl**, supracleithrum. Numbers refer to characters and character states (see text).

1999). *Alepocephalus* is the only other taxon to bear an anterior indentation (and bifurcation) on the basipterygium (Gosline 1969). †*Gasteroclupea*, *Neoopisthopterus*, *Odontognathus*, *Opisthopterus*, *Pliosteostoma*, *Pristigaster* and *Raconda* where coded as inapplicable (-) since they lack the basipterygium.

280. Pelvic-fin insertion (C22, K114): (0) placed anterior to the dorsal-fin origin; (1) at level of the dorsal-fin base; (2) behind the dorsal-fin base and closer to the caudal-fin base than to the pectoral-fin insertion.

Description. In clupeomorphs, the position of the pelvic-fin insertion with respect to the dorsal-fin is quite variable. Among clupeiforms, in *Denticeps*, †*Palaeodenticeps*, †*Leufuichthys*, *Chirocentrus*, all the Engraulidae, the pristigasteroids *Chirocentrodon*, *Ilisha* and *Pellona*, some ehiravids (*Clupeoides*, *Corica*, *Gilchristella*, *Microthrissa* and *Nannothrissa*), the dorosomatid *Rhinosardinia*, (Figs 1A, D-G, J, M; 2A, H), and the †ellimmichthyiforms †*Diplomystus*, †*Ellimmichthys*, †*Foreyclupea*, †*Guiclupea*, †*Eoellimmichthys*, †*Ezkutuberezi* and †*Scutatuspinosus*, the pelvic fins insert anterior to the dorsal-fin origin (Fig. 3D, G, H). In most of the other clupeomorphs the pelvic fins insert at the level of or posterior to the dorsal-fin origin (Figs 1B, I, K, L, N; 2B-G, I, J), but *Etrumeus* (Fig. 1C) and the †paraclupeids †*Rhombichthys* and †*Scutatoclupea* are the only taxa in which the pelvic fins originate behind the dorsal-fin base and closer to the caudal-fin base than to the pectoral-fin insertion (Khalloufi *et al.* 2010; Bannikov 2015). Among the outgroups, *Alepocephalus* is the only one to have pelvic fins originating anterior to the dorsal-fin origin.

Caudal skeleton

281. Number of hypurals (CM21): (0) six; (1) seven; (2) five.

Description. The presence of six hypurals has been considered as a clupeocephalan synapomorphy by Patterson & Rosen (1977). Among the examined taxa, most of the outgroups and clupeomorphs have six hypurals (Figs 28; 29; 30B-F; 31C-F). Among clupeiforms, denticipitids, †*Pseudoellimma* and †*Santanaclupea* have five hypurals (Fig. 28A) (see Greenwood 1968; Maisey 1993; Figueiredo 2009a), as well as the peculiar †ellimmichthyiform †*Sorbinichthys* (Fig. 31A) (Bannikov & Bacchia 2000; Murray & Wilson 2011), and the basal ostariophysan †*Tischlingerichthys* (Arratia 1997). †*Ornategulum* (Fig. 31B), †*Ranulfoichthys* and likely †*Diplomystus shengliensis* are unique in having seven hypurals (Forey 1973a; Chang & Maisey 2003; Alvarado-Ortega 2014).

282. Proximal end of the hypural 1 (CM27): (0) reaching and articulating to the first ural centrum; (1) truncated, failing to articulate to the first ural centrum.

Description. The first hypural is long and articulates with the first ural centrum (or to the compound centrum) in most of teleosts, including *Albula*, *Alepocephalus*, *Osmerus* and †*Tischlingerichthys* (Forey 1973b; Arratia 1997). In clupeomorphs, this appears to be the plesiomorphic condition, being present in denticipitids, the basal clupeiforms †*Leufuichthys*, †*Pseudoellimma*, and †*Santanaclupea*, the basal clupeoids †*Nolfia*, †*Italoclupea* and †*Scombroclupea* (Fig. 28A; 29A, B) (the posterior part of body is missing in †*Cynoclupea*) and in all the †Ellimmichthyiformes (Fig. 31) (Greenwood 1960; Maisey 1993; Chang & Maisey 2003; Zaragüeta Bagils 2004; Figueiredo 2009a, b; Gallo *et al.* 2011). Conversely, in all fossil and extant Clupeoidei (except †*Nolfia*, †*Italoclupea* and †*Scombroclupea*) the first hypural has a reduced proximal region that does not contact the compound centrum, leaving a hiatus in between and resulting in the complete separation of hypural 1 from the compound centrum (Figs 28B-F; 29; 30C-F) (Grande 1985). This latter condition is also shared by *Chanos* (in which it articulates proximally with the parhypural) and *Kneria* (Fink & Fink 1996; Davis *et al.* 2013; Schultze & Arratia 2013).

283. Proximal end of the hypural 1 (Z26): (0) massive, forming a well-developed articulatory process; (1) sharp, with no articulatory process.

Description. The proximal surface of the first hypural in teleosts is usually massive and expanded, forming a broad process articulating with the first ural or compound centrum (like in *Albula*, *Alepocephalus*, *Kneria*, *Osmerus*, †*Tischlingerichthys*) or with the proximal end of the parhypural (e.g., *Chanos*) (Fink & Fink 1996; Davis *et al.* 2013; Schultze & Arratia 2013); this appears to be also the basal condition in Clupeiformes being present in denticipitids, †*Pseudoellimma*, †*Santanaclupea* (Figs 28A; 30A) (Greenwood 1960; Maisey 1993; Gallo *et al.* 2011). A massive proximal end of the first hypural represents the plesiomorphic state in †Ellimmichthyiformes, being present in †*Armigatus* and in most of the †Paraclupeidae (Fig. 31A, D-F) (see Zaragüeta Bagils 2004; Marramà & Carnevale 2023). In †*Leufuichthys* and most of the living and fossil Clupeoidei, including †*Nolfia*, †*Italoclupea* and †*Scombroclupea*, the proximal end of the first hypural is sharp and triangular, with no articulatory process (Figs 28B-F; 29; 30B-F). The same condition is present in the †ellimmichthyiforms †*Ornategulum* and †*Ranulfoichthys*, but also in †*Diplomystus*, †*Gasteroclupea*, †*Guiclupea*, †*Scutatoclupea* and †*Triplomystus* (Fig. 31B, C) (Bannikov 2015; Marramà & Carnevale 2023).

284. Hypural 2 (G4, CM22): (0) autogenous; (1) fused to the first ural centrum.

Description. The fusion between the second hypural and the first ural centrum is traditionally considered a synapomorphy shared by all the clupeomorphs (Figs 28-30; 31B-

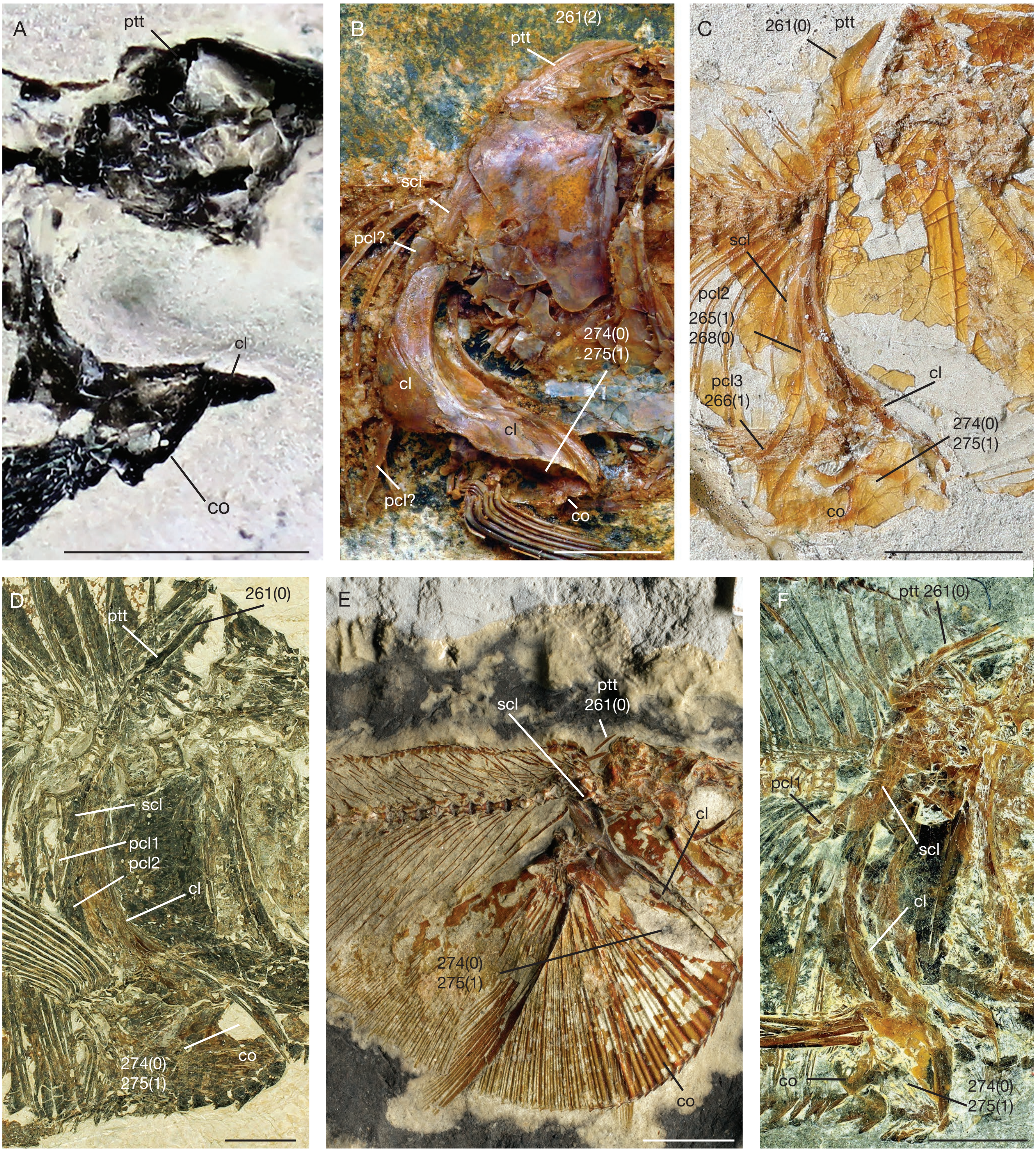

Fig. 27. — Pectoral girdle of selected fossil clupeomorphs. **A**, †*Palaeodenticeps* sp. (Clupeiformes: Denticipitidae), uncatalogued specimen from Museum für Naturkunde, Berlin (photo: courtesy of Gloria Arratia); **B**, †*Santanaclupea silvasantoi* Maisey, 1993 (Clupeiformes: †Cynoclupeidae), AMNH DVP.18968 (photo: courtesy of Lorraine Meeker); **C**, †*Italoclupea nolfi* Taverne, 2007 (Clupeiformes: Clupeoidei *incertae sedis*), MCSNV Na43; **D**, †*Diplomystus dentatus* Cope, 1877 (†Ellimmichthyiformes: †Gasteroclupeidae), NHMUK PV P.52501 (reversed); **E**, †*Gasteroclupea branisai* Signeux, 1964 (†Ellimmichthyiformes: †Gasteroclupeidae), MNHN F.1963.11.1; **F**, †*Armigatus namourensis* Forey, Yi, Patterson & Davies, 2003 (†Ellimmichthyiformes: †Armigatidae), NHMUK PV P.62528. Scale bars: 5 mm. Abbreviations: **cl**, cleithrum; **co**, coracoid; **pcl2**, second postcleithrum; **pcl3**, third postcleithrum; **ptt**, posttemporal; **scl**, supracleithrum. Numbers refer to characters and character states (see text).

F) although not unique to this group (present, e.g., in some characoids) (Grande 1985; Lecointre & Nelson 1996). The †ellimmichthyiform †*Sorbinichthys* is the only clupeomorph in which the hypural 2 is apparently autogenous (Fig. 31A) (Bannikov & Bacchia 2000). The condition is unknown in †*Spratticeps* (Patterson 1970).

285. Shape of the hypural 2 (Z27): (0) triangular, distal end distinctly broader than proximal end; (1) stick-like, distal end as wide as the proximal end; (2) triangular, distal end distinctly narrower than proximal end.

Description. The shape of the second hypural of teleosts usually resembles that of the other hypurals, being triangular, with a distal end broader than its proximal end, as in *Albula*, *Alepocephalus* and *Osmerus* (Forey 1973b; Arratia 2018). In clupeomorphs this shape is only typical of denticipitids (Fig. 28A), the basal clupeiform †*Leufuichthys*, and the †ellimmichthyiform †*Sorbinichthys* (Fig. 31A) (Greenwood 1968; Bannikov & Bacchia 2000; Gallo *et al.* 2011). Conversely, most of the other clupeiforms and †ellimmichthyiforms are unique in having the hypural 2 stick-like, with its distal end as wide as the proximal end (Figs 28B, D-F; 29; 30A, B, D-F; 31B-F), whereas *Dussumieria*, *Etrumeus* and †*Nardoclupea* are unique, among clupeomorphs, in having the hypural 2 triangular with its distal end distinctly narrower than the proximal end (Figs 28C; 30C) (Sato 1994; Taverne 2002).

286. Posterior margin of the hypural 2 (S147): (0) in line with that of the other hypurals; (1) not in line with that of the other hypurals (shorter posteriorly).

Description. In most teleosts the posterior margin of the second hypural is in line with that of the other hypurals (Figs 28A, B, D-F; 29; 30A, B, D-F; 31), whereas *Dussumieria* and †*Nardoclupea* are unique in having the hypural 2 shorter than other hypurals with its posterior margin not in line that of the other hypurals (Figs 28C; 30C).

287. Bases of the hypurals 1 and 2 (new): (0) joined by cartilage; (1) not joined by cartilage (and/ or bone).

Description. In early ontogeny of teleosts hypurals 1 and 2 are joined at their bases by cartilage or bone, as in *Albula*, *Alepocephalus* and *Osmerus*, whereas a cartilaginous connection between the bases of the first two hypurals is lacking in clupeomorphs and ostariophysans (Arratia 1999, 2018). In fossil clupeomorphs, there is no connection between the bases of the hypurals since the second one is always articulated with ural 1 (except in *Sorbinichthys*, where both hypurals are autogenous).

288. Hypural diastema (G21, S148, CM26): (0) present; (1) absent.

Description. The hypural diastema is a space between hypurals 2 and 3, or the notch positioned at the distal regions of these hypurals (Schultze & Arratia 2013). It is usually present in teleosts, including our outgroups and most of the Clupeiformes, including the basal †*Pseudoellimma* and †*Santanaclupea* (Figs 28A-E; 29; 30). The hypural diastema, however, is absent in †*Leufuichthys* and †*Nolfia*, some engraulids (*Encrasicholina*, *Lycothrissa*, *Setipinna* and *Thryssa*) and all the Pristigasteroidea (Fig. 28F), where the ventral posterior edge of the third hypural is nearly flush with that of the hypural 2, leaving no gap between the second and third hypurals (Grande 1985; Sato 1994; Di Dario 2004b). The absence of the hypural diastema is also the most common condition in †Ellimmichthyiformes (Fig. 31B-F), although a diastema was reported in †*Armigatus dalmaticus*, †*Codoichthys*, †"*Ellimmichthys*" *spinosus*, †*Sorbinichthys* (Fig. 31A), †*Tunisiaclupea* and †*Tycheroichthys* (e.g., Bannikov & Bacchia 2000; Murray *et al.* 2016). Contra Chang & Maisey (2003), we found that, like most of the other †ellimmichthyiforms, †*Ellimma branneri* has no diastema.

289. Shape of the hypural diastema (MW32): (0) large triangular cavity; (1) small triangular or concave notch.

Description. In *Chanos* and most clupeiforms, the hypural diastema is usually small, in form of a small and triangular or concave notch at the posterior base of the third hypural (Figs 28; 29; 30B-F). In the basal clupeiforms †*Pseudoellimma* and †*Santanaclupea*, however, the diastema is represented by a large and triangular space or cavity between the hypurals 2 and 3 (Fig. 30A), resembling the condition of the basal teleosts, including all the other outgroups and the few †ellimmichthyiforms that possess the hypural diastema (e.g., †*Sorbinichthys*, Fig. 31A).

290. Size of the hypural 3 (to hypural 1) (S149, FR55): (0) smaller or almost of the same size of hypural 1; (1) larger than hypural 1.

Description. In teleosts (including outgroups and most of the extant and fossil Clupeiformes) the third hypural is usually smaller or has almost the same size as the first hypural. However, in Pristigasteroidea (Fig. 28F) and in some †ellimmichthyiforms (†*Armigatus brevissimus*, †*A. elatus*, †*A. namourensis*, †*A. oligodentatus*, †*A. plinii*, the †Gasteroclupeidae, and the †paraclupeids †*Ellimmichthys*, †*Ezkutuberezi*, †*Paraclupea*, †*Rhombichthys*, †*Scutatuspinosus*, †*Thorectichthys*; Fig. 31C-F) the hypural 3 is larger than the hypural 1.

291. Upward process on the third hypural constraining the fourth hypural to project anteriorly (FR56): (0) absent or very poorly developed; (1) present and massive.

Description. Outgroups and Clupeiformes do not have any process in the proximal end of the hypural 3. Some †ellimmichthyiforms can have a very small upward process on the proximal end of the hypural 3 but not comparable with the larger process present in †*Rhombichthys*, †*Scutatoclupea* and †*Scutatuspinosus*, whose third hypural has an upward process constraining the fourth hypural to project forwardly (Figueiredo & Ribeiro 2016, 2017).

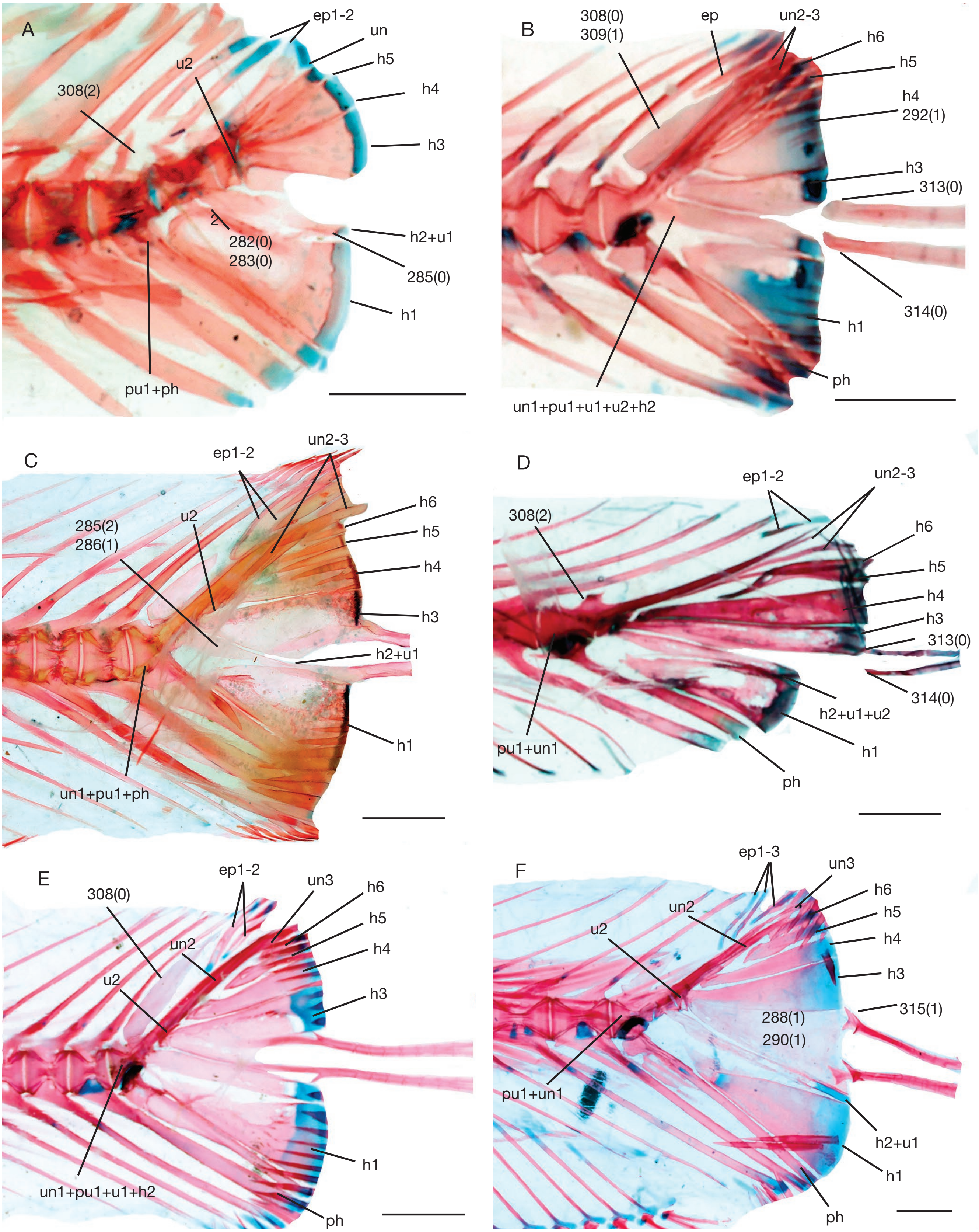

FIG. 28. — Caudal skeleton of selected living clupeiforms: **A**, *Denticeps clupeoides* Clausen, 1959 (Denticipitidae), AMNH 53082; **B**, *Jenkinsia lamprotaenia* (Gosse, 1851) (Spratelloididae), AMNH 28252; **C**, *Dussumieria acuta* Valenciennes, 1847 (Dussumieriidae), AMNH 17555; **D**, *Coilia brachygnathus* Kreyenberg & Pappenheim, 1908 (Engraulidae: Coiliinae), AMNH 10321; **E**, *Anchoa compressa* (Girard, 1858) (Engraulidae: Engraulinae), AMNH 2671; **F**, *Odontognathus mucronatus* Lacepede, 1800 (Clupeiformes: Pristigasteridae), AMNH 20749. Scale bars: 1 mm. Abbreviations: **ep**, epural; **h**, hypural; **ph**, parhypural; **pu**, preural centrum; **u**, ural centrum; **un**, uroneural. Numbers refer to characters and character states (see text).

292. Size of the hypural 4 (to hypural 1) (G*i*, S149): (0) smaller than hypural 1; (1) approximately symmetrical to the hypural 1.

Description. In teleosts (including the outgroups and most of the extant and fossil clupeomorphs) the fourth hypural is usually smaller than the hypural 1 (Figs 28A, C-F; 29-31). However, *Jenkinsia* and *Spratelloides* are unique in having the first and fourth hypurals approximately of the same size (Fig. 28B) (Grande 1985; Sato 1994).

293. Posterior margin of the upper hypurals (S150): (0) in line with the lower hypurals; (1) not in line (projecting more posteriorly).

Description. In most clupeomorphs, the posterior margins of the upper (third to sixth) hypurals are in line with the lower ones, forming a more or less pronounced arc (Figs 28A-C, E, F; 29-31). In the engraulid subfamily Coiliinae (*Coilia*, *Lycothrissa*, *Setipinna*, *Thryssa*), however, due to the posterior inclination of the pleurostylar rod, the upper hypurals (third to sixth in *Coilia*, fifth and sixth in the other genera) are more elongated and their posterior margins therefore project beyond those of the lower hypurals (Fig. 28D) (Grande & Nelson 1985; Sato 1994).

294. Size of the first ural centrum (G15, CM18): (0) approximately the same size as the preural centrum 1; (1) much smaller than the preural centrum 1.

Description. The first ural centrum in lower teleosts that have independent ural vertebrae at least at some ontogenetic stages is usually about equal in size to the first preural centrum. This is the case, e.g., of the outgroups, †Ellimmichthyiformes (except †*Ornategulum*; Forey 1973a), and basal Clupeiformes *Denticeps*, †*Palaeodenticeps*, †*Pseudoellimma* and †*Santanaclupea* (Figs 28A; 30A; 31A, C-F) (Fink & Fink 1981; Maisey 1993; Chang & Maisey 2003). On the other hand, †*Ornategulum* (Fig. 31B) and all the other fossil and extant clupeiforms share the reduction in size of the first ural centrum (Figs 28B-F; 29; 30B-F), considered by Grande (1985) to be a derived character for the Clupeoidei. This character is impossible to observe in the basal clupeiforms †*Cynoclupea* and †*Leufuichthys* due to taphonomic biases (Gallo *et al.* 2011; Malabarba & Di Dario 2017).

295. Caudal complex (PU1, U1, U2) in mature individuals (G*k*, G*o*, S143, 146): (0) all centra autogenous; (1) PU1+U1 fused, U2 autogenous; (2) PU1 autogenous, U1+U2 fused; (3) all PU1+U1+U2 fused.

Description. In teleosts the condition of the caudal complex including PU1, U1, and U2 in mature individuals is highly variable. In *Albula*, *Alepocephalus*, *Osmerus* and most clupeomorphs, the first preural centrum and both the ural centra are autogenous (Figs 28A, C, D, F; 29C-F; 30A, B, D-F; 31). In *Spratelloides*, numerous engraulids (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Encrasicholina*, *Engraulis*, *Lycengraulis* and *Pterengraulis*), most ehiravids (*Clupeichthys*, *Clupeonella*, *Corica*, *Gilchristella*, *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa* and *Stolothrissa*) and †*Scombroclupea*, PU1 is only fused to U1, whereas U2 is autogenous (Figs 28E; 29A, B) (Grande 1985; Sato 1994). *Coilia*, *Lycengraulis* and *Etrumeus* are the only clupeiforms in which PU1 is autogenous, but U1+U2 are fused together (Fig. 28D) (Grande 1985; Sato 1994; Schultze & Arratia 2013), whereas *Jenkinsia* and †*Nardoclupea* are the only clupeomorphs to have all PU1+U1+U2 fused into a single compound centrum (Figs 28B; 30C) (Grande 1985; Taverne 2002), resembling the condition of the ostariophysans *Chanos*, *Kneria* and †*Tischlingerichthys* (Fink & Fink 1981, 1996; Schultze & Arratia 2013).

296. Number of uroneurals (G13, Z29): (0) three or more; (1) two or one.

Description. Clupeiforms usually have three uroneurals (Figs 28B-F; 29; 30B-F). Among them, *Denticeps* and †*Palaeodenticeps* are unique in having lost the posterior two uroneurals (Fig. 28A), whereas †*Santanaclupea* and †*Scombroclupea* have two uroneurals (Fig. 30A) (Greenwood 1968; Maisey 1993; Forey *et al.* 2003). †Ellimmichthyiforms commonly have three uroneurals (Fig. 31) but the loss of one or two of them has been reported in †*Armigatus alticorpus*, †*A. dalmaticus*, †*Rhombichthys*, †*Scutatoclupea applegatei*, †*Triplomystus* and †*Tunisiaclupea* (e.g., Khalloufi *et al.* 2010; Vernygora & Murray 2021). Outgroups with less than three uroneurals include *Albula*, *Chanos* and *Kneria* (e.g., Forey 1973b; Poyato-Ariza *et al.* 2010).

297. Fusion of the first uroneural and first preural centrum, forming pleurostyle (G14, CM24): (0) absent; (1) present.

Description. The fusion of the first uroneural with the first preural centrum, forming pleurostyle, occurs in many ostariophysans (including *Chanos*, *Kneria* and †*Tischlingerichthys*) and the Clupeoidei (Figs 28B-F; 29; 30B-F) (e.g., Grande 1985; Arratia 1999). It does not occur in the Denticipitidae (Fig. 28A), the clupeiforms †*Leufuichthys*, †*Pseudoellimma* and †*Santanaclupea* (Fig. 28A), and in the †Ellimmichthyiformes (Fig. 31), other than in *Albula*, *Alepocephalus* and *Osmerus* (Greenwood 1968; Maisey 1993; Chang & Maisey 2003; Gallo *et al.* 2011).

298. Anterior tip of the first uroneural (CM25): (0) does not reach PU2; (1) reaches or extends anteriorly beyond the posterior margin of PU2.

Description. In *Albula*, *Chanos*, *Kneria* and most Clupeiformes the anterior tip of the first uroneural does not extend beyond the anterior margin of PU1 and lies between its an-

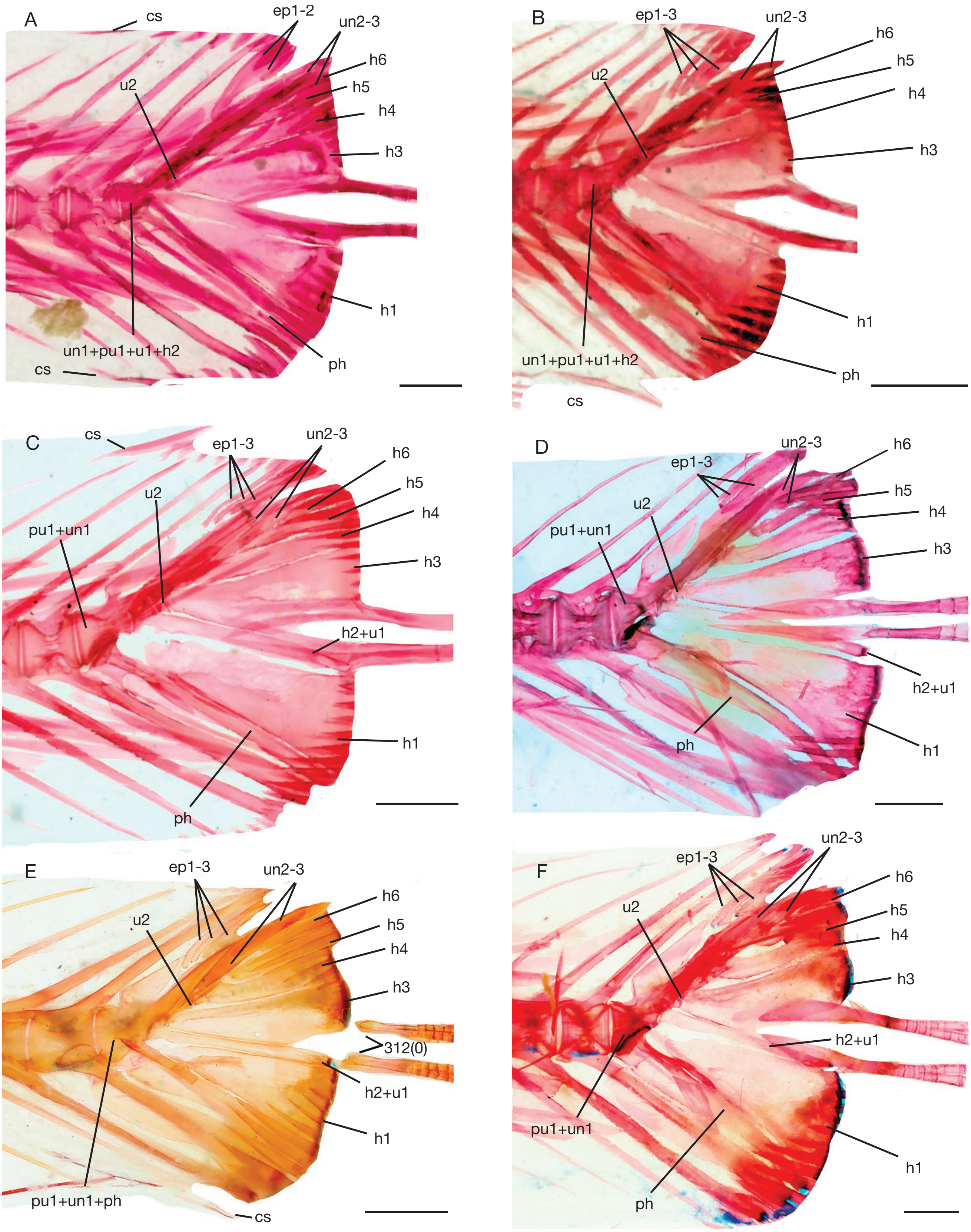

Fig. 29. — Caudal skeleton of selected living clupeiforms: **A**, *Corica soborna* Hamilton, 1822 (Ehiravidae: Ehiravinae), AMNH 55343; **B**, *Microthrissa royauxi* Boulenger, 1902 (Ehiravidae: Pellonulinae), AMNH 5830; **C**, *Hyperlophus vittatus* (Castelnau, 1875) (Hyperlophidae), AMNH 3050; **D**, *Sardinops sagax* (Jenyns, 1842) (Alosidae), AMNH 5449; **E**, *Amblygaster leiogaster* (Valenciennes, 1847) (Dorosomatidae), AMNH 17581; **F**, *Herklotsichthys dispilonotus* (Bleeker, 1852) (Dorosomatidae), AMNH 54611. Scale bars: 1 mm. Abbreviations: **cs**, caudal scute; **ep**, epural; **h**, hypural; **ph**, parhypural; **pu**, preural centrum; **u**, ural centrum; **un**, uroneural. Numbers refer to characters and character states (see text).

terior and posterior margins (or is fused to it) (Figs 28; 29; 30B-F). In †*Santanaclupea* and †*Pseudoellimma*, however, it extends anteriorly to reach or extends anteriorly beyond the posterior margin of the PU2 (Fig. 30A), resembling the condition of *Alepocephalus* and †*Tischlingerichthys*. In the †ellimmichthyiforms the condition is extremely variable. In †*Armigatus carrenoae*, †*A. elatus*, †*A. oligodentatus*, †*A. plinii*, †*Codoichthys*, †"*Ellimmichthys*" *spinosus*, †Gasteroclupeidae, †*Rhombichthys*, †*Scutatoclupea* and †*Sorbinichthys africanus*, the anterior tip of the uroneural 1 does not reach the posterior margin of PU2 (Fig. 31C), whereas in †*Armigatus alticorpus*, †*A. brevissimus*, †*A. dalmaticus*, †*A. felixi*, †*A. namourensis*, †*Ellimma*, †*Ellimmichthys longicostatus*, †*Ezkutuberezi*, †*Ornategulum*, †*Paraclupea*, †*Ranulfoichthys*, †*Sorbinichthys elusivo*, †*Tunisiaclupea* †*Thorectichthys* and †*Triplomystus* the anterior tip of the uroneural 1 reaches or extends anteriorly beyond the posterior margin of PU2 (Fig. 31A, B, D-F).

299. Membranous anterodorsal outgrowth of the uroneural 1 (Z33, DD409): (0) absent; (1) present on the autogenous uroneural 1; (2) present on the uroneural of the pleurostyle.

Description. Several non-eutelosts, including clupeomorphs (Forey 1973b; Di Dario 2004b) have a small, dorsal laminar bony expansion or outgrowth on the first uroneural resembling a stegural, although the homology with the true stegural of the Euteleostei is unlikely (stegural is a modified first uroneural bearing a membranous bony extension at its antero-dorsal border that is considered a synapomorphy of the Euteleostei and that is herein present only in *Osmerus*; Johnson & Patterson 1996; Schultze & Arratia 2013; Arratia 2018). Some authors (e.g., Lecointre 2010; Schultze & Arratia 2013; Arratia 2018) also hypothesize that the laminar outgrowth of the autogenous first uroneural (present for example in Alepocephaloidei, *Denticeps*, †Ellimmichthyiformes) might have different origin from that of the uroneural 1 when is fused to PU1 (e.g., *Chanos* and Clupeoidei). Since it is not clear if these latter two types of bony laminae are homologous, we prefer to include two different states. Dorsal laminar expansion on the autogenous uroneural 1 is present in *Albula*, *Alepocephalus*, *Denticeps* and several †ellimmichthyiforms (†*Armigatus alticorpus*, †*A. brevissimus*, †*A. carrenoae*, †*A. namourensis*, †*Ellimma longipectoralis*, †*Ezkutuberezi*, †*Ornategulum*, †*Ranulfoichthys*, †*Scutatuspinosus*, †*Triplomystus*, †*Tunisiaclupea* (e.g., Forey 1973a; Zaragüeta Bagils 2004). Similarly, a dorsal laminar expansion is present on the uroneural of the pleurostyle of some clupeoids (*Alosa*, *Clupanodon*, *Clupea*, *Clupeichthys*, *Clupeoides*, *Clupeonella*, *Corica*, *Dorosoma*, *Harengula*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Nematalosa*, *Opisthonema*, *Pellonula*, *Potamothrissa Potamalosa*, *Sardinella*, *Sardinops*, *Sprattus*, *Stolothrissa*) (see also Forey 1973a; Di Dario 2004b).

300. Distal end of the second uroneural (Z34): (0) reaching the distal end of the first uroneural; (1) not reaching the distal end of the first uroneural.

Description. The distal end of the second uroneural reaches the distal end of the first uroneural in most outgroups and clupeomorphs (Figs 28B-F; 29-31). However, it does not reach the distal end of the first uroneural in †*Thorectichthys*, †*Tunisiaclupea* and †*Tycheroichthys*. *Denticeps* and *Kneria* where coded as inapplicable (-) because of the absence of uroneural 2.

301. Parhypural (G17, G*h*, S141, CM20): (0) autogenous; (1) fused with the first preural centrum.

Description. The parhypural is ancestrally autogenous in teleosts, so as in *Albula*, *Alepocephalus*, ostariophysans, *Osmerus*, and most Clupeiformes. However, in denticipitids, †*Pseudoellimma*, †*Santanaclupea*, †*Scombroclupea*, *Dussumieria*, *Etrumeus*, †*Nardoclupea*, and some dorosomatids (*Amblygaster*, *Anodontostoma*, *Opisthonema*) the parhypural is fused to PU1 (Figs 28A, C; 29E; 30A, C) (Grande 1985; Sato 1994; Taverne 2002; Forey *et al.* 2003). The parhypural is always fused to the first preural centrum in the †Ellimmichthyiformes (Fig. 31) (e.g., Grande 1985; Chang & Maisey 2003).

302. Hypurapophysis (S142): (0) absent; (1) present.

Description. The hypurapophysis (also called parhypurapophysis) is a small, lateral process on the proximal part of the parhypural that serves as attachment for the hypochordal longitudinal muscle (Nursall 1963). It is present in *Albula*, *Chanos*, *Kneria* and all the Clupeiformes (except in †*Nolfia* and †*Pseudoellimma*) but is absent in *Alepocephalus* (Sato 1994; Mertzen 2019). This process has been reported in several †ellimmichthyiforms, including †*Armigatus*, †*Ellimmichthys*, †*Rhombichthys*, †*Tunisiaclupea*, †*Triplomystus*, †*Tycheroichthys* (e.g, Forey *et al.* 2003a; Khalloufi *et al.* 2010) but is apparently absent in the basal †*Ornategulum*, †*Scutatuspinosus* and †*Diplomystus* (Forey 1973a; Arratia 1999; Figueiredo & Ribeiro 2017).

303. Size of the hypurapophysis (to the parhypural) (new): (0) small; (1) large.

Description. The size of the hypurapophysis in *Albula*, *Chanos*, *Kneria*, *Osmerus*, *Denticeps* and engraulids is very small, in comparison to the rest of the Clupeiformes and †Ellimmichthyiformes in which it is prominent.

304. Number of epurals (G*j*, S152, CM23): (0) three; (1) two (2) one.

Description. Clupeiforms have generally three epurals (although in certain species, some individuals can have two or three epurals). Conversely, *Denticeps*, †*Leufuichthys*, †*Pseudoellimma*, †*Scombroclupea*, *Chirocentrus*, *Dussumieria*, all engraulids (except *Setipinna*), and some other clupeoids (*Brevoortia*, *Clupea*, *Clupeichthys*, *Clupeoides*, *Clupeonella*, *Corica*, *Dorosoma*, *Es-*

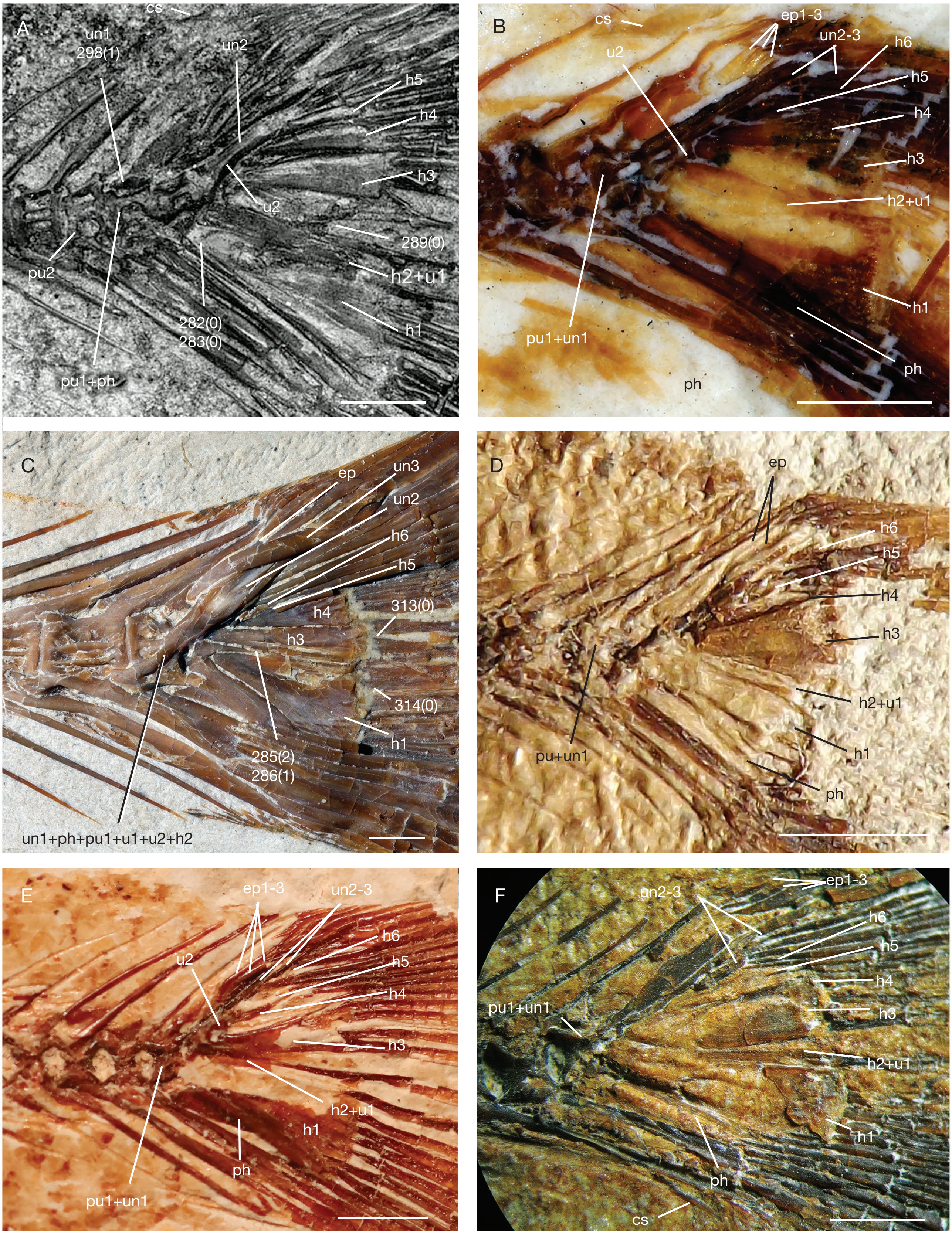

Fig. 30. – Caudal skeleton of selected fossil clupeiforms: **A**, †*Santanaclupea silvasantoi* Maisey, 1993 (†Cynoclupeidae), DNPM DGM 1338-P (photo: courtesy of Lorraine Meeker; reversed); **B**, †*Italoclupea nolfi* Taverne, 2007 (Clupeoidei *incertae sedis*), MCSNV Na538; **C**, †*Nardoclupea grandei* Taverne, 2002 (Dussumieriidae), MCSNV Na250; **D**, †*Eoengraulis fasoloi* Marramà & Carnevale, 2016 (Engraulidae), MCSNV T.54; **E**, †*Knightia eocaena* Jordan, 1907 (Hyperlophidae), MRSN P/109; **F**, †*Bolcaichthys catopygopterus* (Woodward, 1901) (pan-Dorosomatidae), MCSNV II.D.240. Scale bars: 1 mm. Abbreviations: **cs**, caudal scute; **ep**, epural; **h**, hypural; **ph**, parhypural; **pu**, preural centrum; **u**, ural centrum; **un**, uroneural. Numbers refer to characters and character states (see text).

cualosa, *Limnothrissa*, *Nannothrissa*, *Potamothrissa* and *Stolothrissa*) have two epurals (Figs 28A, C-E; 29A; 30D). Finally, *Jenkinsia*, †*Nardoclupea*, *Spratelloides* and †*Trollichthys* have a single epural (Figs 28B; 30C). We agree with Yabumoto & Uyeno (1981) that *Hyperlophus* can have up to three epurals (Fig. 29C). Most of †Ellimmichthyiformes have three epurals (Fig. 31), except †*Ezkutuberezi* that has been reported as having two (Poyato-Ariza *et al.* 2000). Among outgroups, *Albula* has two epurals, *Alepocephalus*, *Osmerus* and †*Tischlingerichthys* have three, the Gonorynchiformes have only a single epural (Forey 1973b; Fink & Fink 1996; Arratia 1997).

305. Position of the epurals (Z38): (0) filling the space between the first uroneural and the neural spine of the first or second preural vertebra; (1) located far from the spine of the first or second preural vertebra, leaving a space between the spine and the first uroneural.

Description. In the outgroups and most clupeomorphs, the epurals are located anterior to the first uroneural, filling the space between this bone and the neural spine of the (first or) second preural vertebra. In some †ellimmichthyiforms like †*Codoichthys*, †*Ornategulum*, †*Diplomystus*, †*Gasteroclupea* and †*Ranulfoichthys* the epurals are located far from the spine of the (first or second) preural vertebra, leaving a space between the spine and the first uroneural (Fig. 31B, C) (Zaragüeta Bagils 2004; Marramà *et al.* 2022).

306. Caudal scutes (CM17): (0) absent; (1) present.

Description. Caudal scutes (dorsal and ventral scutes preceding the caudal fin) are primitively present in teleost and occur also in *Albula*, *Chanos*, †*Tischlingerichthys*, *Osmerus* and clupeomorphs, but not in *Alepocephalus* or *Kneria* (e.g., Fujita 1990; Johnson & Patterson 1996). Caudal scutes are present in several fossil and living clupeiforms except in *Denticeps*, *Chirocentrus*, dussumieriids and spratelloidids, engraulids and pristigasteroids (Figs 28; 29) (Fujita 1990; Di Dario 2004b). We detected at least a dorsal caudal scute in †*Santanaclupea* (Fig. 30A) and likely it was present †*Palaeodenticeps* (contrary to *Denticeps*) as it can be seen in plate 3 of Greenwood (1960). They characterize also †*Italoclupea* (Fig. 30B), †*Nolfia* and †*Scombroclupea* but their presence in unknown in †*Leufuichthys* and †*Pseudoellimma*. Caudal scutes are also present in all the †Ellimmichthyiformes (Fig. 31B-D, F), except in †*Ellimma longipectoralis*, †*Ezkutuberezi*, †*Rhombichthys*, †*Scutatoclupea bacchiai* Bannikov, 2015, †*Sorbinichthys* and †*Tycheroichthys* (Fig. 31A, E) (e.g., Forey 1973a; Hay *et al.* 2007).

307. Size of the caudal scutes (new): (0) reduced, very thin; (1) robust and thick.

Description. In fossil and extant clupeiforms examined, the caudal scutes, when present, are usually very thin, resembling the shape of the dorsal and ventral procurrent rays. Conversely, the caudal scutes of †*Palaeodenticeps*, †*Italoclupea*, †*Nolfia*, †*Santanaclupea*, †*Scombroclupea*, and the †Ellimmichthyiformes are robust and thick, resembling those of *Albula*, *Chanos*, †*Tischlingerichthys* and *Osmerus*, suggesting that this is the ancestral condition in both the clupeomorphs and the clupeiforms.

308. Neural spine of the first preural centrum (S144, CM19): (0) almost as long as the neural spine of PU2; (1) short, about half of the length of the neural spine of PU2; (2) extremely reduced, 1/3 of the length of the neural spine of PU2 or less.

Description. In most of clupeomorphs, the neural spine on PU1 is of moderate size, being long about half of the length of the neural spine of the preceding preural centrum. Within the Clupeiformes, however, *Jenkinsia*, *Spratelloides*, the stem engrauline †*Eoengraulis* and all the engraulines (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Encrasicholina*, *Engraulis*, *Lycengraulis*, *Pterengraulis* and *Stolephorus*) have the neural spine of PU1 almost as long as the neural spine of PU2 (Fig. 28B, E) similar to that of the basal †*Leufuichthys*, †*Nolfia* and †*Pseudoellimma*, whereas *Denticeps* and *Colia* are unique in having an extremely reduced neural spine, being less than 1/3 of the length of the neural spine of PU2 (Fig. 28A, D). Among †ellimmichthyiforms, †*Ellimmichthys longicostatus*, †*Scutatoclupea*, †*Scutatuspinosus*, †*Sorbinichthys* and †*Tunisiaclupea* are the only taxa to possess a long neural spine on PU1 reaching almost the length of the spine of PU2 (Fig. 31A, E) (Bannikov & Bacchia 2000; Figueiredo & Ribeiro 2017). *Alepocephalus*, *Osmerus*, and ostariophysans share the condition of *Denticeps* and *Coilia* in having this spine extremely reduced, whereas it is about half of the length of PU2 in *Albula* (Forey 1973b; Grande & Poyato-Ariza 1999).

309. Fusion between most of the posterior margin of the neural spine of PU1 and the anterior margin of the first uroneural (S145): (0) absent; (1) present.

Description. In outgroups and most clupeomorphs the neural spine of PU1 is broadly separated from the first uroneural. *Chirocentrus*, *Jenkinsia* and *Spratelloides*, however, are unique among clupeomorphs in having the posterior margin of the neural spine of PU1 fused for most of its length to the anterior margin of the first uroneural, leaving no notch between these two structures (Fig. 28B).

310. Procurrent rays deeply inserted in the interneural and interhaemal spaces (MC60): (0) absent; (1) present.

Description. In the outgroups, clupeiforms and most †ellimmichthyiform genera, the procurrent rays of the caudal fin are short and do not reach the neural spines. However, the two species of †*Sorbinichthys* are unique among clupeomorphs in having the anteriormost procurrent rays deeply

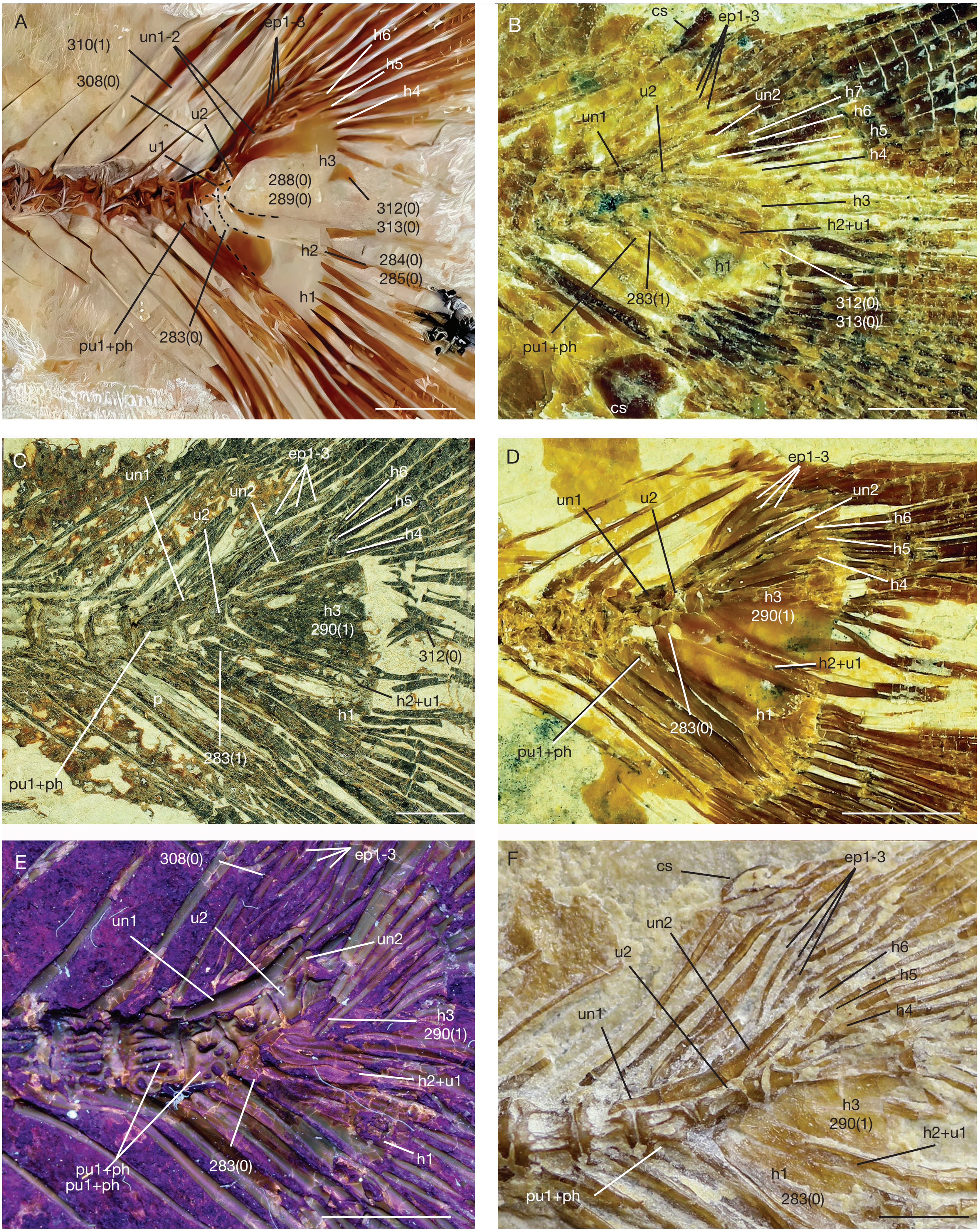

Fig. 31. — Caudal skeleton of selected †ellimmichthyiforms. **A**, †*Sorbinichthys elusivo* (†Sorbinichthyidae), CLC S-431a (photo: courtesy of Luigi Capasso); **B**, †*Ornategulum sardinioides* (†Scutatuspinosidae), NHMUK PV P.63293; **C**, †*Diplomystus dentatus* (†Gasteroclupeidae), NHMUK PV P.52501; **D**, †*Armigatus namourensis* (†Armigatidae), NHMUK PV P.63151; **E**, †*Ellimmichthys longicostatus* (†Paraclupeidae: †Ellimmichthyinae), AMNH 734 (under UV light); **F**, †*Paraclupea pietrarojae* (†Paraclupeidae: †Paraclupeinae), CMSNF M.19254 (reversed). Scale bars: 5 mm. Abbreviations: **cs**, caudal scute; **ep**, epural; **h**, hypural; **ph**, parhypural; **pu**, preural centrum; **u**, ural centrum; **un**, uroneural. Numbers refer to characters and character states (see text).

inserted between interneural and interhaemal spaces of the last caudal vertebrae (Fig. 31A) (Bannikov & Bacchia 2000; Murray & Wilson 2011).

311. Lateral crest of the hypural 1 (DD411): (0) absent; (1) present.

Description. A lateral crest running more or less anteroposteriorly on the first hypural is typically present in most clupeiforms, except in *Coilia*, *Denticeps*, *Chirocentrus*, *Etrumeus*, *Jenkinsia*, *Spratelloides*, most pristigasteroids (but present in *Ilisha* and *Pellona*), *Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*, and some ehiravids (*Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*) (Di Dario 2004b). Outgroups and examined †ellimmichthyiforms have no lateral crest on the first hypural.

312. Proximal region of median caudal-fin rays (S154): (0) not extending anteriorly; (1) extending anteriorly.

Description. In most clupeiforms (including the basal †*Santanaclupea*) the proximal region of the two median rays of the caudal fin extends anteriorly covering laterally about half of the length of the hypurals 2 and 3; however, in denticipitids, *Coilia*, *Amblygaster* and pristigasteroids (except *Ilisha* and *Pellona*; Di Dario 2004b), the proximal region of the two median caudal-fin rays does not extend anteriorly but only contacts or slightly overlaps the posterior margins of these hypurals 2 and 3 (Figs 28A, D, F; 29E). Most of †Ellimmichthyiformes, show the commonest condition seen in clupeiforms, except †*Codoichthys*, †*Diplomystus*, †*Gasteroclupea*, †*Guiclupea*, †*Ornategulum*, †*Scutatoclupea*, †*Scutatuspinosus*, and †*Sorbinichthys* in which median caudal-fin rays only contact the posterior margins of these two hypurals (Fig. 31A-C), resembling the plesiomorphic condition of teleosts, including the outgroups.

313. Peg on upper middle caudal-fin ray (S153): (0) absent; (1) present.

Description. In fossil and extant clupeomorphs the bases of the two middle caudal-fin rays usually show dorsal and ventral “pegs”. The peg on upper middle ray is present in most of the clupeiform taxa, except in denticipitids, *Coilia*, †*Nardoclupea*, *Jenkinsia* and *Spratelloides* (Figs 28A, B, D; 30C), whereas in †ellimmichthyiforms, the peg is absent in †*Ornategulum*, †*Scutatuspinosus* and †*Sorbinichthys* (Fig. 31A, B). The dorsal peg is absent in outgroups.

314. Peg on lower middle caudal-fin ray (S153): (0) absent; (1) present.

Description. The peg on lower middle ray is present in most of the clupeiforms, except in denticipitids, †*Santanaclupea*, †*Nardoclupea*, *Jenkinsia* and *Spratelloides*, the coiliines *Coilia*, *Lycothrissa*, *Setipinna* and *Thryssa*, and the clupeoid *Potamalosa* (Figs 28A, B, D; 30C), whereas in the †ellimmichthyiforms, the peg is always absent (Fig. 31), resembling the condition of the outgroups.

315. Position of the pegs on the middle caudal-fin rays (new): (0) placed in a more medial direction on ray; (1) placed very proximally on ray.

Description. When present, the dorsal and ventral pegs on the middle caudal-fin rays (or just the dorsal peg when it is the only present) of most clupeomorphs are usually placed in a more medial direction on ray, at midway between its proximal tip and the beginning of segmentation, whereas pristigasteroids (except *Ilisha* and *Pellona*; Di Dario 2004b) are unique in having the upper and lower pegs placed proximally on middle rays, next to the posterior margin of the hypurals (Fig. 28F).

316. Shape of the basal segments of the upper middle caudal-fin ray (S154): (0) rod-like; (1) spatulate.

Description. In most clupeomorphs the basal segment of the upper middle caudal-fin ray is usually expanded anteriorly, forming a spatulate blade embracing the third hypural (Sato 1994). Among clupeiforms, however, the basal segment of the upper middle ray is not spatulate but rather rod-like in *Denticeps*, *Coilia*, *Jenkinsia*, *Spratelloides* and pristigasteroids (except *Ilisha* and *Pellona*; Di Dario 2004b) (Fig. 28A, B, D, F) and the same condition can be observed, among †ellimmichthyiforms, only in †*Ornategulum*, †*Scutatuspinosus*, †*Scutatoclupea* and †*Sorbinichthys* (Fig. 31A, B) (Forey 1973a; Bannikov & Bacchia 2000), resembling the condition of the outgroups.

317. Shape of the basal segments of the lower middle caudal-fin ray (S154): (0) rod-like; (1) spatulate.

Description. In most clupeomorphs the basal segment of the lower middle caudal-fin ray is expanded anteriorly, forming a spatulate blade embracing the second hypural. Among clupeiforms, however, the basal segment of the lower middle ray is not spatulate but rather rod-like in *Denticeps*, *Coilia*, *Jenkinsia*, *Spratelloides* and pristigasteroids (Fig. 28A, B, D, F), and the same condition can be observed in all the †ellimmichthyiforms (Fig. 31), except in †*Ranulfoichthys* (Alvarado-Ortega 2014).

Dorsal scutes

318. Predorsal scutes (G6): (0) completely absent; (1) at least one present.

Description. One or more scutes between the occiput and the dorsal-fin origin occur in most clupeomorph groups suggesting that their presence has to be considered the primitive condition in Clupeomorpha, whereas their secondary loss in several different groups is thought to be more plausible than independent acquisition (Grande 1985). One or more predorsal scutes are present in basal engraulids (*Coilia*, *Lycothrissa*, *Setipinna* and *Thryssa*), the pristigasteroid *Pristigaster*, some clupeoideans (*Alosa*, *Clupanodon*, *Dorosoma*, *Harengula*, *Herklotsichthys*, *Hyperlophus*, *Nematalosa*, *Opisthonema*, *Potamalosa* and *Tenualosa*) and in the fossil †*Cynoclupea*, †*Pseudoellimma*, †*Knightia* and †*Gosiutichthys* (Fig. 32) (e.g., Grande 1985; Sato 1994). All the †ellimmichthyiforms possess predorsal scutes (Fig. 33), except †*Foreyclupea*, †*Ornategulum* and †*Ranulfoichthys* (Forey 1973a; Chang & Maisey 2003). All the outgroups are devoid of predorsal scutes.

319. Distribution of the predorsal scute(s) (S155, CM14): (0) incomplete series of predorsal scutes leaving an unscuted area behind occiput; (1) complete series of predorsal scutes; (2) a single predorsal scute just behind occiput; (3) a single predorsal scute just in front of dorsal fin.

Description. Among clupeiforms, †*Gosiutichthys*, †*Knightia*, *Clupanodon*, *Hyperlophus* and *Potamalosa* have a complete series of predorsal scutes from the occiput to the dorsal fin (Fig. 32D, E). Conversely, the pristigasterid *Pristigaster*, the alosid *Alosa*, and the dorosomatids *Dorosoma*, *Harengula*, *Herklotsichthys*, *Nematalosa*, *Opisthonema* and *Tenualosa* have a single predorsal scute just behind occiput (Fig. 32A, B); also, the basal engraulids *Coilia*, *Lycothrissa*, *Setipinna* and *Thryssa* have a single scute, but this is located just in front of the dorsal fin (Fig. 32A). Although †*Pseudoellimma* and †*Cynoclupea* possess some predorsal scutes, their distribution cannot be assessed (?) due to their incompleteness and displacement from their original position (Figueiredo 2009a; Malabarba & Di Dario 2017). †Ellimmichthyiformes with predorsal scutes usually have a complete series (Fig. 33A, B, D), except most armigatids (†*Armigatus alticorpus*, †*A. brevissimus*, †*A. carrenoae*, †*A. elatus*, †*A. felixi*, †*A. oligodentatus*, †*A. plinii*) that are unique in possessing an incomplete series leaving an unscuted gap behind the occiput (Fig. 33C), although a complete series is present in †*A. dalmaticus* and †*A. namourensis* (e.g., Forey *et al.* 2003).

320. Shape of the predorsal scute(s) in the anterior part of the series (G7, Z47): (0) ovoid; (1) subtriangular; (2) subrectangular; (3) heart shaped; (4) subrhombic.

Description. In fossil and extant clupeiforms having scutes in the anterior part of the series (e.g., *Alosa*, *Pristigaster*, †*Knightia*, †*Gosiutichthys*, etc.) they are always ovoid in shape (Fig. 34A), except for †*Cynoclupea* that has subtriangular scutes (Grande 1982b; Malabarba & Di Dario 2017). Among the †ellimmichthyiforms, ovoid scutes in anterior part of the series are typical of †*Codoichthys*, †*Ellimma*, †*Ellimmichthys*, †*Eoellimmichthys*, †*Guiclupea*, †*Scutatuspinosus*, †*Sorbinichthys africanus*, and all the †Paraclupeidae (Fig. 34D), whereas the armigatids having complete dorsal scute series (†*A. alticorpus*, †*A. dalmaticus*, †*A. namourensis*, †*A. oligodentatus*, †*A. plinii*) have scutes in the anterior part of the series heart-shaped. †*Diplomystus*, †*Gasteroclupea* and are unique in having subrectangular scutes in the anterior part of the series (Fig. 34B) (Grande 1985; Marramà *et al.* 2022), whereas †*Sorbinichthys elusivo* has subrhombic-shaped scutes (Fig. 33A) (Bannikov & Bacchia 2000).

321. Shape of the predorsal scute(s) in the posterior part of the series (G7, Z47): (0) ovoid; (1) subtriangular; (2) subrectangular; (3) heart shaped; (4) subrhombic.

Description. Among clupeiforms having scutes in the posterior part of the predorsal series, *Clupanodon*, *Hyperlophus*, *Potamalosa*, †*Knightia* and †*Gosiutichthys* have ovoid scutes (Fig. 34A), whereas †*Pseudoellimma* and the engraulids *Coilia*, *Lycothrissa*, *Setipinna* and *Thryssa* possess subtriangular scutes (Grande 1982a; Figueiredo 2009a). Among †Ellimmichthyiformes, †*Codoichthys*, †*Guiclupea*, †*Sorbinichthys africanus* and the basal †paraclupeid †*Thorectichthys* possess ovoid scutes in the posterior part of the series; all †armigatids and †*Scutatuspinosus* are unique in possessing heart-shaped scutes in the posterior part of the series (Fig. 34C), whereas †*Diplomystus*, †*Gasteroclupea* and all the †paraclupeids (except †*Thorectichthys*) possess scutes with lateral expansion (or wings), which give scutes a subrectangular shape (Fig. 33B; 32B) (e.g., Grande 1985; Marramà *et al.* 2022). †*Sorbinichthys elusivo* has subrhombic-shaped scutes also in the posterior part of the dorsal series (Fig. 33A) (Bannikov & Bacchia 2000).

322. Series of spines on the posterior margin of the lateral wings of the predorsal scutes (G8, Z48): (0) absent; (1) present.

Description. Among clupeomorphs, only the species of the genera †*Diplomystus* and †*Sorbinichthys* are characterized by spines on the posterior margin of the predorsal scutes (Fig. 34B) (Grande 1982a; Bannikov & Bacchia 2000).

323. Prominent median spines on the posteriormost predorsal scute(s) (Z49): (0) absent; (1) present.

Description. A prominent spine on the posteriormost predorsal scutes is present in all the †paraclupeids (Fig. 34D) except †*Thorectichthys* (Zaragüeta Bagils 2004; Murray & Wilson 2013).

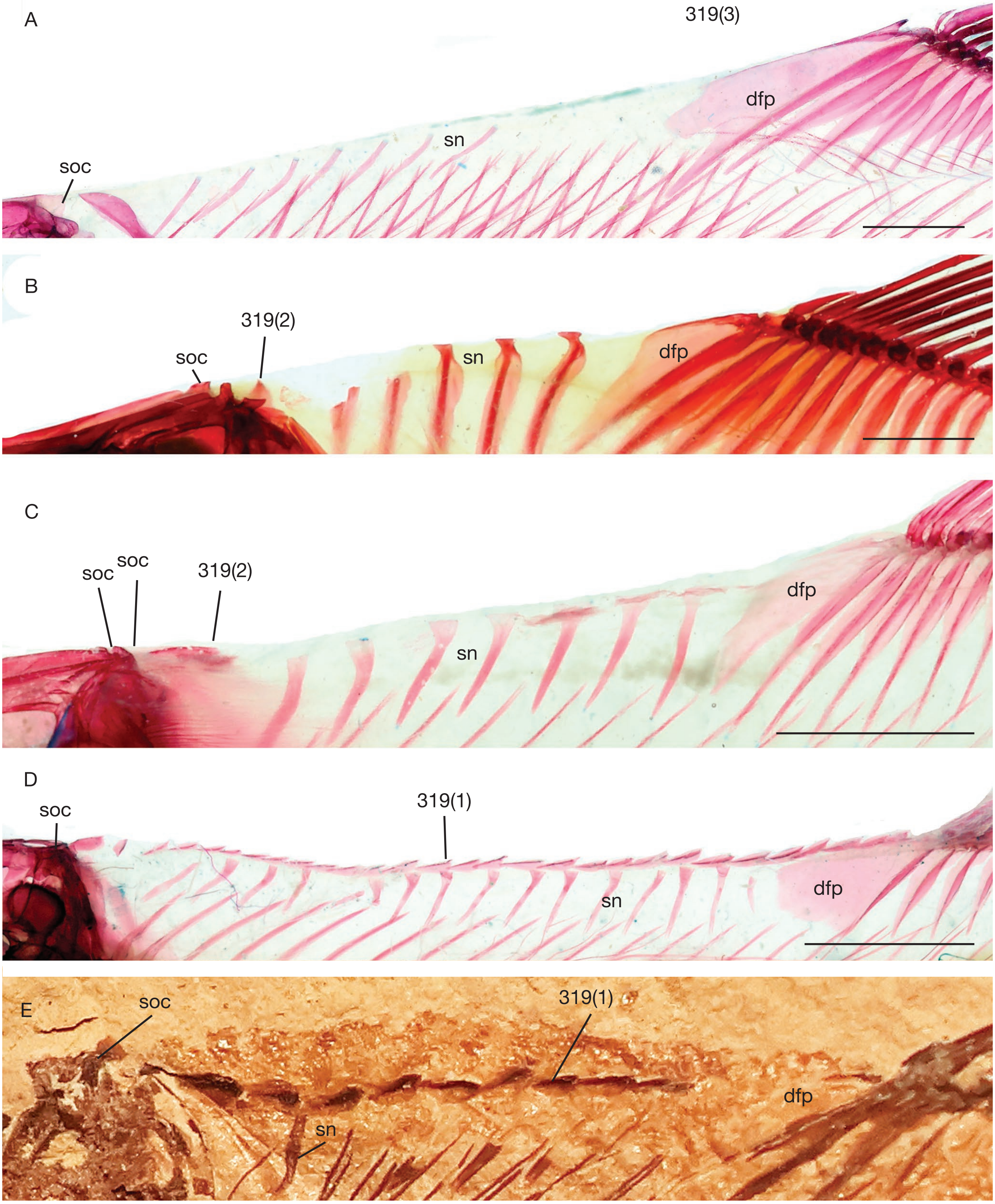

Fig. 32. – Dorsal scute series of selected clupeiforms: **A**, *Setipinna tenuifilis* (Valenciennes, 1848) (Engraulidae), AMNH 17551; **B**, *Pristigaster cayana* Cuvier, 1829 (Pristigasteridae), AMNH 10186; **C**, *Herklotsichthys dispilonotus* (Bleeker, 1852) (Dorosomatidae), AMNH 54611; **D**, *Hyperlophus vittatus* (Castelnau, 1875) (Hyperlophidae), AMNH 3050; **E**, †*Gosiutichthys parvus* Grande, 1982 (Hyperlophidae), MRSN P/111 (reversed). Scale bars: 5 mm. Abbreviations: **dfp**, dorsal-fin pterygiophores; **sn**, supraneurals; **soc**, supraoccipital. Numbers refer to characters and character states (see text).

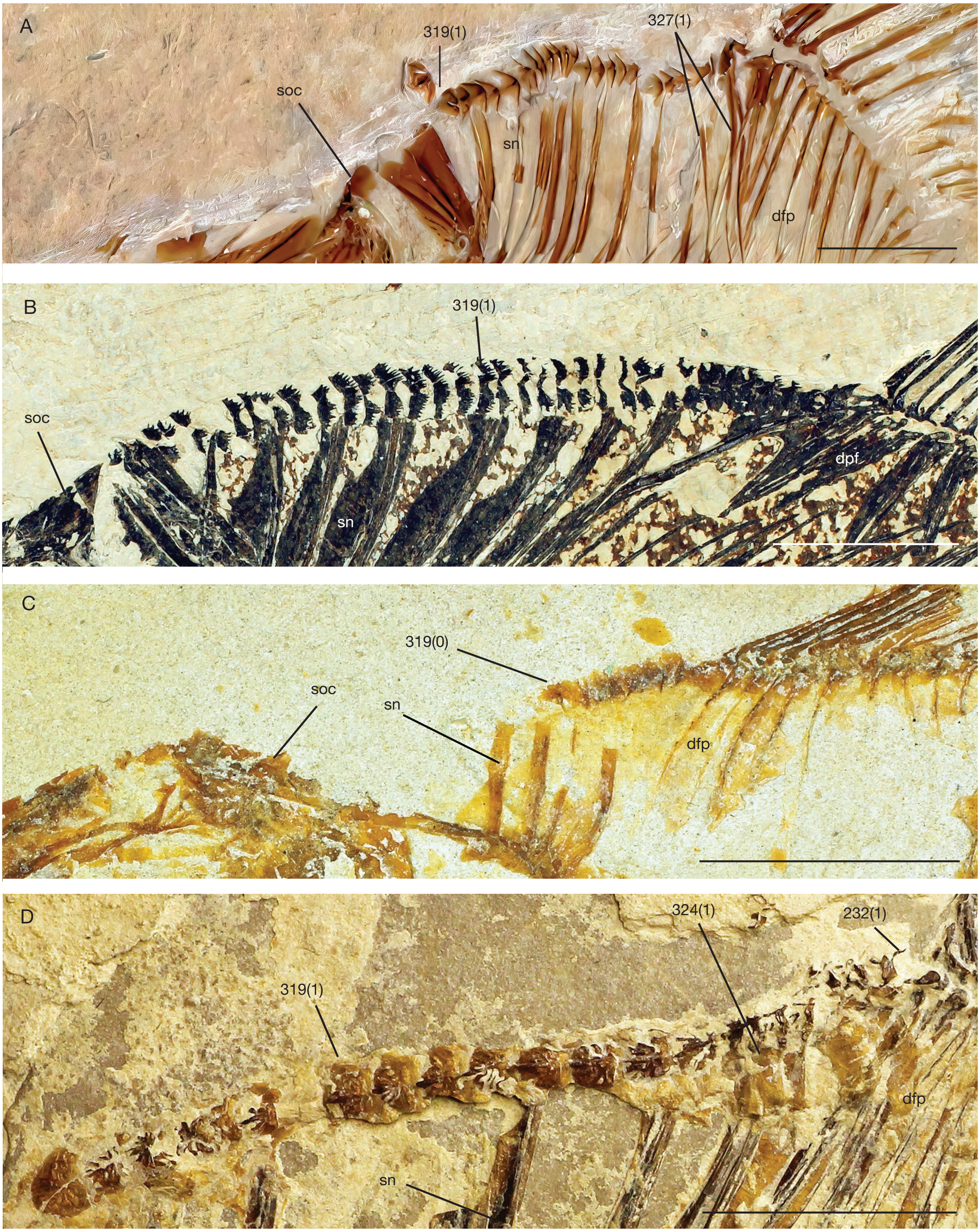

Fig. 33. — Dorsal scute series of selected †ellimmichthyiforms: **A**, †*Sorbinichthys elusivo* Bannikov & Bacchia, 2000 (†Sorbinichthyidae), CLC S-431a (photo: courtesy of Luigi Capasso); **B**, †*Diplomystus dentatus* Cope, 1877 (†Gasteroclupeidae), NHMUK PV P.52501; **C**, †*Armigatus brevissimus* (Blainville, 1818) (†Armigatidae), NHMUK PV P.108; **D**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Paraclupeidae: †Paraclupeinae), CMSNF M.19279 (reversed). Scale bars: 10 mm. Abbreviations: **dfp**, dorsal-fin pterygiophores; **sn**, supraneurals; **soc**, supraoccipital. Numbers refer to characters and character states (see text).

324. Size of the scutes of the predorsal series (if more than one scute) (Z50): (0) all the scutes of the same size; (1) size of scutes increasing posteriorly.

Description. In all clupeiforms and most †ellimmichthyiforms all the predorsal scutes have roughly the same size; however, in representatives of the family †Paraclupeidae the posteriormost scutes are larger than the scutes in the anterior part of the series (Fig. 34D) with this character being considered as a synapomorphy of the group (Zaragüeta Bagils 2004; Murray & Wilson 2013).

325. Ornamentation on the surface of the predorsal scutes (CM15, Z51): (0) absent; (1) present.

Description. In all clupeiforms and most †ellimmichthyiforms the predorsal scutes are always smooth, with no surface ornamentation. Conversely, in some †armigatids (†*A. carrenoae*, †*A. elatus*, †*A. namourensis*), †*Guiclupea*, †*Sorbinichthys elusivo*, and all †paraclupeids (except †*Tunisiaclupea* and †*Tycheroichthys*) the surface of the predorsal scutes is ornamented with circuli or radiating ridges (Fig. 34C, D).

326. Maximum number of predorsal scutes (MW54): (0) 20 or more; (1) 11 to 20; (2) two to ten; (3) only one.

Description. When predorsal scutes are present in clupeiforms, the extant taxa usually possess a single scute, although *Clupanodon* and *Hyperlophus* possess more than 20 scutes and *Potamalosa* about 14; in fossil clupeiforms †*Cynoclupea* and †*Pseudoellimma* this number is unknown, but †*Knightia* and †*Gosiutichthys* possess between 11 and 14 scutes. Among †ellimmichthyiforms, those with up to 10 predorsal scutes include most †*Armigatus* species, †*Codoichthys*, †*Scutatuspinosus*, and the †paraclupeids †*Eoellimmichthys*, †*Ezkutuberezi* and †*Thorectichthys marocensis*. †Ellimmichthyiforms with 11 to 20 predorsal scutes include †*Armigatus dalmaticus*, †*A. namourensis*, and all the other †paraclupeids, except †*Paraclupea pietrarojae* that has more than 20 predorsal scutes, similar to the condition of the †Gasteroclupeidae (†*Diplomystus*, †*Gasteroclupea*, †*Guiclupea*) and †*Sorbinichthys*.

327. Lateral rod-like extensions of the posteriormost predorsal scutes (MC61): (0) absent; (1) present.

Description. This character has been proposed by Marramà & Carnevale (2017) to detect taxon grouping for the two †*Sorbinichthys* species (Fig. 33A) (Bannikov & Bacchia 2000; Murray & Wilson 2011).

328. Postdorsal scute series (AO58): (0) absent; (1) present.

Description. The presence of scutes in the dorsal border of the trunk between the dorsal and caudal fins is shared by the †ellimmichthyiform species of †*Triplomystus* and †*Scutatoclupea*. No other clupeomorph has a postdorsal scute series.

ABDOMINAL SCUTES

329. Pelvic scute just anterior to the pelvic fin (G1, CM16): (0) absent; (1) present.

Description. The presence of one or more abdominal scutes as individual elements crossing the ventral midline of body is one of the main synapomorphies shared by extant and fossil clupeomorphs (Figs 35-37; 38B-E) (Grande 1985). Although prepelvic and/or postpelvic scutes might be absent in some taxa, the pelvic scute, a scute located just in front of the pelvic fin, is always present in clupeomorphs, with the only exception of the clupeiforms *Sundasalanx* (not included in our analysis) and †*Nardoclupea*, and the †ellimmichthyiform †*Ornategulum* (Fig. 38A) (Forey 1973a; Siebert 1997; Taverne 2002). All outgroups lack pelvic, prepelvic and postpelvic scutes.

330. Ventral margin and shape of the pelvic scute (G*f*, S158): (0) keeled, making the scute having V-shaped; (1) unkeeled and concave, making the scute W- or double U-shaped.

Description. The pelvic scute of clupeomorphs is usually keeled with two more or less pronounced ascending arms that make the scute V-shaped. Conversely, the pelvic scute of the dussumieriids (*Dussumieria*, *Etrumeus*), the pan-spratelloidid †*Trollichthys*, and that of living spratelloidids (*Jenkinsia* and *Spratelloides*) is unkeeled and has a concave ventral margin, being W-shaped (Fig. 37B-D). Also the single pelvic scute in immature individuals of *Chirocentrus* is a W-shaped element that in adult individuals is secondarily separated at the midline forming a pair of U-shaped bones (Fig. 37A) (Grande 1985; Sato 1994).

331. Length of the ascending arms of the pelvic scute (Z55): (0) short; (1) long.

Description. In most clupeomorphs the pelvic scute bears a pair of long, lateral ascending arms extended upward and covering the abdominal cavity laterally for at least one quarter of the distance between the ventral margin of the body and the vertebral column. However, the pelvic scute of denticipitids, *Coilia* and †*Santanaclupea* (Fig. 35A, B), and of the †ellimmichthyiforms †*Foreyclupea*, †*Scutatuspinosus* and †*Ranulfoichthys* have extremely reduced lateral wings that cover the abdominal cavity laterally for less than one quarter of the distance between the ventral margin of the body and the vertebral column (Greenwood 1968; Maisey 1993; Alvarado-Ortega 2014; Figueiredo & Ribeiro 2016).

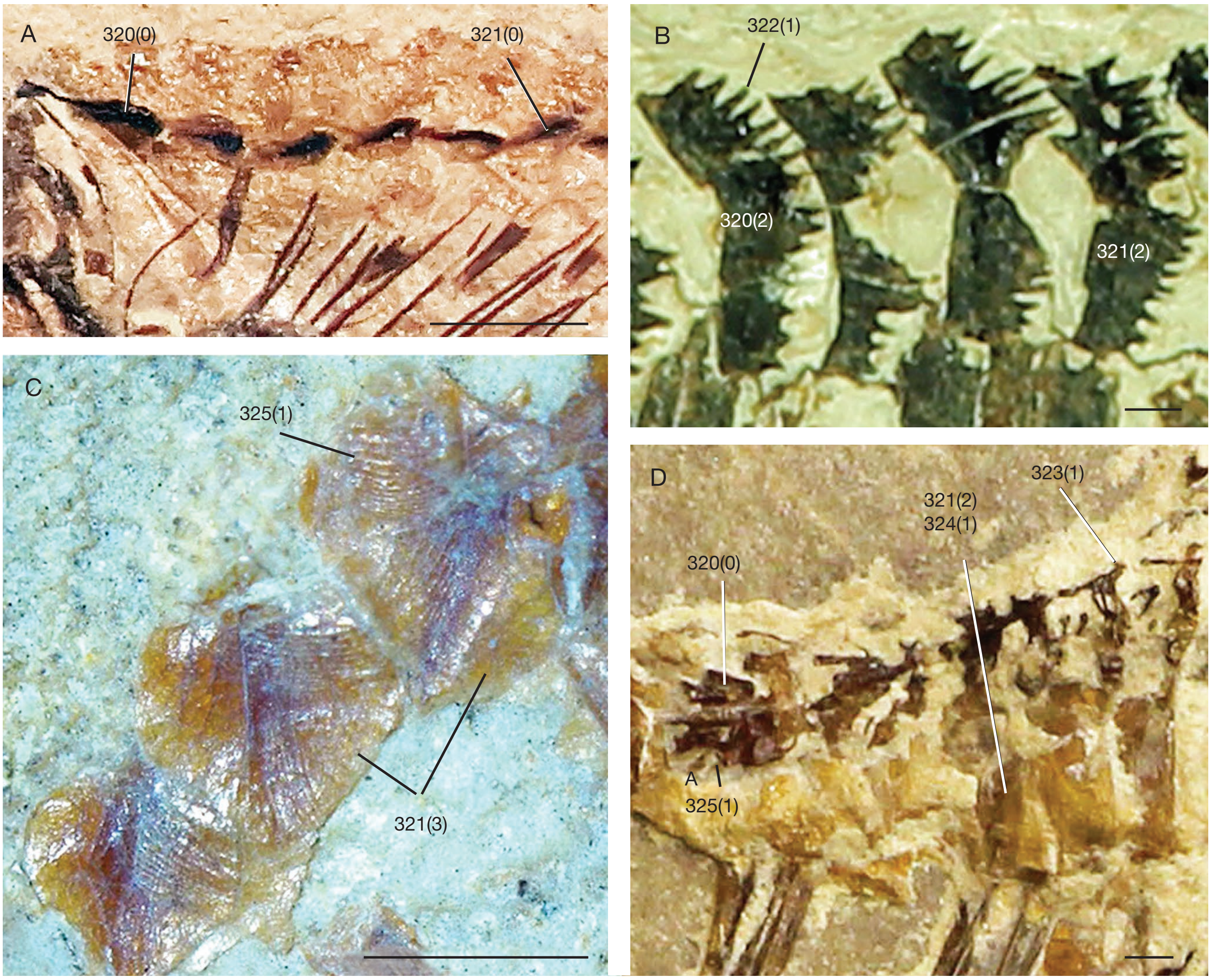

Fig. 34. — Close up of the dorsal scutes of selected clupeomorphs: **A**, †*Gosiutichthys parvus* Grande, 1982 (Clupeiformes: Hyperlophidae), MRSN P/111; **B**, †*Diplomystus dentatus* Cope, 1877 (†Ellimmichthyiformes: †Gasteroclupeidae), NHMUK PV P.52501; **C**, †*Armigatus elatus* (Costa, 1850) (†Ellimmichthyiformes: †Armigatidae), CMSNF M.441; **D**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Paraclupeidae: †Paraclupeinae), CMSNF M.19279 (reversed). Scale bars: 1 mm. Numbers refer to characters and character states (see text).

332. Development of the keel of the pelvic scute (if present) (DD446): (0) poorly developed or inconspicuous; (1) well-developed.

Description. In clupeomorphs, the ventral keel of the pelvic scute, when present, is usually well developed. However, in the engrauline engraulids, *Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*, and the ehiravid *Gilchristella* the pelvic scute is unkeeled or has an inconspicuous keel (Figs 35E, F; 36C; 37).

333. Prepelvic scutes between the pelvic scute and the posterior end of coracoid (DD442): (0) absent; (1) present.

Description. Most clupeomorphs have a series of keeled prepelvic scutes between the pelvic scute and the posterior end of coracoid. However, these are completely absent in *Chirocentrus*, Dussumieriidae and Spratelloididae, †*Nardoclupea*, all New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis Lycengraulis*, *Pterengraulis*), *Engraulis* and in the †ellimmichthyiform †*Ornategulum* (Figs 35C, F; 38A) (see Forey 1973a; Di Dario 2004b).

334. Prepelvic scutes along the ventral edge of the coracoid (DD442): (0) absent; (1) present.

Description. Prepelvic scutes between the anterior and posterior end of coracoid are present in most of clupeomorphs (Figs 35A, B, D; 36A, C, D; 38B-E), except in those taxa lacking prepelvic scutes between the pelvic scute and the posterior end of coracoid (see ch. 333) plus some ehiravids (*Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*, *Limnothrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolo-*

thrissa), †*Italoclupea*, the engraulids *Encrasicholina*, *Eoengraulis*, *Lycothrissa*, *Stolephorus* and the †ellimmichthyiform †*Sorbinichthys*, in which these are instead present only between the pelvic scutes and the posterior tip of the coracoid (Figs 35C, E, F; 36B; 38A).

335. Ascending arms of the prepelvic scutes along the ventral edge of the coracoid (DD444): (0) moderately developed; (1) absent or inconspicuous.

Description. When present, the prepelvic scutes along the ventral edge of the coracoid of the clupeomorphs usually possess ascending arms similarly to those between the posterior tip of coracoid and the pelvic scute, although shorter. However, the prepelvic scutes on ventral edge of the coracoid of denticipitids, *Clupea*, †*Gosiutichthys*, *Hyperlophus*, †*Knightia*, *Lile*, *Platanichthys*, *Potamalosa*, *Rhinosardinia* and *Sprattus* do not possess ascending arms or these are very inconspicuous, making the scales folded in half (Figs 35A; 36C) (Whitehead 1968; Di Dario 2004b). This condition is also present, among †ellimmichthyiforms, in the †scutatuspinosids †*Foreyclupea*, †*Ranulfoichthys* and †*Scutatuspinosus* (Vernygora *et al.* 2016).

336. Prepelvic scutes anterior to the coracoid (S156): (0) absent; (1) present.

Description. The engraulid *Coilia*, all the members of the Pristigasteroidea and the †ellimmichthyiform †*Gasteroclupea* are the only clupeomorphs in which the prepelvic scutes extend beyond the anterior end of coracoid, reaching the gular region between the branchiostegal rays (Figs 36A; 38C) (Di Dario 2004b; Marramà & Carnevale 2017).

337. Length of the ascending arms of the prepelvic scutes between the pelvic scute and the posterior edge of coracoid (Z55, DD443): (0) short; (1) long.

Description. In most clupeomorphs the prepelvic scutes bear a pair of long lateral ascending arms extended upward and covering the abdominal cavity laterally for at least one quarter of the distance between the ventral margin of the body and the vertebral column. However, this is not the case of denticipitids, †*Cynoclupea* and †*Santanaclupea*, whose prepelvic scutes have reduced ascending arms (Greenwood 1968; Maisey 1993; Malabarba & Di Dario 2017); a similar condition characterizes the prepelvic scutes of *Encrasicholina*, †*Eoengraulis* and *Stolephorus*, which possess needle-like prepelvic scutes with extremely reduced lateral wings (Fig. 35A, B, E). Among the †ellimmichthyiforms, only †*Foreyclupea*, †*Scutatuspinosus* and †*Ranulfoichthys* have short ascending arms of the prepelvic scutes (Alvarado-Ortega 2014; Figueiredo & Ribeiro 2016).

338. Postpelvic scutes (Z53, S157): (0) absent; (1) present.

Description. Abdominal scutes between the pelvic fin (or the pelvic scute) and the anal fin are present in most clupeiforms, except *Chirocentrus*, Dussumieriidae, Spratelloididae, †*Nardoclupea*, all New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*), *Engraulis*, *Encrasicholina*, *Stolephorus* and †*Eoengraulis*, and the ehiravid *Gilchristella* (Fig. 35C, E, F). Postpelvic scutes are always present in the †Ellimmichthyiformes, except †*Ornategulum* (Fig. 38A) (Forey 1973a).

339. Posteriorly directed ventral spines on the postpelvic abdominal scutes (Z54): (0) short; (1) prominent and strong.

Description. In most clupeomorphs, the postpelvic scutes bear a small posteriorly directed spine representing a posterior extension of the median keel that is similar in shape to that of the pelvic and prepelvic scutes. The †ellimmichthyiforms of the family †Paraclupeidae are instead characterized by a prominent enlargement of the size and robustness of the ventral spines on the postpelvic scutes (Zaragüeta Bagils 2004; Murray & Wilson 2013).

340. Shape of the ascending arms of the prepelvic and postpelvic scutes (AO57): (0) triangular and spine-like, with large spaces between the wings of adjacent scutes; (1) triangular and wide or spatulate, with wings of adjacent scutes contacting each other for almost their entire length; (2) semicircular to subrectangular, with wings of adjacent scutes contacting each other for their entire length.

Description. In most clupeiforms and †ellimmichthyiforms, the lateral wings of the abdominal scutes are triangular and spine-like, with large spaces between the wings of adjacent scutes (Fig. 35D, E). In *Pristigaster* and all the †paraclupeids (except †*Eoellimmichthys*, †*Ezkutuberezi* and †*Thorectichthys*; Fig. 38D) the wings are triangular, wide or spatulate, contacting with wings of adjacent scutes for almost their entire length (Figs 36A; 38E) (Alvarado-Ortega *et al.* 2008; Marramà *et al.* 2019). The denticipitids, †*Cynoclupea*, †*Santanaclupea*, and the †ellimmichthyiforms †*Codoichthys*, †*Scutatuspinosus* and †*Ranulfoichthys* have scutes with semicircular or subrectangular wings, with wings of adjacent scutes contacting each other for almost their entire length.

341. Number of abdominal scutes (MW61) - ordered: (0) one; (1) two to nine; (2) 10-20; (3) 21-30; (4) more than 30.

Description. A single scute (the pelvic scute) is characteristic of *Chirocentrus*, Dussumieriidae, Spratelloididae (including †*Trollichthys*) and the New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*) plus

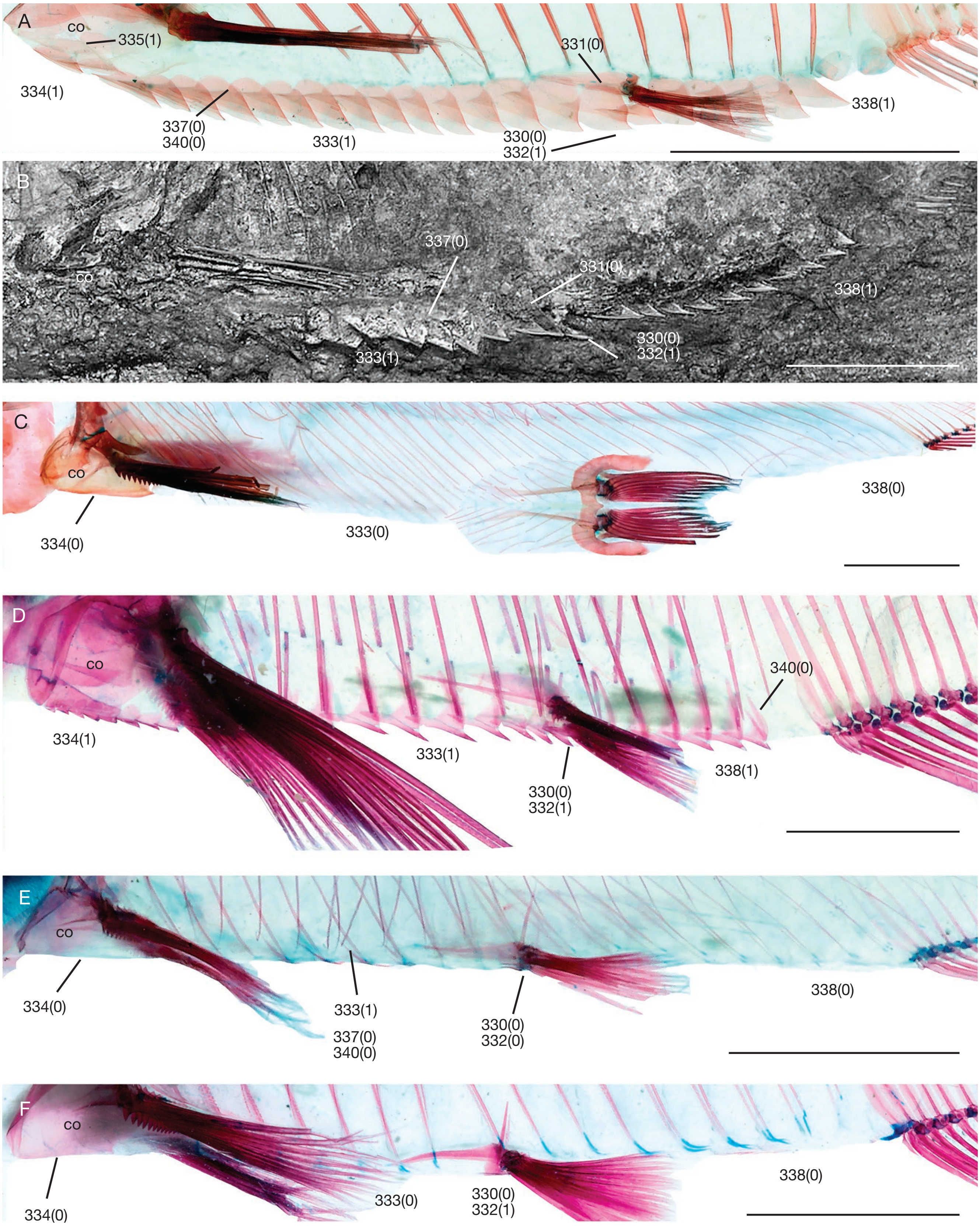

FIG. 35. — Abdominal scute series of selected clupeiforms: **A**, *Denticeps clupeoides* Clausen, 1959 (Denticipitidae), AMNH 53082; **B**, †*Santanaclupea silvasantoi* Maisey, 1993 (†Cynoclupeidae), AMNH DVP.12790 (reversed) (photo: courtesy of Lorraine Meeker); **C**, *Dussumieria acuta* Valenciennes, 1847 (Dussumieriidae), AMNH 17555; **D**, *Setipinna tenuifilis* (Valenciennes, 1848) (Engraulidae: Coiliinae), AMNH 17551; **E**, *Stolephorus indicus* (van Hasselt, 1823) (Engraulidae: Engraulinae), AMNH 32820; **F**, *Anchoviella lepidentostole* (Fowler, 1911) (Engraulidae: Engraulinae); AMNH 40905. Scale bars: 5 mm. Abbreviation : **co**, coracoid. Numbers refer to characters and character states (see text).

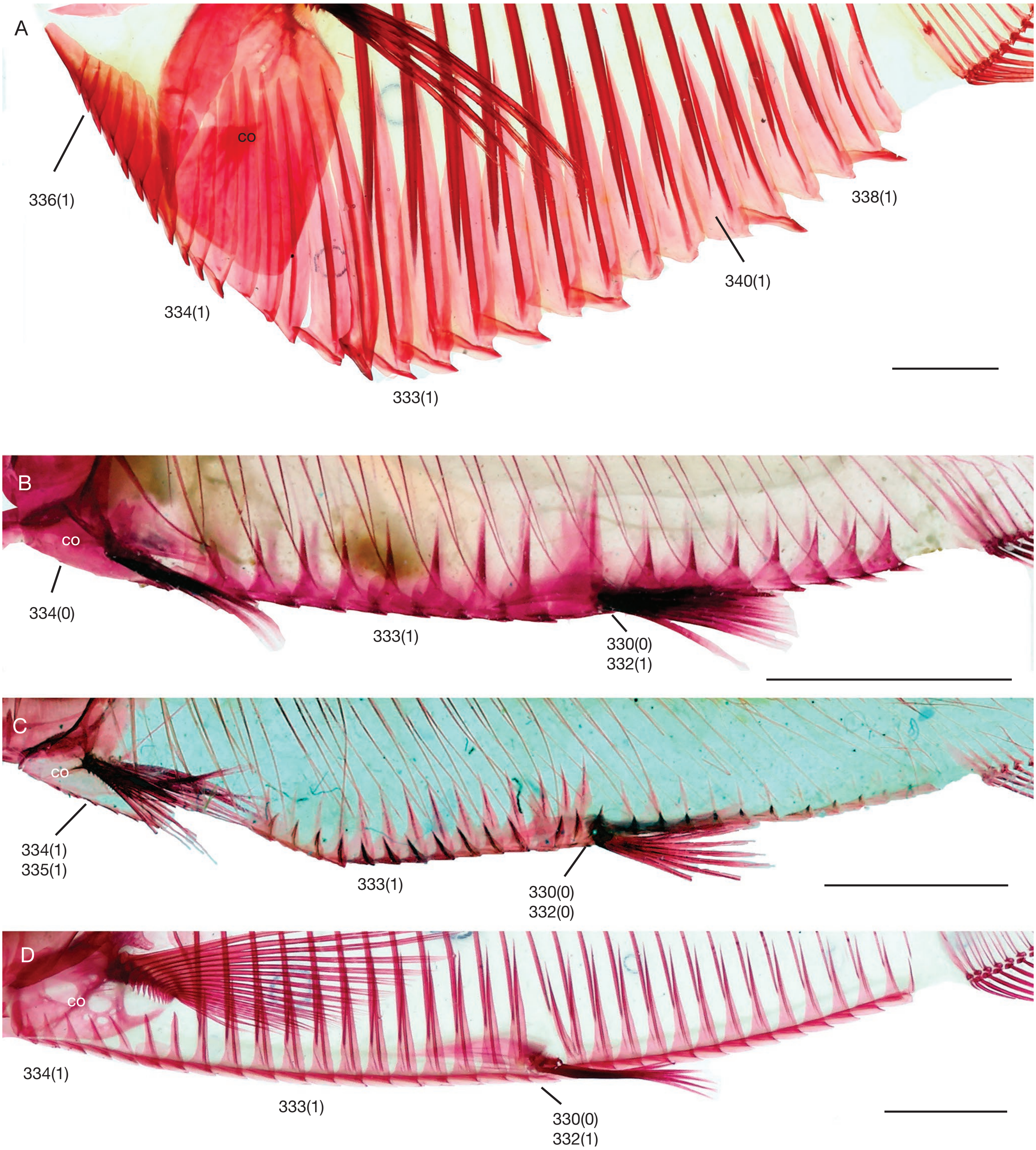

Fig. 36. — Abdominal scute series of selected clupeiforms: **A**, *Pristigaster cayana* Cuvier, 1829 (Pristigasteridae), AMNH 10186; **B**, *Corica soborna* Hamilton, 1822 (Ehiravidae), AMNH 55343; **C**, *Hyperlophus vittatus* (Castelnau, 1875) (Hyperlophidae), AMNH 3050; **D**, *Nematalosa erebi* (Gunther, 1868) (Dorosomatidae), AMNH 28097. Scale bars: 5 mm. Abbreviations: **cl**, cleithrum; **co**, coracoid. Numbers refer to characters and character states (see text).

Engraulis, whereas *Encrasicholina*, *Stolephorus* and †*Eoengraulis* possess (other than the pelvic scute) two to eight prepelvic needle-like scutes. Some Ehiravidae (*Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*, *Nannothrissa*), the engraulid *Lycothrissa*, the pristigasterid *Neoopisthopterus*, and the fossils †*Eoalosa*, †*Leufuichthys*, †*Nolfia* and †*Palaeodenticeps* have between 10 and 20 scutes along the belly. A number comprised between 21 to 30 scutes is typical of *Denticeps*, †*Pseudoellimma*, *Amblygaster*, *Anodontostoma*, †*Bolcaichthys*, *Clupeonella*, *Dorosoma*, *Escualosa*, †*Gosiutichthys*, *Herklotsichthys*, *Hilsa*, †*Italoclupea*, †*Knightia*, *Limnothrissa*, *Microthrissa*, *Nematalosa*, *Odaxothrissa*, *Platanichthys*, *Potamothrissa*, *Rhinosardinia*, *Tenualosa*,

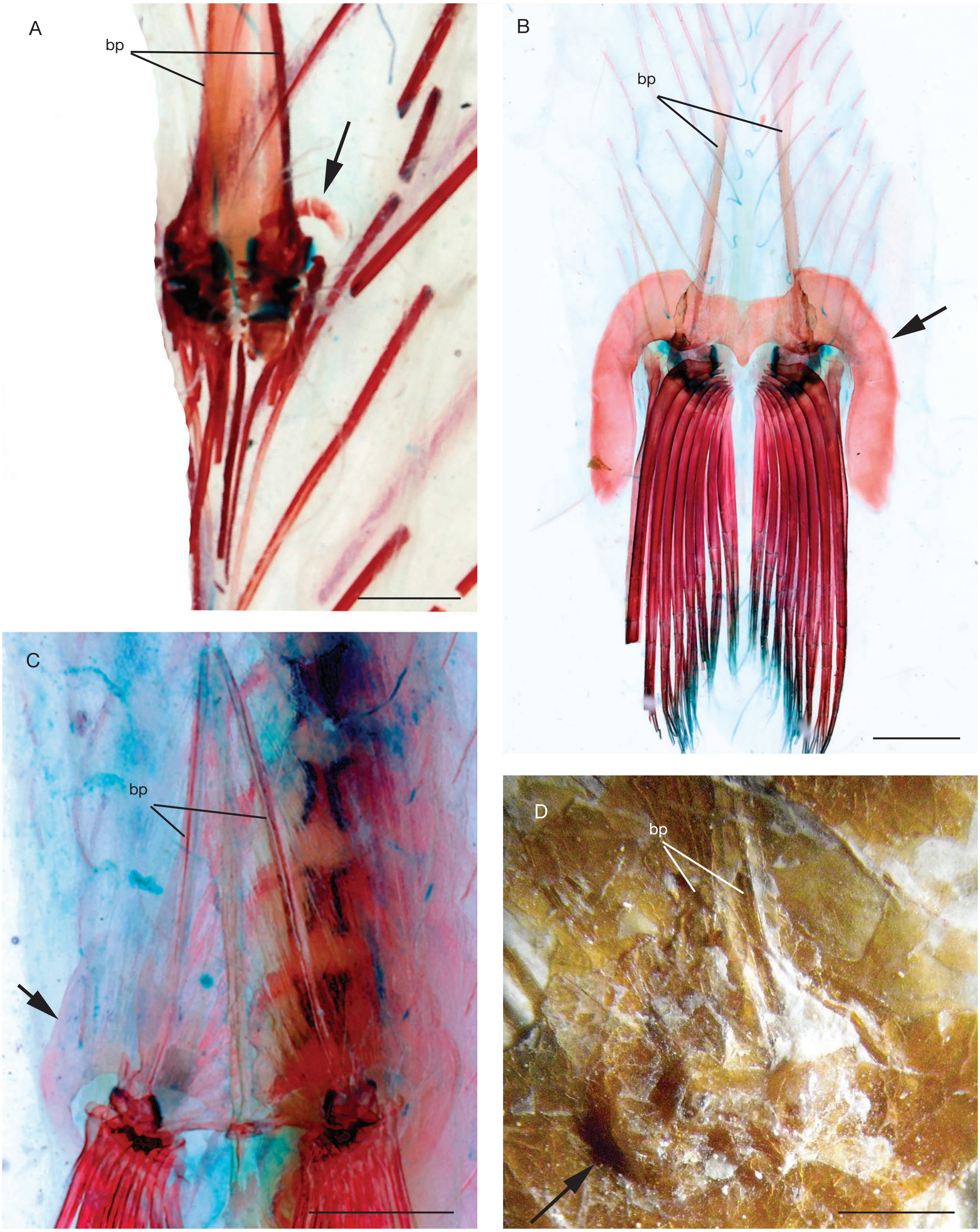

FIG. 37. — The pelvic scute of selected clupeiforms: **A**, *Chirocentrus dorab* (Forsskål, 1775) (Chirocentridae), AMNH 55306; **B**, *Dussumieria acuta* Valenciennes, 1847 (Dussumieriidae), AMNH 17555; **C**, *Spratelloides delicatulus* (Bennett, 1832) (Spratelloididae), AMNH 54621; **D**, †*Trollichthys bolcensis* Marramà & Carnevale, 2015 (pan-Spratelloididae), MCSNV IG.VR.82000. Scale bars: 1 mm. Anterior to the top. **Arrows** indicate the pelvic scute. Abbreviation: **bp**, basipterygia. Numbers refer to characters and character states (see text).

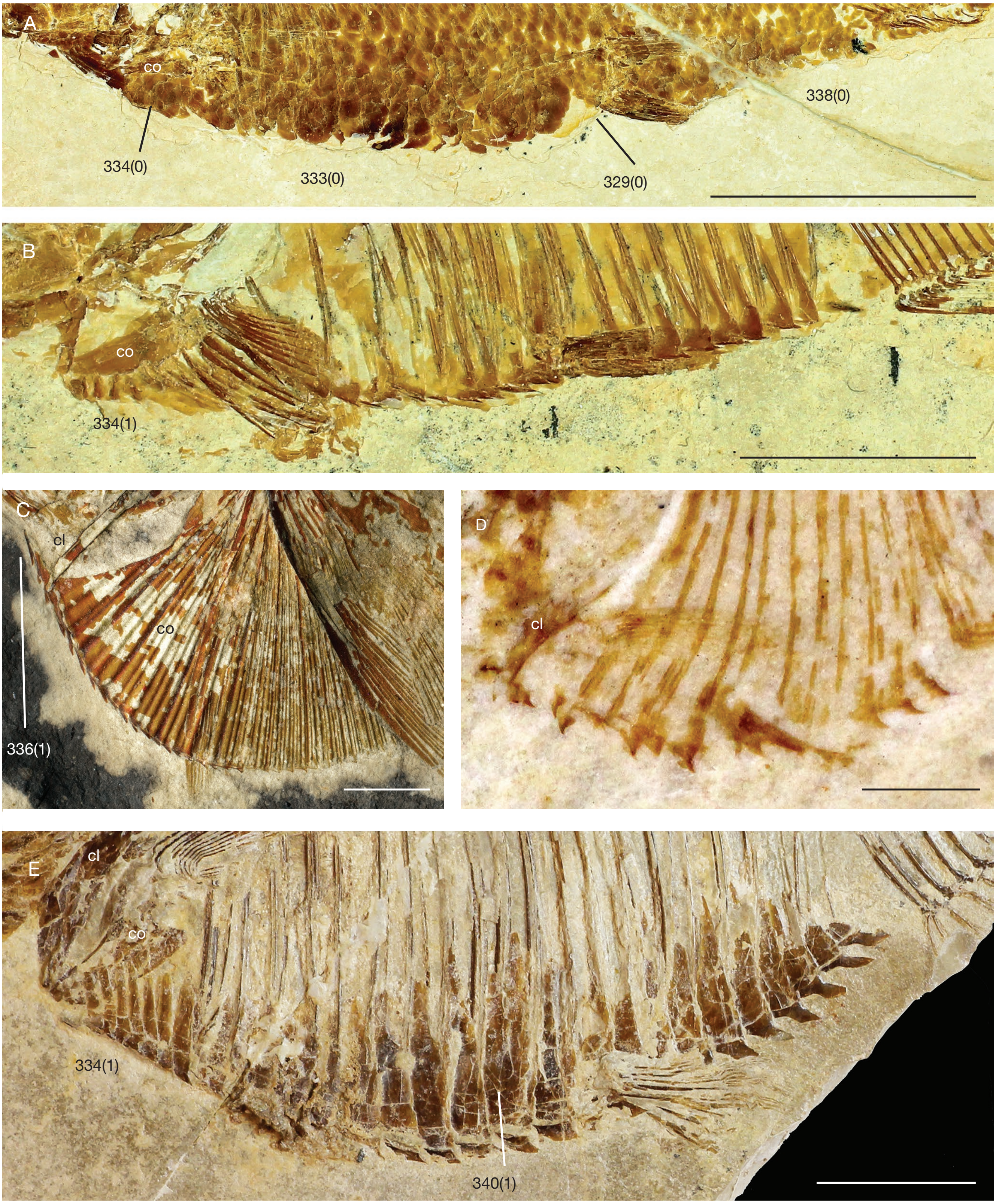

Fig. 38. — Abdominal scute series of selected ellimmichthyiforms: **A**, †*Ornategulum sardinioides* (Pictet, 1850) (†Scutatuspinosidae), NHMUK PV P.63293; **B**, †*Armigatus namourensis* (†Armigatidae), NHMUK PV P.63140; **C**, †*Gasteroclupea branisai* Signeux, 1964 (†Gasteroclupeidae), MNHN F.1963.11.1 (reversed); **D**, †*Eoellimmichthys superstes* Marramà, Bannikov, Kriwet & Carnevale, 2019 (†Paraclupeidae: †Eoellimmichthyinae n. subfam.), MCSNV IG.23695; **E**, †*Paraclupea pietrarojae* Marramà & Carnevale, 2023 (†Paraclupeidae: †Paraclupeinae), CMSNF M.19284 (reversed). Scale bars: **A**, **B**, E 20 mm; **C**, D 2 mm. Abbreviations: **cl**, cleithrum; **co**, coracoid. Numbers refer to characters and character states (see text).

Stolothrissa and †*Scombroclupea*, the engraulids *Setipinna* and *Thryssa*, and the pristigasteroids *Chirocentrodon*, *Odontognathus*, *Opisthopterus*, *Pellona* and *Pliosteostoma*. More than 30 scutes characterize *Alosa*, *Brevoortia*, *Clupanodon*, *Clupea*, *Harengula*, *Hyperlophus*, *Konosirus*, *Opisthonema*, *Potamalosa*, *Sardina*, *Sardinella*, *Sardinops*, the pristigasteroids *Ilisha*, *Pristigaster* and *Raconda*, and the engraulid *Coilia*. Among †ellimmichthyiforms, †*Codoichthys*, †*Eoellimmichthys* and †*Sorbinichthys* have the lowest count (10-20), whereas †*Armigatus*, †*Diplomystus birdi* and †*D. dubertreti*, †*Ellimma*, †*Ellimmichthys longicostatus*, †*Ezkutuberezi*, †*Ranulfoichthys*, †*Scutatuspinosus*, †*Thorectichthys* and †*Triplomystus oligoscutatus* have between 21 and 30 abdominal scutes. All the other †gasteroclupeids and †paraclupeids have more than 30 scutes.

342. Needle-like prepelvic scutes (M6): (0) absent; (1) present.

Description. Needle-like prepelvic scutes (one to seven scutes with needle-like keel projected ventrally and extremely reduced lateral wings) are present uniquely in species of the engraulid genera *Encrasicholina*, *Stolephorus* and †*Eoengraulis* (Whitehead *et al.* 1988; Marramà & Carnevale 2016).

MEDIAN FINS

343. Maximum number of anal-fin pterygiophores (*Ge*): (0) up to 30; (1) 31-55; (2) 56 or more.

Description. All outgroups and most clupeiforms have a small anal fin usually supported by up to 30 pterygiophores. However, in *Chirocentrus*, some engraulids (*Anchoa*, *Anchovia*, *Lycothrissa*, *Setipinna*, *Thryssa*), pristigasteroids (*Chirocentrodon*, *Ilisha*, *Neoopisthopterus*, *Pellona*, *Pliosteostoma*, *Pristigaster*) and *Clupanodon* the anal fin is supported by 31 to 55 pterygiophores, whereas more than 55 pterygiophores are present only in *Coilia*, *Odontognathus*, *Opisthopterus* and *Raconda*. Most †ellimmichthyiforms have up to 30 anal-fin pterygiophores, except †*Diplomystus dentatus*, †*D. shengliensis*, †*Guiclupea* and †*Sorbinichthys* having between 31 and 55 pterygiophores.

344. Anal-fin origin (relative to the dorsal-fin base) (K124): (0) posterior to the dorsal-fin base; (1) below the dorsal-fin base; (2) anterior to the dorsal-fin origin.

Description. In most clupeiforms the anal fin is usually small and, being positioned posterior on body, it originates well behind the dorsal-fin base. In *Chirocentrus*, the engraulids *Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Stolephorus*, and the pristigasteroid *Ilisha*, the anal fin is longer, and its origin lies below the dorsal-fin base. Conversely, in denticipitids, the engraulid *Lycothrissa*, *Pterengraulis* and *Setipinna*, and all the pristigasteroids (except *Pristigaster* having state 0), the anal fin originates anterior to the dorsal-fin origin. Most of †ellimmichthyiforms have the anal fin that originates behind the dorsal-fin base, except in †*Armigatus alticorpus*. †*A. brevissimus*, †*A. plinii*, †*Diplomystus birdi*, †*D. dubertreti*, †*Eoellimmichthys* and †*Sorbinichthys* whose anal fins originate below the dorsal-fin base. All outgroups have the anal fin originating behind the dorsal-fin base, except *Alepocephalus* whose anal fin originates below the dorsal-fin base.

345. Anal finlets (G*r*): (0) absent; (1) present, as Ehiravini-type; (2) present, as †*Scombroclupea*-type.

Description. In most teleosts (and clupeomorphs) the anal-fin rays are supported by a series of equally distant pterygiophores, each made up of a long proximal radial, and small middle and distal radials articulated in series (proximal and middle radials are fused together in clupeomorphs). In some ehiravids (the "Ehiravini" *Clupeichthys*, *Corica* and *Spratellomorpha*) the last two anal-fin rays are set close together and separated from the rest of the preceding rays by a clear gap; this arrangement, forming the anal "finlet" of ehiravid-type, results from the elongation of a single pterygiophore due to the lengthening of a fused proximal and middle radial (Grande 1985; Forey *et al.* 2003). Anal "finlets" are also reported in the Late Cretaceous clupeiforms †*Scombroclupea*, but the associated support structure for each finlet is quite different from that of the Ehiravini-type. In fact, the anal "finlets" of †*Scombroclupea* comprise the posteriormost two to six pterygiophores, each formed by autogenous proximal, middle and distal radials, in which only the middle radials become progressively longer, increasing the space between consecutive fin rays (Forey *et al.* 2003). Therefore, despite some apparent similarities and denomination, the anal finlets of the "Ehiravini" and †*Scombroclupea* were likely not homologous and acquired independently (Grande 1985; Forey *et al.* 2003), resulting in a separate coding in our analysis. The last anal-fin pterygiophore of †*Italoclupea* resembles the †*Scombroclupea*-type finlet but further investigation is needed (?).

346. Last two anal-fin rays (relative to the others) (K126): (0) not elongated; (1) more elongated.

Description. In most clupeomorphs the last two anal-fin rays are similar in size and shape to the others, but in *Clupeonella*, *Amblygaster*, *Sardina*, *Sardinella* and *Sardinops* the last two rays are more elongated than the anterior ones (Whitehead 1985).

347. Anal-fin stay (S140): (0) absent; (1) present.

Description. The last modified anal-fin pterygiophore (stay of Weitzman 1962) is present in *Chanos*, *Kneria* and all the Clupeiformes, except denticipitids and *Coilia* (Sato 1994; Koch *et al.* 2023). All the †Ellimmichthyiformes possess the anal-fin stay (Forey *et al.* 2003; Alvarado-Ortega 2014; Alvarado-Ortega *et al.* 2020).

348. Dorsal-fin position (D90): (0) displaced anteriorly on the body (predorsal length <30% SL); (1) at middle of body (predorsal length 30 to 60% SL); (2) displaced posteriorly on the body (predorsal length >60% SL).

Description. In most clupeomorphs, the dorsal fin lies approximately in the middle of the dorsal profile of body, being their predorsal distance comprised between 30 and 60% of SL. *Coilia* is the only clupeomorph whose dorsal fin is displaced anteriorly on the body (PDL <30% SL), whereas denticipitids, *Chirocentrus* and some pristigasteroids (*Odontognathus*, *Opisthopterus* and *Pliosteostoma*) have the dorsal fin displaced in the posterior part of the body, their predorsal distance reaching at least 60% SL. Although the pristigasterid *Raconda* lacks dorsal-fin rays, the presence of dorsal-fin pterygiophores displaced posteriorly on the body indicates that its condition resembles that of *Odontognathus*, *Opisthopterus* and *Pliosteostoma* (Grande 1985; Di Dario 1999). Among the †Ellimmichthyiformes, only †*Gasteroclupea* and †*Scutatuspinosus* have the dorsal fin displaced posteriorly at least at 60% SL (Figueiredo & Ribeiro 2017; Marramà & Carnevale 2017). All the outgroups have a dorsal fin at mid-length of their dorsal profile, except *Alepocephalus* whose dorsal fin is displaced in the posterior part of the body.

349. Dorsal-fin base (D91): (0) large, covering five or more consecutive neural spines; (1) reduced, covering less than five consecutive neural spines.

Description. In most clupeomorphs, the area between the first and last dorsal-fin pterygiophores is large, being equivalent to a distance greater than five consecutive neural spines. In *Odontognathus* and *Opisthopterus* the area between the first and last pterygiophores of the dorsal fin, without considering its anterior and posterior processes, is equivalent to three or four consecutive neural spines. This latter arrangement can be also recognized in *Raconda* because, despite the absence of external elements, the internal skeleton of the dorsal fin is present (Grande 1985; Di Dario 1999).

350. Number of dorsal-fin pterygiophores reaching the neural spines (D92): (0) two or more; (1) one or none.

Description. In all the outgroups and most clupeomorphs at least two pterygiophores reach the level of the underlying neural spines, inserting in the respective interneural spaces. In *Odontognathus* and *Raconda*, howerer, only one or none of the dorsal pterygiophores reaches the underlying neural spines (Di Dario 1999).

351. Posterior process of the dorsal-fin stay (S138): (0) absent or inconspicuous; (1) very long.

Description. In most clupeomorphs the dorsal-fin stay bear a thin posterior process, but this is absent or inconspicuous in denticipitids, *Coilia*, *Setipinna* and *Thryssa* (Sato 1994). Outgroups and all †Ellimmichthyiformes possess a short or inconspicuous posterior process of the dorsal-fin stay, as for example in †*Armigatus*, †*Diplomystus*, †*Paraclupea*, †*Ranulfoichthys*, etc. (Forey *et al.* 2003; Alvarado-Ortega 2014; Alvarado-Ortega *et al.* 2020; Marramà & Carnevale 2023).

352. Filamentous last dorsal-fin ray (S139): (0) absent; (1) present.

Description. In outgroups and most clupeomorphs the posteriormost ray of the dorsal fin is shorter than the rest of the dorsal-fin rays; however, in *Clupanodon*, *Dorosoma*, *Konosirus*, *Nematalosa* and *Opisthonema* the last dorsal-fin ray is much longer than the others.

353. Greatly elongated second dorsal-fin ray (MC59): (0) absent; (1) present.

Description. According to Murray & Wilson (2011) this character is diagnostic for †*Sorbinichthys*, being exclusively present in this genus among the †Ellimmichthyiformes. It is not present in outgroups and other clupeomorphs.

BODY SCALES

354. Lateral line (G16, CM29): (0) present in most body scales; (1) totally or almost totally absent in most body scales.

Description. Teleosts exhibit basally a complete lateral line on body scales going all the way back to the caudal fin, as in all the outgroups and, among clupeomorphs, in denticipitids, †*Santanaclupea*, and †ellimmichthyiforms (at least those preserving some body scales like e.g., †*Armigatus*, †*Diplomystus*, †*Ellimmichthys*, †*Ornategulum* and †*Ellimma longipectoralis*) (Grande 1982a, 1985; Maisey 1993; Chang & Maisey 2003; Polck *et al.* 2020). Although some clupeoids (e.g., *Alosa*, *Nematalosa*) have one or two anterior lateral-line scales, all members of the Clupeoidei (including all the other Cretaceous and Eocene clupeiforms) lost most or all of the lateral line (Grande 1985).

355. Scale shape (ME-*SS*): (0) circular; (1) cordate; (2) discoidal; (3) oval; (4) quadrilateral; (5) intermediate.

Description. This and the following characters refer to the scale morphology and were taken directly from Mertzen (2019) who analysed the characters of clupeiform scales. Since the various states can be found in different combinations within a single taxon and in different taxa within the same family, we refer directly to that work for the explanation of characters and the states in each taxon. Data on scale morphology for those taxa not included in Mertzen (2019) (e.g., *Escualosa*, *Tenualosa*) was implemented with information taken from Patterson *et al.* (2001) and Purrafee Dizaj *et al.* (2020).

356. Anterior field (ME-*AF*): (0) convex; (1) convex with apex; (2) concave; (3) flattened; (4) flattened with apex; (5) dentate.

357. Posterior field (ME-*PF*): (0) flattened; (1) convex; (2) tapered.

358. Lateral fields (ME-*LF*): (0) convex; (1) convex with apex; (2) concave; (3) flattened; (4) flattened with apex; (5) dentate.

359. Extension of lateral fields (ME-*DM*): (0) extended in the dorso-ventral axis; (1) centric; (2) elongated in antero-posterior axis.

360. Position of focus (ME-*FP*): (0) anterior; (1) antero-central; (2) central; (3) postero-central; (4) posterior.

361. Scale type (ME-*ST*): (0) true cycloid; (1) crenate; (2) spinoid.

362. Posterior margin (ME-*PM*): (0) smooth; (1) crenulate; (2) spinous.

363. Focus (ME-*FO*): (0) indistinct; (1) distinct.

364. Superficial ornamentations (ME-*SO*): (0) absent; (1) waved; (2) irregular.

365. Radii (ME-*RI*): (0) absent; (1) present.

366. Common fracture lines (discontinuous striae) (ME-*COF*): (0) absent; (1) transverse; (2) curvilinear; (3) irregular.

367. Central fracture line (continuous striae) (ME-*CEF*): (0) absent; (1) present.

368. Perforations on body scales (new): (0) absent; (1) present.

Description. Clupeomorph genera usually do not exhibit perforated scales. However, a few clupeoid species are characterized by body scales that are considerably perforated along their entire surface or only in the hind part, including some of *Sardinella* (including *S. maderensis*), *Sardinops*, and *Hilsa* (Wongratana 1980; Whitehead 1985; Purrafee Dizaj *et al.* 2020). Among fossils here considered, perforated body scales have been reported only in †*Eoalosa* (Marramà & Carnevale 2018).

PHYLOGENETIC RESULTS

Our implied weighted analysis of 368 characters coded for 130 taxa (see Appendix 2) produced three equally parsimonious trees that have been used to build the strict con*sensu*s tree having 1978 steps, fitness value of 40.46, CI 0.236, RI 0.762, aiming at resolving the intrarelationships within the Clupeomorpha (Figs 39; 40). The average amount of homoplasy (HI) for the matrix is 0.764. The low CI and high HI indicate that the tree contains a considerable amount of homoplasy, suggesting that many characters have high evolutionary plasticity and/or exhibit convergent evolution and/or reversals, therefore requiring additional evolutionary steps beyond the minimum needed to explain the observed patterns. Despite high homoplasy, the relatively high RI indicates that, once evolved, most characters are retained along branches and character reversal events are relatively uncommon. This implies that certain traits are phylogenetically informative and reliably track the history of the clades in the tree, and the tree has a strong phylogenetic signal, as suggested by the high Bremer support, at least for some nodes (Figs 39; 40). Performing the same analysis and stabilizing the con*sensu*s twice with a factor of 75 results in a tree topology very similar to that of the main analysis. These results indicate that the characters employed in the main analysis are robust and that the resulting systematic arrangement is very stable.

The tree from the main analysis appears to be almost completely resolved, with only a few relationships between species of the ellimmichthyiform †*Paraclupea* and species of the Pellonulinae that remain still unclear. The main tree topology shows that the Clupeomorpha is strongly supported as a monophyletic group (Relative Bremer = 88) having a dichotomous nature, in which the extinct order †Ellimmichthyiformes is sister to the total group Clupeiformes (†*Spratticeps* + Clupeiformes). The †Ellimmichthyiformes is a monophyletic group in which the †Sorbinichthyidae, †*Codoichthys*, †Scutatuspinosidae and †Gasteroclupeidae are successive sister taxa to the clade including the †Armigatidae and †Paraclupeidae, with the topology highly consistent with the last hypotheses (e.g., Marramà *et al.* 2022; Marramà & Carnevale 2023).

†*Spratticeps* can be considered as a stem clupeiform, with the crown group Clupeiformes that includes the suborder Denticipitoidei (†Cynoclupeidae + Denticipitidae), and the stem clupeoids †*Pseudoellimma* and †*Leufuichthys* as successive sister taxa of the Clupeoidei. We therefore identified three major lineages within the Clupeoidei: the pan-Engrauloidea (including fossil and extant round herrings, wolf herrings and anchovies) as sister to a clade formed by the Pristigasteroidea and the Clupeoidea new usage.

We demonstrate that the recovering of the Spratelloididae (*Jenkinsia* and *Spratelloides*) as the basalmost clupeoid clade in the recent hypotheses based on molecular data (e.g., Wang *et al.* 2022) might be an artifact due to missing fossil data. In fact, whereas in our main analysis the total group Spratelloididae (†*Trollichthys*, *Jenkinsia* and *Spratelloides*) is sister to a lineage (the Engrauloidea new usage) that includes †*Nardoclupea*, and the living Dussumieriidae, as successive sisters to the Chirocentridae and the total group Engraulidae, the analysis that excludes fossil taxa (Fig. 41) recovered the Spratelloididae as sister to all remaining Clupeoidei in agreement with the recent molecular analyses (Bloom & Lovejoy 2014; Betancur-R *et al.* 2017; Bloom & Egan 2018; Egan *et al.* 2018; Wang *et al.* 2022).

The pristigasteroids form a monophyletic clade, but within this lineage there is no support for the monophyly of the Pellonidae and Pristigasteridae as proposed by Grande (1985). The Clupeoidea new usage includes the remaining clupeoids. The monophyly of the Clupeidae *sensu* Wang *et al.* (2022) (*Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*) recovered in the recent molecular analyses appears to be an artifact as well, since the inclusion of the Eocene pair †*Gosiutichthys* and †*Knightia*, forming herein a clade with the pair *Hyperlophus* + *Potamalosa* (the Hyperlophidae, new rank), makes the Wang *et al.* (2022) family Clupeidae paraphyletic and highlights the gradual achievement of traits that characterize the more derived and monophyletic clupeoid families (Ehiravidae, Alosidae and Dorosomatidae). In fact, the analysis that excludes fossil taxa (Fig. 41) recovered the living Hyperlophidae as sister to the pair *Clupea* + *Sprattus*, in agreement with the recent molecular analyses (Bloom & Lovejoy 2014; Betancur-R *et al.* 2017; Bloom & Egan 2018; Egan *et al.* 2018; Wang *et al.* 2022).

Time-calibrated trees are depicted in Figs 42-44.

SYSTEMATIC ACCOUNT: THE INTRARELATIONSHIPS OF THE CLUPEOMORPHA (Figs 39-40)

Node 1
Superorder Clupeomorpha Greenwood, Rosen, Weitzman & Myers, 1966 (*sensu* Grande 1985)

TAXA INCLUDED AND RELATIONSHIPS. — †Ellimmichthyiformes + (†*Spratticeps* + Clupeiformes).

UNAMBIGUOUS SYNAPOMORPHIES. — Skull roof ornamented (16:0>1); anterior frontal fontanelle absent (24:1>0); anterior arm of the orbitosphenoid short, not reaching the ethmoid region (44:1>0); otophysic connection involving a diverticulum of the swim bladder that penetrates the exoccipital and extends into the prootic (48:0>1); prootic bulla present (50:0>1); central shaft of the maxilla long (96:1>0); anterior ceratohyal short, its length less than five times its depth (144:1>0); first and second postcleithra present (262:0>1, 263:0>1); parhypural fused with PU1 (301:0>1); pelvic scute present (329:0>1); prepelvic scutes present between the pelvic scute and the posterior end of the coracoid (333:0>1); postpelvic scutes present (338:0>1).

SUPPORT. — Relative Bremer = 88%.

REMARKS. — The superorder Clupeomorpha is strongly supported by 13 unambiguous synapomorphies and encompasses all the taxa considered in our ingroups. All the taxa can be included within two orders Clupeiformes and †Ellimmichthyiformes, containing four and ten of the families traditionally recognized, respectively. †*Spratticeps* is considered herein as a stem-clupeiform. Grande (1982a) divided the clade in two “Divisions”, with “Division 1” including only †*Ornategulum*, originally described by Forey (1973a) as a “primitive clupeomorph”, and “Division 2” including †*Armigatus*, his †Ellimmichthyiformes (including only †*Diplomystus* and †*Ellimmichthys longicostatus*) and the Clupeiformes. Later, Grande (1985) excluded †*Ornategulum* from the Clupeomorpha and included †*Erichalcis* in his “Division 1”. Today, the Grande’s Division 1 is invalid because †*Erichalcis*, originally described by Forey (1975) as a “primitive clupeomorph”, has been later proved to be a basal euteleost (Arratia 1997, 1999; Hermus *et al.* 2004). By excluding the Division 1 from the group, the synapomorphies of the Clupeomorpha as recognized by Grande (1985) include 1) the presence of abdominal (pelvic, prepelvic and postpelvic) scutes, 2) an otophysic connection involving a diverticulum of the swim bladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase, forming ossified bullae in the prootic, 3) supratemporal commissural sensory canal passing through parietals and supraoccipital, 4) second hypural fused with the first ural centrum, 5) a well-defined pre-epioccipital fossa, and 6) keeled dorsal scutes. Of these, our analysis solely recognized the first two characters as clupeomorph synapomorphies.

Although the presence of a complete series of abdominal scutes is one of the distinctive features of the clupeomorphs, the presence of taxa with a single scute (e.g., Dussumieriidae, Spratelloididae, and some engraulids), which were considered as “basal” (e.g., Whitehead 1963), resulted in a debate about the possession of a fully developed series of abdominal scutes in the most recent common ancestor (MRCA hereafter) of the clupeomorphs or whether the absence of scutes (e.g., †*Ornategulum*) represents a distinctive character of the basal bauplan of clupeomorphs or not, or if the taxa devoid of a complete series of abdominal scutes should be regarded as genuine clupeomorphs (see, e.g., Grande 1982a, 1985). In this perspective, our analysis supports the hypothesis that the MRCA of clupeomorphs had a complete series of abdominal scutes, which have been secondarily reduced (e.g., in *Chirocentrus*, round herrings, and New World anchovies) or completely lost (e.g., †*Nardoclupea*, †*Ornategulum*). Using the logical basis for morphological characters in phylogenetics (e.g., Sereno 2007) we distinguished the presence of otophysic connection, and of pterotic and prootic bullae as three distinct characters, highlighting that, beside the presence of otophysic connection involving penetration of the exoccipital by a swim bladder diverticulum, the presence of prootic bullae can be considered as a synapomorphy of the Clupeomorpha as well.

The third synapomorphy proposed by Grande (1985) (supratemporal commissural sensory canal primitively passing through parietals, or through parietals and supraoccipital) was not identified as a synapomorphy of the Clupeomorpha in our analysis for two reasons: 1) character 2 of Grande (1985) has been split in two distinct characters; 2) the supratemporal canal passing through parietals is a feature that characterizes, other than all clupeomorphs, also *Chanos* and †*Tischlingerichthys* making the state as a synapomorphy of the pair formed by Ostariophysi + Clupeomorpha, whereas the supratemporal canal passing also through the supraoccipital is a synapomorphy of the clade that includes †*Spratticeps* + Clupeiformes.

Also the fourth synapomorphy proposed by Grande (1985) (second hypural fused with the first ural centrum) was not identified as synapomorphy of the Clupeomorpha in our analysis, since the basalmost †ellimmichthyiform †*Sorbinichthys* retains the plesiomorphic teleost condition in which all the hypurals are autogenous (Bannikov & Bacchia 2000; Murray & Wilson 2011) and, at the same time, the condition is unknown in the stem Clupeiformes †*Spratticeps* (Patterson 1970) making impossible to detect the condition in the MRCA.

As far as the fifth synapomorphy proposed by Grande (1985) is concerns, although a large, well developed pre-epioccipital fossa has been detected in †*Cynoclupea*, †*Santanaclupea*, and most extant and fossil Clupeoidei, it is small or even absent in †*Spratticeps*, *Denticeps*, †*Pseudoellimma*, Engrauloidea and †Ellimmichthyiformes (Patterson 1970; Grande 1985; Sato 1994), thereby precluding it to represent a synapomorphy of the Clupeomorpha. The same can be said for the presence of predorsal scutes, considered as a distinctive feature of the Division 2 of Grande (1982a, 1985), since it was not identified as synapomorphy of the Clupeomorpha; although most †ellimmichthyiforms possess predorsal scutes, only a few clupeiforms possess them and their presence in key basal taxa (†*Spratticeps*, †*Santanaclupea*) is unknown, making their presence a synapomorphy of the †Ellimmichthyiformes rather than of the clupeomorphs.

Interestingly, the presence of a parhypural fused with the first preural centrum (or to the compound centrum) was recovered as a key clupeomorph synapomorphy. Although Grande (1985, pp. 259-260) clearly noticed that †ellimmichthyiforms and denticipitoids have the parhypural fused to the first preural centrum, with secondary separation in clupeoids, he did not consider it as a key synapomorphy of the Clupeomorpha.

Node 2
Order †Ellimmichthyiformes Grande, 1982

Taxa included and relationships. — †Sorbinichthyidae + (†*Codoichthys* + (†Scutatuspinosidae + (†Gasteroclupeidae + (†Armigatidae + †Paraclupeidae))).

Unambiguous synapomorphies. — Basipterygoid process of the parasphenoid present (33:0>1); striations on the ventral part of opercle (201:0>1); anteriormost ribs articulate with pits, followed by ribs articulating with parapophyses (220:0>1); at least one predorsal scute present (318:0>1).

Support. — Relative Bremer = 6%.

Remarks. — The order †Ellimmichthyiformes was created by Grande (1982a) to contain the non-clupeiform clupeomorphs †*Diplomystus dentatus* and †*Ellimmichthys longicostatus* (but excluding †*Armigatus brevissimus*, †*Ellimma branneri* and †*Ornategulum sardinioides*) and defined by the lateral expansion of dorsal scute "wings" that give scutes a subrectangular shape. The same topology and diagnosis have been maintained by Grande (1985). After the discovery of new double-armored herrings, Chang & Maisey (2003) include also †*Armigatus*, †*Ellimma* and †*Paraclupea chetungensis* (but not †*Ornategulum*) within the †Ellimmichthyiformes, now diagnosed by the presence of basipterygoid process of parasphenoid, beryciform foramen in anterior ceratohyal and dorsal scutes, whereas Zaragüeta Bagils (2004) diagnosed it (excluding †*Armigatus*, †*Diplomystus* and †*Ornategulum*) by the dorsal margin of the body with a marked angle at the insertion of the dorsal fin and prominent spine on the postpelvic scutes. Forey (2004) by including †*Armigatus*, †*Diplomystus*, †*Ellimmichthys*, †*Paraclupea*, †*Sorbinichthys*, and †*Triplomystus* proposed the presence of a S-shaped cleithrum as the only synapomorphy of the †Ellimmichthyiformes, whereas Alvarado-Ortega *et al.* (2008) excluded †*Armigatus* and diagnosed the †Ellimmichthyiformes using the presence of predorsal scutes with a subrectangular shape in the posterior part of predorsal series. More recently, Murray & Wilson (2013) diagnosed the †Ellimmichthyiformes (including †*Armigatus*) as clupeomorphs showing medioparietal condition, frontals and parietals ornamented, basipterygoid process, beryciform foramen, predorsal scutes and three epurals; with these features, tree topology and group composition were in general retained in subsequent analyses (e.g., Murray *et al.* 2016; Alvarado-Ortega *et al.* 2020; Marramà & Carnevale 2023). Our analysis corroborates the most recent hypotheses about the composition of the order that can be diagnosed by the presence of basipterygoid process of parasphenoid and dorsal scutes, but not by the presence of a beryciform foramen, since it is also present in basal clupeiforms (e.g., †*Santanaclupea*, †*Scombroclupea*, †*Italoclupea*). The presence of anteriormost ribs articulating with pits, followed by ribs articulating with parapophyses can be considered an additional unambiguous synapomorphy of the †Ellimmichthyiformes, being this pattern present in most taxa. Although the presence of endopterygoid teeth and the medioparietal condition have been often regarded as typical of the double-armoured herrings, the presence of endopterygoid teeth in several clupeiforms (e.g., Sato 1994), their absence in some †ellimmichthyiforms, and the lateroparietal condition in the basalmost †ellimmichthyiform †*Sorbinichthys*, suggest that these characters cannot be recognized as a synapomorphies in our hypothesis. Recent morphological and combined (morphological + molecular) analyses (Vernygora 2020; Kevrekidis *et al.* 2024) recovered the †Ellimmichthyiformes within the Clupeiformes, even nested within the Clupeoidei. However, as we show later, these analyses were affected by incomplete character sampling.

Node 3
Family †Sorbinichthyidae
Bannikov & Bacchia, 2000

Taxa included and relationships. — †*Sorbinichthys elusivo* + †*S. africanus*.

Unambiguous synapomorphies. — Anterior dorsal margin of the body forming a marked angle at the dorsal-fin insertion (1:0>1); lower jaw length three or more times its depth (109:0>1); endopterygoid teeth present (115:0>1); pleural ribs/vertebrae ratio of 0.20-0.40 (231:2>0); elongated upper pectoral-fin rays (256:0>1); dorsal process of the posttemporal subtriangular, wider at distal tip than at its midlength (261:0>2); hypural 2 triangular, with its distal end distinctly broader than the proximal end (285:0>2); caudal scutes absent (306:1>0); procurrent rays deeply inserted in the interneural and interhaemal spaces (310:0>1); spines on the posterior margin of the predorsal scutes (322:0>1); lateral extensions of the posteriormost predorsal scutes (327:0>1); 31 to 55 anal-fin pterygiophores (343:0>1); anal-fin origin below the dorsal-fin base (344:0>1); greatly elongated second dorsal-fin ray (353:0>1).

Support. — Relative Bremer = 84%.

Remarks. — The family †Sorbinichthyidae was created by Bannikov & Bacchia (2000) to include the peculiar clupeomorph †*Sorbinichthys elusivo* from the Cenomanian of Namoura (Lebanon). The peculiar mix of †ellimmichthyiform (pectinate predorsal scutes, large U1, uroneural 1 autogenous) and clupeiform (beryciform foramen apparently absent, lateroparietal condition of the skull) features led the authors to leave the family as Clupeomorpha *incertae sedis*. Subsequent analyses (Forey 2004; Zaragüeta Bagils 2004) included †*Sorbinichthys* within the †Ellimmichthyiformes, with these hypotheses later corroborated by the discovery of new species (*S. africanus*) that exhibits a large beryciform foramen, basipterygoid processes, and anteriormost ribs articulate with pits, followed by ribs articulating with parapophyses (Murray & Wilson 2011). Other analyses placed †*Diplomystus* in the family †Sorbinichthyidae because they share spines on the posterior

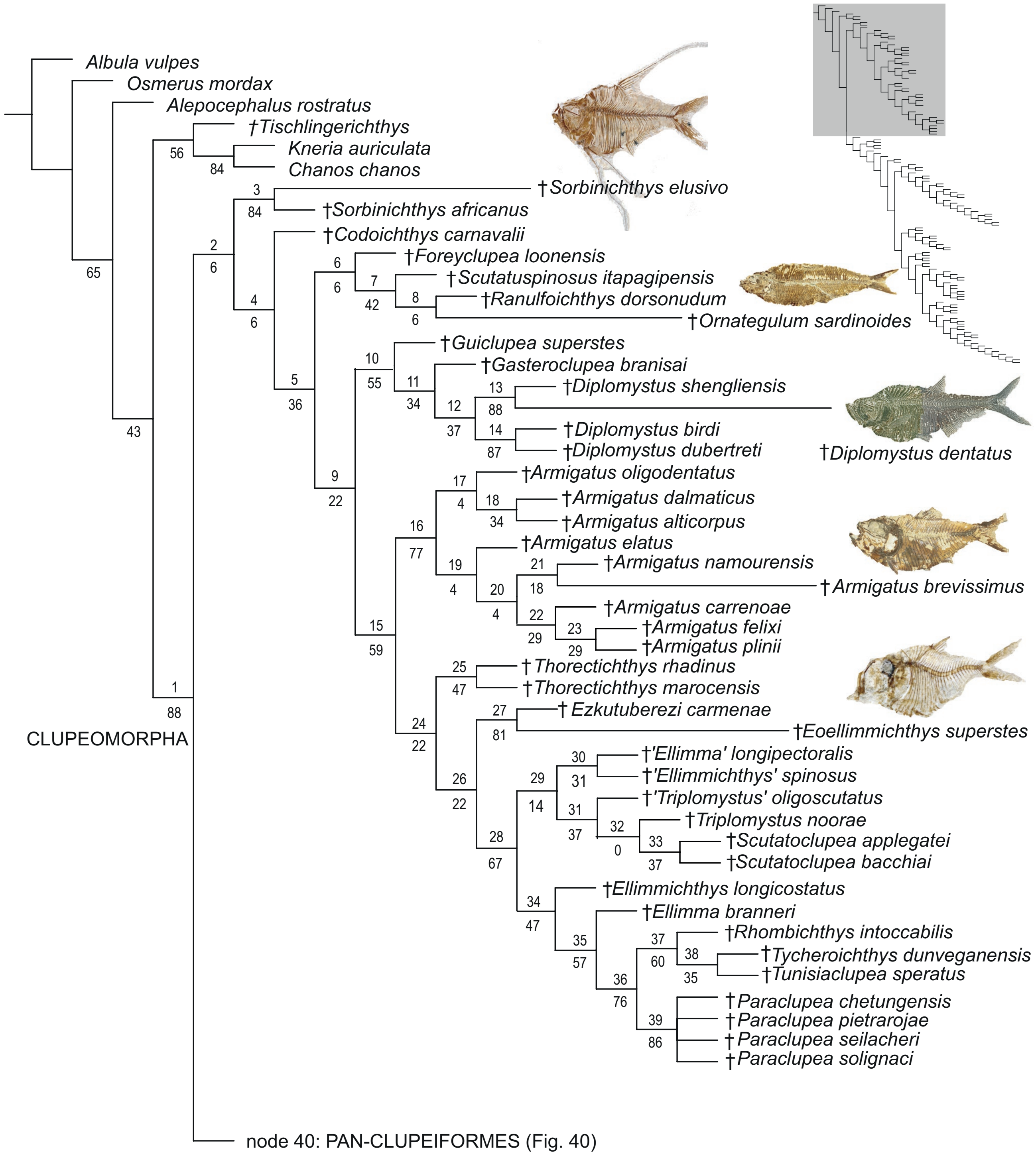

Fig. 39. — Strict consensus tree from three equally parsimonious trees retrieved in TNT v.1.6 based on 368 morphological characters and all 130 terminal taxa highlighting the interrelationships of node 2 (†Ellimmichthyiformes) within the Clupeomorpha. Numbers above nodes indicate the node number. Numbers below the nodes indicate the Bremer support. Extinct taxa are marked with a dagger. The unambiguous synapomorphies on each node are explained in the text.

margin of predorsal scutes (Alvarado-Ortega *et al.* 2008). Our analysis, however, excludes the close relationship of †*Diplomystus* with †*Sorbinichthys*, because it recovered this latter sister to all the remaining †ellimmichthyiform taxa, likely due to the presence of plesiomorphic traits like lateroparietal condition, and the absence of more derived †ellimmichthyiform characters (see below), resembling some of the most recent hypotheses (e.g., Murray *et al.* 2016; Figueiredo & Ribeiro 2017; Marramà *et al.* 2022).

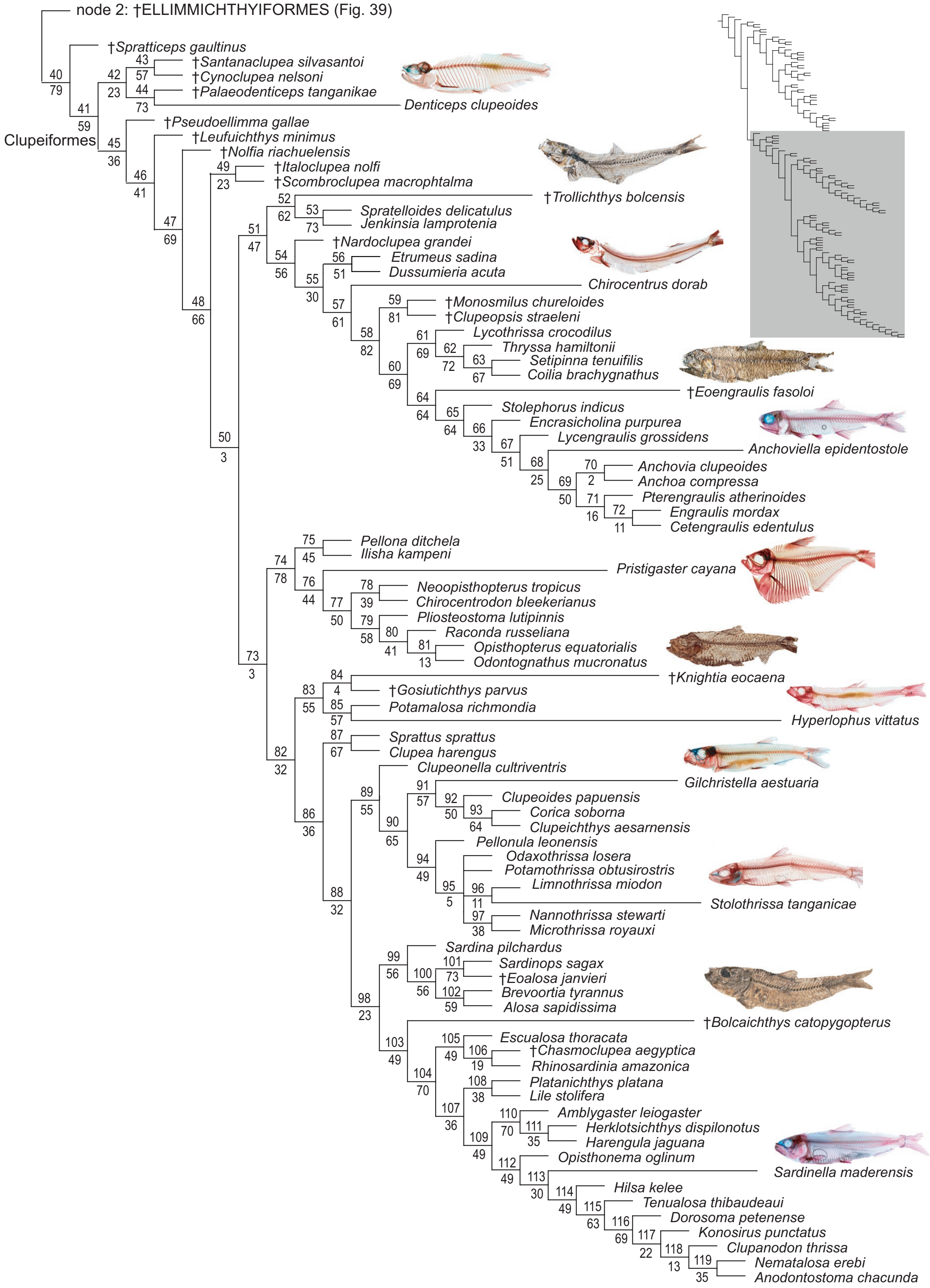

FIG. 40. — Strict consensus tree from three equally parsimonious trees retrieved in TNT v.1.6 based on 368 morphological characters and all 130 terminal taxa highlighting the interrelationships of node 40 (the total group Clupeiformes) within the Clupeomorpha. Numbers above nodes indicate the node number. Numbers below the nodes indicate the Bremer support. Extinct taxa are marked with a dagger. The unambiguous synapomorphies on each node are explained in the text.

Node 4
Unnamed clade

Taxa included and relationships. — †*Codoichthys* + (†Scutatuspinosidae + (†Gasteroclupeidae + (†Armigatidae + †Paraclupeidae))).

Unambiguous synapomorphies. — Mediopariental condition (4:1>0); coronoid process located in the anterior part of the lower jaw (110:0>1).

Support. — Relative Bremer = 6%.

Remarks. — The genus †*Codoichthys* from the Late Aptian of Brazil was created by Santos (1994) who referred it to as Clupeomorpha *incertae sedis*, although he recognized affinities with non-clupeiform clupeomorphs. Figueiredo & Ribeiro (2016) recovered †*Codoichthys* as the basalmost †Paraclupeidae because of the presence of some homoplastic features shared with the members of that family (absence of teeth on parasphenoid and low number of predorsal scutes), whereas more recent analyses recovered it as a basal †ellimmichthyiform having more affinities with †*Foreyclupea*, †*Ornategulum*, †*Ranulfoichthys* and †*Scutatuspinosus* (Marramà *et al.* 2022; Marramà & Carnevale 2023), in agreement with our results.

Node 5
Unnamed clade

Taxa included and relationships. — †Scutatuspinosidae + (†Gasteroclupeidae + (†Armigatidae + †Paraclupeidae)).

Unambiguous synapomorphies. — Hypural diastema absent (288:0>1); 21-30 abdominal scutes (341:2>3).

Support. — Relative Bremer = 36%.

Node 6
Family †Scutatuspinosidae
Silva Santos & Silva Corréa, 1985
(*sensu* Vernygora *et al.* 2016)

Taxa included and relationships. — †*Foreyclupea* + (†*Scutatuspinosus* + (†*Ranulfoichthys* + †*Ornategulum*)).

Unambiguous synapomorphies. — Ornamentation of the supramaxillae present (87:0>1); length of the ascending arms of the pelvic scute short (331:1>0); ascending arms of the prepelvic scutes along the ventral edge of the coracoid absent or inconspicuous (335:0>1); length of the ascending arms of the prepelvic scutes between the pelvic scute and the posterior edge of coracoid short (337:1>0).

Support. — Relative Bremer = 6%.

Remarks. — Vernygora *et al.* (2016) elevated the subfamily †Scutatuspinosinae Silva Santos & Silva Correa, 1985 to the family level (Scutatuspinosidae) to include †*Foreyclupea*, †*Ranulfoichthys*, and †*Scutatuspinosus*, and the clade diagnosed by anterior dorsal margin of the body with no angle at dorsal-fin origin, abdominal scutes with short ascending arms and absence of a diastema between hypurals 2 and 3. Our analysis agrees with Vernygora *et al.* (2016) in recovering this clade if also †*Ornategulum* is included. Although †*Ornategulum* has no abdominal scutes, its ornamented supramaxillae and the numerous osteological traits shared with †*Ranulfoichthys* (Forey 1973a; Alvarado-Ortega 2014) support its placement within the †Scutatuspinosidae.

Node 7
Unnamed clade

Taxa included and relationships. — †*Scutatuspinosus* + (†*Ranulfoichthys* + †*Ornategulum*).

Unambiguous synapomorphies. — Ascending arms of the prepelvic and postpelvic scutes semicircular to subrectangular, contacting each other for the entire length (340:0>2).

Support. — Relative Bremer = 42%.

Node 8
Unnamed clade

Taxa included and relationships. — †*Ranulfoichthys* + †*Ornategulum.*

Unambiguous synapomorphies. — Supratemporal commissure sensory canal passing through the supraoccipital present (8:0>1); coronoid process displaced from the middle to the posterior part of the dentary (110:1>0); more than 10 branchiostegal rays (153:1>2); seven hypurals (281:0>1); proximal end of the first hypural not reaching the first ural centrum (283:0>1); anterior tip of the first uroneural reaches or extends anteriorly beyond the posterior margin of PU2 (298:0>1).

Support. — Relative Bremer = 6%.

Node 9
Unnamed clade

Taxa included and relationships. — †Gasteroclupeidae + (†Armigatidae + †Paraclupeidae).

Unambiguous synapomorphies. — Pre-epioccipital fenestra present (22:0>1); basisphenoid absent (40:0>1); dentary teeth restricted to the region near the mandibular symphysis (106:1>0); endopterygoid teeth present (115:p>1); striations on ventral part of opercle absent (201:1>0); proximal region of supraneurals with an antero-posterior laminar expansion that covers most of the bone length (210:0>2); cleithrum S-shaped (257:0>1); peg on the upper middle ray of caudal fin present (313:0>1).

Support. — Relative Bremer = 22%.

Remarks. — The most recent phylogenetic analyses of the †Ellimmichthyiformes recurrently recovered the clade formed by †Gasteroclupeidae + (†Armigatidae + †Paraclupeidae) as monophyletic due to the absence of the basisphenoid, striations on the ventral part of the opercle, presence of third hypural being the largest of the series, and S-shaped cleithrum (Marramà *et al.* 2022; Marramà & Carnevale 2023). The clade is diagnosed herein roughly by the same set of unambiguous synapomorphies plus a few others.

Node 10
Family †Gasteroclupeidae
(*sensu* Marramà *et al.* 2022)

Taxa included and relationships. — †*Guiclupea* + (†*Gasteroclupea* + †*Diplomystus*).

Unambiguous synapomorphies. — Mouth superterminal, upward turned (2:0>2); high supraoccipital crest (11:0>1); posterior process of infraorbital 1 present (76:0>1); quadrate-mandibular articulation anterior to orbit (131:1>2); pleural ribs-preural vertebrae ratio between 0.41 and 0.46 (231:2>1); proximal end of hypural 1 sharp, with no articulatory process (283:0>1); 20 or more predorsal scutes (326:2>0); more than 30 abdominal scutes (341:3>4).

Support. — Relative Bremer = 55%.

Remarks. — The subfamily †Gasteroclupeinae has been created by Signeaux (1964) to contain the peculiar fossil clupeomorph †*Gasteroclupea* from the Upper Cretaceous-Paleocene non-marine deposits of South America. Although the author recognized some affinities with the genus †*Diplomystus* (e.g., medioparietal condition of the skull roof, complete series of predorsal scutes with subrectangular lateral wings, etc), its general body physiognomy and the absence of pelvic fins led some authors to classify it within the Pristigasteroidea (Grande 1985; Gayet & Meunier 1998). Thanks to the recent detailed redescription and, particularly, the new observations of the caudal skeleton, †*Gasteroclupea* has been reclassified as an †ellimmichthyiform clupeomorph with affinities with †*Diplomystus* and †*Guiclupea*, leading Marramà *et al.* (2022) to elevate the Gasteroclupeinae Signeaux, 1964 to the rank of family (†Gasteroclupeidae) and containing these three genera.

Node 11
Unnamed clade

Taxa included and relationships. — †*Gasteroclupea* + †*Diplomystus*.

Unambiguous synapomorphies. — Subrectangular predorsal scutes in the anterior part of the series (320:0>2); subrectangular predorsal scutes in the posterior part of the series (321:0>2); predorsal scutes with no surface ornamentation (325:1>0).

Support. — Relative Bremer = 34%.

Node 12
Genus †*Diplomystus* Cope, 1877

Taxa included and relationships. — (†*D. dentatus* + †*D. shengliensis*) + (†*D. birdi* + †*D. dubertreti*).

Unambiguous synapomorphies. — More than 10 branchiostegal rays (153:1>2); 7-9 supraneurals (208:1>2); pleural rib/preural vertebrae ratio between 0.20 and 0.40 (231:1>0); spines on the posterior margin of the lateral wings of the predorsal scutes (322:0>1).

Support. — Relative Bremer = 37%.

Node 13
Unnamed clade

Taxa included and relationships. — †*Diplomystus dentatus* + †*D. shengliensis*.

Unambiguous synapomorphies. — 41-50 preural vertebrae (218:3>2); 31-55 anal-fin pterygiophores (343:0>1).

Support. — Relative Bremer = 88%.

Remarks. — This clade unites the two Eocene non-marine †*Diplomystus* species †*D. dentatus* and †*D. shengliensis* from North America and China, respectively, compared to the two marine species from the Upper Cretaceous of Lebanon (see below), with this phylogenetic hypothesis therefore reflecting similarity in anatomy, age and habitat preference.

Node 14
Unnamed clade

Taxa included and relationships. — †*Diplomystus birdi* + †*D. dubertreti*.

Unambiguous synapomorphies. — 21 to 30 abdominal scutes (341:4>3); anal-fin origin below the dorsal-fin base (344:0>1).

Support. — Relative Bremer = 87%.

Node 15
Unnamed clade

Taxa included and relationships. — †Armigatidae + †Paraclupeidae.

Unambiguous synapomorphies. — Skull roof ornamented with strong grooves and numerous fine, radiating ridges (17:0>1); six or fewer supraneurals (208:1>3); proximal region of median rays of the caudal fin extends anteriorly covering laterally about the half of the length of the hypurals 2 and 3 (312:0>1).

Support. — Relative Bremer = 59%.

Node 16
Family †Armigatidae Murray & Wilson, 2013

Taxa included and relationships. — (†*Armigatus oligodentatus* + (†*A. alticorpus* + †*A. dalmaticus*)) + (†*A. elatus* + ((†*A. brevissimus* + †*A. namourensis*) + (†*A. carrenoae* + (†*A. plinii* + †*A. felixi*)))).

Unambiguous synapomorphies. — Incomplete series of predorsal scutes, leaving a gap posterior to occiput (319:1>0); heart-shaped predorsal scutes in the anterior part of the series (320:0>3); heart-shaped predorsal scutes in the posterior part of the series (321:0>3).

Support. — Relative Bremer = 77%.

Remarks. — The genus †*Armigatus* was established by Grande (1982a) to distinguish the fossil species †*Clupea brevissima* Blainville, 1818 from the Cenomanian deposits in Lebanon (previously placed in the genus †*Diplomystus*) from the other †*Diplomystus* species. The initial diagnosis of †*Armigatus* provided by Grande (1985) included some diagnostic features, which Forey *et al.* (2003) subsequently expanded. Murray & Wilson (2013) later created the family †Armigatidae to include †*Armigatus* and †*Diplomystus*, though later analyses suggested this grouping was paraphyletic. Further studies have refined the diagnostic traits of †*Armigatus* and recognized the family †Armigatidae of Murray & Wilson (2013) as paraphyletic. Although a few studies recovered †*Armigatus* to be a paraphyletic assemblage (e.g., Boukhalfa *et al.* 2018; Than-Marchese & Alvarado-Ortega 2022) the most recent analyses (including our implied-weighting one) strongly support the hypothesis that both †*Armigatus* species can be grouped into a single monotypic family (e.g., Marramà & Carnevale 2023; this study). The relationships between the †*Armigatus* species seem to agree with their age and palaeogeographical settings, supporting the hypothesis that that both the main lineages originated from an early Lower Cretaceous ancestor in the western Tethys, as the study of a new upper Hauterivian-lower Barremian species confirmed (Amalfitano *et al.* 2025).

Node 17
Unnamed clade

Taxa included and relationships. — †*Armigatus oligodentatus* + (†*A. alticorpus* + †*A. dalmaticus*).

Unambiguous synapomorphies. — Skull roof unornamented (16:1>0).

Support. — Relative Bremer = 4%.

Node 18
Unnamed clade

Taxa included and relationships. — †*A. alticorpus* + †*A. dalmaticus*.

Unambiguous synapomorphies. — Pleural ribs/preural vertebrae ratio of 0.41-0.46 (231:2>1); hypural 3 equal or smaller than hypural 1 (290:1>0); less than three uroneurals (296:0>1); anterior tip of first uroneural reaches or extends anteriorly beyond the posterior margin of PU2 (298:0>1).

Support. — Relative Bremer = 34%.

Node 19
Unnamed clade

Taxa included and relationships. — †*A. elatus* + ((†*A. brevissimus* + †*A. namourensis*) + (†*A. carrenoae* + (†*A. plinii* + †*A. felixi*))).

Unambiguous synapomorphies. — Teeth on the parasphenoid present (34:0>1).

Support. — Relative Bremer = 4%.

Node 20
Unnamed clade

Taxa included and relationships. — (†*A. brevissimus* + †*A. namourensis*) + (†*A. carrenoae* + (†*A. plinii* + †*A. felixi*)).

Unambiguous synapomorphies. — Radial striations on the ventral part of the opercle present (201:0>1).

Support. — Relative Bremer = 4%.

Node 21
Unnamed clade

Taxa included and relationships. — †*A. brevissimus* + †*A. namourensis*.

Unambiguous synapomorphies. — All the ribs articulate with the parapophyses (220:1>0); anterior tip of first uroneural reaches or extends anteriorly beyond the posterior margin of PU2 (298:0>1).

Support. — Relative Bremer = 4%.

Node 22
Unnamed clade

Taxa included and relationships. — †*A. carrenoae* + (†*A. plinii* + †*A. felixi*).

Unambiguous synapomorphies. — Supramaxillae ornamented (87:0>1); foramen in the posterior ceratohyal present (125:0>1).

Support. — Relative Bremer = 29%.

Node 23
Unnamed clade

Taxa included and relationships. — †*A. plinii* + †*A. felixi*.

Unambiguous synapomorphies. — Pleural ribs/preural vertebrae ratio of 0.41-0.46 (231:2>1); ornamentation on the surface of the predorsal scutes absent (325:1>0).

Support. — Relative Bremer = 29%.

Node 24
Family †Paraclupeidae Chang & Chou, 1977

Taxa included and relationships. — †Thorectichthyinae + (†Eoellimmichthyinae + (((“†*Ellimmichthys*” *spinosus* + “†*Ellimma*” *longipectoralis*) + †Triplomystinae) + †Paraclupeinae)).

Unambiguous synapomorphies. — Anterior tip of the first uroneural reaching or extending anteriorly beyond the posterior margin of PU2 (298:0>1); predorsal scutes increasing in size posteriorly (324:0>1); posteriorly directed ventral spines on the postpelvic abdominal scutes (339:0>1).

Support. — Relative Bremer = 22%.

Remarks. — Chang & Chou (1977) created the family †Paraclupeidae (= †Ellimmichthyidae of Grande 1982a) that was defined by a single character (dorsal scutes broader than long) and that accounted until then all non-clupeiform clupeomorphs (†*Diplomystus*, †*Ellimmichthys* and †*Paraclupea*). After the recognition of †*Armigatus* as a separate genus (that included †*Diplomystus brevissimus*) by Grande (1982a), Chang & Maisey (2003) emended the diagnosis of the family in order to include †*Armigatus*, †*Diplomystus*, †*Ellimma*, †*Ellimmichthys* and †*Paraclupea* that share the presence of laterally expanded, subrectangular dorsal scutes with some having a median keel extending posteriorly over the adjacent scute in the form of a pointed prominent spine. After the discovery of new †ellimmichthyiform genera and the inclusion of new characters, Alvarado-Ortega *et al.* (2008) recovered the family †Paraclupeidae as a monophyletic group that excluded †*Armigatus*, †*Diplomystus* and †*Sorbinichthys* but included all the other †ellimmichthyiforms that have 1) scutes of the predorsal series that increase in size posteriorly, and 2) with the posterior most ones bearing a prominent and strong spine. Subsequent studies generally agree in recovering these two synapomorphies as typically characterizing the †Paraclupeidae, although a few genera (e.g., †*Codoichthys*, †*Scutatuspinosus*) fall within or outside the family depending on the different interpretation of some states or the inclusion of new characters (e.g., Vernygora *et al.* 2016; Vernygora & Murray 2021).

Node 25
Subfamily †Thorectichthyinae
Murray & Wilson, 2013

Taxa included and relationships. — †*Thorectichthys marocensis* + †*T. rhadinus*.

Unambiguous synapomorphies. — Premaxilla long, equal or more than 50% of the maxillary length (92:0>1); distal end of the second uroneural not reaching the distal end of the first uroneural (300:0>1).

Support. — Relative Bremer = 47%.

Remarks. — Murray & Wilson (2013) created the genus †*Thorectichthys* and its own subfamily †Thorectichthyinae to include two new †ellimmichthyiform species from the late Cenomanian or early Turonian of Morocco, †*T. marocensis* and †*T. rhadinus*, the monophyly of the subfamily being supported by the absence of the median strong spine on posteriormost predorsal scutes, usually present in other paraclupeids. This is one of the reasons why this monotypic subfamily is often recovered as the basalmost †paraclupeid (e.g., Boukhalfa *et al.* 2018; Marramà *et al.* 2022). The genus †*Thorectichthys* has been recovered as paraphyletic due to a certain degree of dissimilarity of the two known species, regarding differences in the outline of the dorsal margin, skull roof ornamentation and other traits (e.g., Marramà & Carnevale 2023). However, the present analysis corroborates the validity of the genus, as also detected by another analysis performed after the discovery of a third species, †*T. fideli* from the Cenomanian deposits of southeastern Mexico (Than-Marchese *et al.* 2024).

Node 26
Unnamed clade

Taxa included and relationships. — †Eoellimmichthyinae + (((“†*Ellimmichthys*” *spinosus* + “†*Ellimma*” *longipectoralis*) + †Triplomystinae) + †Paraclupeinae).

Unambiguous synapomorphies. — Epipleurals in the caudal region absent (227:1>0); subrectangular predorsal scutes in the posterior part of the series (321:0>2); prominent median spine in posteriormost predorsal scutes (323:0>1).

Support. — Relative Bremer = 22%.

Node 27
Subfamily †Eoellimmichthyinae n. subfam.

urn:lsid:zoobank.org:act:9EF46A8F-EB14-4774-AEB9-3D322A81A3EF

Taxa included and relationships. — †*Eoellimmichthys* + †*Ezkutuberezi*.

Unambiguous synapomorphies. — Preural ribs/preural vertebrae ratio of less of 0.20-0.40 (331:2>0); pelvic-fin insertion anterior to the dorsal-fin origin (280:1>0).

Support. — Relative Bremer = 81%.

Diagnosis. — A new †paraclupeid subfamily diagnosed by the following combination of characters: body deep (60-80% SL); preanal length 67-69% SL; posterior supramaxilla with anterior process as long as the main body of the bone; preural ribs/preural vertebrae ratio of less of 0.20-0.40; dorsal process of the posttemporal subtriangular and distally sharp; last dorsal scute claw-shaped and hypertrophied, more than twice the size of the preceding scute; ascending arms of the abdominal scutes spine-like with large spaces between the wings of the adjacent scutes; pelvic-fin insertion anterior to the dorsal-fin origin; 23-25 anal-fin pterygiophores.

Remarks. — This new subfamily is created herein to include two †paraclupeids (†*Eoellimmichthys*, from the marine Ypresian limestone of Bolca, Italy, and †*Ezkutuberezi* from the upper Valanginian-middle Barremian brackish deposit of the Spanish Basque Country) that are frequently recovered as sisters, since they share at least two unambiguous synapomorphies (see above) other than a number of similar morphological and meristic features, including a deep body (60-80% SL), posterior supramaxilla with anterior process as long as the main body of the bone, last dorsal scute claw-shaped and hypertrophied, more than twice the size of preceding scute, 23-25 anal-fin pterygiophores, and preanal length 67-69% SL (Poyato-Ariza *et al.* 2000; Marramà *et al.* 2019). The new subfamily can be also distinguished from the other paraclupeid subfamilies because of the presence of a subtriangular and distally sharp dorsal process of the posttemporal (vs. sub-rectangular and plate-like in other paraclupeids, except in †*Thorectichthys*), ascending arms of the abdominal scutes spine-like, with large spaces between the wings of adjacent scutes (vs. wide or spatulate, contacting each other for most of their length, except in †*Thorectichthys*). At the same time, alignment of †*Eoellimmichthys* and †*Ezkutuberezi* with the subfamily †Thorectichthyinae can be ruled out because of the absence of epipleurals in the caudal region (vs. present in †*Thorectichthys*) and the presence of a prominent median spine on the posteriormost predorsal scutes (vs. absent in †*Thorectichthys*). The †Eoellimmichthyinae n. subfam. includes taxa (†*Eoellimmichthys*) that represent the youngest and last marine record for the †Ellimmichthyiformes (Marramà *et al.* 2019).

Node 28
Unnamed clade

Taxa included and relationships. — ((“†*Ellimmichthys*” *spinosus* + “†*Ellimma*” *longipectoralis*) + †Triplomystinae) + †Paraclupeinae.

Unambiguous synapomorphies. — Dorsal process of the posttemporal sub-rectangular and plate-like (261:0>1); 11-20 predorsal scutes (326:2>1); lateral wings of the abdominal scutes wide or spatulate, contacting with wings of adjacent scutes for almost their entire length (340:0>1).

Support. — Relative Bremer = 67%.

Node 29
Unnamed clade

Taxa included and relationships. — ("†*Ellimmichthys*" *spinosus* + "†*Ellimma*" *longipectoralis*) + †Triplomystinae.

Unambiguous synapomorphies. — Premaxillary teeth absent (93:1>0).

Support. — Relative Bremer = 14%.

Node 30
Unnamed clade

Taxa included and relationships. — "†*Ellimmichthys*" *spinosus* + "†*Ellimma*" *longipectoralis.*

Unambiguous synapomorphies. — Endopterygoid teeth absent (115:1>0); first and second postcleithra absent (262:1>0; 263:1>0).

Support. — Relative Bremer = 31%.

Remarks. — Our analysis emphasises the necessity of performing phylogenetic analyses before assessing the taxonomic status of a new †ellimmichthyiform species. We show that the genus †*Ellimma* (type species †*E. branneri*) is polyphyletic if "†*Ellimma*" *longipectoralis* is included, as this species is distantly related to †*Ellimma branneri*, therefore disagreeing with the taxonomic placement suggested by Polck *et al.* (2020). The same can be said for the genus †*Ellimmichthys* that is polyphyletic if "†*Ellimmichthys*" *spinosus* is included. This latter taxon shares more characters with "†*Ellimma*" *longipectoralis* compared to †*Ellimmichthys longicostatus* (see Figueiredo & Gallo 2021).

Node 31
Subfamily †Triplomystinae
Murray & Wilson, 2013 (new rank)

Taxa included and relationships. — "†*Triplomystus*" *oligoscutatus* + (†*Triplomystus noorae* + †*Scutatoclupea*).

Unambiguous synapomorphies. — Proximal end of the first hypural sharp, with no articulatory process (283:0>1); two or one uroneurals (296:0>1); postdorsal scute series present (328:0>1).

Support. — Relative Bremer = 37%.

Remarks. — Murray & Wilson (2013) created the tribe †Triplomystini to include species of the genus †*Triplomystus*, namely †*T. noorae* from the Cenomanian strata of Namoura, Lebanon (Forey *et al.* 2003) and †*T. applegatei* from the Albian of Chiapas, Mexico (Alvarado-Ortega & Ovalles-Damián 2008) sharing the presence of a third (postdorsal) series of scutes. After the description of †*Scutatoclupea bacchiai*, another Cretaceous triple-armored herring from Lebanon, Bannikov (2015) referred †"*T.*" *applegatei* to this genus, since the Mexican species shares more features with †*S. bacchiai* than with †*T. noorae* and †*T. oligoscutatus*, including general body physiognomy, similar body proportions and meristic counts, relative position of the fin origins and other skeletal features. Our analysis however, recovered †*Triplomystus* (including †*T. noorae* and †*T. oligoscutatus*) paraphyletic due to a certain degree of dissimilarity of the two species, actually showing differences in body proportions and meristic counts, although their sister group relationship can be recovered in a non-implied weighting analysis. Due to the recurrent recovery of †*Scutatoclupea* and †*Triplomystus* as sister taxa here and in most of the previous analyses (e.g., Marramà & Carnevale 2023) we propose to elevate the tribe †Triplomystini Murray & Wilson, 2013 to the subfamily level.

Node 32
Unnamed clade

Taxa included and relationships. — †*Triplomystus noorae* + †*Scutatoclupea.*

Unambiguous synapomorphies. — More than 30 abdominal scutes (341:3>4).

Support. — Relative Bremer = 0%

Node 33
Genus *Scutatoclupea* Bannikov, 2015

Taxa included and relationships. — †*S. applegatei* + †*S. bacchiai.*

Unambiguous synapomorphies. — Pelvic fins posterior to the dorsal-fin base and closer to the caudal-fin base than to the pectoral-fin insertion (280:1>2); neural spine on PU1 almost as long as the neural spine of PU2 (308:1>0).

Support. — Relative Bremer = 37%.

Remarks. — Our analysis supports the hypothesis of Bannikov (2015) that †"*Triplomystus*" *applegatei* Alvarado-Ortega & Ovalles-Damián, 2008 can be included within the genus †*Scutatoclupea*.

Node 34
Subfamily Paraclupeinae
Chang & Chou, 1977, new usage

Taxa included and relationships. — †*Ellimmichthys longicostatus* + (†*Ellimma branneri* + (†*Paraclupea* + (†*Rhombichthys* + (†*Tunisiaclupea* + †*Tycheroichthys*)))).

Unambiguous synapomorphies. — Striations on the ventral part of the opercle present (201:0>1).

Support. — Relative Bremer = 57%.

Remarks. — Chang & Grande (1997) emended the diagnosis of the subfamily †Paraclupeinae to include †*Paraclupea chetungensis* as sister to †*Ellimmichthys longicostatus* based on the presence of an angle along the dorsal margin of the body at level of the dorsal-fin origin, skull roofing bones strongly sculptured with radiating ridges, supraoccipital ridge small and low, eight to nine predorsal scutes broader than long and ornamented with ridges, gap between hypural 2 and hypural 3, uroneural 2 extending to PU2. After the discovery of new †paraclupeid genera and the inclusion of new characters in phylogenetic analyses, the composition of the family has been emended to include †*Triplomystus* and †*Tycheroichthys* but excluding †*Ellimmichthys* (Murray & Wilson 2013). Our re-examination of the holotype of †*Ellimmichthys longicostatus* AMNH 734 (Fig. 3H) indicates that this taxon shows opercle striation, supporting its inclusion within this family, along with †*Ellimma branneri*, †*Rhombichthys*, †*Tycheroichthys* and †*Tunisiaclupea* that share several features and are morphologically more similar to the †*Paraclupea* species than to other †paraclupeids.

Node 35
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — †*Ellimma branneri* + (†*Paraclupea* + (†*Rhombichthys* + (†*Tunisiaclupea* + †*Tycheroichthys*))).

UNAMBIGUOUS SYNAPOMORPHIES. — Ornamentation of the supramaxillae present (87:0>1).

SUPPORT. — Relative Bremer = 57%.

Node 36
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — †*Paraclupea* + (†*Rhombichthys* + (†*Tunisiaclupea* + †*Tycheroichthys*)).

UNAMBIGUOUS SYNAPOMORPHIES. — More than 30 abdominal scutes (341:3>4).

SUPPORT. — Relative Bremer = 76%.

Node 37
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — †*Rhombichthys* + (†*Tunisiaclupea* + †*Tycheroichthys*).

UNAMBIGUOUS SYNAPOMORPHIES. — Dorsal process of the post-temporal sharp (261:1>0); two or one uroneurals (296:0>1)

SUPPORT. — Relative Bremer = 60%.

Node 38
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — †*Tunisiaclupea* + †*Tycheroichthys*.

UNAMBIGUOUS SYNAPOMORPHIES. — Hypural diastema present (288:1>0); hypural 3 smaller or almost of the same size of hypural 1 (290:1>0); distal end of the second uroneural not reaching the distal end of the first uroneural (300:0>1); ornamentation on the surface of the predorsal scutes absent (325:1>0).

SUPPORT. — Relative Bremer = 34%.

Node 39
Genus †*Paraclupea* Sun, 1956

TAXA INCLUDED AND RELATIONSHIPS. — †*P. chetungensis*, †*P. pietrarojae*, †*P. seilacheri*, †*P. solignaci*.

UNAMBIGUOUS SYNAPOMORPHIES. — Supratemporal commissure sensory canal present on the supraoccipital (8:0>1).

SUPPORT. — Relative Bremer = 86%.

Node 40
Pan-Clupeiformes

TAXA INCLUDED AND RELATIONSHIPS. — †*Spratticeps* + Clupeiformes.

UNAMBIGUOUS SYNAPOMORPHIES. — Supratemporal canal passing through the supraoccipital (8:0>1); temporal foramen present (29:0>1).

SUPPORT. — Relative Bremer = 79%.

REMARKS. — This clade can be considered as the total group Clupeiformes that includes †*Spratticeps* as sister to crown Clupeiformes. †*Spratticeps gaultinus* Patterson, 1970 was described as a basal clupeomorph on the basis of incomplete braincases from the middle Albian strata (*c.* 110-107.5 Mya; Gallois & Owen 2019) of the Gault Formation of Folkestone (Kent, UK) (Patterson 1970). This taxon was regarded to as a clupeomorph because of the presence of a swim bladder diverticulum entering exoccipital and forming a very large prootic bulla, post-temporal fossa roofed, sensory canals bone enclosed, pre-epioccipital fossa, and ornamented skull roof. †*Spratticeps* exhibits a mix of †ellimmichthyiform and clupeiform characters; like the †ellimmichthyiforms it has no recessus lateralis, pterotic diverticulum nor bulla, auditory fenestra, and has skull roof heavily ornamented, without supratemporal fossa or posterior frontal fontanelles, whereas like clupeiforms it possesses a temporal foramen (although not exposed), basisphenoid, supraoccipital separating the parietals (lateroparietal condition), and supratemporal commissure passing through the parietals and supraoccipital, and occipital condyle formed by the basioccipital only. This mosaic of plesiomorphic and derived characters led several authors to consider it as an *incertae sedis* clupeomorph, although Grande (1985) considered †*Spratticeps* as an *incertae sedis* clupeiform. Our analysis, the first one to include †*Spratticeps* in a phylogenetic framework, recovered it as sister taxon to the Clupeiformes, if this group is diagnosed by possessing the three synapomorphies defined by Grande (1985): recessus lateralis (absent in †*Spratticeps*), parietals completely separated by the supraoccipital (present), and beryciform foramen absent (unknown in †*Spratticeps*). Moreover, †*Spratticeps* also lacks other features typically present in clupeiforms (pterotic diverticulum and bullae, sinus temporalis, auditory fenestra) and like most of †ellimmichthyiforms it has skull roof strongly ornamented (Patterson 1970).

Node 41
Order Clupeiformes Bleeker, 1859

TAXA INCLUDED AND RELATIONSHIPS. — Denticipitoidei + (†*Pseudoellimma* + (†*Leufuichthys* + Clupeoidei)).

UNAMBIGUOUS SYNAPOMORPHIES. — Auditory fenestra present (23:0>1); recessus lateralis present (31:0>1); supratemporal system present (39:0>1); vertical process of the basisphenoid absent (41:0>1); pterotic bulla present (55:0>1).

SUPPORT. — Relative Bremer = 59%.

REMARKS. — In the comprehensive review by Grande (1985) the order Clupeiformes comprises all the non-†ellimmichthyiform clupeomorphs grouped in two suborders, Denticipitoidei and Clupeoidei, diagnosed by the presence of the recessus lateralis, parietals separated by the supraoccipital (lateroparietal condition), and loss of the beryciform foramen (chs 9 to 11 of Grande 1985). Di Dario & De Pinna (2006), recognizing the supratemporal system also in *Denticeps* (until then considered exclusive of the Clupeoidei) considered the presence of this character as a further synapomorphy of the Clupeiformes. Our analysis recognizes the presence of recessus lateralis and supratemporal system as synapomorphies of the

Clupeiformes. The laterotemporal condition is not exclusive of the Clupeiformes, since it also occurs in *Osmerus*, *Alepocephalus*, *Chanos* and the basal †ellimmichthyiform †*Sorbinichthys*, evidencing that the MRCA of the Clupeomorpha had the lateroparietal condition (Figs 7B; 8B-D) that has been secondarily lost in more advanced †ellimmichthyiforms. Moreover, the absence of the beryciform foramen cannot be considered a synapomorphy of the Clupeiformes as suggested by Grande (1985) since it still occurs as large perforation in some basal extinct clupeiforms (†*Santanaclupea*), in some basal fossil clupeoids (†*Italoclupea* and †*Scombroclupea*) and, although reduced in size, it is still present in some living clupeoids (*Alosa*, *Brevoortia*, *Clupea*, *Hyperlophus*, *Sardinops* and *Sprattus*) (Maisey 1993; Sato 1994; Segura & De Astarloa 2004; Taverne 2007). Interestingly, our analysis recognized the presence of the auditory fenestra, the pterotic bulla and the absence of the vertical process of basisphenoid as clupeiform synapomorphies. The auditory fenestra is a large or moderate opening in the otic region surrounded by prootic, exoccipital, and basioccipital that is likely unique of the Clupeiformes since the "auditory foramen or fenestra" present in some characiforms and osteoglossomorphs (Weitzman 1962; Hilton 2003) is likely not homologous of the auditory fenestra of the Clupeiformes (Fink & Fink 1981; Mertzen 2019). Although all the clupeomorphs possess prootic bullae, the presence of pterotic bullae can be considered a synapomorphy restricted to the Clupeiformes, as they are absent in †*Spratticeps* and likely in all the †ellimmichthyiforms. Their absence in the extant clupeoids *Clupeonella*, *Ethmidium* and *Sprattus* must be therefore considered as a secondary lost (Grande 1985).

Node 42
Suborder Denticipitoidei Greenwood, Rosen, Weitzman & Myers, 1966, new usage

Taxa included and relationships. — †Cynoclupeidae + Denticipitidae.

Unambiguous synapomorphies. — Maxillo-premaxillary gap absent (88:0>1); lower jaw length three or more times its depth (109:1>2); pleural ribs/preural vertebrae ratio of 0.41-0.46 (231:2>1); two or one uroneurals (296:0>1); ascending arms of the pelvic scute short (331:1>0); ascending arms of the prepelvic scutes between the pelvic scute and the posterior edge of the coracoid short (337:1>0); ascending arms of the prepelvic and postpelvic scutes semicircular to subrectangular, contacting with those of adjacent scutes for almost their entire length (340:0>2).

Support. — Relative Bremer = 23%.

Emended diagnosis. — Clupeiform fishes (having recessus lateralis and medioparietal condition) retaining the following plesiomorphic features: first ural centrum large, its size approximately similar (or slightly less) as that of the first preural centrum (vs. U1 reduced in clupeoids); first hypural articulated to the first ural centrum through massive proximal head forming a well-developed articulatory process (vs. hypural 1 not reaching the first ural centrum and having sharp proximal head, with no articulatory process); parhypural fused to PU1 (vs. autogenous); first uroneural autogenous (vs. fused to PU1, forming the pleurostyle); two or one uroneural (vs. three); complete lateral line present (vs. mostly or totally absent); keeled abdominal scutes with short or reduced semicircular to subrectangular ascending arms.

Remarks. — The suborder Denticipitoidei was introduced by Greenwood *et al.* (1966) to contain the family Denticipitidae Clausen, 1959 represented by extant freshwater denticle herring *Denticeps clupeoides* and the Middle Eocene †*Palaeodenticeps tanganikae* (Greenwood 1960, 1968). Although the family and both the genera have been formally diagnosed, the suborder Denticipitoidei appears to lack formal diagnosis in its original description by Greenwood *et al.* (1966), although it was based on the presence of plesiomorphic morphological traits that distinguish *Denticeps* and †*Palaeodenticeps* from the other members of the Clupeiformes (i.e., the Clupeoidei), whose morphological distinctiveness has been instead satisfactory provided (see Grande 1985). In this perspective, although the suborder Denticipitoidei has not been explicitly diagnosed with unique characters, Greenwood *et al.* (1966: 359) provided a list of morphological characters that support its difference with respect to the other clupeiforms, and that can be used here to provide a formal diagnosis of the suborder, including features of the caudal skeleton and lateral line system, whereas the presence of odontodes (denticles) and reduction of the number of uroneurals to a single one, used traditionally since Grande (1985) to define the Denticipitoidei, are instead used herein as distinctive features of the family Denticipitidae, rather than the whole suborder. Since the features listed by Greenwood *et al.* (1966) are shared with the basal clupeiforms †*Cynoclupea* and †*Santanaclupea*, that our analysis recognized as closely related to the Denticipitidae to form a clade, we propose the inclusion of these two taxa within the suborder providing herein a formal diagnosis.

Node 43
Family †Cynoclupeidae
Malabarba & Di Dario, 2017, new usage

Taxa included and relationships. — †*Cynoclupea* + †*Santanaclupea.*

Unambiguous synapomorphies. — Pre-epioccipital fossa large and well defined (21:0>1); suspensorium posteriorly inclined (119:0>1); quadrate-mandibular articulation posterior to the orbit (131:1>0); 7-9 supraneurals (208:1>2).

Support. — Relative Bremer = 57%.

Emended diagnosis. — A denticipitoid family distinguished from all the other members of the suborder by the following combination of characters: head triangular in lateral view; pre-epioccipital fossa large and well defined; snout acuminated; long and straight lower jaws with a conspicuous dentition extending well back along the oral margin of the dentary; suspensorium slightly inclined obliquely backward; quadrate-mandibular articulation posterior to the orbit; odontodes absent.

Remarks. — The monotypic family †Cynoclupeidae was established by Malabarba & Di Dario (2017) to contain the peculiar Early Cretaceous (Barremian) clupeiform †*Cynoclupea nelsoni* collected in the shales of the Morro do Chaves Formation of the Sergipe-Alagoas Basin in NE, Brazil, that the authors hypothesized to be closely related to the Chirocentridae and Engraulidae due to the shared presence of the dorsal tip of the symplectic in line with the dorsal margin of the quadrate, with this latter bone possessing a laminar outgrowth on its anterior margin, and conspicuous dentition in the lower jaws extending well back along the oral margin of the dentary. Our analysis, instead, suggests that †*Cynoclupea* is sister to †*Santanaclupea silvasantoi* from the late Aptian to early Albian (or late Aptian; see Melo *et al.* 2020) Romualdo Formation (NE Brazil) (Maisey 1993), this relationship being supported by four unambiguous synapomorphies. Since the family †Cynoclupeidae has not been formally diagnosed, we propose a new usage for the family †Cynoclupeidae, which is now diagnosed by characters shared by †*Cynoclupea* and †*Santanaclupea*, most of them actually solely used to diagnose †*Cynoclupea* by Malabarba & Di Dario (2017).

Node 44
Family Denticipitidae Clausen, 1959

Taxa included and relationships. — *Denticeps* + †*Palaeodenticeps.*

Unambiguous synapomorphies. — Odontodes present (3:0>1); ornamentation of the skull roof absent (16:1>0); exoccipital expanded, reaching posteriorly to the level of the basioccipital (47:0>1); anterior and posterior supramaxillae absent (83:1>0; 84:0>1); posterior arm of the preopercle present (204:0>1); gap between the posteriormost ossified supraneural and the first dorsal-fin pterygiophore (217:0>1); halves of neural arches of most abdominal vertebrae fused into a spine (219:0>1); second postcleithrum absent (263:0>1); pelvic-fins anterior to the dorsal-fin origin (280:1>0); hypural 2 triangular, its distal end distinctly broader than the proximal end (285:1>0); hypural diastema small, in form of a concave notch (289:0>1); ascending arms of the prepelvic scutes along the ventral edge of the coracoid absent or inconspicuous (335:0>1); anal-fin origin anterior to the dorsal-fin origin (344:0>2); dorsal fin displaced posteriorly on the body (348:1>2).

Support. — Relative Bremer = 73%.

Remarks. — Recent studies have questioned the monophyly of Clupeiformes, as *Denticeps clupeoides*, the sole extant member of the Denticipitoidei, has been variously placed within the Ostariophysi or as a sister group to the clade formed by Ostariophysi + Clupeoidei (e.g., Li & Ortí 2007; Bloom & Lovejoy 2014; Bloom & Egan 2018), although bootstrap or posterior probability values were low and arrangements likely resulting from nucleotide compositional bias (Li & Ortí 2007). Conversely, evidence supporting the inclusion of *Denticeps* within the Clupeiformes are more robust and comes from mitogenomic (Lavoué *et al.* 2007, 2013; Near *et al.* 2012; Wang *et al.* 2022) and morphological data (Grande 1985; Di Dario 2004b; Di Dario & De Pinna 2006), these latter including the presence of the recessus lateralis, pterotic bullae, supratemporal system and hypural 2 fused with the second ural centrum. Although we recovered the †Cynoclupeidae sisters of the Denticipitidae, our analysis still supports the traditional arrangement of the Clupeiformes since the clade formed by these families (Denticipitoidei) is still recovered sister to the pan-Clupeoidei (†*Pseudoellimma* + (†*Leufuichthys* + Clupeoidei)), and therefore, within the Clupeiformes.

Node 45
Pan-Clupeoidei

Taxa included and relationships. — †*Pseudoellimma* + (†*Leufuichthys* + Clupeoidei).

Unambiguous synapomorphies. — Dentary teeth absent (104:1>0): one to three canals branching from the main preopercular canal at its angle (203:1>0).

Support. — Relative Bremer = 36%.

Remarks. — The basal clupeiform †*Pseudoellimma gallae* Figueiredo, 2009 comes from the Barremian (Lower Cretaceous) of the Sergipe-Alagoas Basin (NE Brazil) (Figueiredo 2009a). Although the presence of plesiomorphic features in the caudal skeleton (e.g., lack of pleurostyle, parhypural fused to PU1) led the author to consider †*Pseudoellimma* as a non-clupeoid clupeiform, the presence of some derived features of the neurocranium (e.g., presence of an accessory opening of the temporal canal, parallel longitudinal ridges on the skull roof, etc.) suggested a sister-group relationship or at least its close affinity with the Clupeoidei (Figueiredo 2009a). Our analysis corroborates this hypothesis, placing †*Pseudoellimma* as the basalmost stem clupeoid, recovering the lack of dentary teeth and the reduction in the number of canals branching at the angle of preopercle as supportive of this hypothesis, indicating that divergence between Denticipitoidei and Clupeoidei occurred before 121.4 million years ago.

Node 46
Unnamed clade

Taxa included and relationships. — †*Leufuichthys* + Clupeoidei.

Unambiguous synapomorphies. — Proximal end of hypural 1 sharp, with no articulatory process (283:0>1); parhypural autogenous (301:1>0).

Support. — Relative Bremer = 41%.

Remarks. — †*Leufuichthys minimus* Gallo, Calvo & Kellner, 2011 was described from the Upper Cretaceous (late Turonian-early Coniacian) fluvial deposits of the Portezuelo Formation, of the Neuquén Group (Argentina) as an *incertae sedis* clupeomorph based on the presence of abdominal scutes, haemal spines of the third and fourth preural vertebrae fused to the centra, and autogenous first hypural (Gallo *et al.* 2011). Although its poor preservation prevented the authors to recognize synapomorphies clearly supporting its placement into one of the two clupeomorph orders, our main analysis recognized this taxon as a crown clupeiform likely due to possession of some plesiomorphic features that characterize most of representatives of the Clupeiformes, including the presence of a basisphenoid, autogenous parhypural and absence of basipterygoid processes, but also of two of the characters typical of the Clupeoidei (an autogenous parhypural, and the proximal end of hypural 1 with no articulatory process) recovering its sister group relationship with the Clupeoidei. However, the lack of pleurostyle (its first uroneural tip is not fused to PU1; Gallo *et al.* 2011) and the impossibility to determine the size of U1 and presence of lateral line rules out its inclusion within the crown group.

Node 47
Suborder Clupeoidei Bleeker, 1859
(*sensu* Greenwood *et al.* 1966)

Taxa included and relationships. — †*Nolfia* + ((†*Italoclupea* + †*Scombroclupea*) + ((Pan-Engrauloidea + (Pristigasteroidea + Clupeoidea)))).

Unambiguous synapomorphies. — Third postcleithrum present (264:0>1); second postcleithrum rod-like (265:0>1); fusion of first uroneural and first ural centrum, forming a pleurostyle (297:0>1); three epurals (304:1>0).

Support. — Relative Bremer = 69%.

Remarks. — The Clupeoidei is the most diverse clupeiform suborder, sister to the Denticipitoidei, with its monophyly supported by several morphological characters (Grande 1985), including: 1) fusion of the first uroneural with the first preural centrum, forming a pleurostyle; 2) reduction in size of the first ural centrum; 3) loss of lateral line scales; and 4) autogenous parhypural. Patterson (1970) suggested the presence of the supratemporal system as a synapomorphy of the Clupeoidei but Di Dario & De Pinna (2006), recognizing the supratemporal system also in *Denticeps*, and considered this character a synapomorphy of the Clupeiformes. The inclusion of some basalmost clupeiforms in our analysis highlights for the first time the gradual achievement of the traits that characterize the extant clupeoids. †*Pseudoellimma* lacks three of the clupeoid characters and the absence of lateral line scales cannot be checked due to incompleteness (Figueiredo 2009a), so it cannot be considered as a clupeoid. Although the separation of parhypural from PU1 was already achieved by †*Leufuichthys*, this taxon lacks at least one of the clupeoid synapomorphies (the pleurostyle), whereas the size of the first ural and absence of lateral line scales cannot be detected. Because of the impossibility to detect the state of these latter characters in a key taxon like †*Leufuichthys*, our analysis was not able to recognize them as synapomorphies of the Clupeoidei. Separation of parhypural from PU1 cannot be detected as synapomorphy of the Clupeoidei because it was already achieved in a non-clupeoid clupeiform (†*Leufuichthys*). †*Nolfia riachuelensis* Figueiredo, 2009, a clupeiform species from the Albian Taquari Member of the Riachuelo Formation, in the Sergipe-Alagoas Basin (NE Brazil) is the basalmost clupeiform in which three out of four clupeoid synapomorphies can be observed (Figueiredo 2009b). Although the loss of lateral line scales cannot be checked in this species due to inadequate preservation, this synapomorphy can be inferred, as it was detected in the congeneric species †*Nolfia kwangoensis* Taverne, 1976 from the Cenomanian deposits of the Democratic Republic of Congo (Taverne 1997). In this perspective, it is possible to consider †*Nolfia* as the basalmost clupeoid. Figueiredo (2009b) considered †*Nolfia* as member of the Clupeidae mainly based on the presence of two rod-like postcleithra, the only character used by Grande (1985) to diagnose this family. However, recent studies recovered neither molecular nor morphological support for the monophyly of the Clupeidae *sensu* Grande (1985). Nelson (1967b) suggested that the absence of abdominal scutes might be the ancestral condition within the Clupeoidei (as he considered the Dussumieriidae to be a "primitive" group within the family Clupeidae). Our analysis discards this hypothesis and is more consistent with Lavoué *et al.* (2014), suggesting that the MRCA of the Clupeoidei had a complete series of abdominal scutes and that the reduction in their number has been secondarily achieved at least twice within this suborder.

Node 48
Unnamed clade

Taxa included and relationships. — (†*Italoclupea* + †*Scombroclupea*) + (Pan-Engrauloidea + (Pristigasteroidea + Clupeoidea)).

Unambiguous synapomorphies. — Dentary teeth present (104:0>1); interzygapophysal articulation present (243:0>1); neural spine on PU1 short, about half the length of the neural spine of PU2 (308:0>1).

Support. — Relative Bremer = 66%.

Node 49
Unnamed clade

Taxa included and relationships. — †*Italoclupea* + †*Scombroclupea*.

Unambiguous synapomorphies. — Anterior arm of the orbitosphenoid long, reaching the lateral ethmoid (44:0>1); posterior process of the lateral ethmoid present (65:0>1); more than 10 branchiostegal rays (153:1>2).

Support. — Relative Bremer = 23%.

Remarks. — †*Italoclupea nolfi* and †*Scombroclupea macrophthalma* are two clupeiform fishes from the Upper Cretaceous (Campanian) of Nardò (southern Italy) and the Cenomanian strata of Lebanon, respectively (Forey *et al.* 2003; Taverne 2007). Interestingly, despite they are undoubtedly part of the Clupeoidei, as demonstrated by the uroneural fused to the first preural centrum, they still retain some plesiomorphic traits of the basalmost clupeiforms, including a large beryciform foramen, contralateral halves of most abdominal neural arches unfused, therefore not forming a neural spine, proximal end of the first hypural long, articulating to the first ural centrum, and large caudal scutes, indicating that the traits characterizing the clupeoid body plan of modern type was achieved only later in the clupeoid evolution.

Node 50
Unnamed clade

Taxa included and relationships. — Pan-Engrauloidea + (Pristigasteroidea + Clupeoidea)

Unambiguous synapomorphies. — Anterior frontal fontanelle present (24:0>1); 41-50 preural vertebrae (218:3>2); neural arches of most abdominal vertebrae with fused halves forming a median neural spine (219:0>1); proximal end of the first hypural truncated, failing to articulate to the first ural centrum (282:0>1); caudal scutes reduced, very thin (307:1>0).

Support. — Relative Bremer = 3%.

Remarks. — This clade includes the clupeoids of "modern type", i.e., all the Cenozoic and extant clupeoids (plus the late Upper Cretaceous †*Nardoclupea*). Its members are characterized by the absence (or reduction) of the foramen on the anterior ceratohyal and by the proximal tip of the first hypural truncated, not reaching the first ural centrum. Grande (1985) considered the loss of the beryciform foramen as a synapomorphy of the Clupeiformes, being a large foramen on anterior ceratohyal absent in *Denticeps* and living clupeoids. However, the inclusion in our analysis of †*Santanaclupea*, and two fossil clupeoids (†*Italoclupea* and †*Scombroclupea*) possessing a large beryciform foramen, indicates that its complete loss occurred later in the evolution of clupeiforms and, therefore, that its absence cannot be considered as a synapomorphy of the Clupeiformes. Another character considered by Grande (1985) (also mentioned by Cavender 1966) as characteristic of clupeoids is the complete separation of hypural 1 from ural centrum 1. However, this character appeared subsequently in the evolution of clupeoids, since †*Nolfia*, †*Italoclupea* and †*Scombroclupea*, which can be considered as crown clupeoids, actually possess a long hypural 1 reaching and likely articulating with the first ural centrum (Forey *et al.* 2003; Figueiredo 2009b). Interestingly, the presence of neural arches of most abdominal vertebrae with fused halves forming a median neural spine appears to be another feature of the clupeoids of modern type.

Node 51
Pan-Engrauloidea

Taxa included and relationships. — Pan Spratelloididae + Engrauloidea.

Unambiguous synapomorphies. — Skull roof unornamented (16:1>0); abdominal epipleurals (distally) long, extending ventrally at least to the midlength between the vertebrae and the ventral margin of the body (223:1>0); single epural present (304:0>2); ventral margin of the pelvic scute unkeeled and concave, making the scute W- or double U-shaped (330:0>1); prepelvic scutes posterior to the coracoid absent (333:1>0); prepelvic scutes along the ventral edge of the coracoid absent (334:1>0); postpelvic scutes absent (338:1>0); single abdominal scute (341:2 or 3>0)

Support. — Relative Bremer = 47%.

Remarks. — This clade include the fossil and extant taxa traditionally known as round herrings, i.e., the pan-Spratelloididae, †*Nardoclupea*, and Dussumieriidae as successive sisters to the Chirocentridae

+ Engraulidae. However, the sister-group relationship between the extant Spratelloididae (*Jenkinsia* and *Spratelloides*) and the rest of the extant taxa of this clade is not recovered if fossil species are excluded from the analysis, since *Denticeps* and the Spratelloididae are recovered sister to the remaining Clupeoidei, resembling the tree topologies of recent molecular analyses. This might suggest that the topologies recovered by molecular analyses (based on extant taxa alone) might be biased by the lack of data from the fossil record. Conversely, our analyses agree with the most recent molecular studies in recognizing the Dussumieriinae as defined by Grande (1985) as non-monophyletic, finding robust evidence that *Jenkinsia* and *Spratelloides* are distantly related to *Dussumieria* and *Etrumeus*.

Node 52
pan-Spratelloididae

TAXA INCLUDED AND RELATIONSHIPS. — †*Trollichthys* + Spratelloididae.

UNAMBIGUOUS SYNAPOMORPHIES. — Five infraorbitals (75:0>1); dentary teeth absent (104:1>0); palatine teeth absent (114:1>0); first two supraneurals in close proximity (215:0>1); first two supraneurals having different shape to the others (216:0>1); gap between the posteriormost supraneural and the first dorsal-fin pterygiophore present (217:0>1); parapophysis on the third vertebra reduced (241:0>1); distal tip of the parapophysis on the third vertebra rounded, truncated or irregular (242:1>0); caudal complex formed by fused PU1+U1, U2 autogenous (295:0>1).

SUPPORT. — Relative Bremer = 62%.

REMARKS. — †*Trollichthys bolcensis*, an Eocene (Ypresian, *c.* 50 Mya) round herring from Bolca (Marramà & Carnevale 2015a), is recovered as sister to the extant spratelloidids (*Jenkinsia* and *Spratelloides*), sharing with them the presence of a W-shaped pelvic scute, five infraorbitals, first ural centrum fused to PU1, single epural, but still retaining primitively at least two rod-like postcleithra (vs. none in extant spratelloidids) and a fourth hypural smaller than the first one (vs. approximately symmetrical to the hypural 1). Our main parsimony analysis placed the pan-Spratelloididae sister to the Engrauloidea, i.e., †*Nardoclupea* + (Dussumieriidae + (Chirocentridae + Engrauloidae n. epifam.)). This recovery is not surprising as several molecular studies (Lavoué *et al.* 2007; Li & Ortí 2007; Wilson *et al.* 2008; Wang *et al.* 2022) hypothesized a sister group relationship between the Chirocentridae and a clade composed of some genera traditionally assigned to the Dussumieriinae by Grande (1985). In other analyses, topology tests failed to reject an alternative hypothesis of a sister group relationship between the Chirocentridae and Engrauloidea (Li & Ortí 2007). Interestingly, our analysis that excludes fossil taxa (Fig. 41) recovered the Spratelloididae as sister to all remaining Clupeoidei in agreement with the recent molecular analyses suggesting that this clade splits early from the other Clupeoidei (Bloom & Lovejoy 2014; Betancur-R *et al.* 2017; Bloom & Egan 2018; Egan *et al.* 2018; Wang *et al.* 2022), thereby indicating that the different results of molecular analyses might be due to the lack of fossil data.

Node 53
Family Spratelloididae Jordan, 1925
(*sensu* Bloom & Egan 2018)

TAXA INCLUDED AND RELATIONSHIPS. — *Jenkinsia* + *Spratelloides*.

UNAMBIGUOUS SYNAPOMORPHIES. — Anterior arm of the orbitosphenoid long, reaching the lateral ethmoid (44:0>1); posterior process of lateral ethmoid present (65:0>1); quadrate-metapterygoid fenestra present (126:0>1); dorsal process of posttemporal subtriangular, wider at distal tip than at its midlength (261:0>2); second and third postcleithra absent (263:1>0; 264:1>0); hypural 4 approximately symmetrical to the hypural 1 (292:0>1); neural spine of the first preural centrum almost as long as the neural spine of PU2 (308:1>0); fusion between most of the posterior margin of PU1 neural spine and the anterior margin of first uroneural (309:0>1).

SUPPORT. — Relative Bremer = 73%.

REMARKS. — The small round herrings *Jenkinsia* and *Spratelloides* have been traditionally recognized to form either a subfamily of the family Dussumieriidae (the Spratelloidinae of Whitehead 1963) or a tribe within the subfamily Dussumieriinae (the Spratelloidini of Grande 1985). In both cases, their alignment with the round herring *Dussumieria* and *Etrumeus* was due to the presence of a single unkeeled W-shaped pelvic scute, along with the absence of pre- and post-pelvic scutes (Whitehead 1963; Grande 1985). We therefore follow the taxonomic ranking proposed by Bloom & Egan (2018) and consider the Spratelloidinae/-ini as a family-level lineage. The close relationship between Spratelloididae or pan-Spratelloididae and the rest of the Engrauloidea is not recovered if fossil taxa are excluded from the analysis, but the Spratelloididae is instead recovered as sister to the living Clupeoidei, resembling the tree topologies of recent molecular analyses (see Remarks of node 52). Once again, this might suggest that the topologies recovered in molecular analysis (based on living taxa alone) might be biased by the lack of fossil data.

Node 54
Superfamily Engrauloidea Nelson, 1970, new usage

TAXA INCLUDED AND RELATIONSHIPS. — †*Nardoclupea* + (Dussumieriidae + (Chirocentridae + Engrauloidae n. epifam.)).

UNAMBIGUOUS SYNAPOMORPHIES. — Anterior lateral process of mesethmoid for articulation of palatine absent (63:1>0); premaxillae subrectangular (90:0>1); central shaft of the maxilla short, almost equal or shorter than the length of the articular head (96:0>1); posterior blade of the maxilla approximately of the same size or slender than the central shaft (97:0>1); dorsal and ventral profile of the maxilla nearly straight (98:0>1); ectopterygoid teeth present (132:0>1); more than 10 branchiostegal rays (153:1>2); parapophyses on the first vertebra absent (238:1>0); basal segments of the upper middle caudal-fin ray spatulate (317:0>1).

SUPPORT. — Relative Bremer = 56%.

REMARKS. — This clade includes the peculiar extinct “round herring” †*Nardoclupea grandei* Taverne, 2002 from the Upper Cretaceous (Campanian) of Nardò (Lecce Province, southern Italy) as sister to the remaining engrauloids. Taverne (2002) described †*Nardoclupea* as a large-sized dussumieriine having more affinities with *Dussumieria* and *Etrumeus* than with *Jenkinsia* and *Spratelloides*. The re-examination and inclusion of this taxon in a phylogenetic context makes †*Nardoclupea* and the Dussumieriidae (*Etrumeus* + *Dussumieria*) successive sister of the clade formed by the Chirocentridae + the total group Engraulidae, highlighting a step-by-step achievement of traits in the evolution of the Engrauloidea new usage.

After the introduction of the superfamily Engrauloidae n. epifam. by Nelson (1970), Grande (1985) renamed the clade as Engrauloidea to standardize the suffix (-oidae is used at epifamilial level) rather than reflect a fundamental change in the taxonomic composition of the group. The superfamily was originally created to contain the

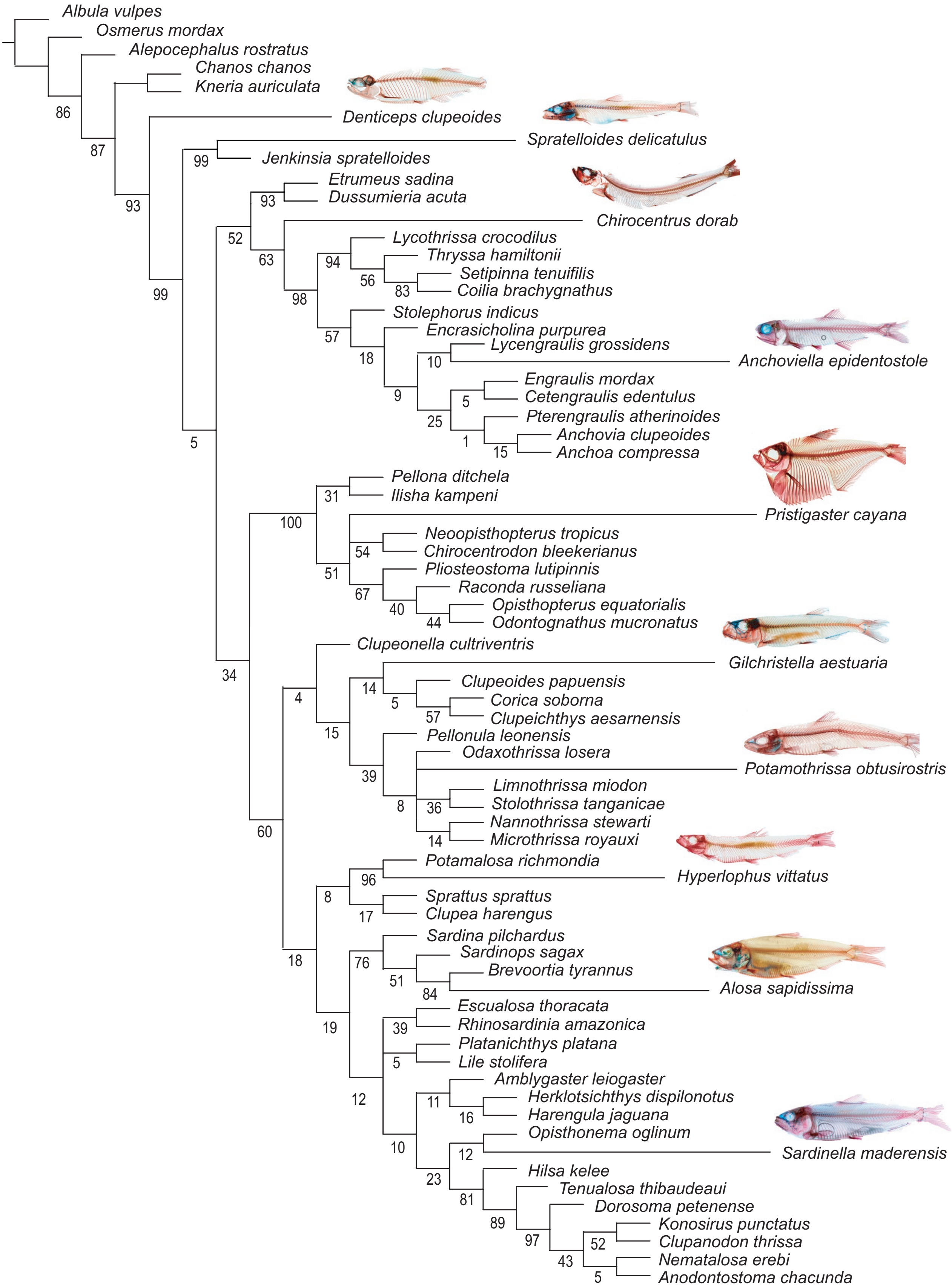

Fig. 41. — Bootstrap consensus tree (1000 replicates) retrieved in TNT v.1.6 based on 368 morphological characters and 69 terminal taxa highlighting the interrelationships of the living Clupeiformes. Numbers below nodes indicate the bootstrap values.

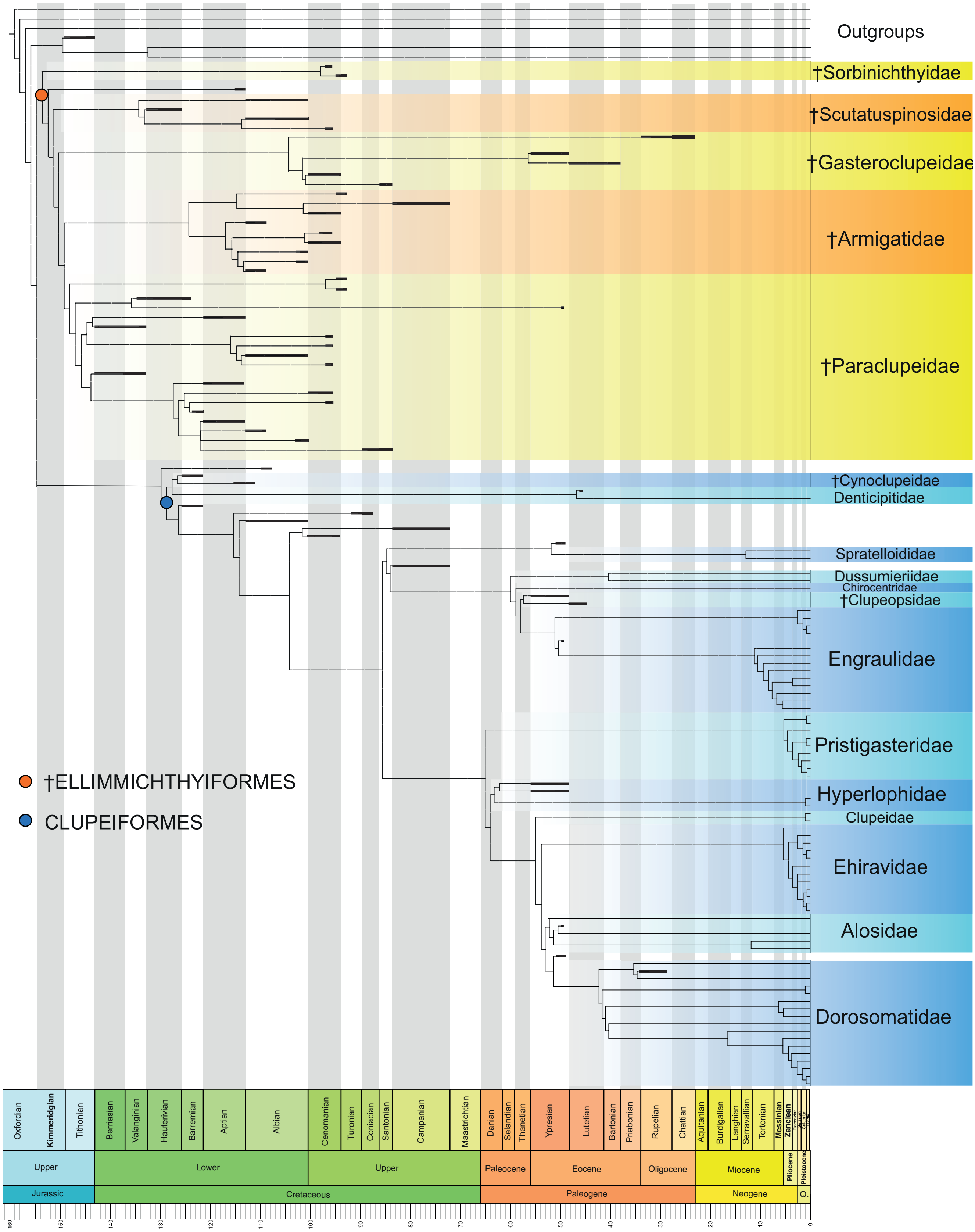

FIG. 42. — Time-calibrated strict consensus tree from the main parsimony-based phylogenetic analysis based on 368 morphological characters and 130 terminal taxa highlighting the interrelationships within the Clupeomorpha. The black bars represent the known stratigraphic range of the taxa.

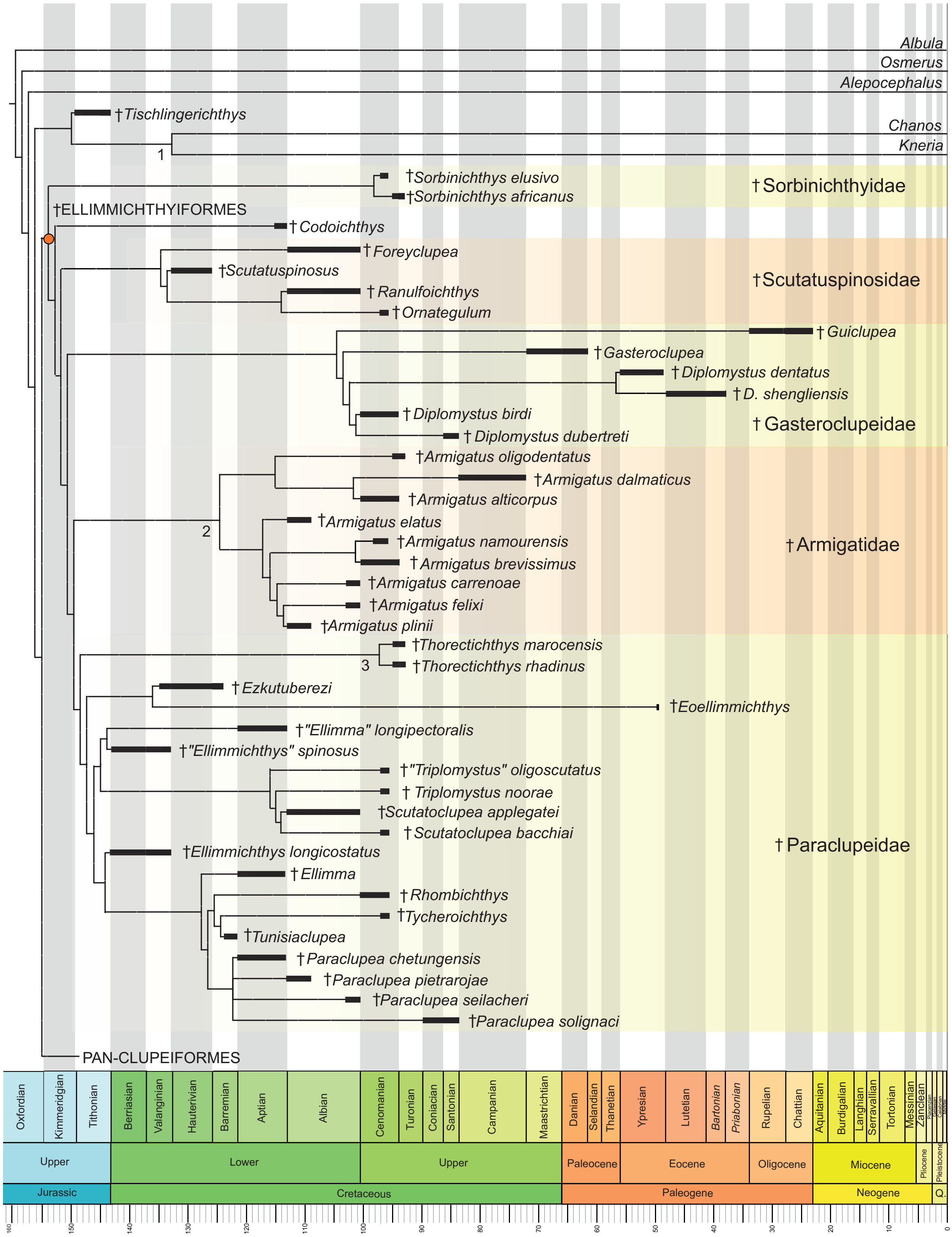

Fig. 43. — Time-calibrated strict consensus tree from the main parsimony-based phylogenetic analysis based on 368 morphological characters and 130 terminal taxa highlighting the interrelationships of the †Ellimmichthyiformes (node 2) within the Clupeomorpha. The black bars represent the known stratigraphic range of the taxa. Numbers at nodes indicates additional calibration points based on fossils not included in the analysis (see Material and Methods): 1) †*Rubiesichthys gregalis* Wenz, 1984 (Berriasian-Valanginian of Montse, Lerida, Spain; Poyato-Ariza 1996; Near & Thacker 2024); 2) †*Armigatus simonettoi* Amalfitano, Marrama, Bannikov, Dalla Vecchia & Carnevale, 2025 (upper Hauterivian-lower Barremian of Vernasso, NE Italy; Amalfitano *et al.* 2025); 3) †*Thorectichthys fideli* Than-Marchese, Alvarado-Ortega, Murray, Velasquez-Velasquez & Dominguez, 2024 (early Cenomanian of Chiapas, southeastern Mexico; Than-Marchese *et al.* 2024).

family Engraulidae Gill, 1861 with two subfamilies (Coiliinae and Engraulinae) characterized by five traits of the branchial arches: 1) reduction of the basihyal and loss of its ossification center; 2) reduction and loss of the basihyal tooth plate; 3) elongation of the second basibranchial; 4) elongation of the dorsal parts of the gill arches; 5) fusion of tooth plates with the first and third basibranchials. Grande (1985) added two new skeletal traits: 6) suspensorium inclined obliquely backward; and 7) mesethmoid projecting anterior to vomer making the snout pig-like. Later, Di Dario (2009) suggested that the monotypic Chirocentridae (*Chirocentrus*) is more closely related to the Engraulidae than to the Clupeidae, and therefore proposed a new classification of the Engrauloidea, with the inclusion of the Chirocentridae based on the presence of seven characters (see remarks of node 57), this latter hypothesis being supported by molecular and morphology-based analyses (Di Dario 2004b; Bloom & Lovejoy 2014; Bloom & Egan 2018; Bloom *et al.* 2018; Vernygora 2020; Kevrekidis *et al.* 2024). The close affinity of representatives of the Dussumieriini of Grande (1985) with *Chirocentrus* is not unusual, as molecular analyses often recovered the close relationship of *Chirocentrus* with *Dussumieria* (Wang *et al.* 2022), *Etrumeus* (Lavoué *et al.* 2013), or with the pair *Jenkinsia* + *Spratelloides* (Li & Ortí 2007; Milec *et al.* 2022), or, alternatively, nested within a clade formed by *Etrumeus* + (*Chirocentrus* + (*Jenkinsia* + *Spratelloides*)) (Lavoué *et al.* 2017a, 2019). In this perspective, we propose the inclusion of *Etrumeus* and *Dussumieria* into the superfamily Engrauloidea of Di Dario (2009) also because this relationship is still recovered if fossil taxa are excluded from the analysis (Fig. 41). Moreover, since *Dussumieria* and *Etrumeus* are found to be sister taxa also when fossil taxa are excluded and are sufficiently unique in respect to the other engrauloid families (i.e., Chirocentridae, Engraulidae, Spratelloididae) they can be included in a taxonomic rank equivalent to that of the other established families within the Engrauloidea, the Dussumieriidae Gill, 1861.

Node 55
Unnamed clade

Taxa included and relationships. — Dussumieriidae + (Chirocentridae + Engrauloidae n. epifam.).

Unambiguous synapomorphies. — Teeth on vomer present (69:0>1); lower jaw length three or more times its depth (109:0>1); endopterygoid teeth present (115:0>1); anterior margin of the non-laminar area of the tubular branch of the hyomandibula with a crescent-shaped concavity along most of its length (121:0>1); length of the anterior ceratohyal more than 2.5 times the length of the posterior ceratohyal (145:0>1); two epurals (304:2>1); peg on lower middle caudal-fin ray present (314:0>1).

Support. — Relative Bremer = 30%.

Remarks. — This clade includes the Dussumieriidae (*Etrumeus* and *Dussumieria*) as sister to the Chirocentridae plus the pan-Engraulidae. *Etrumeus* and *Dussumieria* have been traditionally considered to form a clade within the Clupeidae (the Dussumieriini of Grande 1985) closely related to *Jenkinsia* and *Spratelloides* (the Spratelloidini of Grande 1985), all four genera forming the Dussumieriinae (Grande 1985). However, recent studies do not recognize *Etrumeus* and *Dussumieria* as sister taxa (e.g., Milec *et al.* 2022) and in some cases they are considered as distantly related from each other (Wilson *et al.* 2008; Lavoué *et al.* 2017a; Bloom & Egan 2018; Wang *et al.* 2022). Our analysis, instead, support the more traditional view, in line with molecular analyses of Vernygora (2020) and the Bayesian analysis of the 6-gene dataset of Egan *et al.* (2018).

Node 56
Family Dussumieriidae Gill, 1861

Taxa included and relationships. — *Etrumeus* + *Dussumieria.*

Unambiguous synapomorphies. — Anterior arm of the orbitosphenoid long, reaching the lateral ethmoid (44:0>1); dorsal medial lamella on orbitosphenoid present (45:0>1); posterior process of lateral ethmoid present (65:0>1); three or more branchiostegal rays on posterior ceratohyal (156:2>3); ossified occipital epineurals present (233:0>1).

Support. — Relative Bremer = 51%.

Node 57
Unnamed clade

Taxa included and relationships. — Chirocentridae + Engrauloidae n. epifam.

Unambiguous synapomorphies. — Supratemporal commissure passing through the parietals not bony enclosed (7:1>0); posterior border of the maxilla posterior to the orbit (101:0>2); coronoid process displaced on the posterior part of the dentary (110:1>0); anterior margin of the metapterygoid located anterior to the anterior margin of the quadrate (120:0>2); ventral limb of the hyomandibula meeting the posterior margin of the quadrate (not separated by the metapterygoid) (123:0>1); posterodorsal margin of the metapterygoid in line with the condyle of articulation of the hyomandibula with the opercle (125:0>1); laminar outgrowth on the anterior margin of the quadrate present (127:0>1); quadrate shaped as isosceles triangle (129:0>1); dorsal tip of the symplectic in line with the proximal margin of the quadrate (130:0>1); dorsal process of the ectopterygoid absent (134:1>0); teeth on the third hypobranchial present (181:0>1); contralateral paired infrapharyngobranchials distant from each other (185:1>0); angle between the dorsal and ventral parts of the lateral line canal of the preopercle ≥130° (202:0>1); accessory neural arch present (205:0>1); gap between the posteriormost supraneural and the first dorsal-fin pterygiophore present (217:0>1), dorsal process of the posttemporal subtriangular, wider at distal tip than at its midlength (261:0>2); cleithrum-coracoid fenestra reduced (275:1>0); seven pelvic-fin rays (277:2>1); pelvic fins placed anterior to the dorsal-fin origin (280:1>0).

Support. — Relative Bremer = 61%.

Remarks. — The family Chirocentridae Bleeker, 1849, currently comprises two species of the wolf herring *Chirocentrus* (*C. dorab* and *C. nudus*), and has been traditionally included within the superfamily Clupeoidea of Grande (1985), as sister to his family Clupeidae (including Alosinae, Clupeinae, Dorosomatinae, Dussumieriinae and Pellonulinae) (Grande 1985). Di Dario (2009) refuted the monophyly of the Grande's Clupeoidea, recognizing that the Chirocentridae was more closely related to the Engraulidae than to the Clupeidae, this relationship being supported by seven characters: 1) anterior margin of the metapterygoid located anterior to the quadrate; 2) ventral limb of the hyomandibula and quadrate not separated by the metapterygoid; 3) posterodorsal margin of the metapterygoid in line with the condyle of articulation of the hyomandibula with the opercle; 4) presence of a laminar outgrowth of the anterior margin of the quadrate; 5) endochondral portion of the quadrate in the shape of an isosceles triangle; 6) presence and arrangement of the autogenous tooth plates on ceratobranchials 1 to 3; 7) posterior region of infraorbital 1 well developed and extending along the ventral margin of the infraorbital 2. The close relationship between Chirocentridae and Engraulidae appears reliably supported by molecular (Bloom & Lovejoy 2014; Bloom & Egan 2018; Bloom *et al.* 2018) and morphology-based parsimony analyses (Di Dario 2004b; Vernygora 2020; Kevrekidis *et al.* 2024). Our analysis strongly corroborates this relationship (Relative Bremer = 61%), recovering 19 unambiguous synapomorphies uniting the Chirocentridae and the clade formed by Clupeopsidae n. fam. + Engraulidae, i.e., the new epifamily Engrauloidae n. epifam.

Node 58
Epifamily Engrauloidae n. epifam.

Taxa included and relationships. — Clupeopsidae n. fam. + Engraulidae.

Unambiguous synapomorphies. — Lateral expansion of the frontal bone above the orbit present (13:0>1); pterotic bulla greatly expanded dorsally, obliterating the pre-epioccipital fossa (56:0>1); dorsal process of the mesethmoid projecting in advance of the vomer (61:0>2); vomerine teeth grouped into two well-defined groups, each at anterolateral end of the vomer (71>0); suspensorium inclined obliquely backward (119:0>1); articulation between the ventral limb of the hyomandibula and quadrate present (124:0>1); dorsal tip of the symplectic ventral to the proximal margin of the quadrate (130:1>2); quadrate-mandibular articulation posterior to the orbit (131:1>0); basihyal reduced or absent (170:1>0).

Support. — Relative Bremer = 82%.

Diagnosis. — A new engrauloid epifamily diagnosed by the following unique combination of characters: lateral expansion of the frontal bone above the orbit; pterotic bulla greatly expanded dorsally, obliterating the pre-epioccipital fossa; dorsal process of the mesethmoid projecting in advance of the vomer; vomerine teeth grouped into two well-defined groups, each at anterolateral end of the vomer; suspensorium inclined obliquely backward; articulation between the ventral limb of the hyomandibula and quadrate; dorsal tip of the symplectic ventral to the proximal margin of the quadrate; quadrate-mandibular articulation posterior to the orbit; basihyal reduced or absent.

Remarks. — Capobianco *et al.* (2020) redescribed in detail the Ypresian stem-engraulid †*Clupeopsis straeleni* Casier, 1946 and described the Lutetian †*Monosmilus chureloides* Capobianco *et al.*, 2020 from Pakistan, bases on three-dimensional fossils. A number of derived features (e.g., suspensorium posteriorly inclined, mesethmoid projecting in advance of the vomers, substantial portion of the metapterygoid situated anterodorsal to the quadrate, ventral limb of the hyomandibula meeting the posterior margin of the quadrate and absence of the bony basihyal and basihyal tooth plate) support their close affinity with the Engraulidae, leading their inclusion into the Engrauloidea. However, †*Clupeopsis* and †*Monosmilus* lack at least one of the engraulid synapomorphies listed by Nelson (1970) (i.e., first basibranchial and basibranchial tooth plate not fused) plus other typical engraulid features (anteriorly - rather than posteriorly - directed articular surface of the quadrate) that exclude them from the crown Engraulidae (Capobianco *et al.* 2020). Since our analysis corroborates the hypotheses proposed by Capobianco *et al.* (2020), we propose to include these two taxa and the Engraulidae in their own epifamily, the Engrauloidae n. epifam., that can be diagnosed by the characters recovered by our analysis.

Node 59
Family Clupeopsidae n. fam.

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Taxa included and relationships. — †*Clupeopsis* + †*Monosmilus.*

Unambiguous synapomorphies. — Anterior arm of orbitosphenoid long, reaching the lateral ethmoid (44:0>1); posterior process of lateral ethmoid present (65:0>1); vomerine teeth massive and fang-like (70:0>1); maxillary teeth absent (103:1>0); endopterygoid teeth absent (115:1>0); ectopterygoid teeth absent (132:1>0); lateral horizontal lamina of the ectopterygoid present (136:0>1).

Support. — Relative Bremer = 81%.

Diagnosis. — A new engrauloid family whose representatives are characterized by a unique autapomorphy (lateral horizontal lamina of the ectopterygoid that overlies the maxilla) and the following combination of characters: a single massive, enlarged vomerine tooth (fang); single row of enlarged dentary fangs; maxilla edentulous; endopterygoid and ectopterygoid toothless.

Remarks. — Since our analysis corroborates the hypothesis of Capobianco *et al.* (2020) about the sister group relationships between †*Clupeopsis* and †*Monosmilus*, we propose the creation of a new family diagnosed by the combination of characters recovered by our parsimony analysis and the features already evidenced by Capobianco *et al.* (2020).

Node 60
Family Engraulidae Gill, 1861

Taxa included and relationships. — Coiliinae + pan-Engraulinae.

Unambiguous synapomorphies. — Pre-epioccipital fossa reduced or obliterated (21:1>0); four discrete openings present in the otic region: the opening for the infraorbital sensory canal opens between sphenotic, pterotic and frontal; the preopercular sensory canal and the cephalic sensory canal open on the pterotic; the accessory temporal canal opens on the pterotic and frontal (32:0>1); anterior ceratohyal length five times or more than its dept (144:0>1).

Support. — Relative Bremer = 69%.

Remarks. — Anchovies constitute a monophyletic group (the Engraulidae) that is traditionally divided in two distinct subgroups: the subfamily Coiliinae (=Coiliidae or Old World anchovies of Grande & Nelson 1985), including *Coilia*, *Lycothrissa*, *Papuengraulis*, *Setipinna* and *Thryssa*, and the subfamily Engraulinae (=Engraulidae of Grande & Nelson 1985) including *Stolephorus*, *Encrasicholina*, *Engraulis*; and the New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*). The family and both the subfamilies are recurrently recovered as monophyletic in morphological and molecular analyses, and our analysis corroborates this assumption. Nelson (1970) provided five diagnostic characters to distinguish anchovies from other clupeoid fishes: 1) reduction of the basihyal and loss of its ossification center; 2) reduction and loss of the basihyal tooth plate; 3) elongation of the second basibranchial; 4) elongation of the dorsal parts of the gill arches; 5) fusion of tooth plates with the first and third basibranchials. Grande (1985) added two further skeletal traits: 6) suspensorium inclined obliquely backward; and 7) mesethmoid projecting in advance of vomer making the snout pig-like. Stephens (2010) evidenced the role of an expanded orbital reticulum of the cephalic lateralis system as potential further synapomorphy of the Engraulidae. However, since it cannot be detected in †*Clupeopsis* or †*Monosmilus*, our analysis was not able to detect it as synapomorphy of the group.

Node 61
Subfamily Coiliinae Bleeker, 1872
(*sensu* Grande & Nelson 1985)

Taxa included and relationships. — *Lycothrissa* + (*Thryssa* + (*Setipinna* + *Coilia*)).

Unambiguous synapomorphies. — Basihyal teeth or tooth plate absent (171:1>0); first mediopharyngobranchial cartilage present (192:0>1); Baudelot's ligament originates at both first and second vertebra (235:1>2); Baudelot's ligament not ossified (236:1>0); hypural diastema absent (288:0>1); hypurals 5 and 6 not in line with the lower hypurals (projecting more posteriorly) (293:0>1); peg on the lower middle caudal-fin ray absent (314:1>0); at least one predorsal scute present (318:0>1); postpelvic scutes present (338:0>1); 10-20 abdominal scutes (341:1>2).

Support. — Relative Bremer = 69%.

Remarks. — Whitehead (1972) divided the Engraulidae into two subfamilies, the Engraulinae and the monotypic Coiliinae, this latter including *Coilia* only, to separate the peculiar rat-tailed anchovy from the other members of the family. Grande (1985) considered this division as artificial because most of the Old World anchovy genera (*Lycothrissa*, *Thryssa*, *Papuengraulis*, *Setipinna*) are more closely related to *Coilia* than to other anchovies, as also suggested by Jordan & Seale (1926). Grande (1985) and Grande & Nelson (1985) tentatively assumed that the Coiliinae form a distinct clade from the other anchovies, with their monophyly supported by at least three morphological features: 1) loss of the peg on the lower middle caudal-fin ray, 2) posterior margin of the fifth and sixth hypurals not in line with that of the lower elements of the series, and 3) absence (or remarkable reduction) of the posteroventral notch in the third hypural. The monophyly of the Coiliinae tentatively assumed by Grande & Nelson (1985) was later confirmed by several molecular studies (e.g., Lavoué *et al.* 2010, 2013; Wang *et al.* 2018, 2022), other than by our analysis that was able to recover six additional unambiguous synapomorphies supporting the clade.

Node 62
Unnamed clade

Taxa included and relationships. — *Thryssa* + (*Setipinna* + *Coilia*).

Unambiguous synapomorphies. — Posterior border of the maxilla just reaching or even exceeding the posterior margin of preopercle (100:0>1/2); prepelvic scutes present between the anterior and posterior end of the coracoid (334:0>1); 21-30 abdominal scutes (341:1>2).

Support. — Relative Bremer = 72%.

Node 63
Unnamed clade

Taxa included and relationships. — *Setipinna* + *Coilia*.

Unambiguous synapomorphies. — Anterior dorsal margin of the body forming a marked angle at the dorsal-fin insertion (1:0>1); temporal foramen unexposed, almost completely obliterated by frontal (30:0>1); posterior ramus of the parasphenoid not extending posteriorly to the neurocranium (37:1>0); posterior ramus of the parasphenoid with no posterior bifurcation (38:1>0); posterior medial opening that communicates with the posterior myodome absent or vestigial (54:1>0); vomer wider than long (67:1>0); Baudelot's ligament originates at the second vertebra (235:2>3); upper fin rays of pectoral fin extremely elongated (256:0>1).

Support. — Relative Bremer = 67%.

Node 64
pan-Engraulinae

Taxa included and relationships. — †*Eoengraulis* + Engraulinae.

Unambiguous synapomorphies. — Ectopterygoid and metapterygoid fused (133:0>1); no bony flange on the outer surface of the opercle close to the joint area with the hyomandibula (200:1>0); cleithrum-coracoid fenestra absent (274:0>1); neural spine on the first preural centrum almost as long as the neural spine on PU2 (308:1>0); ascending arms of the prepelvic scutes reduced (337:1>0); needle-like prepelvic scutes (342:0>1).

Support. — Relative Bremer = 64%.

Remarks. — †*Eoengraulis fasoloi*, an Eocene engraulid from Bolca, Italy, is the earliest known anchovy in the record (Marramà & Carnevale 2016). This genus is supposed to be a stem-Engraulinae based on the presence of at least four of the synapomorphies of the subfamily (possession of needle-like pre-pelvic scutes; nearly full spine on the first preural centrum; two epurals; fused ecto- and metapterygoid; Grande & Nelson 1985). However, it is excluded from the crown Engraulinae, since it still lacks two of the other distinctive traits of the engraulines: gap in the tooth row of the dentary and anteriormost two supraneurals in close proximity.

Node 65
Subfamily Engraulinae Gill, 1861
(*sensu* Grande & Nelson 1985)

Taxa included and relationships. — *Stolephorus* + (*Encrasicholina* + Engraulini)

Unambiguous synapomorphies. — Gap in the tooth row of the dentary present (107:0>1); anteriormost two supraneurals in close proximity (215:0>1); anteriormost two supraneurals having different shape respect to the others (216:0>1); keel of the pelvic scute poorly developed or inconspicuous (332:1>0).

Support. — Relative Bremer = 64%.

Remarks. — Nelson (1983) provided osteological evidence (ramifications of preopercular and temporal sensory canals; first epibranchial with fused tooth plate; caudal skeleton with first preural and first ural centra) that the New World anchovies plus the cosmopolitan *Engraulis* and the Indo-Pacific *Encrasicholina* form a well-defined monophyletic group. Grande (1985) expanded the list of synapomorphies of this group, adding the loss of the dorsal scutes (although still present in some species of *Stolephorus*). Grande & Nelson (1985) further demonstrated that the genus *Stolephorus* is the closest relative to this assemblage, jointly forming the subfamily Engraulinae (Engraulidae of Grande & Nelson 1985), because all of them can be diagnosed by the presence of oval eggs, nearly complete spine on the first preural centrum, two epurals, rear edge of hypurals 5 and 6 in line with the lower hypurals, close positioning of the first two supraneurals, fusion of ecto- and metapterygoid, gap in the tooth row of the dentary. *Stolephorus* and *Encrasicholina* were supposed to be successive sisters to the New World genera plus *Engraulis*, since they still retain less than nine needle-like prepelvic scutes with reduced lateral wings, which are absent in the remaining engrauline genera. Our analysis corroborates this hypothesis, similarly to several molecular analyses (Bloom & Lovejoy 2012; Lavoué *et al.* 2017b; Bloom & Egan 2018).

Node 66
Unnamed clade

Taxa included and relationships. — *Encrasicholina* + Engraulini.

Unambiguous synapomorphies. — First epibranchial fused to a tooth plate (162:0>1); first postcleithrum absent (262:1>0); caudal complex formed by fused PU1+U1, and autogenous U2 (295:0>1).

Support. — Relative Bremer = 33%.

Remarks. — Nelson (1983) identified several key osteological features that unify the Indo-Pacific *Encrasicholina* to the New World anchovies (including *Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis* and *Pterengraulis*) plus *Engraulis* as a monophyletic group. These features include 1) modifications in the preopercular and temporal sensory canals, 2) fusion of a tooth plate on the first epibranchial, and 3) fusion of the first preural and first ural centra (the latter two features recovered also in this study). Grande (1985) expanded the list of synapomorphies of this group, including 4) the absence of dorsal scutes (still found in some *Stolephorus* species) and 5) the absence of scutes along the ventral edge of the coracoid (also present in *Lycothrissa*).

Node 67
Tribe Engraulini
(*sensu* Grande & Nelson 1985)

Taxa included and relationships. — *Lycengraulis* + (*Anchoviella* + ((*Anchovia* + *Anchoa*) + (*Pterengraulis* + (*Cetengraulis* + *Engraulis*)))).

Unambiguous synapomorphies. — Posterior frontal fontanelles closed in adult individuals (28:1>0); contralateral paired infrapharyngobranchials close to each other (185:0>1); prepelvic scutes between the pelvic scute and the posterior end of the coracoid absent (333:1>0); single abdominal scute (341:1>0).

Support. — Relative Bremer = 51%.

Remarks. — This tribe includes *Engraulis* and the so called New World anchovies (*Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Lycengraulis*, *Pterengraulis*) that share the absence of abdominal scutes, except for the pelvic scute just in front of pelvic fins (Jordan & Seale 1926; Grande & Nelson 1985). Although this group is recurrently recovered as monophyletic in several morphological and molecular analyses, there is usually no con*sensu*s about the intrarelationships of the taxa included within the clade [compare, e.g., Di Dario (2004b), Vernygora (2020) and this work with, e.g., Bloom & Lovejoy (2012), Bloom & Egan (2018), Bloom *et al.* (2018)]. Due to limited sampling of Engraulini species, our analysis cannot test the hypothesis of Bloom & Lovejoy (2012) about the separation of the so called "marine clade" from the "freshwater clade" since we included only marine species, except for a single freshwater taxon (*Pterengraulis atherinoides*).

Node 68
Unnamed clade

Taxa included and relationships. — (*Anchoviella* + ((*Anchovia* + *Anchoa*) + (*Pterengraulis* + (*Cetengraulis* + *Engraulis*)))).

Unambiguous synapomorphies. — Teeth on the third hypobranchial absent (181:1>0).

Support. — Relative Bremer = 25%.

Node 69
Unnamed clade

Taxa included and relationships. — (*Anchovia* + *Anchoa*) + (*Pterengraulis* + (*Cetengraulis* + *Engraulis*)).

Unambiguous synapomorphies. — "Panamensis" condition of the head sensory-canal system (9:0>1); peritoneal tunic covering the swim bladder non-silvered (49:1>0); basihyal teeth absent (171:1>0); four pectoral-fin proximal radials (254:1>0) first postcleithrum present (262:0>1).

Support. — Relative Bremer = 50%.

Node 70
Unnamed clade

Taxa included and relationships. — *Anchovia* + *Anchoa.*

Unambiguous synapomorphies. — Posterior border of the maxilla reaching onto preopercle but not exceeding its posterior margin (100:0>1); 31-55 anal-fin pterygiophores (343:0>1).

Support. — Relative Bremer = 37%.

Node 71
Unnamed clade

Taxa included and relationships. — *Pterengraulis* + (*Cetengraulis* + *Engraulis*).

Unambiguous synapomorphies. — Teeth on first hypobranchial absent (179:1>0).

Support. — Relative Bremer = 16%.

Node 72
Unnamed clade

Taxa included and relationships. — *Cetengraulis* + *Engraulis.*

Unambiguous synapomorphies. — Posterior border of the maxilla does not reach the preopercle (102:1>0); epibranchial organs present (195:0>1).

Support. — Relative Bremer = 11%.

Node 73
Unnamed clade

Taxa included and relationships. — Pristigasteroidea + Clupeoidea.

Unambiguous synapomorphies. — Ridge between orbital wall and levator arcus palatini fossa on the frontal and sphenotic absent or poorly developed (14:0>1); anterior frontal fontanelle very large (25:0>1); all four sensory canals of the recessus lateralis confluent into a single opening between the sphenotic, pterotic and frontal (32:0>7); single branchiostegal ray on the distinct posteroventral process of the anterior ceratohyal (155:0>1); two branchiostegal rays on the posterior ceratohyal (156:2>1); posterior process on the second basibranchial reaching the third basibranchial (177:0>1); cleithrum-coracoid fenestra absent (274:0>1); peg on the lower middle caudal-fin ray present: (314:0>1).

Support. — Relative Bremer = 3%.

Remarks. — This node includes the monotypic superfamily Pristigasteroidea (including the family Pristigasteridae only) as sister to a clade formed by the rest of clupeoids forming herein the superfamily Clupeoidea, new usage (= i.e., the Clupeoidea of Grande 1985, excluding *Chirocentrus* and his Dussumieriinae). Recent parsimony analyses based on morphological data were unable to detect this relationship, since they recovered the pristigasterids, e.g., sister to a clade that includes dussumieriids, *Chirocentrus* and Engraulidae (Di Dario 2004b), or nested within the Clupeoidea *sensu* Grande (1985) minus *Chirocentrus* (Sato 1994) or minus spratelloidines (Kevrekidis *et al.* 2024), or in polytomous relationship with some of these subfamilies (Vernygora 2020). The same can be said for some molecular analyses, as they are mostly inconsistent to each other in recovering Pristigasteroidea sister to any specific clade, being the pristigasteroids recovered sister to the Engraulidae (Egan *et al.* 2018), to the Clupeoidea *sensu* Grande (1985) (Lavoué *et al.* 2007, 2010, 2017a, 2019; Milec *et al.* 2022), nested within the Clupeoidea *sensu* Grande (1985) as sister to the Alosinae or *Chirocentrus* (Bloom & Egan 2018; Egan *et al.* 2018), sister to (*Chirocentrus* + Dussumieriinae) (Wang *et al.* 2022; Near & Thacker 2024), or in polytomy with all of these taxa (Li & Ortí 2007). Interestingly, our analysis is mostly consistent with the Bayesian relaxed clock analysis of the mitogenomic dataset of Lavoué *et al.* (2013, fig. 3), the molecular time-calibrated phylogeny including 1990 species of bony fishes of Betancur-R *et al.* (2017, fig. 2 a), with that of Bloom & Lovejoy (2014, fig. 3 and supplementary material) and Bloom *et al.* (2018, fig. 1), except for the placement of *Etrumeus* that falls within our Clupeoidea in these latter two analyses.

Node 74
Superfamily Pristigasteroidea Nelson, 1970
Family Pristigasteridae Bleeker, 1872

Taxa included and relationships. — (*Ilisha* + *Pellona*) + (*Pristigaster* + ((*Chirocentrodon* + *Neoopisthopterus*) + (*Pliosteostoma* + (*Raconda* + (*Opisthopterus* + *Odontognathus*))))).

Unambiguous synapomorphies. — Mouth superterminal (upward turned) (1:0>2); supratemporal commissure passing through parietals not bony enclosed (7:1>0); parietal-epioccipital ridge present (19:0>1); posterior frontal fontanelles present (open) (27:0>1); ethmopalatine cartilage present (46:0>1); nasal small, bearing a bony flange to form a narrow groove for the supraorbital canal opening posteriorly (73:0>1); sclerotic bones large, their total length representing almost the entire circumference of the orbit (82:0>1); quadrate-mandibular articulation anterior to the orbit (131:0>2); dorsal process of the ectopterygoid elongated and slender (135:0>1); dorsal process of the posterior ceratohyal well-definite and large (147:0>1); dorsal blade of the urohyal present and well developed (149:0>1); ventral process of the second basibranchial well developed (178:0>1); teeth on the first and second hypobranchials present (179:0>1; 180:0>1); basibranchial tooth plates 1-3 fused with the second basibranchial (182:0>1); supraneurals oriented vertically or inclined forward (209:0>1); dorsal fork of the epipleurals not projecting dorsally beyond the level of the epicentrals (225:1>0); epicentrals and anterior ribs unfused (230:1>0); pleural ribs/preural vertebrae ratio 0.20-0.40 or 0.41-0.46 (231:2>0/1); interzygapophysal articulation absent (243:1>0); postzygapophyses more developed than prezygapophyses (244:0>2); anterior bony expansion in the parapophyses of the third vertebra present (245:0>1); bony process on the first pleural rib present (248:0>1); second and third postcleithra absent (263:1>0; 264:1>0); pelvic fin placed anterior to the dorsal-fin origin (280:1>0); hypural diastema absent (288:0>1); hypural 3 larger than hypural 1 (290:0>1); prepelvic scutes anterior to the coracoid present (336:0>1); 31-55 anal-fin pterygiophores (343:0>1).

Support. — Relative Bremer = 78%.

Remarks. — Nelson (1970) assigned the pristigasterids the rank of a superfamily due to their distinct and consistent gill arch characters (fusion of tooth plates with the second hypobranchials, and sometimes with the first, third, or both first and third hypobranchials, lacking other traits distinctive of engrauloids and clupeoids) which were supposed sufficiently unique to warrant a rank equivalent to other established clupeoid superfamilies, i.e., Chirocentroidea, Engrauloidea, and Clupeoidea. After the introduction of the superfamily "Pristigasteroidae" by Nelson (1970), Grande (1985) renamed the clade as Pristigasteroidea to standardize the suffix rather than reflect a fundamental change in the taxonomic composition of the group and added two new skeletal traits: supraneurals oriented either vertically or inclined anterodorsally and loss of the interlobar notch (hypural diastema) in the third hypural. Within the clade, Grande (1985) recognized three major groups at family level: 1) the Pristigasteridae (including "*Ilisha*" *africana*, *Odontognathus*, *Opisthopterus*, *Pristigaster* and *Raconda*) supported by the presence of a bony process on the first pleural rib which articulates with the shoulder girdle; and 2) the Pellonidae (including *Chirocentrodon*, *Neoopisthopterus*, *Pellona* and *Pliosteostoma*) supported by the maxillary-premaxillary gap covered by bone; and 3) the genus *Ilisha* (minus "*Ilisha*" *africana*). Although the monophyly of the Pristigasteroidea is well supported by several morphological and molecular based analyses (Sato 1994; Di Dario 2004b; Li & Ortí 2007; Lavoué *et al.* 2013; Bloom & Egan 2018; Egan *et al.* 2018; Wang *et al.* 2022) the relationships between the genera have not yet been comprehensively understood and these three groups have not been always recognized, mostly because pristigasteroids are usually undersampled in these analyses. Former parsimony-based phylogenetic analyses often recovered a clade formed by *Chirocentrodon* and *Odontognathus* in polytomy with *Ilisha* and *Pellona* (Sato 1994), or sister to *Ilisha* + *Pellona* (Vernygora 2020), or sister to *Ilisha africana* (Kevrekidis *et al.* 2024), or species of a paraphyletic *Pellona* that are successive sister of a clade formed by *Ilisha* and *Opisthopterus* (Di Dario 2004b). Our tree topology about the intrarelationships of the monotypic Pristigasteroidea, however, is not comparable to most of the morphological or molecular analyses as these included only a few genera (mostly two to five), whereas our topology is, at least in part, consistent with that of Di Dario (1999). In conclusion, since the Pellonidae and Pristigasteridae *sensu* Grande (1985) have never been recognized in molecular or parsimony approaches, we confirm the monotypic nature of the Pristigasteroidea, including a single family (Pristigasteridae) pending further detailed analyses. The putative fossil pristigasteroid †*Gasteroclupea branisai* Signeaux, 1964 has been re-described in detail by Marramà & Carnevale (2017) who recovered this clupeomorph to be a member of the †Ellimmichthyiformes (see family Gasteroclupeidae), as confirmed also in this study.

Node 75
Unnamed clade

Taxa included and relationships. — *Ilisha* + *Pellona*.

Unambiguous synapomorphies. — Posterodorsal region of the lateral aspect of the skull high and truncated (59:0>1); antorbital crescent or oval, with bony constituent (flange or tube) for sensory canal (74:0>1); anterior border of the infraorbital 3 concave (79:0>1); ectopterygoid teeth present (132:0>1); posteriorly facing process on infrapharyngobranchial 1 present (191:0>1); anterior notch (and bifurcation) of the basipterygium present (279:0>1); lateral crest on hypural 1 present (311:0>1).

Support. — Relative Bremer = 45%.

Node 76
Unnamed clade

Taxa included and relationships. — *Pristigaster* + ((*Chirocentrodon* + *Neoopisthopterus*) + (*Pliosteostoma* + (*Raconda* + (*Opisthopterus* + *Odontognathus*))))).

Unambiguous synapomorphies. — Ventral process of quadrate short, with its distal end not reaching the posterior margin of the main body of the quadrate (128:1>0); teeth or tooth plate over infrapharyngobranchial 4 absent (189:1>0); dorsal myorhabdoi present (232:0>1); anteriorly facing bony expansions at the base of the neural arches of the first abdominal vertebrae absent (237:0>1); posteriorly directed process on the posteroventral margin of the coracoid absent (270:0>1); pelvic fins absent (276:0>1); basipterygium absent (278:0>1); proximal region of the middle rays of the caudal fin not extending anteriorly (312:1>0); pegs on the middle caudal-fin rays placed very proximally (315:0>1); basal segments of the upper middle caudal-fin ray rod-like (316:1>0).

Support. — Relative Bremer = 44%.

Node 77
Unnamed clade

Taxa included and relationships. — (*Chirocentrodon* + *Neoopisthopterus*) + (*Pliosteostoma* + (*Raconda* + (*Opisthopterus* + *Odontognathus*))))).

Unambiguous synapomorphies. — Distal region of the supraneurals expanded or greatly expanded. (211:0>1); abdominal epipleurals proximally trifurcated (224:1>2); anal fin anterior to the dorsal-fin origin (344:0>2).

Support. — Relative Bremer = 50%.

Node 78
Unnamed clade

Taxa included and relationships. — *Chirocentrodon* + *Neoopisthopterus*.

Unambiguous synapomorphies. — Maxillo-premaxillary gap absent (88:0>1); dentary teeth extending well back to the border of the coronoid process (106:0>1); quadrate-mandibular articulation below the orbit (131:2>1); ectopterygoid teeth present (132:0>1); tooth patch on the dorsal surface of the dorsal hypohyal present (169:0>1); spoon-like expansion of the rib head present (221:0>1); mesocoracoid absent (269:0>1).

Support. — Relative Bremer = 39%.

Node 79
Unnamed clade

Taxa included and relationships. — (*Pliosteostoma* + (*Raconda* + (*Opisthopterus* + *Odontognathus*))).

Unambiguous synapomorphies. — Posterodorsal region of the lateral aspect of the skull high and truncated (59:0>1); proximal region of most supraneurals greatly expanded near the tip (210:0>1); abdominal epipleurals distally multifurcated (226:0/1>2); ossified occipital epineurals present (233:0>1); dorsal fin displaced posteriorly on the body (predorsal length >60% SL) (348:1>2).

Support. — Relative Bremer = 58%.

Node 80
Unnamed clade

Taxa included and relationships. — *Raconda* + (*Opisthopterus* + *Odontognathus*).

Unambiguous synapomorphies. — Temporal foramen unexposed, almost completely obliterated by frontal (30:0>1); supraneurals extending beyond their posterior neural spine (214:0>1); articulation between the first pleural rib and cleithrum present (249:0>1); coracoid large, its depth at least 1/3 (or more) of the body depth (271:0>1); 56 or more anal-fin pterygiophores (343:1>2); dorsal-fin base reduced, covering less than five consecutive neural spines (349:0>1).

Support. — Relative Bremer = 41%.

Node 81
Unnamed clade

Taxa included and relationships. — *Opisthopterus* + *Odontognathus*.

Unambiguous synapomorphies. — Supraoccipital crest high (11:0>1); spoon-like expansion of rib head present (221:0>1); dorsal process of the posttemporal sub-rectangular and plate-like (261:0>1).

Support. — Relative Bremer = 13%.

Node 82
Superfamily Clupeoidea Cuvier, 1816,
new usage

Taxa included and relationships. — Hyperlophidae + (Clupeidae + (Ehiravidae + (Alosidae + pan-Dorosomatidae))).

Unambiguous synapomorphies. — Anterior arm of the orbitosphenoid long, reaching the lateral ethmoid (44:0>1); posterior process of the lateral ethmoid present (65:0>1); palatine teeth absent (114:1>0); teeth or tooth plates on ceratobranchial 1 small

(158:0>1); teeth or tooth plates on ceratobranchials 2 and 3 small (160:0>1); cartilage process of the anterior margin of the fourth ceratobranchial directed medially, forming a bridge over the ventral surface of the fourth basibranchial (161:0>1); cartilage chevron at the distal tip of the epicentrals present (229:0>1); parapophyses on third vertebra reduced (241:1>0); medial process of the cleithrum present (258:0>1); basal segments of the upper middle caudal-fin ray spatulate (317:0>1); body scales of crenate type (361:0>1); posterior margin of the body scales crenulate (362:0>1).

Support. — Relative Bremer = 32%.

Remarks. — The traditional composition of the superfamily Clupeoidea has been proposed by Grande (1985) to include the families Chirocentridae (*Chirocentrus*) and his Clupeidae (Alosinae, Clupeinae, Dorosomatinae, Dussumieriinae, Pellonulinae) with the monophyly of the group thought to be supported by single condition, increase in pleural rib to preural vertebrae ratio (≥0.47), and possibly by a peculiar type of connection between the swim bladder and gut in a more posterior position of the esophagous with respect to other clupeiforms (Nelson 1970). The Clupeoidea *sensu* Grande (1985) was later proposed to be more closely related to the engraulids based on the presence of cartilage chevrons at the tips of the epicentrals, posteriorly directed parapophyses of the second vertebra, and interzygapophysal articulation (Di Dario 2002). Di Dario (2009) rejected the monophyly of the Clupeoidea *sensu* Grande (1985), in that *Chirocentrus* was supposed to be more closely related to the Engraulidae than to the other Clupeidae. Miyashita (2010) proposed an alternative hypothesis in which the Clupeoidea *sensu* Grande (1985) is closer to the Pristigasteroidea than to the Engrauloidea because they all share "a unique occipital articulation with the first vertebra". Our analysis rejects the monophyly of the Clupeoidea and Clupeidae *sensu* Grande (1985), since *Chirocentrus*, *Dussumieria*, *Etrumeus*, *Jenkinsia* and *Spratelloides* are basal or more closely related to the Engraulidae than to the other clupeoids. For this reason, we propose a new usage for the superfamilial rank Clupeoidea that would include all the remaining clupeoid taxa.

Node 83
Family Hyperlophidae Ogilby, 1897, new rank

Taxa included and relationships. — (†*Gosiutichthys* + †*Knightia*) + (*Hyperlophus* + *Potamalosa*).

Unambiguous synapomorphies. — At least one predorsal scute present (318:0>1); 11 to 20 predorsal scutes (326:3>1).

Support. — Relative Bremer = 55%.

Remarks. — The subfamily Hyperlophinae was established by Ogilby (1897) to contain *Hyperlophus* and *Potamalosa*, two small to medium sized double-armored herring genera inhabiting the marine and freshwater/brackish habitats of the Australia (Whitehead 1985). The subfamily has been diagnosed by the presence of complete abdominal and predorsal scute series and a single (posterior) supramaxilla, and a dorsal fin inserted above or just behind the pelvic-fin insertion (Ogilby 1897). In our analysis, the pair formed by the putative clupeine †*Gosiutichthys* and the putative pellonuline †*Knightia* from the Paleocene to Middle Eocene freshwater deposits of North America (Grande 1982b) is recovered sister to the extant Hyperlophinae, since most of them also share similar number of predorsal scutes (11-20). Despite recent molecular analyses recurrently recover the pair *Hyperlophus* + *Potamalosa* as sister to the clade formed by *Clupea* + *Sprattus*, in the family Clupeidae *sensu* Wang *et al.* (2022), our analysis might suggest that results from gene datasets might be biased by the lack of fossil data, since we recover these two pairs as successive sisters to the rest of clupeoids. The counterproof is that when fossil taxa are removed the pair (*Hyperlophus* +*Potamalosa*) form a monophyletic group with the pair (*Clupea* + *Sprattus*) (Fig. 41). For these reasons, we propose to keep the distinctiveness of these two pairs, elevating the subfamily Hyperlophinae Ogilby, 1897 at familial level, and considering *Clupea* and *Sprattus* as the sole members of the family Clupeidae Cuvier, 1816.

Node 84
Unnamed clade

Taxa included and relationships. — †*Gosiutichthys* + †*Knightia*.

Unambiguous synapomorphies. — 7-9 supraneurals (208:1>2); 30-40 preural vertebrae (218:2>3).

Support. — Relative Bremer = 4%.

Node 85
Unnamed clade

Taxa included and relationships. — *Hyperlophus* +*Potamalosa*.

Unambiguous synapomorphies. — Posterior frontal fontanelles open (27:0>1); more than 30 abdominal scutes (341:3>4).

Support. — Relative Bremer = 57%.

Remarks. — Because of the presence of a single (posterior) supramaxilla, Grande (1985) considered *Potamalosa* and *Hyperlophus* as pellonulines, although he pointed out that "separation of this group based on this character is tenuous" as the anterior supramaxilla is absent also in other non-pellonuline clupeoids and because there are no other characters that unite these two taxa to the Pellonulinae. Our analysis, in agreement with the results of several molecular studies (Lavoué *et al.* 2013; Bloom & Lovejoy 2014; Bloom *et al.* 2018; Wang *et al.* 2022) demonstrates that *Potamalosa* and *Hyperlophus* are not related to the Pellonulinae but are more closely related to the clupeines *Clupea* and *Sprattus*, as clearly shown by the analysis that excludes fossil taxa (Fig. 41), in which the Hyperlophidae is sister to the pair *Clupea* + *Sprattus* (the family Clupeidae new usage).

Node 86
Unnamed clade

Taxa included and relationships. — Clupeidae + (Ehiravidae + (Alosidae + pan-Dorosomatidae)).

Unambiguous synapomorphies. — Unique W-shaped articulation between the first and second vertebrae (207:0>1); abdominal epipleurals long, extending ventrally at least to the midlength between the vertebrae and the ventral margin of the body (223:1>0); lateral flange of cleithrum present (260:0>1); membranous anterodorsal outgrowth of uroneural 1 present (299:0>2).

Support. — Relative Bremer = 36%.

Node 87
Family Clupeidae Cuvier, 1816, new usage

Taxa included and relationships. — *Clupea* + *Sprattus*.

Unambiguous synapomorphies. — Participation of the pterotic in the sub-epioccipital fossa (58:1>0); anterior region of the mesethmoid keel perforated (62:0>1); olfactory nerve foramen of the lateral ethmoid surrounded by the lateral ethmoid and mesethmoid (66:1>2); teeth on the vomer present (69:0>1); ventral process of the quadrate short (128:0>1); foramen on the anterior ceratohyal produced by the overlap between lateral and medial foramina of the hyoid arterial duct present (140:0>1); foramen in the fourth epibranchial present (163:0>1); posterior concavity on the fourth epibranchial (166:0>1); holes on the surface of the coracoid present (272:0>1); keel of the pelvic scute absent (332:1>0); more than 30 abdominal scutes (341:3>4); focus of the body scales in postero-central position (360:2>3).

Support. — Relative Bremer = 67%.

Node 88
Unnamed clade

Taxa included and relationships. — Ehiravidae + (Alosidae + pan-Dorosomatidae).

Unambiguous synapomorphies. — First mediopharyngobranchial cartilage present (192:0>1); bony flange on the outer surface of the opercle close to the joint area with the hyomandibula absent (200:1>0); ossified occipital epineurals present (233:0>1); lateral crest of hypural 1 present (311:0>1).

Support. — Relative Bremer = 32%.

Node 89
Family Ehiravidae Deraniyagala, 1929, new usage

Taxa included and relationships. — *Clupeonella* + (Ehiravinae + Pellonulinae).

Unambiguous synapomorphies. — Skull roof unornamented (16:1>0); posterior frontal fontanelles open and large (27:0>1; 28:0>1); teeth or tooth plates on ceratobranchial 1 absent (157:1>0); teeth or tooth plates on ceratobranchials 2 and 3 absent (159:1>0); medial process of the cleithrum absent (258:1>0); caudal complex formed by fused PU1+U1 and autogenous U2 (295:0>1); two epurals (304:0>1); true cycloid body scales (361:1>0); posterior margin of the body scales smooth (362:1>0).

Support. — Relative Bremer = 56%

Remarks. — The family Ehiravidae new usage comprises the subfamily Pellonulinae *sensu* Grande (1985) to the exclusion of *Hyperlophus* and *Potamalosa* but including *Clupeonella* (a clupeine according to Grande 1985). The Pellonulinae was the only subfamily of the Clupeidae, along with the Dussumieriinae, for which Grande (1985) provided a diagnosis, whereas the Alosinae, Dorosomatinae and Clupeinae were merely considered to be "groups of convenience" because of the difficulty to recognize unambiguous diagnostic characters. Grande (1985) diagnosed his Pellonulinae by the presence of a single ambiguous synapomorphy, the loss of the anterior supramaxilla, although he pointed out that "separation of this group based on this character is tenuous" because the anterior supramaxilla is absent also in other non-pellonuline clupeoids and because there are no other features that unite *Potamalosa* and *Hyperlophus* to the members of the pellonulines. Our analysis in agreement with many recent molecular analyses (Lavoué *et al.* 2013, 2014, 2017a; Bloom & Lovejoy 2014; Wang *et al.* 2022) corroborates the molecular results, indicating that *Potamalosa* and *Hyperlophus* are not related to the Pellonulinae, whereas *Clupeonella* is resolved herein to be the basalmost ehiravid. However, contrary to molecular analyses that recovers the tribe Pellonulini *sensu* Grande (1985) nested within the Dorosomatidae, we recovered *Clupeonella* sister to the pair formed by the Ehiravidae *sensu* Wang *et al.* (2022) (here represented by *Clupeichthys*, *Clupeonella*, *Corica* and *Gilchristella*) and the Pellonulini *sensu* Grande (1985) (including *Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, and *Stolothrissa*) that are re-ranked herein at the subfamilial level (Fig. 44).

Node 90
Unnamed clade

Taxa included and relationships. — Ehiravinae + Pellonulinae.

Unambiguous synapomorphies. — Anterior supramaxilla absent (83:1>0); accessory neural arch absent (205:1>0); first postcleithrum absent (262:1>0); anterior margin of the second rod-like postcleithrum not expanded (267:1>0); prepelvic scutes along the ventral edge of the coracoid absent (334:1>0).

Support. — Relative Bremer = 65%.

Node 91
Subfamily Ehiravinae Deraniyagala, 1929, new rank

Taxa included and relationships. — *Gilchristella* + (*Clupeoides* + (*Corica* + *Clupeichthys*)).

Unambiguous synapomorphies. — Lateral wings of the urohyal absent (151:1>0); unique W-shaped articulation between the first and second vertebrae absent (207:1>0); pelvic fins inserted anterior to the dorsal-fin origin (280:1>0); lateral crest of hypural 1 absent (311:1>0); 10-20 abdominal scutes (341:3>2).

Support. — Relative Bremer = 57%.

Node 92
Unnamed clade

Taxa included and relationships. — *Clupeoides* + (*Corica* + *Clupeichthys*).

Unambiguous synapomorphies. — First mediopharyngobranchial cartilage absent (192:1>0); parapophyses on the first vertebrae absent (238:1>0).

Support. — Relative Bremer = 50%.

Node 93
Unnamed clade

Taxa included and relationships. — *Corica* + *Clupeichthys*.

Unambiguous synapomorphies. — Teeth or tooth plates over ceratobranchials 2 and 3 present (159:0>1); teeth or tooth plates over infrapharyngobranchial 2 and 3 present (187:0>1; 188:0>1); 30-40 preural vertebrae (218:2>3); anal finlets (of Ehiravini-type) present (345:0>1).

Support. — Relative Bremer = 64%.

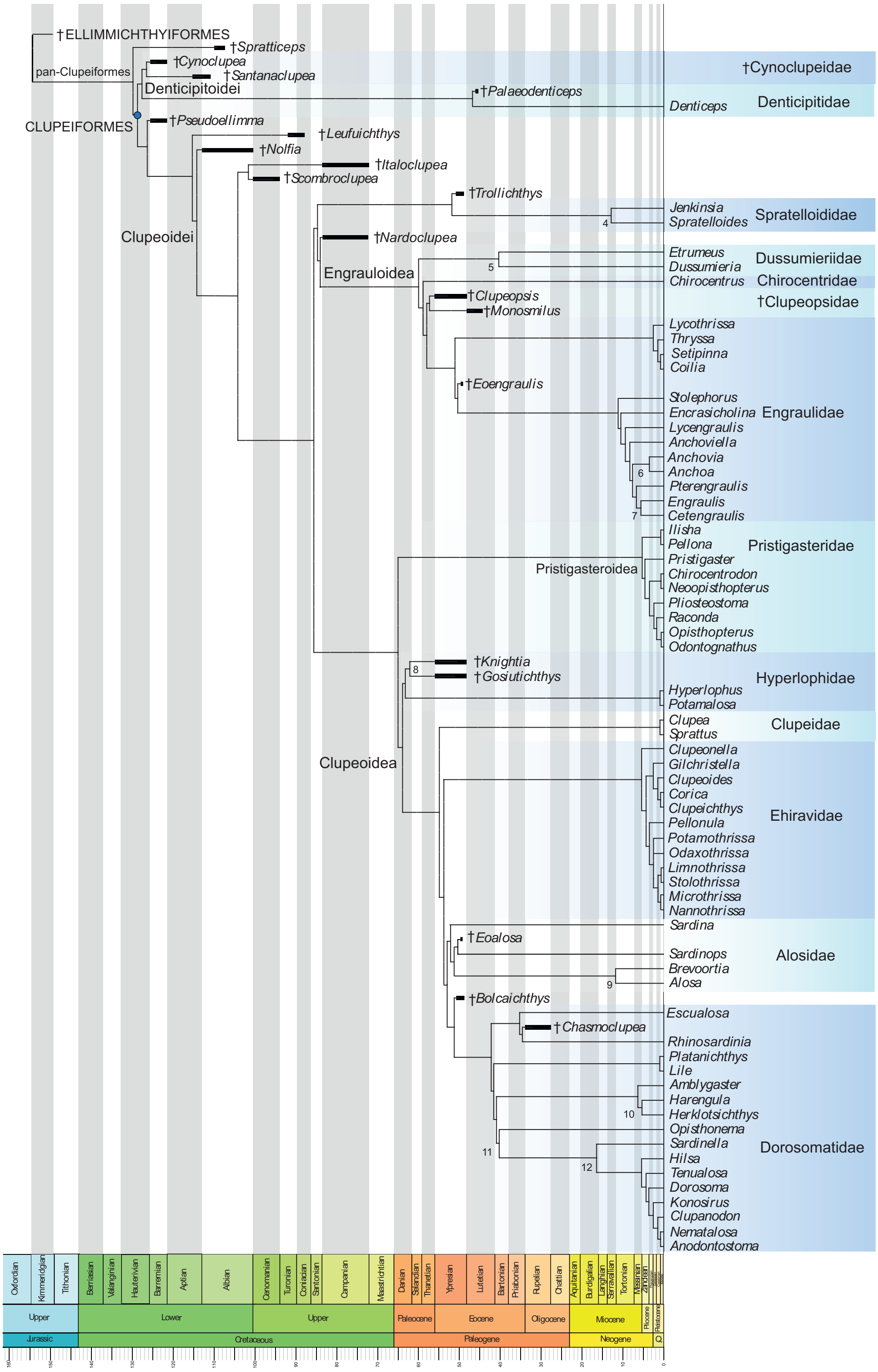

FIG. 44. — Time-calibrated strict consensus tree from the main parsimony-based phylogenetic analysis based on 368 morphological characters and 130 terminal taxa highlighting the interrelationships of the pan-Clupeiformes (node 40) within the Clupeomorpha. The black bars represent the known stratigraphic range of the taxa. Numbers at nodes indicates additional calibration points based on fossils not included in the analysis (see Material and Methods): 4) *Spratelloides* sp. (Badenian of St. Margarethen, Austria; pers. obs. GC); 5) †*Etrumeus hafizi* Arambourg, 1966 (lower Bartonian of Pabdeh Formation; Arambourg 1966); 6) *Anchoa* sp. (early Pliocene of Onzole Formation, Ecuador; Carnevale *et al.* 2011); 7) †*Engraulis tethensis* Grande & Nelson, 1985 (Messinian of the Mesaoria Group, Cyprus; Grande & Nelson 1985); 8) †*Knightia vetusta* Grande, 1982 (middle Paleocene Tongue River Formation, Montana; Grande 1982b); 9) †*Alosa elongata* Agassiz, 1842 (Upper Tortonian of the Mediterranean area); (e.g., Arambourg 1927; Gaudant & Cavallo 2008); 10) *Harengula* sp. (Messinian of Central Italy; Carnevale & Schwarzhans 2022); 11) †*Opisthonema persicum* Arambourg, 1966 (lower Bartonian of the Pabdeh Formation; Arambourg 1966); 12) †*Sardinella miyanoshitaensis* Sato & Uyeno, 1999 (late Burdigalian of Japan; Sato & Uyeno 1999).

Node 94
Subfamily Pellonulinae Svetovidov, 1952, new rank

Taxa included and relationships. — *Pellonula* + (*Potamothrissa*, *Odaxothrissa*, (*Stolothrissa* + *Limnothrissa*), (*Microthrissa*, *Nannothrissa*)).

Unambiguous synapomorphies. — Ventral blade of the urohyal absent or inconspicuous (150:1>0); posterior process of the fifth epibranchial absent or inconspicuous (168:1>0); teeth or tooth plates over infrapharyngobranchial 4 absent (189:1>0); distal region of most supraneurals greatly expanded (211:0>1); articulation of the first rodlike postcleithrum (=second postcleithrum) with the supracleithrum well behind the cleithrum (268:0>1).

Support. — Relative Bremer = 49%.

Node 95
Unnamed clade

Taxa included and relationships. — *Potamothrissa*, *Odaxothrissa*, (*Stolothrissa* + *Limnothrissa*), (*Microthrissa*, *Nannothrissa*).

Unambiguous synapomorphies. — First mediopharyngobranchial cartilage absent (192:1>0); ossified occipital epineurals absent (233:1>0).

Support. — Relative Bremer = 5%.

Node 96
Unnamed clade

Taxa included and relationships. — *Stolothrissa* + *Limnothrissa*.

Unambiguous synapomorphies. — Dorsal blade of the urohyal absent or inconspicuous (149:1>0); four to nine branchiostegal rays on the anterior ceratohyal (excluding those rays on the distinct posteroventral process, if present) (154:2>3).

Support. — Relative Bremer = 11%.

Node 97
Unnamed clade

Taxa included and relationships. — *Microthrissa* + *Nannothrissa*.

Unambiguous synapomorphies. — 7-9 supraneurals (208:1>2); Baudelot's ligament originating on the cranium (235:1>0); pelvic fins inserting anterior to the dorsal-fin origin (280:1>0).

Support. — Relative Bremer = 38%.

Node 98
Unnamed clade

Taxa included and relationships. — Alosidae + pan-Dorosomatidae.

Unambiguous synapomorphies. — Ridge between the orbital wall and the levator arcus palatini fossa on the frontal and sphenotic present and fully developed (14:1>0); vertical process of the basisphenoid present (41:1>0); two or more basihyal cartilages (172:0>1); epibranchial organs large (196:0>1).

Support. — Relative Bremer = 23%.

Node 99
Family Alosidae Svetovidov, 1953
(*sensu* Wang *et al.* 2022)

Taxa included and relationships. — *Sardina* + ((†*Eoalosa* + *Sardinops*) + (*Alosa* + *Brevoortia*)).

Unambiguous synapomorphies. — Four discrete openings present in the otic region: the opening for the infraorbital sensory canal opens between sphenotic, pterotic and sometimes frontal; all other openings open on pterotic (32:7>0); posterior pterotic spine present (57:0>1); anterior border of the third infraorbital concave (79:0>1); posterior cartilage of the fourth epibranchial formed by three cartilaginous elements fused into one with posterior process well developed, but neither anterior process nor medial expansion developed (167:3>4); radial striations on the ventral part of the opercle (201:0>1); more than 30 abdominal scutes (341:3>4).

Support. — Relative Bremer = 56%.

Remarks. — The Alosinae (shads) was one of the artificial subfamilies considered as "groups of convenience" by Grande (1985), since no osteological characters were recognized to support its monophyletic status. Traditionally, alosines included seven extant genera (*Alosa*, *Brevoortia*, *Ethmalosa*, *Ethmidium*, *Gudusia*, *Hilsa* and *Tenualosa*) (Grande 1985; Whitehead 1985) united by a set of plesiomorphic characters, including their large size (up to 60 cm in SL), the possession of strong and well-developed abdominal scutes, and the presence of a median notch between the two contralateral premaxillae, plus some features of the gill arches and digestive tract (e.g., Nelson 1967a, b; Whitehead 1973, 1985). However, numerous molecular (Lavoué *et al.* 2007, 2014; Bloom & Lovejoy 2014; Wang *et al.* 2022) and morphology-based analyses (Vernygora 2020; Kevrekidis *et al.* 2024) recurrently recovered *Alosa* and *Brevoortia* close to the putative clupeines *Sardina* and *Sardinops*, in agreement with our analyses that highlight seven unambiguous synapomorphies supporting this clade. Re-examination of the clupeomorph †*Pugliaclupea nolardi* from fossiliferous Upper Cretaceous (Campanian; Schlüter *et al.* 2008) levels of Nardò (southern Italy), considered as the oldest putative alosid or pan-alosid (Taverne 2004; Near & Thacker 2024), ruled out this hypothesis since the holotype clearly shows diagnostic features of the †Ellimmichthyiformes, particularly of the †Armigatidae (G.M. pers. obs.).

Node 100
Unnamed clade

Taxa included and relationships. — (†*Eoalosa* + *Sardinops*) + (*Alosa* + *Brevoortia*).

Unambiguous synapomorphies. — Anterior region of the mesethmoid keel perforated (62:0>1); quadrate-metapterygoid fenestra present (126:0>1); ventral process of the quadrate short (128:1>0); foramen on the anterior ceratohyal produced by the overlap between lateral and medial foramina of the hyoid arterial duct present (140:0>1); foramen in the posterior ceratohyal present (146:0>1); posterior process of the fifth epibranchial well developed (168:1>2); posterior process on the second basibranchial not reaching the third basibranchial (177:1>0).

Support. — Relative Bremer = 56%.

Node 101
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — †*Eoalosa* + *Sardinops*.

UNAMBIGUOUS SYNAPOMORPHIES. — Perforations on body scales present (368:0>1).

SUPPORT. — Relative Bremer = 73%.

REMARKS. — †*Eoalosa* is an Eocene (Ypresian, *c.* 50 Mya) clupeoid fish from Bolca, Italy that has been tentatively aligned to the Alosinae due to a combination of features, in particular the presence or absence of certain homoplastic characters, including its large size, perforated scales and the possession of strong and well-developed abdominal scutes (Marramà & Carnevale 2018). Our analysis supports this previous interpretation. Although there is no trace of the large ovoid quadrate-metapterygoid fenestra that are characteristic of *Alosa*, *Brevoortia* and *Sardinops* (Ridewood 1904b; Phillips 1942; Sato 1994), the small notch visible along the dorsal margin of the quadrate in †*Eoalosa* (Marramà & Carnevale 2018: 112, fig. 2), the few feeble striations on the ventral part of the opercle and the perforations on body scales support this relationship.

Node 102
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — *Alosa* + *Brevoortia.*

UNAMBIGUOUS SYNAPOMORPHIES. — Lateral expansion of the frontal above the orbit present (13:0>1); distinct median notch or cleft between the premaxillae when seen from front present (91:0>1); striation on the lateral surface of the maxilla present (99:0>1); anterior margin of the metapterygoid located at same level of the quadrate (120:0>1).

SUPPORT. — Relative Bremer = 59%.

Node 103
Pan-Dorosomatidae

TAXA INCLUDED AND RELATIONSHIPS. — †*Bolcaichthys* + ((*Escualosa* + (†*Chasmoclupea* + *Rhinosardinia*)) + ((*Platanichthys* + *Lile*) + ((*Amblygaster* + (*Harengula* + *Herklotsichthys*)) + (*Opisthonema* + (*Sardinella* + (*Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*))))))))))).

UNAMBIGUOUS SYNAPOMORPHIES. — Eight or more fronto-parietal striae (18:0>1); coronoid process of the dentary located very close to the anterior end of the maxilla (110:1>2).

SUPPORT. — Relative Bremer = 49%.

REMARKS. — Since no osteological characters were found to support its monophyly, the Dorosomatinae (*Anodontostoma*, *Clupanodon*, *Dorosoma*, *Gonialosa*, *Konosirus* and *Nematalosa*) was another artificial subfamily referred by Grande (1985) to as "group of convenience". However, Nelson (1970) recognized that *Harengula*, *Herklotsichthys*, *Hilsa*, *Opisthonema* and *Sardinella* (traditionally representing putative Alosinae or Clupeinae) could have been closely related to the Dorosomatinae because of similarities in the structure of the fins and gill arches (e.g., the non-overlap of the gill rakers). However, neither Whitehead (1985a, b) nor Grande (1985) followed this taxonomic arrangement. Our study, similarly to morphology-based (Vernygora 2020; Kevrekidis *et al.* 2024) and molecular analyses (Lavoué *et al.* 2007, 2014; Bloom & Lovejoy 2014; Wang *et al.* 2022) supports the hypothesis proposed by Nelson (1970); however, molecular studies found the Pellonulini *sensu* Grande (1985) (*Pellonula*, *Odaxothrissa*, *Nannothrissa*, *Microthrissa*, *Potamothrissa*, *Stolothrissa*, *Limnothrissa*) sister to or nested within the Dorosomatidae (e.g., Wilson *et al.* 2008; Lavoué *et al.* 2013; Wang *et al.* 2022). †*Bolcaichthys catopygopterus*, the commonest clupeoid fish from the Eocene of Bolca, Italy, was tentatively aligned to the Clupeinae based on the presence or absence of some plesiomorphic characters (Marramà & Carnevale 2015b), it is recovered herein as sister to the extant dorosomatids. However, since it is impossible to observe in †*Bolcaichthys* most of the diagnostic characters that have been used to diagnose the living dorosomatids (e.g., gill arches toothless in adults, non-overlap of the gill rakers, large epibranchial organs, etc; Nelson 1970; Nelson & Rothman 1973), we prefer to consider this fossil as a pan-dorosomatid. The Oligocene clupeoid †*Chasmoclupea aegyptica* Murray, Simons & Attia, 2005, tentatively assigned to the alosines or clupeines by Murray *et al.* (2005), results instead nested within the crown Dorosomatidae, corroborating the hypothesis proposed by Vernygora (2020).

Node 104
Family Dorosomatidae Bleeker, 1872,
new usage

TAXA INCLUDED AND RELATIONSHIPS. — (*Escualosa* + (†*Chasmoclupea* + *Rhinosardinia*)) + ((*Platanichthys* + *Lile*) + ((*Amblygaster* + (*Harengula* + *Herklotsichthys*)) + (*Opisthonema* + (*Sardinella* + (*Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*)))))))))).

UNAMBIGUOUS SYNAPOMORPHIES. — Distal region of the supraneurals greatly expanded (211:0>1); membranous anterodorsal outgrowth of uroneural 1 absent (299:2>0).

SUPPORT. — Relative Bremer = 70%.

Node 105
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — *Escualosa* + (†*Chasmoclupea* + *Rhinosardinia*).

UNAMBIGUOUS SYNAPOMORPHIES. — Two branchiostegal rays on the anterior ceratohyal (excluding those rays on the distinct posteroventral process) (154:2>1); cartilage process of the anterior margin of the fourth ceratobranchial directed medially, forming a bridge over the ventral surface of the fourth basibranchial absent (161:1>0); 30-40 preural vertebrae (218:2>3); two epurals (304:0>1).

SUPPORT. — Relative Bremer = 49%.

Node 106
Unnamed clade

TAXA INCLUDED AND RELATIONSHIPS. — †*Chasmoclupea* + *Rhinosardinia*.

UNAMBIGUOUS SYNAPOMORPHIES. — Pelvic fins inserted anterior to the dorsal-fin origin (280:1>0).

SUPPORT. — Relative Bremer = 19%.

Node 107
Unnamed clade

Taxa included and relationships. — (*Platanichthys* + *Lile*) + ((*Amblygaster* + (*Harengula* + *Herklotsichthys*)) + (*Opisthonema* + (*Sardinella* + (*Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*)))))))))).

Unambiguous synapomorphies. — Dentary teeth present (104:0>1); ectopterygoid teeth present (132:0>1).

Support. — Relative Bremer = 36%.

Node 108
Unnamed clade

Taxa included and relationships. — *Platanichthys* + *Lile*.

Unambiguous synapomorphies. — Premaxillary teeth present (93:0>1); palatine teeth present (114:0>1); proximal region of the abdominal epipleurals bifurcated (224:0>1).

Support. — Relative Bremer = 38%.

Node 109
Unnamed clade

Taxa included and relationships. — (*Amblygaster* + (*Harengula* + *Herklotsichthys*)) + (*Opisthonema* + (*Sardinella* + (*Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*))))))))).

Unambiguous synapomorphies. — Ventral process of the quadrate short (128:1>0); posterior cartilage of the fourth epibranchial formed by three cartilaginous elements fused into one; anterior and posterior processes well developed, but medial expansion not developed (167:3>5); posterior process of the fifth epibranchial well developed (168:1>2); medial process of the cleithrum large, reaching or almost reaching the anterior margin of the dorsal arm of the cleithrum (259:0>1).

Support. — Relative Bremer = 49%.

Node 110
Unnamed clade

Taxa included and relationships. — *Amblygaster* + (*Harengula* + *Herklotsichthys*).

Unambiguous synapomorphies. — Ethmopalatine cartilage present (46:0>1).

Support. — Relative Bremer = 70%.

Node 111
Unnamed clade

Taxa included and relationships. — *Harengula* + *Herklotsichthys*.

Unambiguous synapomorphies. — Up to seven fronto-parietal striae (18:1>0); premaxillary teeth present (93:0>1); at least one predorsal scute present (318:0>1).

Support. — Relative Bremer = 35%.

Node 112
Unnamed clade

Taxa included and relationships. — *Opisthonema* + (*Sardinella* + (*Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*))))))).

Unambiguous synapomorphies. — Posterior pterotic spine present (57:0>1); endopterygoid teeth absent (115:1>0); teeth or tooth plates on ceratobranchials 2 and 3 absent (159:1>0); surface of the fourth epibranchial perforated by several holes (164:0>1); second mediopharyngobranchial cartilage present (193:0>1).

Support. — Relative Bremer = 49%.

Remarks. — This clade highlights a step-by-step achievement of traits (reduction and loss of teeth on jaws, basibranchials, ceratobranchials, increase in the number of ceratobranchial gill rakers, also supported by mediopharyngobranchial cartilages) for enhancing cross-flow filtering, which are highly related to planktivorous feeding behaviour (e.g., Whitehead 1985).

Node 113
Unnamed clade

Taxa included and relationships. — *Sardinella* + (*Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*)))))).

Unambiguous synapomorphies. — Over 165 lower gill rakers (198:0>1); dorsal myorhabdoi present (232:0>1).

Support. — Relative Bremer = 30%.

Node 114
Unnamed clade

Taxa included and relationships. — *Hilsa* + (*Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*))))).

Unambiguous synapomorphies. — Maxillary teeth absent (103:1>0); dentary teeth absent (104:1>0); coronoid process located from midlength to the anterior third of the lower jaw (110:2>1); foramen in the posterior ceratohyal present (146:0>1); anterior facet of the fourth epibranchial not projected anteriorly (165:0>1); teeth or tooth plate on basibranchial 2 absent (174:1>0); fifth upper pharyngeal connected to the fourth epibranchial (197:0>1).

Support. — Relative Bremer = 49%.

Node 115
Unnamed clade

Taxa included and relationships. — *Tenualosa* + (*Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*)))).

Unambiguous synapomorphies. — Lateral expansion of the frontal bone above the orbit present (13:0>1); prominent keel on the parasphenoid (36:0>1); dorsal process of mesethmoid at the same level of the anterior tip of vomer (61:0>1); anterior region of the mesethmoid keel perforated (62:0>1); ventral margin of the dentary concave at symphysis (108:0>1); teeth or tooth plates on ceratobranchial 1 absent (157:1>2); teeth or tooth plates overlying the fifth ceratobranchial absent (184:1>0); teeth or tooth plates over infrapharyngobranchial 5 absent (190:1>0); third mediopharyngobranchial cartilage present (194:0>1); at least one predorsal scute present (318:0>1).

Support. — Relative Bremer = 63%.

Node 116
Unnamed clade

Taxa included and relationships. — *Dorosoma* + (*Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*))).

Unambiguous synapomorphies. — Premaxilla long, 50% or more of the maxillary length (92:0>1); posterior blade of the maxilla approximately of the same size or slender than the central shaft (97:0>1); lateral wings of the urohyal well-developed, with triangular profile in dorsal or ventral view (152:0>1); basihyal cartilage single, undivided (172:1>0); Baudelot's ligament ossified (236:0>1); surface of the coracoid perforated by holes (272:0>1); filamentous last dorsal-fin ray present (352:0>1); true cycloid body scales (361:1>0); posterior margin of the body scales smooth (362:1>0).

Support. — Relative Bremer = 69%.

Node 117
Unnamed clade

Taxa included and relationships. — *Konosirus* + (*Clupanodon* + (*Anodontostoma* + *Nematalosa*)).

Unambiguous synapomorphies. — Mouth inferior or subterminal (2:0>1); anterior supramaxilla absent (83:1>0); dorsal profile of the maxilla convex, ventral profile concave (98:0>2).

Support. — Relative Bremer = 22%.

Node 118
Unnamed clade

Taxa included and relationships. — *Clupanodon* + (*Anodontostoma* + *Nematalosa*).

Unambiguous synapomorphies. — Two branchiostegal rays on the distinct posteroventral process of the anterior ceratohyal (155:1>2); one branchiostegal ray on the posterior ceratohyal (156:1>0).

Support. — Relative Bremer = 13%.

Node 119
Unnamed clade

Taxa included and relationships. — *Anodontostoma* + *Nematalosa*.

Unambiguous synapomorphies. — Central shaft of the maxilla short, almost equal or shorter than the length of the articular head (96:0>1); coronoid process located very close to the anterior end of the dentary (110:1>2); body scales of crenate type (361:0>1); posterior body scale margin (362:0>1).

Support. — Relative Bremer = 35%.

Ancestral habitat reconstruction of the Clupeomorpha

The character evolution reconstructions of the habitat preferences indicate that the most recent common ancestor of the Clupeomorpha was very likely marine (proportional likelihood, PL: 92.6%) (Fig. 45). The initial clupeomorph diversification occurred in marine environments, since also the MRCAs of the two main clupeomorph lineages were likely marine (†Ellimmichthyiformes PL: 91.9%; pan-Clupeiformes PL: 87.6%; Clupeiformes; PL: 40.6%), although we cannot fully exclude that the MRCA of the Clupeiformes was already euryhaline (PL: 39.6%). We inferred a minimum of nine transitions from marine to euryhaline or freshwater environments within five of the 28 main clupeomorph lineages recognized in this study.

Seven of these transitions occurred within five different lineages of the †Ellimmichthyiformes: a transition from marine to euryhaline habitats possibly occurred in the Late Jurassic (giving rise to the lineage including †*Codoichthys*), whereas the other six occurred at the Jurassic-Cretaceous boundary or in the Early Cretaceous: a transition from marine to euryhaline habitats within the †Scutatuspinosidae, another one giving rise to the likely freshwater (PL: 82.1%) MRCA ancestor of the †Gasteroclupeidae and three other occurred early in the evolution of the †Paraclupeidae (one giving rise to the lineage including †*Ezkutuberezi*, one giving rise to the euryhaline MRCA of the clade including "*Ellimmichthys*" *spinosus* and "*Ellimma*" *longipectoralis*, one involving the *Scutatoclupea* lineage), and one giving rise to the likely freshwater MRCA of the Paraclupeinae.

Conversely, if the MRCA of the Clupeiformes was marine (PL: 40.6%), two main transitions toward non-marine habitats occurred early in the evolution of the Clupeiformes (Fig. 46). One of these gave rise to the euryhaline common ancestor of the Denticipitoidei (PL: 49.6%) with some of its descendants that later gave rise to the very likely freshwater (PL: 91.5%) MRCA of the Denticipitidae, in agreement with the marine-to-freshwater transition process inferred by Lavoué (2020). The other one, produced the Early Cretaceous euryhaline MRCA of the pan-Clupeoidei (PL: 50.8%).

A single, secondary transition from non-marine to marine habitats occurred in the late Lower Cretaceous, leading to the rise of the MRCA of the Clupeoidei that, in agreement with the results of Lavoué *et al.* (2013), was very likely marine (PL: 88.2%). We then inferred a minimum of four transitions from marine to non-marine environments within three of our 14 main clupeoid lineages. Three of these transitions occurred after the K-Pg boundary: the first one gave rise to the lineage including the euryhaline *Dussumieria*, whereas the other two gave rise independently to the likely freshwater (PL: 46.0%) and euryhaline (PL: 89.4%) MRCAs of the Coiliinae and Engraulinae, respectively. Only one of these four transitions predated or occurred around the end-Cretaceous extinction giving rise to the likely euryhaline (PL: 67.1%) MRCA of the clade that includes the superfamilies Pristigasteroidea and Clupeoidea. Within the Pristigasteridae, a further transition toward freshwater environments was achieved by the *Pristigaster* lineage,

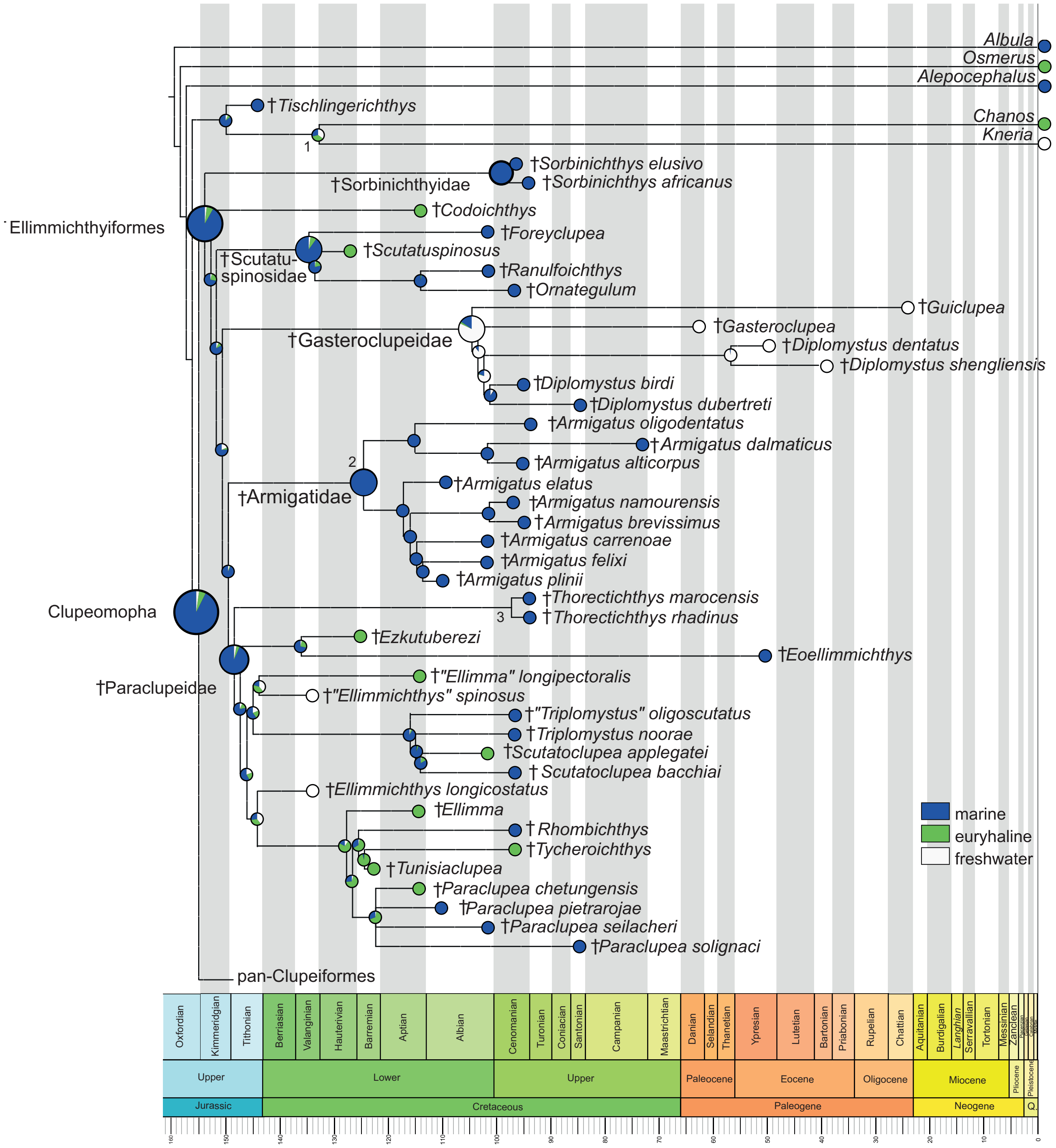

FIG. 45. — Ancestral state reconstruction of the salinity preference evolution within the †Ellimmichthyiformes (node 2) using the maximum clade credibility tree through the "Mk1" evolutionary model of the Likelihood approach. Pie charts at nodes show the proportional likelihood. Black bars representing the known stratigraphic range of the taxa are omitted.

whereas *Pliosteostoma* became secondarily marine. Within the Hyperlophidae, a further transition toward freshwater lacustrine habitats of the Green River Formation likely occurred around the K-Pg transition or at the beginning of the Paleogene, whereas within the Clupeidae the *Clupea* lineage became secondarily marine. Two further transitions from euryhaline toward freshwater habitats occurred in the Neogene within the Ehiravidae, one of these following the entrance in the Afrotropical freshwaters of a clade within the Pellonulinae. A single transition towards marine habitat might have occurred within the Alosidae and three independent transitions within the Dorosomatidae, whereas three lineages (†*Chasmoclupea*, *Tenualosa* and *Nematalosa*) occupied freshwater habitats within the Dorosomatidae.

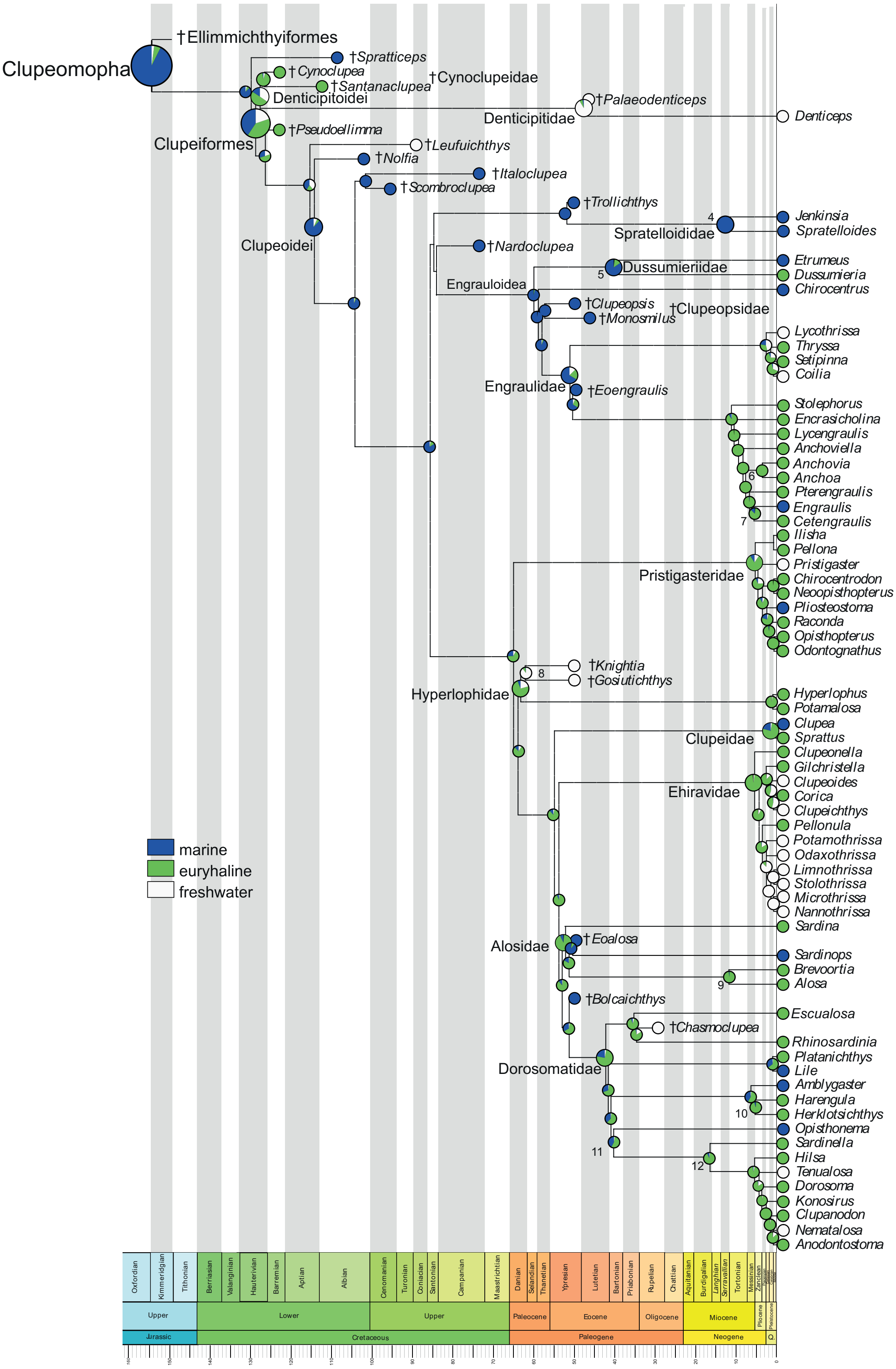

FIG. 46. – Ancestral state reconstruction of the salinity preference evolution within the pan-Clupeiformes (node 40) using the maximum clade credibility tree through the "Mk1" evolutionary model of the Likelihood approach. Pie charts at nodes show the proportional likelihood. Black bars representing the known stratigraphic range of the taxa are omitted.

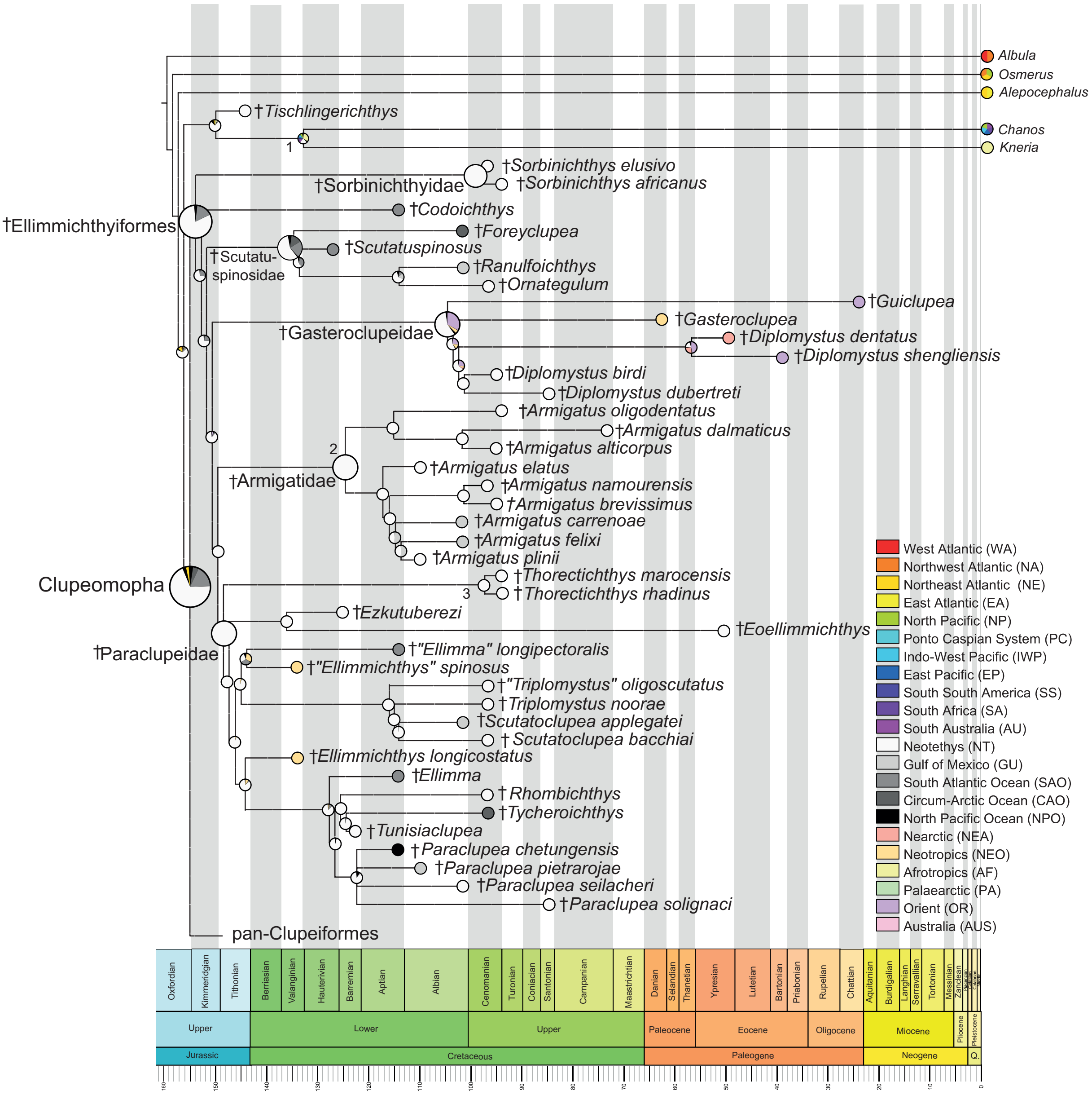

Fig. 47. — Ancestral area reconstruction of the †Ellimmichthyiformes (node 2) using the maximum clade credibility tree through the "Mk1" evolutionary model of the Likelihood approach. Pie charts at nodes show the proportional likelihood. Black bars representing the known stratigraphic range of the taxa are omitted.

Ancestral area reconstruction of the Clupeomorpha

The ancestral area reconstruction using the "Mk1" evolutionary model of the Likelihood approach indicates that most recent common ancestor of the Clupeomorpha very likely (PL: 69.2%) lived in the Neotethys in the Late Jurassic about 155 million years ago (Mya) (Fig. 47). At the end of the period, the first event of diversification of the Clupeomorpha was likely a within-Tethyan event of speciation that gave rise to the Tethyan (PL:80.8%) MRCA of the †Ellimmichthyiformes.

The diversification of the †Ellimmichthyiformes was in large part a Neotethyan event, since five of the six main lineages (†Sorbinichthyidae, †Scutatuspinosidae, †Gasteroclupeidae, †Armigatidae and †Paraclupeidae) originated in the Neotethys (proportional likelihoods for each clade between 57.4 and *c.* 100%), whereas only a single south-westward event of dispersion from the Tethys to the northern coastal margins of South America (that were bounded by the Equatorial Segment of the South Atlantic Ocean) led to the South Atlantic MRCA of the †*Codoichthys* lineage.

Within the †Scutatuspinosidae, at least three independent dispersal events occurred, one toward the marine Circum-Arctic habitats (†*Foreyclupea*), one toward the brackish habitats of the South Atlantic Ocean (†*Scutatuspinosus*), and another toward the marine habitats of Gulf of Mexico (†*Ranulfoichthys*).

As far as the ancestral area reconstruction of the †Gasteroclupeidae is concerned, we observe inconsistencies between ancestral salinity preference (freshwater) and geographic origin (Tethyan) of its MRCA. It could be explained by one or more of the following factors: later ecological adaptations, uncertainties in geological or ecological data, or a more complex and dynamic evolutionary history that cannot be easily reduced to a single geographic or ecological origin. We cannot rule out the hypothesis that the ancestor was able to occupy a range of different environments, or that the original environment was a transitional area, such as estuaries or coastal zones, where fresh and marine water mix. The existence of an approximately 50-million-year-long ghost lineage, following the divergence of the †Gasteroclupeidae, may be closely related to this discrepancy in ancestral reconstructions. The long-time span implies a period of fossil uncertainty, which could reflect ecological, evolutionary adaptation, or geological changes not yet fully documented, but which may have led to the transition from a marine habitat (Tethys) to a freshwater preference. In any case, within the †Gasteroclupeidae successive independent dispersal events by the end of the Early Cretaceous occurred: one from the Tethys toward the Neotropical freshwaters (†*Gasteroclupea*), and two toward Oriental freshwaters, one giving rise to the †*Guiclupea* lineage, and the other one giving rise to the MRCA of the clade including †*Diplomystus dentatus* and †*D. shengliensis*.

Within the †Armigatidae, whose MRCA originated in the Neotethys (PL:*c.* 100%), a single westward dispersal event occurred during the Albian from the western Neotethys to the marine environments of the Gulf of Mexico, where the MRCA of the clade (†*Armigatus carrenoae* + (†*A. felixi* + †*A. plinii*)) originated.

Finally, within the Tethyan (PL:*c.* 100%) †Paraclupeidae, at least seven further independent dispersal events occurred, two toward the likely freshwater habitats of the Neotropics (giving rise to the †*Ellimmichthys longicostatus* lineage and to the MRCA of the pair "†*Ellimmichthys*" *spinosus* + "†*Ellimma*" *longipectoralis*), two toward the estuarine environments of Gulf of Mexico (†*Paraclupea seilacheri*, †*Scutatoclupea applegatei*), one toward the brackish environments of South Atlantic Ocean (†*Ellimma branneri*), one toward the Circum-Arctic Ocean (†*Tycheroichthys*) and one toward the North Pacific Ocean (†*Paraclupea chetungensis*). Interestingly, all these dispersal events coincide with transitions from marine to euryhaline, or from euryhaline to freshwater habitats.

According to our likelihood-based ancestral area reconstruction, the MRCA of pan-Clupeiformes most likely originated in the South Atlantic Ocean (PL: 37.7%) during the Early Cretaceous. However, while the South Atlantic Ocean has the highest individual likelihood, the combined likelihood of the Tethyan and Circum-Arctic realms (PL: 50.2%) moderately exceeds it, suggesting that a northern hemispheric marine origin cannot be ruled out and may be more probable if these regions are considered as a connected paleogeographic continuum, implying that the second main event of diversification within the Clupeomorpha likely occurred within the Tethys-Circum-Arctic.

If so, after the early separation from the MRCA of the pair †*Spratticeps* + Clupeiformes and a single westward dispersal event from the Circum Arctic or Tethyan realm, the most recent common ancestor of the Clupeiformes originated (PL: 91.0%) in the northern part of the South Atlantic Ocean around 130 Mya. Also the MRCA of the Denticipitoidei originated in this region (PL: 90.7%), with the common ancestor the †Cynoclupeidae that originated in the same biogeographic context (PL: 99.7%), whereas early representatives of its sister lineage (Denticipitidae) likely dispersed into euryhaline habitats and then freshwater habitats of the Afrotropical freshwaters during the early rift phase of the South America-Africa breakup when only a narrow seaway still separated the two continents (Maisey 2000; Luft-Souza *et al.* 2022) (PL: 97.6%).

The MRCA of the Clupeoidei very likely originated in the South Atlantic Ocean (PL: 90.0%) around 115 Mya. This disagrees with the Indo-West Pacific/Tethyan origin of the Clupeoidei as hypothesized by Lavoué *et al.* (2013) and Avaria-Llautureo *et al.* (2021). After a secondary eastward dispersal event toward the Western Tethys, the MRCA of the clade that includes all main living clupeoid lineages (Spratelloididae, Engrauloidea, Pristigasteroidea, Clupeoidea) likely originated in the Neotethys (84.7%) at the beginning of the Late Cretaceous.

Our analysis indicates the Tethyan origin of the MRCAs of the pan-Spratelloididae, Dussumieriidae, Chirocentridae and Engraulidae (PLs between 88.6 and 98.3%). Also, the MRCA of the pair Pristigasteroidea + Clupeoidea likely originated in the Neotethys (PL: 38.8%) around the K-Pg boundary and soon after, at least two or three dispersal events occurred. The first event of dispersion from the Neotethys was likely toward the western margin of the North Atlantic Ocean where the modern West Atlantic later established leading to the most recent common ancestor of the Pristigasteridae (PL WA: 23.7%). However, the hypothesis of an East Atlantic origin proposed by Lavoué *et al.* (2013) cannot be completely discarded as we did not include *Ilisha africana* in our analysis.

The MRCA of the Clupeoidea likely originated after a second event of western dispersion toward the eastern margins of the North Atlantic Ocean, which is the precursor of the modern Northeast Atlantic (PL: 25.1%).

Due to the bipolar distribution of the terminal taxa of the Hyperlophidae lineage (South Australian for *Hyperlophus* and *Potamalosa*, Nearctic for †*Knightia* and †*Gosiutichthys*), our analysis was not able to detect with certainty the direction of the second event of dispersal nor the most likely ancestral area of origin of the subfamily, because of the similar values of the proportional likelihoods for their origin in South Australia (PL: 34.32%) or in Nearctic freshwaters (PL: 34.28%).

The analysis supports a Northeast Atlantic origin (PL: 86.2%) for the MRCA of the Clupeidae lineage including *Clupea* and *Sprattus*. This biogeographic region was already well-established in the early Paleogene, when the Clupeidae likely diverged from the other clupeoids.

If Ehiravinae plus Pellonulinae constitute a genuine monophyletic lineage within the family Ehiravidae, as detected in our parsimony analyses, the ancestral area reconstruction indicates a Neogene Ponto-Caspian (Paratethyan) origin for the family (PL: 39.7%). During the Miocene, profound geological and climatic changes, including regressive and transgressive events, would have facilitated the bidirectional dispersal of this ancestral lineage: on the one hand towards West and Central Africa along Atlantic coastal and river routes, leading to the colonization of the Afrotropical freshwaters (PL: 98.3%) and the subsequent radiation of the Pellonulinae (see, e.g., Wilson *et al.* 2008); on the other hand, along the coasts of the Indo-West Pacific (PL: 52.6%), the ancestor of the Ehiravinae (*Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*, *Sauvagella*, etc.) would have progressively colonized coasts and freshwaters of India, Madagascar and Southern Africa.

The MRCA of the pair Alosidae + pan-Dorosomatidae might have originated in the North Atlantic (PL: 58.0%) around the Paleocene-Eocene boundary or in the early Eocene. Whereas the MRCA of the Alosidae originated in this paleogeographic context (PL: 74.1%), the most recent common ancestor of the Dorosomatidae likely originated in the Indo-West Pacific (PL: 53.7%), a hypothesis that agrees with that of the Tethyan origin for the total group (the pan-Dorosomatidae; PL: 40.5%).

DISCUSSION

Updated classification of the Clupeomorpha

In addition to the newly proposed hypothesis regarding clupeomorph relationships, we propose an updated classification for the superorder Clupeomorpha (Table 1). Many of the clades identified over the past few decades (e.g., Grande 1985; Sato 1994; Wang *et al.* 2022) have been confirmed, although some clades are proposed herein as new usage and a few clades, recurrently recovered in past analyses, have been proposed for the first time. New lineages have been identified and some fossil taxa have been referred to different families or subfamilies. The main findings presented here are the follow:

1. Clupeomorpha was recovered monophyletic with a dichotomous nature due to the early divergence of two distinct lineages, both monophyletic, representing the orders †Ellimmichthyiformes and Clupeiformes. Morphological support for the Clupeomorpha is consistent with the diagnostic features proposed since Greenwood *et al.* (1966), including the otophysic connection between the swim bladder and inner ear involving a diverticulum of the swim bladder penetrating the exoccipital, presence of prootic bullae, parhypural fused to PU1 and one or more abdominal scutes, whereas fusion between the second hypural and the first ural centrum cannot be definitely assessed.

2. The monophyly of the †Ellimmichthyiformes is confirmed. They include fossil non-clupeiform clupeomorphs characterized by the lack of the recessus lateralis, presence of dorsal scutes, basipterygoid process of the parasphenoid, and anteriormost ribs articulating with lateral pits on the centra followed by ribs articulating with parapophyses. The tree topology includes †Sorbinichthyidae, †*Codoichthys*, †Scutatuspinosidae and †Gasteroclupeidae as successive sister groups of the pair †Armigatidae plus †Paraclupeidae. Within the †Paraclupeidae, a new subfamily, †Eoellimmichthyinae n. subfam., is introduced to accommodate the Eocene †*Eoellimmichthys* and the Early Cretaceous †*Ezkutuberezi*, representing one of the most basal lineage of the family †Paraclupeidae.

3. The middle Albian †*Spratticeps* is closer to the Clupeiformes than to the †Ellimmichthyiformes, corroborating the hypothesis of Forey (2004). Although †*Spratticeps* exhibits some traits of the †ellimmichthyiforms (absence of recessus lateralis, pterotic diverticulum and bulla, auditory fenestra, skull roof heavily ornamented, without supratemporal fossa or posterior frontal fontanelles), our analysis recovered it to as sister taxon to the Clupeiformes, since it exhibits a temporal foramen (although unexposed), basisphenoid, lateroparietal condition, supratemporal commissure passing through the parietals and supraoccipital, and occipital condyle formed by the basioccipital only (Patterson 1970), suggesting that the Clupeiformes possibly achieved their key traits (recessus lateralis, pterotic diverticulum and bulla, auditory fenestra, supratemporal fossa, an exposed temporal foramen, fusion of median and lateral extrascapulars with the supraoccipital and parietal) early after their divergence from the †Ellimmichthyiformes.

4. The unexpected closer relationships of †*Santanaclupea* and †*Cynoclupea* with members of the family Denticipitidae bring us to propose a new usage and an emended diagnosis for the suborder Denticipitoidei that can be defined as a clupeiform clade whose representatives retain primitive features, including a large first ural centrum, first hypural articulated to the first ural centrum through massive proximal head forming a well-developed articulatory process, parhypural fused with the first preural centrum, first uroneural autogenous, and complete lateral line.

5. †*Pseudoellimma* and †*Leufuichthys*, originally considered as Clupeiformes and Clupeomorpha *incertae sedis*, respectively (Figueiredo 2009a; Gallo *et al.* 2011) are recovered herein as stem-Clupeoidei. The analysis of the phylogenetic relationships suggests that the body plan of the Clupeoidei is the result of the gradual accumulation of traits that started at least 115 million years ago, after the divergence between the Denticipitoidei and Clupeoidei.

6. †*Nolfia* and †*Italoclupea*, previously hypothesized as belonging to the Clupeidae *sensu* Grande, 1985 (Taverne 2007; Figueiredo 2009b) and †*Scombroclupea*, formerly referred to the Clupeoidea *sensu* Grande, 1985 (Giersch *et al.* 2011) are all recovered as crown-Clupeoidei but not closely related to any of the extant families or superfamilies.

7. The interrelationships recovered within the suborder Clupeoidei and the newly proposed classification are generally consistent with the results of the recent molecular analyses. The Clupeoidei includes three main monophyletic lineages (pan-Engrauloidea + (Pristigasteroidea + Clupeoidea)).

8. The Spratelloididae (*Jenkinsia* and *Spratelloides*), which are recognized as the basalmost clupeoid lineage in several recent molecular analyses, might be considered as the basal clade in the line that led to the advanced engrauloids. In fact, the analysis with no fossil taxa (Fig. 41), recovered the Spratelloididae as the basalmost clupeoid lineage but with high support (relative Bremer 99%). This suggests that the molecular results might be biased by the lack of fossil data, since in the main analysis conducted herein the spratelloidids are grouped together with the Dussumieriidae, †*Nardoclupea*, Chirocentridae, Clupeopsidae n. fam. and Engraulidae.

9. The close relationship between Chirocentridae (*Chirocentrus*), †Clupeopsidae n. fam. (†*Clupeopsis* and †*Monosmilus*), and Engraulidae confirms the hypothesis of Capobianco *et al.* (2020) that the fang-like dentition, indicative of piscivorous diets, may represent the ancestral condition for the Engraulidae. Within this lineage, a new clupeoid epifamily, Engrauloidae n. epifam., is introduced to accommodate a new family, †Clupeopsidae n. fam. (including the stem-engraulids †*Clupeopsis* and †*Monosmilus*), and all the extant and fossil Engraulidae.

10. Consistent with previous morphological and molecular studies (Grande, 1985; Grande & Nelson, 1985; Lavoué *et al.* 2010, 2013; Bloom *et al.* 2018), our phylogenetic analysis recovered the Engraulidae as a well-supported (relative Bremer 69%) monophyletic group including two subfamilies, Engraulinae and Coiliinae, with †*Eoengraulis* confirmed to be a stem-Engraulinae (see Marramà & Carnevale 2016).

11. The monotypic Pristigasteroidea (longfin herrings) is a monophyletic group well-supported by several characters that includes a single family, Pristigasteridae, since the traditional families recognized by Grande (1985) (Pristigasteridae and Pellonidae) are resolved as nonmonophyletic.

12. The rest of clupeoid taxa, i.e., the Grande's (1985) Pellonulinae, Clupeinae, Alosinae and Dorosomatinae, can be included into the third superfamily, Clupeoidea new usage. The family Clupeidae *sensu* Grande (1985) is therefore confirmed not to be a natural group.

13. Within the Clupeoidea new usage, the Clupeidae *sensu* Wang *et al.* 2022 (*Clupea*, *Hyperlophus*, *Potamalosa*, *Sprattus*) is recovered as non-monophyletic in the main analyses but monophyletic in the analysis that excludes fossil taxa (Fig. 41), suggesting that molecular analyses might be biased by the lack of fossil data. The close evolutionary relationship between †*Gosiutichthys*, †*Knightia*, *Hyperlophus*, and *Potamalosa* (the family Hyperlophidae, new rank) is supported by the presence of a complete series of predorsal scutes

14. The pellonulines (*Limnothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa*, *Stolothrissa*), which are recovered as nested within the Dorosomatidae in molecular analyses (e.g., Lavoué *et al.* 2014; Wang *et al.* 2022), are recognized herein to form a monophyletic group with some of the Ehiravidae *sensu* Wang *et al.* 2022 (*Clupeichthys*, *Clupeoides*, *Corica*, *Gilchristella*). In this perspective, the recovery of the anadromous Ponto-Caspian *Clupeonella* as the most basal ehiravid (as also hypothesized by molecular results) suggests that the hypothesis that the whole clade derived from a Paratethyan ancestor cannot be excluded. If this is true (relative Bremer 65%), the transition from marine/euryhaline to freshwater habitats of the clupeoid fishes of the Tanganyika Lake, South and West Africa occurred only once. Future analyses that will include other ehiravid taxa (e.g., *Ehirava*, *Dayella*, *Sauvagella*, *Sierrathrissa*, etc.) and *Ethmalosa fimbriata* (Bowdich, 1825), an estuarine dorosomatid species widespread along the coasts of West Africa considered the sister taxon of the Pellonulinae in molecular analyses (e.g., Wilson *et al.* 2008; Lavoué *et al.* 2013) might help to clarify the discrepancy between molecular analyses that place the Pellonulinae within the Dorosomatidae, and our morphological analysis, which places it as a sister taxon to Ehiravinae. The putative pellonulines (*sensu* Grande 1985) *Hyperlophus* and *Potamalosa* are confirmed not to be part of this group.

15. The family Alosidae (*Alosa*, *Brevoortia*, *Sardina* and *Sardinops*) is confirmed as a monophyletic group, as suggested by molecules, with the marine Ypresian Tethyan genus †*Eoalosa* confirmed as part of the family, whereas the Dorosomatidae includes all the other tropical and subtropical clupeoids, plus the Eocene genus †*Bolcaichthys* representing the early diverging offshoot of the group.

Ancestral character state reconstruction and the evolution of key features of Clupeomorpha

Our study provides, for the first time, an exhaustive comparative analysis combined with explicit hypotheses of homology for the skeletal and soft tissue features of the Clupeomorpha. Our study confirms that the Clupeomorpha are characterized by extensive degree of morphological homoplasy. In this paragraph, we focus on those key morphological characters that were traditionally regarded as synapomorphies supporting the major clades within the Clupeomorpha, to corroborate their status of synapomorphies or to recognize their homoplastic nature.

Synapomorphies of the superorder Clupeomorpha:
Presence of abdominal keeled scutes (Grande 1985, ch. 1). Our analysis confirms that the MRCA of the Clupeomorpha had a complete series of abdominal scutes from the posterior tip of the coracoid to the anal-fin origin as seen in denticipitoids and †Sorbinichthyidae, but it is not clear if scutes were also present along the ventral edge of coracoid as well. We can therefore reject the hypothesis that the presence of only a few or even a single scute was the original condition in the MRCA or, eventually, that taxa with no scutes (e.g., †*Ornategulum*) represent the basal condition of clupeomorphs. That means that abdominal scutes have been only later secondarily reduced (like in *Chirocentrus*, round herrings, some ehiravids, and New World anchovies) or completely lost (like in †*Nardoclupea* and †*Ornategulum*).

The otophysic connection involving a diverticulum of the swim bladder penetrating the exoccipital and extending into the prootic within the lateral wall of the braincase (Grande 1985, ch. 2). This character is definitely confirmed as a synapomorphy (autapomorphy) of the Clupeomorpha.

Supratemporal commissural sensory canal primitively passing through the parietals, or through the parietals and supraoccipital (Grande 1985, ch. 3). Our analysis corroborates that the MRCA of clupeomorphs had a supratemporal commissural sensory canal primitively passing through the parietals, although this must be considered a synapomorphy of the Otocephala (Ostariophysi + Clupeomorpha) rather than an autapomorphy of the Clupeomorpha. A supratemporal commissural sensory canal passing also through the supraoccipital, instead, can be considered a synapomorphy of the pan-Clupeiformes (†*Spratticeps* + Clupeiformes).

Hypural 2 fused to the first ural centrum (Grande 1985, ch. 4). Pending further studies and new fossil findings, this feature can no longer be considered with absolutely certainty as synapomorphy of the Clupeomorpha, since the †Sorbinichthyidae (the basalmost †ellimmichthyiform in our analysis) have an autogenous hypural (Bannikov & Bacchia 2000) and the condition of the stem-Clupeiformes †*Spratticeps* is unknown. If the MRCA of clupeomorphs had a hypural 2 fused to the first ural centrum, that means that this bone secondarily separated from the centrum in †*Sorbinichthys*, whereas if it was autogenous in the MRCA, then it fused with the first ural centrum independently in Clupeiformes and in the other †Ellimmichthyiformes.

Presence of a well-defined pre-epioccipital fossa (Grande 1985, ch. 5). After Forey (2004) clarified the distinction between the "pre-epioccipital fossa" (=pre-epioccipital fenestra) of the †Ellimmichthyiformes and the true pre-epioccipital fossa of the Clupeiformes, this trait cannot be considered as valid synapomorphy of the Clupeomorpha. Although a large, well developed pre-epioccipital fossa has been detected in †*Cynoclupea*, †*Santanaclupea* and most of the extant and fossil Clupeoidei, it is small or even absent in †*Spratticeps*, *Denticeps*, †*Pseudoellimma*, Engrauloidea and †Ellimmichthyiformes (Patterson 1970; Grande 1985; Sato 1994). According to our tree topology, a well-defined pre-epioccipital fossa might have been independently achieved by the †Cynoclupeidae and Clupeoidei (with secondary loss or reduction in the Engraulidae), whereas the MRCA of the Clupeomorpha likely had small or inconspicuous pre-epioccipital fossa.

Presence of keeled dorsal scutes (Grande 1985, ch. 6). Although most †ellimmichthyiforms possess predorsal scutes, only a few clupeiforms possess them. Moreover, their presence in key basal taxa (†*Spratticeps*, †*Santanaclupea*) is unknown, making this trait a synapomorphy of the †Ellimmichthyiformes rather than of the whole superorder, as originally hypothesized by Chang & Maisey (2003). Analysis of our character mapping cannot lead us to rule out the hypothesis that the predorsal scutes of some clupeiforms (†*Cynoclupea*, †*Pseudoellimma*, Coiliinae, Hyperlophidae and a few other clupeoids) are not homologous to the predorsal scutes of the †Ellimmichthyiformes.

Synapomorphies of the order †Ellimmichthyiformes:
Lateral expansion of dorsal scute wings, which give scute a subrectangular shape (Grande 1985, ch. 7). This must be considered as synapomorphy of the †ellimmichthyiform pair †*Gasteroclupea* + †*Diplomystus*, rather than of the whole order.

Presence of beryciform foramen (Chang & Maisey 2003, ch. 12). The presence of a large perforation on the anterior ceratohyal, the so-called beryciform foramen, cannot be considered an unambiguous synapomorphy of the †Ellimmichthyiformes nor of the Clupeomorpha because, despite it is present, other than in †ellimmichthyiforms, also in some basal clupeiforms (†*Italoclupea*, †*Santanaclupea*, †*Scombroclupea*) its presence is impossible to determine in †*Spratticeps* and most of the basal clupeiforms. If the MRCA of Clupeomorpha had a large perforation on anterior ceratohyal, it has been secondarily reduced (as in *Clupea*, *Hyperlophus*, *Sprattus* and Alosidae) or disappeared in the advanced clupeoids.

Other putative †ellimmichthyiform synapomorphies proposed in the past, including dorsal margin of body with a marked angle at the insertion of the dorsal fin, prominent spine on postpelvic scutes, S-shaped cleithrum, medioparietal conditions, frontals and parietals ornamented, and three epurals (e.g., Forey 2004; Zaragüeta Bagils 2004; Alvarado-Ortega *et al.* 2008; Murray & Wilson 2013) can no longer be considered synapomorphies of the †Ellimmichthyiformes, but rather of some of the †ellimmichthyiform families.

Synapomorphies of the order Clupeiformes:
Presence of recessus lateralis (Grande 1985, ch. 9). It is confirmed to be an unambiguous synapomorphy and autapomorphy of this clade.

Parietals completely separated (*medially*) *by the supraoccipital* (Grande 1985, ch. 10). Our character mapping shows that this trait was already present in the MRCA of the Clupeomorpha and likely in the MRCA of the Otomorpha *sensu* Arratia (2018), and inherited by †*Spratticeps* and Clupeiformes. Conversely, since the †Sorbinichthyidae still have the lateroparietal condition, the medioparietal condition was clearly achieved only later in the evolution of the †Ellimmichthyiformes and must be therefore considered a derived condition for the Clupeomorpha.

Loss of the beryciform foramen (Grande 1985, ch. 11). Being a large foramen on the anterior ceratohyal retained in basal clupeiforms (†*Italoclupea*, †*Santanaclupea*, †*Scombroclupea*) and, although reduced, in some clupeoids (*Clupea*, *Hyperlophus*, *Sprattus* and alosids), its loss can no longer be considered a synapomorphy of the Clupeiformes (see above).

Synapomorphies of the suborder Clupeoidei:
Fusion of the first uroneural with the first preural centrum (Grande 1985, ch. 14). Our analysis corroborates the hypothesis that this fusion should be considered as an unambiguous synapomorphy of the Clupeoidei, independently achieved by the Ostariophysi (see Arratia 1999)

Reduction in relative size of the first ural centrum (Grande 1985, ch. 15). Although our character mapping shows that this trait was clearly present in the MRCA of Clupeoidei, the difficulty of determining the size of the first ural centrum in the stem-clupeoid †*Leufuichthys*, makes it impossible to detect if a reduced centrum was already present also in the MRCA of the clade formed by †*Leufuichthys* + Clupeoidei. An independent reduction also occurred in the †ellimmichthyiform †*Ornategulum*.

Loss of lateral line scales (Grande 1985, ch. 16). The difficulty in detecting this trait in the basal clupeoid †*Nolfia*, makes it problematic to determine whether a complete lateral line was already present in the MRCA of the Clupeoidei or not. In any case, being a complete lateral line present in *Denticeps*, and recovered in some †ellimmichthyiforms, †*Santanaclupea* and †*Palaeodenticeps*, our analysis suggests that it was therefore present in the MRCA of the Clupeomorpha, corroborating the hypothesis that it is a retention of the plesiomorphic condition shared with other teleost lineages.

Separation of the parhypural from the first ural centrum (Grande 1985, ch. 17). Our character mapping shows that the MRCA of the Clupeomorpha had a parhypural fused to the first preural centrum and that their separation occurred already in the stem-clupeoid †*Leufuichthys*. The clupeoids therefore retained this plesiomorphic condition, demonstrating that the modern clupeoid body plan was the result of gradual achievement of its traits. Secondary fusion of parhypural and first ural centrum occurred later and independently in †*Scombroclupea*, Dussumieriidae and in different lineages of dorosomatids (e.g., *Amblygaster*, *Anodontostoma* and *Opisthonema*).

Synapomorphies of the superfamily Engrauloidea:
Suspensorium inclined obliquely backward (Grande 1985, ch. 18; Di Dario (2009)). This trait must be considered a synapomorphy of the epifamily Engrauloidae n. epifam. and not of the Engraulidae only, as it also characterizes the stem engraulids †*Clupeopsis* and †*Monosmilus*. Our analysis demonstrates that this condition has been independently achieved by the Cynoclupeidae †*Cynoclupea* and †*Santanaclupea*, thereby rejecting the hypothesis that these taxa are closely related to the Engrauloidae n. epifam. (Malabarba & Di Dario 2017).

Mesethmoid projecting in advance of the vomer (Grande 1985, ch. 18). This feature must be considered as a synapomorphy of the epifamily Engrauloidae n. epifam., as it also characterizes at least the stem engraulid †*Clupeopsis* (the condition in †*Monosmilus* is unknown).

Our analysis confirms most of the seven traits recovered by Di Dario (2009) as synapomorphies of the clade formed by Chirocentridae + (†Clupeopsidae n. fam. + Engraulidae) (his Engrauloidea), although the presence of autogenous teeth or tooth plates on ceratobranchial 1 to 3 and the presence of a developed posterior process of the infraorbital 1 extending along the ventral margin of infraorbital 2 were not recovered as synapomorphies, being unknown their state in the †Clupeopsidae n. fam.

Synapomorphies of the superfamily Pristigasteroidea:
Vertically or anterodorsally inclined supraneurals (Grande 1985, ch. 20). Our analysis confirms this trait as an autapomorphy of the Pristigasteroidea.

Absence of the interlobar notch (*diastema*) *in the third hypural* (Grande 1985, ch. 21). Our analysis confirms this trait as synapomorphy of the Pristigasteroidea. Our analysis suggests that a hypural diastema (or notch) characterized the MRCA of the Clupeomorpha, with independent loss in advanced †Ellimmichthyiformes, Pristigasteroidea, †*Leufuichthys*, †*Nolfia*, Coiliinae and Encrasicholina.

Synapomorphies of the superfamily Clupeoidea:
High pleural rib to preural vertebrae ratio (≥*0.47*) (Grande 1985, ch. 22). Thought to reflect a general trend of increasing relative abdominal cavity size in the group, our analysis does not support an increase of this ratio in the evolution of the clupeomorphs. Conversely, our analysis suggests that the MRCA of the Clupeomorpha already had a relatively large abdominal cavity size (pleural rib to preural vertebrae ratio (≥0.47), inherited from the Ostariophysi. Several lineages of clupeomorphs seemed to have independently achieved reduction in size of the abdominal cavity (due to decrease of pleural ribs/vertebrae ratio), including the Denticipitoidei, Engraulidae (with secondary increase in filter-feeding taxa, like *Engraulis* and *Anchoviella*), Pristigasteroidea and several †ellimmichthyiform lineages (some †armigatid and †paraclupeid taxa, and all the †Gasteroclupeidae).

Synapomorphies of the family Clupeidae sensu Grande (1985):
Presence of two long, rodlike postcleithra (Grande 1985). Thought to be a synapomorphy of the subfamilies Alosinae, Clupeinae, Dorosomatinae, Dussumieriinae and Pellonulinae *sensu* Grande 1985, our analysis shows that rod-like second and third postcleithra must be considered present in the MRCA of the Clupeoidei, being this feature present also in †*Nolfia*, †*Italoclupea* and likely †*Scombroclupea* (e.g., Figueiredo 2009b; Than-Marchese *et al.* 2020). The absence of rodlike postcleithra in the "more advanced" Chirocentridae, Engraulidae, Spratelloididae (but present in †*Trollichthys*) is actually due to the artifact that these taxa lack both the second and third postcleithra (Grande 1985; Sato 1994; Di Dario 2004b). Conversely, the MRCA of the Clupeomorpha had at least a second scale-like postcleithrum.

CONFLICTS AND AGREEMENTS WITH PREVIOUS PHYLOGENETIC HYPOTHESES

The main objective of our study was to generate a robust, morphology-based phylogeny of the Clupeomorpha that tested both its monophyly and the interrelationships between the different groups of †Ellimmichthyiformes and Clupeiformes. Accordingly, our taxon sampling encompassed many taxa and lineages that were proposed to be variously related between each other by both morphological and molecular studies (see Figs 4 and 5).

Our analysis recovers Clupeomorpha as monophyletic, supported by 13 unambiguous synapomorphies, with †Ellimmichthyiformes sister to a clade formed by †*Spratticeps* and the Clupeiformes. This result is in line with the traditional hypothesis of Forey (2004). At the same time, our results contradict some recent hypotheses that found denticipitids (*Denticeps* and †*Palaeodenticeps*) as sister to the pair †Ellimmichthyiformes + Clupeoidei, or that proposed the †ellimmichthyiforms nested within the Clupeoidei (see Vernygora 2020; Kevrekidis *et al.* 2024). It is likely that these analyses were affected by incomplete character and taxon sampling that led to the recovery of a closer relationship between †Ellimmichthyiformes and Clupeoidei, rather than recovering a sister-group relationship between Denticipitoidei and Clupeoidei, or even to the recovering of the †ellimmichthyiforms nested within the clupeoids. For example, Kevrekidis *et al.* (2024) did not consider the inclusion of phylogenetically relevant characters like the presence/absence of auditory fenestra and vertical process of the basisphenoid, and both studies underestimated the importance of considering the presence/absence of the supratemporal system, temporal foramen, as well as the decoupling of the presence of supratemporal commissure through the parietal and supraoccipital in their analyses. Moreover, the analysis of Kevrekidis *et al.* (2024) did not test the monophyly of Clupeomorpha, Clupeiformes and †Ellimmichthyiformes without a proper taxon sampling, being the †ellimmichthyiforms there represented only by two taxa (†*Armigatus alticorpus* and †*Diplomystus dentatus*), lacking important basal taxa like †*Sorbinichthys* that still retains some traits of the MRCA of the Clupeiformes (Bannikov & Bacchia 2000). Our analysis also contradicts some molecular hypotheses (Li & Ortí 2007; Bloom & Egan 2018) that recovered *Denticeps* as more closely related to the Ostariophysi than to the Clupeoidei. The incomplete character or taxon sampling might also explain why Than-Marchese & Alvarado-Ortega (2022) recovered some †ellimmichthyiforms (†*Ornategulum*, †*Ranulfoichthys* and †*Scutatuspinosus*) as successive sisters to the pair (Clupeiformes + †Ellimmichthyiformes).

As far as the interrelationships between the different †ellimmichthyiform lineages is concerned, our tree topology is consistent with the latest updated analyses based on well-represented taxon and character sampling (e.g., Marramà *et al.* 2022; Marrrama & Carnavale 2023) even after the further inclusion of more than 270 characters that have been previously only used to detect the intrarelationships of the Clupeiformes. †*Armigatus* is confirmed to be monophyletic, as also recognized in many other studies (e.g., Marramà *et al.* 2019, 2022; Vernygora & Murray 2021; Marramà & Carnevale 2023). This contradicts a few hypotheses (Boukhalfa *et al.* 2018; Than-Marchese & Alvarado-Ortega 2022) that found †*Armigatus* to be non-monophyletic.

As far as the clupeoid interrelationships at high taxonomic level (superfamily and family) are concerned, our tree topology based on an unconstrained parsimony analysis that excludes fossil taxa (Fig. 41) is consistent with most of the molecular analyses although some differences need to be addressed.

For example, the tree topology of Bloom & Lovejoy (2014) and Bloom *et al.* (2018) are the most similar to ours in recovering the Spratelloididae sister to all the other clupeoids, with the pair Chirocentridae + Engraulidae sister to a clade that includes the Pristigasteridae, Clupeidae and Ehiravidae as successive sister to the pair formed by Alosidae and Dorosomatidae. The only difference with our topology is that both studies recovered *Etrumeus* as sister to the Clupeidae, and the pellonulines *Limnothrissa*, *Microthrissa*, *Odaxothrissa*, *Pellonula*, *Potamothrissa* and *Stolothrissa* as nested within the Dorosomatidae.

Similarly to our analysis, the Bayesian analysis of the mitochondrial DNA dataset of Bloom & Egan (2018) recovered the sister group relationship between *Chirocentrus* and Engraulidae, although they found the pair (*Clupea* + *Etrumeus*) and Dorosomatidae as successive sisters of the pair Pristigasteridae + Alosidae. Their topology based on Bayesian analysis of the mDNA dataset found Spratelloididae to be the most basal clupeoid taxon and the Dorosomatidae sister to the Alosidae.

Similarly to our analysis, in their concatenated Bayesian analysis of the 6-gene dataset Egan *et al.* (2018) recovered the Spratelloididae sister to all the other clupeoids, with the Clupeidae and Ehiravidae as successive sister to the pair Alosidae + Dorosomatidae. However, *Chirocentrus* is sister to the rest of the clupeoids (to the exclusion of Spratelloididae), the Dussumieriidae (*Etrumeus* + *Dussumieria*) sisters to the Clupeidae, and the pellonulines *Pellonula* and *Microthrissa* are nested within the Dorosomatidae. Another phylogeny inferred by concatenated Bayesian analysis of the 4-gene dataset by Egan *et al.* (2018) also recovered the Spratelloididae sister to all the other clupeoids.

The results of the mitogenome-based phylogenetic Bayesian analysis of Lavoué *et al.* (2013) were similar to our topology in recovering the Pristigasteridae, Clupeidae and Ehiravidae as successive sisters to the pair Alosidae + Dorosomatidae, although differences can be seen in their recognition of the Spratelloididae as sister to all non-engraulid clupeoids. In addition, also in this case the Pellonulini are nested within our Dorosomatidae.

The results of the mitogenome-based phylogenetic analyses of Lavoué *et al.* (2017, 2019) were similar to our topology in recovering the Engraulidae and Pristigasteridae as successive sisters to the other clupeoids, and the Ehiravidae sister to the pair Alosidae + Dorosomatidae; however, their analysis mainly differs in recovering a clade formed by *Chirocentrus* and Spratelloididae sister to the clade (Ehiravidae + (Alosidae + Dorosomatidae)) with *Pellonula* nested within the Dorosomatidae.

The tree topology of Wang *et al.* (2022) is similar to that presented herein in recovering *Denticeps*, Spratelloididae and Engraulidae as successive sisters to the other clupeoids, and a clade formed by the Ehiravidae sister to the pair Alosidae + Dorosomatidae. However, they also recovered this latter clade sister to a clade formed by Clupeidae + (Pristigasteridae + (*Dussumieria* + *Chirocentrus*)).

Finally, the molecular topologies in Li & Ortí (2007), Lavoué *et al.* (2010, 2014) and Milec *et al.* (2022) consistently differ from the topologies presented in this study.

As far as the comparison with morphology-based analyses are concerned, our tree topology is not comparable with the unconstrained parsimony analyses (we will not consider their results from constrained analyses) of Kevrekidis *et al.* (2024) when *Chanos* is used as outgroup. To the exclusion of the Spratelloididae sister to the rest of clupeoids, and *Chirocentrus* sister to the Engraulidae, they recovered a tree topology which is also inconsistent with the results of the molecular analyses mentioned above. In fact, their analysis recovered the Dussumieriidae, the Ehiravidae and *Potamalosa* sister to the rest of clupeoids, with Clupeidae and Dorosomatidae being non monophyletic, and a clade that includes *Clupeonella*, *Hyperlophus* and Pristigasteridae as sister of the Engrauloidea. Even their constrained analysis could not detect the monophyly of some families (Dorosomatidae, Ehiravidae, Clupeidae) with most of the monophyletic taxa (Dussumieriidae + Spratelloididae, Chirocentridae + Engraulidae, Pristigasteridae) recovered in large polytomies (Kevrekidis *et al.* 2024, figs 14, 15). These results change considerably when the more distantly related *Alepocephalus* is used as outgroup instead of *Chanos* in unconstrained analyses, preventing their outgroup, taxon and character sampling from resolving the relationships between the main clupeomorph and clupeiform lineages.

Although the analyses of Sato (1994) and Vernygora (2020) recovered the monophyly of the main clupeoid clades (Engraulidae, Pristigasteridae, Dorosomatidae, Alosidae), the clupeoid intrarelationships were mostly left unsolved, with large polytomies among families and subfamilies.

Finally, Di Dario (2004b), whose study mainly focused on the relationship between Clupeiformes and Ostariophysi recovered, similarly to our analysis, the monophyly of the Dussumieriidae, Spratelloididae, Pristigasteridae and Engraulidae but not the monophyly of Clupeidae, Ehiravidae, Alosidae and Dorosomatidae. Similarly to our results, Di Dario (2004b) recovered *Denticeps* sister to the Clupeoidei, and a clade formed by Dussumieriidae and Chirocentridae as successive sisters to the Engraulidae. However, contrary to our topology, he found the Pristigasteridae sister to the clade formed by Dussumieriidae and Chirocentridae as successive sisters to the Engraulidae.

THE DIVERGENCE TIME ESTIMATES OF THE MAIN LINEAGES OF CLUPEOMORPHA

Based on the minimum branch length of one million years applied, the most recent common ancestor of the Clupeomorpha should have already originated 154.0 Mya ago in the early Kimmeridgian (Late Jurassic) (Figs 42, 43), which appears to be a more cautious hypothesis compared to the *c.* 214 Mya estimated by Vernygora (2020).

The MRCA of the †Ellimmichthyiformes might have arisen in the early Kimmeridgian (159.8-149.2 Mya). Conversely, Vernygora (2020) estimated a Lower Jurassic (*c.* 195 Mya) origin for MRCA of the †Ellimmichthyiformes.

Our estimated Early Cretaceous (Hauterivian: 132.6-125.8 Mya) origin of the MRCA of the Clupeiformes appears more consistent with the estimates based on molecular analyses of Wang *et al.* (2022) (138.9-125.4 Mya), Lavoué *et al.* (2013) (145.0-125.0 Mya), rather than with the Late Jurassic (Egan *et al.* 2018, 2024; Milec *et al.* 2022) or the Late Triassic age estimates (Bloom & Lovejoy 2014).

†*Nolfia riachuelensis* from the Albian of Brazil, identified as the most basal clupeoid in our analysis, suggests an Aptian age (121.4-113.2 Mya) for the origin of the crown Clupeoidei. This age estimate aligns with the origin ranges proposed, e.g., by Lavoué *et al.* (2013), who estimated the most recent common ancestor (MRCA) of Clupeoidei to have emerged around 119 Mya, but also with that of Bloom & Egan (2018) (130.0-110.0 Mya) and Egan *et al.* (2018) (143.1-100.5 Mya). In contrast, other studies place the origin of the Clupeoidei earlier, such as *c.* 150 Mya (Bloom & Lovejoy 2014), 139.0-137.0 Mya (Egan *et al.* 2024), or even later, between 107.5 and 75.0 Mya (Wang *et al.* 2022).

As far as the main clupeoid lineages are concerned, we can estimate a Santonian (85.7-83.6 Mya) origin for the clade (the pan-Engrauloidea) that gave rise to the Spratelloididae, Dussumieriidae, Chirocentridae and Engraulidae. The pan-Spratelloididae likely diverged in this period. Dussumieriidae, Chirocentridae and Engraulidae diverged in the Paleocene (66.0-56.0 Mya) but the MRCA of the Engraulidae should be found in the Ypresian (56.0-48.1 Mya). The Pristigasteroidea likely diverged from the Clupeoidea around the end-Cretaceous extinction (*c.* 66.0 Mya) or during the Paleocene. The absence of crown Pristigasteridae in the fossil record creates a long ghost lineage. The Hyperlophidae should have been already present in the Danian (66.0-61.66 Mya), whereas the lineage that gave rise to the modern Atlantic and Mediterranean species of *Clupea* and *Sprattus*, originated a little bit later during the Ypresian (56.0-48.07 Mya). During the early Eocene a further burst in the clupeoid evolution gave rise to the Alosidae, Dorosomatidae and Ehiravidae, as evidenced by the Ypresian crown alosid †*Eoalosa* and the pan-dorosomatid †*Bolcaichthys* and the Bartonian crown dorosomatid †*Opisthonema persicum* (Arambourg 1966; Marramà & Carnevale 2015b, 2018). The lack of ehiravid fossil taxa makes impossible to detect the age of their MRCA in our analysis (there is no reason to consider †*Lecceclupea* Taverne, 2011 as an ehiravid; G.M. pers. obs.).

Looking at the origin of the MRCA of the main clupeoid families (Spratelloididae, Engraulidae, Pristigasteridae, Hyperlophidae, Clupeidae, Ehiravidae, Alosidae and Dorosomatidae) detected by previous analyses based on molecular data, our analysis is more consistent with that of Lavoué *et al.* (2013) and Bloom & Egan (2018) since our estimates of the MRCAs of Hyperlophidae, Clupeidae, Alosidae, Dorosomatidae and Engraulidae fall within the estimated ranges of these studies. Lavoué *et al.* (2013), similarly to our analysis, estimated ages of 90.0-50.0 Mya for the Clupeidae, 65.0-24.0 Mya for Alosidae. Bloom & Egan (2018) detected similar ranges for the MRCA of the Engraulidae (*c.* 50.0 Mya) and Dorosomatidae (50.0-20.0 Mya).

Ancestral habitat and area reconstructions

Our phylogenetic reconstruction hypothesizes the origin of the most recent common ancestor (MRCA) of the Clupeomorpha in the Neotethys during the Late Jurassic (*c.* 155 Mya) (Fig. 47), a time of dynamic paleogeographic transformation associated with the breakup of Pangaea. This region was characterized by shallow epicontinental seas, high eustatic level, and a greenhouse climate, creating a network of marine and marginal habitats along the Tethyan margins (Luft-Souza *et al.* 2022; Scotese *et al.* 2025). These environmental conditions fostered early clupeomorph diversification in the western and central Neotethys.

The †Ellimmichthyiformes shows a predominantly Tethyan diversification pattern with five of the six main family-level lineages (†Sorbinichthyidae, †Scutatuspinosidae, †Gasteroclupeidae, †Armigatidae, and †Paraclupeidae) that likely originated in the Neotethys (Fig. 47). These findings reinforce previous hypotheses that emphasized a Tethyan origin for these and other teleost taxa (e.g., Maisey 2000; Chang & Maisey 2003; Murray & Wilson 2013) and highlight the role of the Neotethys for early clupeomorph radiation. The ecological flexibility of †Ellimmichthyiformes to occupy fluctuating conditions is consistent with ecological data from estuary-associated fishes globally, which show resilience and dispersal capability across marginal marine systems (Harrison & Whitfield 2022). These fishes occupied a range of habitats, from marine to brackish and freshwater systems, demonstrating considerable ecological plasticity in the course of their evolutionary history.

Several independent dispersal events from the Tethys by the end of Late Jurassic expanded the distribution of the †Ellimmichthyiformes. One of these, a southwestward dispersal into northern South America, resulted in the †*Codoichthys* lineage. This event is consistent with geological and paleontological evidence supporting intermittent marine ingressions into interior basins such as the Parnaíba during the Aptian (Arai 2014, 2016; Lindoso *et al.* 2016). Fossil evidence from the Codó Formation suggests a restricted, lacustrine-dominated setting punctuated by Tethyan marine influence, a pattern indicated also by the shared ichthyofaunal elements between the Codó, Santana, and Riachuelo Formations (Lindoso *et al.* 2016; Nery do Amaral *et al.* 2024). The fish assemblage provides evidence of early Neotethyan-derived lineages adapted to new environments across interior basins of South America. The Sergipe-Alagoas Basin, in particular, records a well-stratified sequence of late Barremian-Albian marine ingressions with relevant Tethyan affinities in its fossil assemblages, highlighting its role as a marine corridor during early South Atlantic opening (Luft-Souza *et al.* 2022).

Within the †Scutatuspinosidae, whose phylogenetic roots trace back to the Neotethys, three additional dispersals likely followed marine regressions and transgressions in the Early Cretaceous. The †*Foreyclupea* lineage colonized the Circum-Arctic, †*Scutatuspinosus* entered brackish South Atlantic margins, and †*Ranulfoichthys* reached the Gulf of Mexico. These events coincide with late Barremian-Albian eustatic rises, which enabled episodic marine connections between marginal basins in NE Brazil and proto-Caribbean and Boreal systems (Arai 2014; Luft-Souza *et al.* 2022).

The dispersal events of the †*Codoichthys* and †*Scutatuspinosus* lineages were associated with habitat transitions—from marine to euryhaline or freshwater conditions—and coincide with the rifting of western Gondwana and the establishment of early trans-Atlantic connections (Luft-Souza *et al.* 2022; Scotese *et al.* 2025).

Within the †Gasteroclupeidae, whose MRCA also traces back to the Neotethys, different lineages radiated widely across Laurasia, reaching the Neotropical (†*Gasteroclupea*), Oriental (†*Guiclupea*, †*Diplomystus shengliensis*), and the Nearctic regions (†*Diplomystus dentatus*) by the end of the Early Cretaceous). The ability of the family to occupy both marine and freshwater systems likely reflects a high degree of salinity tolerance, consistent with sedimentological and ecological interpretations from their fossil localities (Marramà & Carnevale 2017; Chen *et al.* 2021; Zheng *et al.* 2022). The distribution of †*Diplomystus* in East Asia and North America support high-latitude, potentially estuarine-to-freshwater migration routes. These corridors were opened or intensified during intervals of polar warmth and reduced salinity (Chang & Maisey 2003; Capobianco & Friedman 2019).

Diversification within the Neotethyan †Armigatidae reflects continued dispersal via Tethyan-Atlantic connection. For example, the MRCA of the clade including †*Armigatus carrenoae* and †*A. felixi* originated in the Gulf of Mexico (PL: 50.1%) following westward migration from the western Neotethys around the Aptian-Albian boundary—a period marked by a transgressive episode that expanded shallow marine carbonate platforms across the northern margins of South America (Maisey 2000; Scotese *et al.* 2025).

The †Paraclupeidae represent the most dispersive †ellimmichthyiform family, with at least seven independent dispersal events across Gondwana, Laurasia, and Tethyan margins that coincide also with transitions from marine to euryhaline, or from euryhaline to freshwater habitats. The widespread distribution of the †paraclupeid taxa that, from their original Neotethys, reached Northwestern Pacific Ocean (†*Paraclupea chetungensis*), northern margins of South America (†*Ellimma branneri*), Mexico (†*Paraclupea seilacheri* and †*Scutatoclupea applegatei*) and Arctic Canada (†*Tycheroichthys*) confirms the ecological versatility of the entire group. The repeated colonization of marginal and inland waters suggests an adaptive response to fluctuating sea levels and coastal fragmentation during the opening of the South Atlantic. In particular, the occurrence of †*Paraclupea chetungensis* in SE China during the Aptian (*c.* 120 Mya) reflects Tethyan biogeographic affinity and is consistent with the early dispersal pathways (Chen

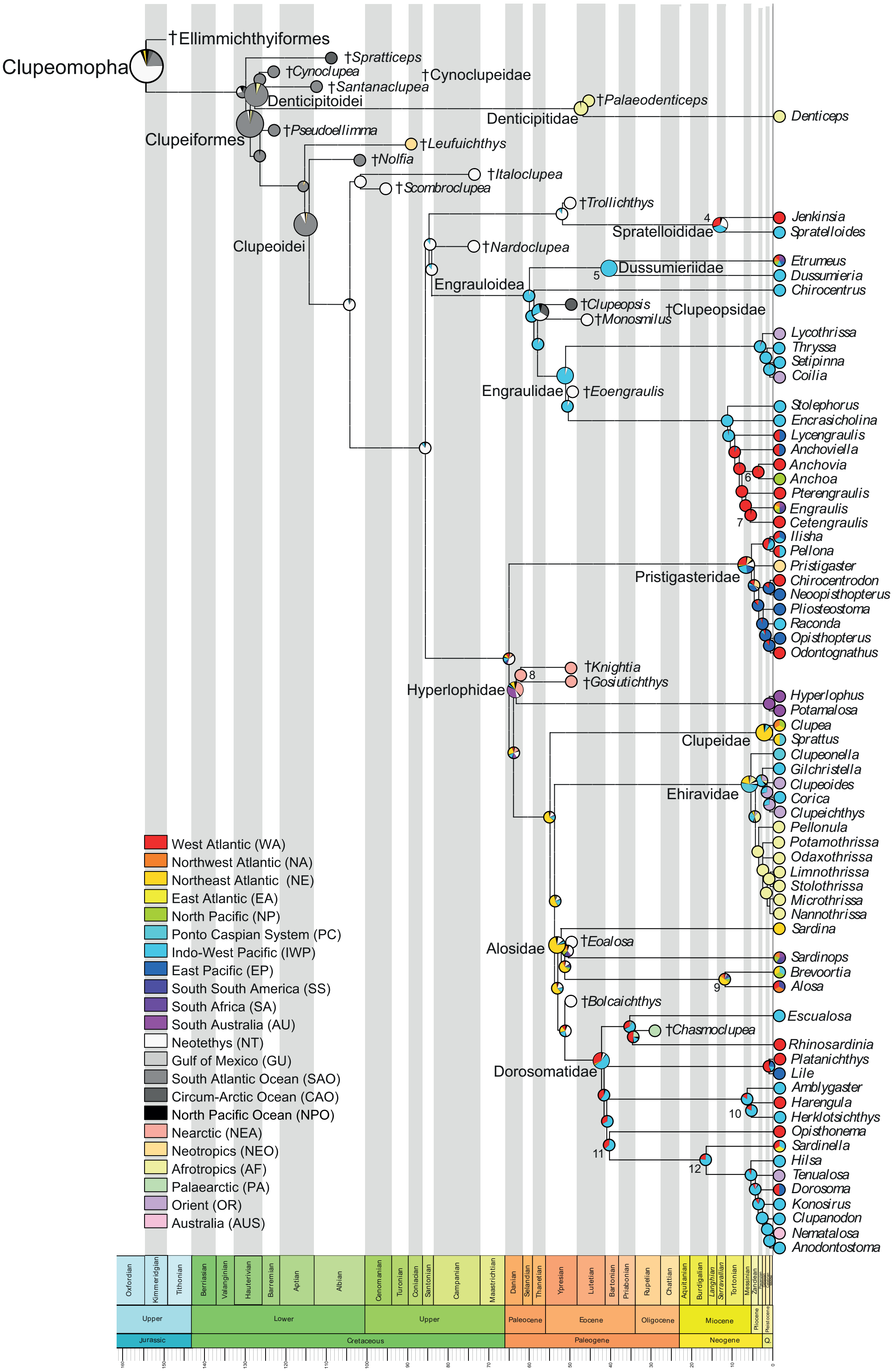

Fig. 48. — Ancestral area reconstruction of pan-Clupeiformes (node 40) using the maximum clade credibility tree through the “Mk1” evolutionary model of the Likelihood approach. Pie charts at nodes show the proportional likelihood. **Black bars** representing the known stratigraphic range of the taxa are omitted.

et al. 2021; Gao *et al.* 2022). Moreover, its association with marine-influenced sediments suggests tolerance to a range of salinities and paleoenvironments (Gao *et al.* 2022).

These patterns reinforce the role of sea-level change and paleogeographic connectivity in shaping the †Ellimmichthyiformes evolution. During the Aptian-Albian, eustatic transgressions and the progressive opening of the Equatorial Atlantic created temporary corridors between the Tethys and nascent Atlantic basins (Arai 2014; Luft-Souza *et al.* 2022). The marine flooding of Brazilian coastal basins like Sergipe-Alagoas, evidenced by Tethyan-affiliated marine fossils and stratigraphic transitions from continental to open marine conditions, represents key dispersal windows. In contrast, periods of regression likely contributed to provincialism and isolation of freshwater-adapted lineages. This pattern of widespread dispersal aligns with the growing con*sensu*s that dispersal, not vicariance, played the dominant role in shaping the biogeography of freshwater and euryhaline teleosts during the Mesozoic (Cavin 2017). While early vicariant models linked fish distributions to the breakup of Pangaea, updated phylogenetic and paleogeographic evidence, particularly for groups like the †Ellimmichthyiformes, supports more dynamic biogeographic histories, often involving marine incursions, ecological transitions, and the exploitation of epicontinental seaways and rift basins.

The occurrence of a pan-Clupeiformes (†*Spratticeps*) in the Early Cretaceous Circum-Arctic realm that was connected to western Neotethys, likely reflects Tethyan origin and subsequent dispersal events (particularly toward the South America) for the lineage that includes extant clupeomorphs. This trend reflects that of the †Ellimmichthyiformes, with both lineages that likely benefited from their pelagic planktivory and shoaling behaviours, that, combined with the extensive marine connectivity of the Cretaceous world, enabled rapid geographic expansion of their occupied area.

The MRCA of Clupeiformes, however, likely emerged in the northern South Atlantic Ocean during the Early Cretaceous, consistent with geological evidence for early marine flooding of marginal South American basins during the Aptian-Albian (Maisey 2000; Arai 2014; Luft-Souza *et al.* 2022). This marine corridor, which expanded during the drift phase of South Atlantic rifting, likely enabled the rapid westward dispersal of the Boreal/Neotethyan-originated clupeiform lineage. The MRCA of Denticipitoidei, as well as one of its two families, the †Cynoclupeidae, originated in this South Atlantic context during the Early Cretaceous. Their sister lineage, Denticipitidae, likely colonized the Afrotropical freshwaters after early dispersal into transitional euryhaline systems, in agreement with scenarios of early brackish-freshwater occupation proposed for other southern hemisphere teleosts (Capobianco & Friedman 2019).

Our analysis also places the MRCA of the sister group of the Denticipitoidei, the Clupeoidei, in the South Atlantic Ocean during the Early Cretaceous (*c.* 115 Mya), challenging previous hypotheses such as that of Lavoué *et al.* (2013), who inferred an Indo-West Pacific (=Tethyan) origin based on mitogenomic data and the modern distribution of basal clades. While Lavoué *et al.* (2013) identified the Neotethys as the center of clupeoid diversification, our data indicate a west-to-east dispersal: following their origin and early diversification in the South Atlantic Ocean, the MRCA of all major clupeoid lineages (Spratelloididae, Engrauloidea, Pristigasteroidea, Clupeoidea) likely emerged in the Neotethys during the Late Cretaceous during renewed Tethyan transgressions that reconnected the Atlantic and Indo-Tethyan systems.

These findings partially reconcile the conflicting views of Lavoué *et al.* (2013) and Avaria-Llautureo *et al.* (2021). While Lavoué *et al.* (2013) emphasized a tropical marine Indo-West Pacific (IWP)/Tethyan origin, Avaria-Llautureo *et al.* (2021) hypothesized the Clupeoidei MRCA near the western Tethys and eastern Proto-Atlantic, also with marine habitat preference. Our model, integrating paleogeographic and eustatic data, suggests an earlier South Atlantic marine origin for the Clupeoidei, followed by eastward expansion into the Neotethys and then, to the IWP. This sequence of events fits better the timing of major marine transgressions and tectonic opening of equatorial seaways (Scotese *et al.* 2025), and aligns with the dispersal pathways inferred for early engraulids and dussumieriids.

Specifically, our analysis places the origins of Engraulidae, Chirocentridae, Dussumieriidae and Spratelloididae within the Neotethys, supporting both their early tropical marine ecology and the subsequent wide dispersal, similarly to the findings of Lavoué *et al.* (2013).

Our results further indicate that the MRCA of the Pristigasteridae emerged in the West Atlantic suggesting a westward dispersal from the Neotethys during the Late Cretaceous. However, this inference has low support because of our incomplete taxonomic sampling within the Pristigasteridae (e.g., *Ilisha africana* was not included in our study), but it also indicates that multiple dispersal routes—eastward and westward—may have operated simultaneously in the Cretaceous tropics.

Origin and diversification of modern Clupeidae (*Clupea*, *Sprattus*) occurred in the Northeastern Atlantic during the early Paleogene, in a temperate marine context already distinct from tropical Tethyan faunas. Our scenario suggests that clupeids did not directly arise from the eastern Tethyan-IWP region but instead represent a separate temperate radiation following marine cooling and the establishment of the North Atlantic basin.

We inferred a Paratethyan origin during the Miocene for the tentatively grouped Ehiravidae and a bidirectional dispersal eastward toward the Indo-West Pacific (Ehiravinae) and toward the East Atlantic and then to the Afrotropical freshwaters where the Pellonulinae originated. This hypothesis complements the historical framework of biogeographic barriers and dispersal routes outlined by Harrison & Whitfield (2022), and the size-dispersal dynamics documented by Avaria-Llautureo *et al.* (2021). Specifically, the closure of the Tethys Sea and subsequent separation of the tropical faunas in the Atlantic and Indo-Pacific regions are key events that could have influenced the dispersal and diversification of the Ehiravidae.

TABLE 1. — Revised classification of the Clupeomorpha (Teleostei: Otomorpha).

- Subcohort Clupei Wiley & Johnson, 2010
  - Superorder Clupeomorpha Greenwood, Rosen, Weitzman & Myers, 1966 (*sensu* Grande, 1985)
    - Order †Ellimmichthyiformes Grande, 1982
      - Unranked: †*Codoichthys* Santos, 1994
      - Family †Sorbinichthyidae Bannikov & Bacchia, 2000
        - †*Sorbinichthys Bannikov & Bacchia, 2000*
      - Family †Scutatuspinosidae Silva Santos & Silva Correa, 1985 (*sensu* Vernygora *et al.* 2016)
        - †*Foreyclupea* Vernygora *et al.*, 2016, †*Ornategulum* Forey, 1973, †*Ranulfoichthys* Alvarado-Ortega, 2014, †*Scutatuspinosus* Silva Santos & Silva Corrêa, 1985
      - Family †Gasteroclupeidae Signeaux 1964 (*sensu* Marramà *et al.* 2022)
        - †*Diplomystus* Cope, 1877, †*Gasteroclupea* Signeux, 1964, †*Guiclupea* Chen *et al.*, 2021
      - Family †Armigatidae Murray & Wilson, 2013
        - †*Armigatus* Grande, 1982
      - Family †Paraclupeidae Chang & Chou, 1997
        - Unranked: "†*Ellimmichthys*" *spinosus* Figueiredo & Gallo, 2021, "†*Ellimma*" *longipectoralis* Polck *et al.*, 2020
        - Subfamily †Thorectichthyinae Murray & Wilson, 2013
          - †*Thorectichthys* Murray & Wilson, 2013
        - Subfamily †Eoellimmichthyinae n. subfam.
          - †*Eoellimmichthys* Marramà *et al.*, 2019, †*Ezkutuberezi* Poyato-Ariza *et al.*, 2000
        - Subfamily †Triplomystinae Murray & Wilson, 2013 (new rank)
          - †*Triplomystus* Forey *et al.*, 2003, †*Scutatoclupea* Bannikov, 2015
        - Subfamily †Paraclupeinae Chang & Chou, 1977 (*sensu* Marramà *et al.* 2022)
          - †*Ellimma* Jordan, 1913, †*Ellimmichthys* Cope, 1886, †*Paraclupea* Sun, 1956, †*Rhombichthys* Khalloufi *et al., 2010*, †*Tunisiaclupea* Boukhalfa *et al.*, 2019, †*Tycheroichthys* Hay *et al.*, 2007
    - pan-Clupeiformes
      - †*Spratticeps* Patterson, 1970
    - Order Clupeiformes Bleeker, 1859
      - Suborder Denticipitoidei Greenwood, Rosen, Weitzman & Myers, 1966 (new usage)
        - Family †Cynoclupeidae Malabarba & Di Dario, 2017 (new usage)
          - †*Cynoclupea* Malabarba & Di Dario, 2017, †*Santanaclupea* Maisey, 1993
        - Family Denticipitidae Clausen, 1959
          - *Denticeps* Clausen, 1957, †*Palaeodenticeps* Greenwood, 1960
      - pan-Clupeoidei
        - †*Leufuichthys* Gallo *et al.*, 2011, †*Pseudoellimma* De Figueiredo, 2009
      - Suborder Clupeoidei Bleeker, 1859 (*sensu* Greenwood *et al.* 1966)
        - Unranked: †*Italoclupea* Taverne, 2007, †*Nolfia* Taverne, 1976, †*Scombroclupea* Kner, 1863
        - pan-Engrauloidea
          - pan-Spratelloididae
            - †*Trollichthys* Marramà & Carnevale, 2015
          - Family Spratelloididae Jordan, 1925 (*sensu* Bloom & Egan 2018)
            - *Jenkinsia* Jordan & Evermann, 1896, *Spratelloides* Bleeker, 1851
        - Superfamily Engrauloidea Nelson, 1970 (new usage)
        - Unranked: †*Nardoclupea* Taverne, 2002
          - Family Dussumieriidae Gill, 1861 (*sensu* Bloom & Egan 2018)
            - *Dussumieria* Valenciennes, 1847, *Etrumeus* Bleeker, 1853
          - Family Chirocentridae Bleeker, 1872
            - *Chirocentrus* Cuvier, 1816
          - Epifamily Engrauloidae n. epifam.
          - Family Clupeopsidae n. fam.
            - †*Clupeopsis* Casier, 1946, †*Monosmilus* Capobianco *et al.*, 2020
          - Family Engraulidae Gill, 1861
            - Subfamily Coiliinae Bleeker, 1872 (*sensu* Grande & Nelson 1985)
            - *Coilia* Gray, 1830, *Lycothrissa* Günther, 1868, *Setipinna* Swainson, 1839, *Thryssa* Cuvier, 1829
            - pan-Engraulinae
            - †*Eoengraulis* Marramà & Carnevale, 2016
            - Subfamily Engraulinae Gill, 1861 (*sensu* Grande & Nelson 1985)
            - *Anchoa* Jordan & Evermann, 1927, *Anchovia* Jordan & Evermann, 1895, *Anchoviella* Fowler, 1911, *Cetengraulis* Günther, 1868, *Encrasicholina* Fowler, 1938, *Engraulis* Linnaeus, 1758, *Lycengraulis* Günther, 1868, *Pterengraulis* Günther, 1868, *Stolephorus* Lacepède, 1803
        - Superfamily Pristigasteroidea Nelson, 1970
          - Family Pristigasteridae Bleeker, 1872
            - *Chirocentrodon* Günther, 1868, *Ilisha* Richardson, 1846, *Neoopisthopterus* Hildebrand, 1948, *Odontognathus* Lacepède, 1800, *Opisthopterus* Gill, 1861, *Pellona* Valenciennes, 1847, *Pliosteostoma Norman, 1923, Pristigaster* Cuvier, 1816, *Raconda* Cuvier, 1816
        - Superfamily Clupeoidea Cuvier, 1816 (new usage)
          - Family Clupeidae Cuvier, 1816 (new usage)
            - *Clupea* Linnaeus, 1758, *Sprattus* Girgensohn, 1846
          - Family Hyperlophidae Ogilby, 1897 (new rank)
            - †*Gosiutichthys* Grande, 1982, *Hyperlophus* Ogilby, 1892, †*Knightia* Jordan, 1907, *Potamalosa* Ogilby, 1897
          - Family Ehiravidae Deraniyagala, 1929 (new usage)
            - Unranked: *Clupeonella* Kessler, 1877

Table 1. — Continuation.

Subfamily Ehiravinae Deraniyagala, 1929 (new rank)
Clupeichthys Fowler, 1935, *Clupeoides* Bleeker, 1851, *Corica* Hamilton, 1822, *Gilchristella* Fowler, 1935
Subfamily Pellonulinae Svetovidov 1952 (new rank)
Limnothrissa Regan, 1917, *Microthrissa* Boulenger, 1902, *Nannothrissa* Poll, 1965, *Odaxothrissa* Boulenger, 1899, *Pellonula* Günther, 1868, *Potamothrissa* Regan, 1917, *Stolothrissa* Regan, 1917
Family Alosidae Svetovidov, 1953 (*sensu* Wang *et al.* 2022)
Alosa Linck, 1790, *Brevoortia* Gill, 1861, †*Eoalosa* Marramà & Carnevale, 2018, *Sardina* Antipa, 1904, *Sardinops* Hubbs, 1929
pan-Dorosomatidae
†*Bolcaichthys* Marramà & Carnevale, 2015
Family Dorosomatidae Bleeker, 1872 (new usage)
Amblygaster Bleeker, 1849, *Anodontostoma* Bleeker, 1849, †*Chasmoclupea* Murray *et al.*, 2005, *Clupanodon* Lacepède, 1803, *Dorosoma* Rafinesque, 1820, *Escualosa* Whitley, 1940, *Harengula* Valenciennes, 1847, *Herklotsichthys* Whitley, 1951, *Hilsa* Regan, 1917, *Konosirus* Jordan & Snyder, 1900, *Lile* Jordan & Evermann, 1896, *Nematalosa* Regan, 1917, *Opisthonema* Gill, 1861, *Platanichthys* Whitehead, 1968, *Rhinosardinia* Eigenmann, 1912, *Sardinella* Valenciennes, 1847, *Tenualosa* Fowler, 1934

The inferred origin of the MRCA of the Alosidae + pan-Dorosomatidae clade in the North Atlantic around the Paleocene-Eocene transition is supported by regional paleogeographic and ecological conditions that would have promoted lineage divergence. By this time, the North Atlantic had substantially widened and was flanked by newly forming marginal marine provinces, while the Tethys Ocean was becoming increasingly restricted (Scotese *et al.* 2025). This created a dynamic marine setting conducive to dispersal and regional isolation. Our reconstruction suggests that the MRCA of the Alosidae originated in this North Atlantic realm, likely tracking temperate marine conditions, whereas a coeval westward dispersal event led to the MRCA of both the total group and crown group Dorosomatidae in the IWP/Tethyan system. These hypotheses align with that of Lavoué *et al.* (2013). The ecological model presented by Harrison & Whitfield (2022) underscores that euryhaline fishes, such as many dorosomatids, are especially responsive to eustatic sea-level changes, with marine transgressions promoting coastal expansion and colonization. These conditions were prominent in the early Paleogene, facilitating the spread of euryhaline lineages (e.g., *Dorosoma*, *Harengula*, *Opisthonema*, *Rhinosardinia*) into the low-salinity habitats of the proto-Gulf of Mexico and western Atlantic embayments.

While Lavoué *et al.* (2013) proposed an Indo-West Pacific origin for many clupeoid lineages, the recognition of multiple Cenozoic dispersal events and independent freshwater transitions supports a framework in which alosids and dorosomatids could have differentiated regionally from a North Atlantic common ancestor. Thus, the divergence of Alosidae and Dorosomatidae appears to reflect both tectonic and ecological partitioning within an evolving North Atlantic system, mediated by marine connectivity and habitat specialization.

Overall, our findings highlight a more complex evolutionary and biogeographic history of Clupeiformes than previously proposed. While Lavoué *et al.* (2013) emphasized an Neotethyan/Indo-West Pacific marine origin for the Clupeoidei, our results suggest that their early diversification occurred in the South Atlantic Ocean, with secondary dispersals into the Neotethys and North Atlantic coastal systems. The integration of eustatic and paleogeographic data clarifies how major marine transgressions opened and closed dispersal routes across the Cretaceous and Paleogene oceans. Combined with ecological traits like planktivory, diadromy, and salinity tolerance, these changes explain the remarkably broad ecological and geographic ranges of modern clupeiforms. The apparent differences between the results of our study and that of Lavoué *et al.* (2013) about the origin of the Clupeoidei may stem from different calibration schemes and methods; our topology incorporates fossil-calibrated ancestral range reconstructions, whereas the mitogenomic tree of Lavoué *et al.* (2013) was uncalibrated in time and relied heavily on extant distributions.

Based on our results it is reasonable to suggest that the present biogeographic distribution of most clupeiform lineages (Engraulidae, Dussumieriidae, Clupeidae, Chirocentridae, Pristigasteridae, Ehiravidae, Alosidae, Dorosomatidae) can be primarily explained by dispersal. Conversely, only a few lineages show today geographically restricted distributions (Denticipitidae, Hyperlophidae) that might be related to ancient tectonic and geographic events.

CONCLUSIONS

The results of this study support a robust phylogenetic framework for the Clupeomorpha, integrating morphological, biogeographic and habitat data to resolve the evolutionary relationships among extant and extinct lineages. Despite the relatively high homoplasy observed in the morphological data the overall congruence across different parsimony analyses reveals a consistent signal of clupeomorph monophyly. This framework supports the traditional recognition of two main lineages within the Clupeomorpha, the †Ellimmichthyiformes and the Clupeiformes, rejecting recent hypotheses that considered the †Ellimmichthyiformes as crown Clupeiformes or crown Clupeoidei. The internal interrelationships among higher-level taxa within the †Ellimmichthyiformes and Clupeiformes are broadly consistent with current molecular classifications. However, our results also indicate that the subfamilies Ehiravinae and Pellonulinae constitute a monophyletic group (family Ehiravidae).

Divergence time estimates further suggest that the split between †Ellimmichthyiformes and Clupeiformes occurred before the Cretaceous, with the origin of the total group Clupeomorpha dating back to the Late Jurassic, approximately 155 million years ago. These findings provide a refined phylogenetic and temporal framework for future evolutionary, biogeographic, and ecological studies of this diverse, widespread and economically important teleost fish clade.

Ancestral habitat and area reconstructions further suggest that the Clupeomorpha originated in the shallow marine environments of the Neotethys during the Late Jurassic, with early diversification of the main clades occurring within connected Tethyan and proto-Atlantic systems. Our analysis additionally recovers the ancient South Atlantic Ocean, particularly along the northern South American margin, as the ancestral area for both Denticipitoidei and Clupeoidei, indicating that these groups initially diversified in marine settings during the early opening of the South Atlantic and subsequently dispersed into the Neotethys, North Atlantic, and African freshwater systems.

The repeated and widespread dispersal events observed across the phylogeny can be attributed in part to the notable clupeomorph euryhalinity – an ecological trait that enabled multiple transitions between marine, brackish, and freshwater environments, and allowed clupeomorphs to exploit newly emerging coastal and epicontinental habitats shaped by Mesozoic and Cenozoic sea-level fluctuations.

Summarizing, the evolutionary and biogeographic history of the Clupeomorpha have been shaped by a complex interplay of paleogeographic connectivity, ecological transitions, and adaptive capabilities. Our results integrate and refine prior hypotheses and provide new resolution on the timing, directionality, and ecological context of major dispersal events that characterized the evolutionary history of this clade.

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APPENDICES

Appendix 1. — List of living and fossil clupeomorph taxa and specimens examined.

Outgroups (cleared and stained specimens):
Kneria auriculata (Pellegrin, 1905): AMNH 27461;
Osmerus mordax (Mitchill, 1814): AMNH 3088.

Extant Clupeiformes (cleared and stained specimens):
Alosa sapidissima (Wilson, 1811): AMNH 32707;
Amblygaster leiogaster (Valenciennes, 1847): AMNH 17581;
Anchoa compressa (Girard, 1858): AMNH 2671;
Anchovia clupeoides (Swainson, 1839): AMNH 224937;
Anchoviella lepidentostole (Fowler, 1911): AMNH 40905;
Brevoortia tyrannus (Latrobe, 1802): AMNH 27686;
Cetengraulis edentulus (Cuvier, 1829): AMNH 37073;
Chirocentrodon bleekerianus (Poey, 1867): AMNH 55306;
Chirocentrus dorab (Forsskål, 1775): AMNH 55306;
Clupanodon thrissa (Linnaeus, 1758): AMNH 28122;
Clupea harengus Linnaeus, 1758: AMNH 49397;
Coilia brachygnathus Kreyenberg & Pappenheim, 1908: AMNH 10321;
Corica soborna Hamilton, 1822: AMNH 55343;
Denticeps clupeoides Clausen, 1959: AMNH 53082;
Dorosoma petenense (Günther, 1867): AMNH 54607;
Dussumieria acuta Valenciennes, 1847: AMNH 17555;
Ehirava fluviatilis Deraniyagala, 1929: AMNH 229124;
Encrasicholina purpurea (Fowler, 1900): AMNH 54601;
Engraulis mordax Girard, 1854: AMNH 54600;
Escualosa thoracata (Valenciennes, 1847): AMNH 32502;
Etrumeus sadina (Mitchill, 1814): AMNH 736;
Gilchristella aestuaria (Gilchrist, 1913): AMNH 232905;
Gudusia variegata (Day, 1870): AMNH 8355;
Harengula jaguana Poey, 1865: AMNH 28283;
Herklotsichthys dispilonotus (Bleeker, 1852): AMNH 54611;
Hilsa kelee (Cuvier, 1829): AMNH 32828;
Hyperlophus vittatus (Castelnau, 1875): AMNH 3050;
Jenkinsia lamprotaenia (Gosse, 1851): AMNH 28252;
Lile stolifera (Jordan & Gilbert, 1882): AMNH 7100;
Lycengraulis grossidens (Spix & Agassiz, 1829): AMNH 20751;
Microthrissa royauxi Boulenger, 1902: AMNH 5830;
Nannothrissa stewarti Poll & Roberts, 1976: AMNH 55289;
Nematalosa erebi (Günther, 1868): AMNH 28097;
Neoopisthopterus tropicus (Hildebrand, 1946): AMNH 53084;
Odaxothrissa losera Boulenger, 1899: AMNH 236933;
Odontognathus mucronatus Lacépède, 1800: AMNH 20749;
Opisthonema oglinum (Lesueur, 1818): AMNH 54613;
Opisthopterus equatorialis Hildebrand, 1946: AMNH 10188;
Pellonula leonensis Boulenger, 1916: AMNH 233688;
Potamothrissa obtusirostris (Boulenger, 1909): AMNH 5843;
Potamalosa richmondia (MacLeay, 1879): AMNH 1737;
Pristigaster cayana Cuvier, 1829: AMNH 10186;
Pterengraulis atherinoides (Linnaeus, 1766): AMNH 48888;
Rhinosardinia amazonica (Steindachner, 1879): AMNH 40923;
Sardinella aurita Valenciennes, 1847: AMNH 44437;
Sardinella maderensis (Lowe, 1838): AMNH 44448;
Sardinops sagax (Jenyns, 1842): AMNH 5449;
Setipinna tenuifilis (Valenciennes, 1848): AMNH 17551;
Spratelloides delicatulus (Bennett, 1832): AMNH 54621;
Sprattus sprattus (Linnaeus, 1758): AMNH 36845;
Stolephorus indicus (van Hasselt, 1823): AMNH 32820;
Thryssa hamiltonii Gray, 1835: AMNH 38188;

Fossil Clupeiformes:
†*Apricenaclupea ridewoodi* Taverne, 2014: MCSNV Ap5, Ap6;
†*Bolcaichthys catopygopterus* (Woodward, 1901): NHMUK PV P.3829a; MCSNV IG.VR.57598/57599; MCSNV IG.VR.71407/71408; MCSNV T.361; 283 additional specimens listed in Supplementary Data 1 in Marramà & Carnevale (2015b);
†*Eoalosa janvieri* Marramà & Carnevale, 2018: MNHN F.Bol475;
†*Eoengraulis fasoloi* Marramà & Carnevale, 2016: MCSNV T.54;
†*Garganoclupea svetovidovi* Taverne, 2014: MCSNV Ap2, Ap8, Ap9, Ap10, Ap49,
†*Gosiutichthys parvus* Grande, 1982: MRSN P/111 (eight specimens);
†*Italoclupea nolfi* Taverne, 2007: MCSNV Na5, Na7, Na28, Na33, Na38, Na39, Na42, Na43, Na77, Na85, Na90, Na92, Na134, Na151, Na267, Na526, Na530, Na533, Na538;
†*Knightia eocaena* Jordan, 1907; MRSN P/109;
†*Lecceclupea ehiravaensis* Taverne, 2011: MCSNV Na271, Na374, Na551, Na552, Na553, Na554;
†*Nardoclupea grandei* Taverne, 2002: MCSNV Na1, Na2, Na4, Na10, Na35, Na56, Na61, Na110, Na129, Na221, Na231, Na231, Na247, Na250, Na435, Na437, Na438, Na443, Na445, Na452, Na463;
†*Portoselvaggioclupea whiteheadi* Taverne, 2007: MCSNV Na542;
†*Santanaclupea silvasantoi* Maisey, 1993: AMNH 12789, 12790, 18968;
†*Scombroclupea macrophthalma* (Heckel, 1849): MNHN F.HAK454, F.HAK465, F.HAK468, F.HAK675, F.HAK688, F.HAK701, F.HAK1252, F.HAK1413, F.HAK1474; MRSN P/1939;
†*Trollichthys bolcensis* Marramà & Carnevale, 2015: MSNM V2890, V235, IG.VR.24388, IG.VR.132573/132574, IG.VR.81999/82000, IG.VR.82193/82194; NHMUK PV OR.37227;

†Ellimmichthyiformes:
†*Armigatus alticorpus* Forey, Yi, Patterson & Davies, 2003: NHMUK PV P.63134;
†*Armigatus brevissimus* (Blainville, 1818): MNHN F.BOL448; F.HAK481, F.HAK661, F.HAK654, F.HAK659, F.HAK1014, F.HAK1015; F.HAK1023; NHMUK PV P.3825, P.47890/1, P.47316, P.49488, P.51673, P.106, P.108;

†*Armigatus elatus* (Costa, 1850): CMSNF M.538, M.442, M.537/M.441;
†*Armigatus namourensis* Forey, Yi, Patterson & Davies, 2003: NHMUK PV P.59808, P.62527, P.62528, P.62529, P.63135, P.63140, P.63146, P.63151;
†*Armigatus plinii* Marramà & Carnevale, 2023: CMSNF M.536;
†*Diplomystus birdi* Woodward, 1895: MNHN F.HAK409, F.HAK381, F.HAK1953G, F.HAK1724, F.320, F.321;
†*Diplomystus dentatus* Cope, 1877: MGPTPU 130443; MRSN P/107 (three specimens), P/109; NHMUK PV P.52501;
†*Diplomystus dubertreti* Signeux, 1951: MNHN F.SHA2052, F.SHA2053;
†"*Diplomystus*" *goodi* Eastman, 1912: AMNH 819, 6145, 6146, 6153, 6155, 6156, 6160;
†*Ellimma branneri* (Jordan, 1910): AMNH 10048, 10057, 10060;
†*Ellimmichthys longicostatus* (Cope, 1886) AMNH 734 (two specimens);
†*Eoellimmichthys superstes* Marramà, Bannikov, Kriwet & Carnevale, 2019: MCSNV IG.23695;
†*Gasteroclupea branisai* Signeux, 1964: AMNH 8672, 8674; MNHN F.1963.11.1, F.1963.11.2, F.1963.11.10, F.1963.11.13, F.1963.11.14, F.1963.11.16, F.1963.11.20;
†*Ornategulum sardinioides* (Pictet, 1850): NHMUK PV P.63293;
†*Paraclupea chetungensis* Sun, 1956: silicon mould of IVPP V3002.19;
†*Paraclupea pietrarojae* Marramà & Carnevale, 2023: MRSN P/260.3, P/260.11, P/260.2; CMSNF M.19254, M.19279, M.19283, M.19284, M.19433, M.19456, M.19285, M.19262;
†*Paraclupea solignaci* (Gaudant & Gaudant, 1971): MNHN F.PSA215;
†*Pugliaclupea nolardi* Taverne, 2004: MCSNV Na75, Na76, Na543;
†*Sorbinichthys elusivo* Bannikov & Bacchia, 2000: MNHN F.NRA40, F.NRA61, F.NRA62, F.NRA102;
†*Triplomystus* sp.: MNHN F.NRA6, F.NRA7, F.NRA9, F.NRA25a, F.NRA25b, F.NRA27, F.NRA39, F.NRA89;
†*Triplomystus noorae* Forey, Yi, Patterson & Davies, 2003: MNHN F.NRA76;

Appendix 2. — Data matrix used in the phylogenetic analysis. https://doi.org/10.7934/X31508

Appendix 3. — List of the living and fossil taxa included in this study, with information about their temporal range (including First Appearance Datum [FAD] and Last Appearance Datum [LAD] in million years), habitat preferences, fossil locality and their past geographic realm used for calibration and ancestral state reconstruction analyses.

Fossil taxon	**Geological age**	**FAD**	**LAD**	**Habitat**	**Fossil Locality**	**Geographic realm**	**References**
†*Armigatus alticorpus*	Cenomanian	100.5	93.9	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey *et al.* 2003
†*Armigatus brevissimus*	Cenomanian	100.5	93.9	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey *et al.* 2003
†*Armigatus carrenoae*	middle-late Albian	103.0	100.5	marine	Middle Member of Tlayúa Fm, Mexico	Gulf of Mexico	Alvarado-Ortega *et al.* 2020
†*Armigatus dalmaticus*	Campanian	83.6	72.2	marine	Dalmatia, Croatia	Neotethys	Vernygora & Murray 2021
†*Armigatus elatus*	early Albian	113.2	109.0	marine	Pietraroja Plattenkalk, Italy	Neotethys	Marramà & Carnevale 2023
†*Armigatus felixi*	middle-late Albian	103.0	100.5	marine	Middle Member of Tlayúa Fm, Mexico	Gulf of Mexico	Than-Marchese & Alvarado-Ortega 2022
†*Armigatus namourensis*	middle Cenomanian	97.0	95.5	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey *et al.* 2003
†*Armigatus oligodentatus*	late Cenomanian-early Turonian	95.0	93.0	marine	Akrabou Fm, Morocco	Neotethys	Vernygora & Murray 2016
†*Armigatus plinii*	early Albian	113.2	109.0	marine	Pietraroja Plattenkalk, Italy	Neotethys	Marramà & Carnevale 2023
†*Bolcaichthys catopygopterus*	late Ypresian	50.7	48.96	marine	Bolca Lagerstatte, Italy	Neotethys	Marramà & Carnevale 2015b
†*Chasmoclupea aegyptica*	Rupelian	33.9	27.3	freshwater	Jebel Qatrani Fm, Fayum, Egypt	Palaearctic	Murray *et al.* 2005
†*Clupeopsis straeleni*	Ypresian	56.0	48.7	marine	Dubois clay pit, Belgium	Circum-Arctic Ocean	Capobianco *et al.* 2020
†*Codoichthys carnavalii*	late Aptian	115.0	113.2	euryhaline	Upper Unit of Codó Formation, NE Brazil	South Atlantic Ocean	Figueiredo & Ribeiro 2016; Lindoso *et al.* 2016
†*Cynoclupea nelsoni*	Barremian	125.77	121.4	euryhaline	Morro do Chaves Fm (Coruripe Group), Brazil	South Atlantic Ocean	Malabarba & Di Dario 2017; Luft-Souza *et al.* 2022
†*Diplomystus birdi*	Cenomanian	100.5	93.9	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Grande 1982a
†*Diplomystus dentatus*	Ypresian	56.0	48.7	freshwater	Fossil Lake, Green River Fm, USA	Nearctic	Grande 1982a
†*Diplomystus dubertreti*	Santonian	85.7	83.6	marine	Sahel Alma Lagerstatte, Chekka Fm, Lebanon	Neotethys	Grande 1982a
†*Diplomystus shengliensis*	Lutetian-Bartonian	48.07	37.71	freshwater	Shahejie Fm, Shandong, China	Orient	Chang & Maisey 2003; Zheng *et al.* 2022
†*Ellimma branneri*	Aptian	121.4	113.2	euryhaline	Muribeca Fm (Coruripe Group), Brazil	South Atlantic Ocean	Chang & Maisey 2003; Lindoso *et al.* 2016; Luft-Souza *et al.* 2022
†*Ellimma longipectoralis*	Aptian	121.4	113.2	euryhaline	Barra Velha Fm, Santos Basin, Brazil	South Atlantic Ocean	Polck *et al.* 2020
†*Ellimmichthys longicostatus*	Berriasian-Valanginian	143.1	132.6	freshwater	Candeias Fm (Recôncavo Basin) Brazil	Neotropics	Figueiredo & Gallo 2021; Nery do Amaral *et al.* 2024
†*Ellimmichthys spinosus*	Berriasian-Valanginian	143.1	132.6	freshwater	Candeias Fm Recôncavo Basin) Brazil	Neotropics	Figueiredo & Gallo 2021; Nery do Amaral *et al.* 2024
†*Eoalosa janvieri*	late Ypresian	49.7	49.5	marine	Bolca Lagerstatte, Italy	Neotethys	Marramà & Carnevale 2018
†*Eoellimmichthys superstes*	late Ypresian	49.7	49.5	marine	Bolca Lagerstatte, Italy	Neotethys	Marramà *et al.* 2019
†*Eoengraulis fasoloi*	late Ypresian	49.7	49.5	marine	Bolca Lagerstatte, Italy	Neotethys	Marramà & Carnevale 2016
†*Ezkutuberezi carmenae*	upper Valanginian–middle Barremian	135.0	124.0	euryhaline	Villaro Member of Villaro Fm, Spain	Neotethys	Poyato-Ariza *et al.* 2000
†*Foreyclupea loonensis*	Albian	113.2	100.5	marine	Loon River Fm, Canada	Circum-Arctic Ocean	Vernygora *et al.* 2016
†*Gasteroclupea branisai*	Maastrichtian-Danian	72.2	61.7	freshwater	Molino Fm, Chaunaca Fm, Santa Lucía Fm, Navay Fm, Yacoraite Fm, South America	Neotropics	Marramà & Carnevale 2017
†*Gosiutichthys parvus*	Ypresian	56.0	48.7	freshwater	Fossil Lake, Green River Fm, USA	Nearctic	Grande 1982b
†*Guiclupea superstes*	Oligocene	33.9	23.04	freshwater	Ningming Fm, Yongning Fm, China	Orient	Chen *et al.* 2021

Appendix 3. — Continuation.

Fossil taxon	Geological age	FAD	LAD	Habitat	Fossil Locality	Geographic realm	References
†*Italoclupea nolfi*	Campanian	83.6	72.2	marine	“Calcari di Melissano”, Nardò, Italy	Neotethys	Taverne 2007; Schlüter *et al.* 2008
†*Knightia vetusta*	Salendian	61.7	59.2	freshwater	Tongue River Fm, USA	Nearctic	Grande 1982b
†*Leufuichthys minimus*	late Turonian-early Coniacian	93.0	87.0	freshwater	Neuquén Group of Portezuelo Fm, Argentina	Neotropics	Gallo *et al.* 2011
†*Monosmilus chureloides*	early Lutetian	48.1	45.0	marine	NP 15 zone of Domanda Fm, Pakistan	Neotethys	Capobianco *et al.* 2020
†*Nardoclupea grandei*	Campanian	83.6	72.2	marine	“Calcari di Melissano”, Nardò, Italy	Neotethys	Taverne 2002; Schlüter *et al.* 2008
†*Nolfia riachuelensis*	Albian	113.2	100.5	marine	Riachuelo Fm (Sergipe Group), Brazil	South Atlantic Ocean	Figueiredo 2009b; Luft-Souza *et al.* 2022
†*Ornategulum sardinioides*	middle Cenomanian	97.0	95.5	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey 1973a
†*Palaeodenticeps tanganikae*	Lutetian	46.0	45.7	freshwater	Maar lake of Mahenge, Iramba Plateau, Tanganyika Territory, Tanzania	Afrotropics	Greenwood 1960
†*Paraclupea chetungensis*	early Aptian	121.4	113.2	euryhaline	Chawan Fm, China	North Pacific Ocean	Chang & Grande 1997; Gao *et al.* 2022
†*Paraclupea pietrarojae*	early Albian	113.2	109.0	marine	Pietraroja Plattenkalk, Italy	Neotethys	Marramà & Carnevale 2023
†*Paraclupea seilacheri*	middle-late Albian	103.0	100.5	marine	Middle Member of Tlayúa Fm, Mexico	Gulf of Mexico	Alvarado-Ortega & Melgarejo-Damián 2017
†*Paraclupea solignaci*	Coniacian-Santonian	89.8	83.6	marine	El Hamma (Gabès, Tunisia)	Neotethys	Marramà *et al.* 2022
†*Pseudoellimma gallae*	Barremian	125.77	121.4	euryhaline	Coqueiro Seco Fm (Coruripe Group), Rift Stage of the Sergipe-Alagoas, Brazil	South Atlantic Ocean	Figueiredo 2009a; Luft-Souza *et al.* 2022
†*Ranulfoichthys dorsonudum*	Albian	113.2	100.5	marine	Middle Member of Tlayúa Fm, Mexico	Gulf of Mexico	Alvarado-Ortega 2014
†*Rhombichthys intoccabilis*	early-middle Cenomanian	100.5	95.5	marine	Bet Meir or Amminadav Fm, Palestine	Neotethys	Khalloufi *et al.* 2010
†*Santanaclupea silvasantoi*	late Aptian-early Albian	115.0	109.0	euryhaline	Romualdo Fm (previously member of Santana Fm) (Araripe Basin), Brazil	South Atlantic Ocean	Maisey 1993; Melo *et al.* 2020
†*Scombroclupea macrophthalma*	Cenomanian	100.5	93.9	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey *et al.* 2003
†*Scutatoclupea applegatei*	Albian	113.2	100.5	euryhaline	Sierra Madre Fm, Mexico	Gulf of Mexico	Alvarado-Ortega & Ovalles-Damián 2008
†*Scutatoclupea bacchiai*	middle Cenomanian	97.0	95.5	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Bannikov 2015
†*Scutatuspinosus itapagipensis*	Hauterivian	132.6	125.77	euryhaline	Marfim Fm (Recôncavo Basin), Brazil	South Atlantic Ocean	Figueiredo & Ribeiro 2017
†*Sorbinichthys africanus*	late Cenomanian-early Turonian	95.0	93.0	marine	Akrabou Fm, Morocco	Neotethys	Murray & Wilson 2011
†*Sorbinichthys elusivo*	middle Cenomanian	97.0	95.5	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Bannikov & Bacchia 2000
†*Spratticeps gaultinus*	middle Albian	113.2	100.5	marine	Gault Fm, England	Circum-Arctic Ocean	Patterson 1970; Gallois & Owen 2019
†*Thorectichthys marocensis*	late Cenomanian-early Turonian	95.0	93.0	marine	Akrabou Fm, Morocco	Neotethys	Murray & Wilson 2013
†*Thorectichthys rhadinus*	late Cenomanian-early Turonian	95.0	93.0	marine	Akrabou Fm, Morocco	Neotethys	Murray & Wilson 2013
†*Tischlingerichthys viohli*	Tithonian	149.2	143.1	marine	Solnhofen Limestone, Germany	Neotethys	Arratia 1997
†*Triplomystus noorae*	middle Cenomanian	97.0	95.5	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey *et al.* 2003
†*Triplomystus oligoscutatus*	middle Cenomanian	97.0	95.5	marine	Sannine Lagerstatte, Sannine Fm, Lebanon	Neotethys	Forey *et al.* 2003
†*Trollichthys bolcensis*	late Ypresian	50.7	48.96	marine	Bolca Lagerstatte, Italy	Neotethys	Marramà & Carnevale 2015a
†*Tunisiaclupea speratus*	upper Barremian	125.77	121.4	euryhaline	Sidi Aich Fm, Tunisia	Neotethys	Boukhalfa *et al.* 2018
†*Tycheroichthys dunveganensis*	middle Cenomanian	97.0	95.5	euryhaline	Dunvegan Fm, Canada	Circum-Arctic Ocean	Hay *et al.* 2007

Appendix 3. — Continuation.

Living taxon	Geological age	FAD	LAD	Habitat	Fossil Locality	Geographic realm	References
Albula vulpes	Holocene	0.01	0	marine	–	West Atlantic, Northwest Atlantic	Froese & Pauly 2025
Alepocephalus rostratus	Holocene	0.01	0	marine	–	Northeast Atlantic, East Atlantic	Froese & Pauly 2025
Alosa sapidissima	Holocene	0.01	0	euryhaline	–	Northeast Atlantic, North Pacific, Ponto-Caspian System	Froese & Pauly 2025
Amblygaster leiogaster	Holocene	0.01	0	marine	–	Indo-West Pacific	Froese & Pauly 2025
Anchoa compressa	Holocene	0.01	0	euryhaline	–	North Pacific	Froese & Pauly 2025
Anchovia clupeoides	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Anchoviella lepidentostole	Holocene	0.01	0	euryhaline	–	West Atlantic, East Pacific	Froese & Pauly 2025
Anodontostoma chacunda	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Brevoortia tyrannus	Holocene	0.01	0	euryhaline	–	Northwest Atlantic, West Atlantic, South South America	Froese & Pauly 2025
Cetengraulis edentulus	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Chanos chanos	Holocene	0.01	0	euryhaline	–	Indo-West Pacific, South Africa, East Pacific, North Pacific, South Australia	Froese & Pauly 2025
Chirocentrodon bleekerianus	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Chirocentrus dorab	Holocene	0.01	0	marine	–	Indo-West Pacific	Froese & Pauly 2025
Clupanodon thrissa	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Clupea harengus	Holocene	0.01	0	marine	–	Northwest Atlantic, Northeast Atlantic, North Pacific	Froese & Pauly 2025
Clupeichthys aesarnensis	Holocene	0.01	0	freshwater	–	Orient	Froese & Pauly 2025
Clupeoides papuensis	Holocene	0.01	0	freshwater	–	Orient	Froese & Pauly 2025
Clupeonella cultriventris	Holocene	0.01	0	euryhaline	–	Ponto-Caspian System	Froese & Pauly 2025
Coilia brachygnathus	Holocene	0.01	0	freshwater	–	Orient	Froese & Pauly 2025
Corica soborna	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Denticeps clupeoides	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Dorosoma petenense	Holocene	0.01	0	euryhaline	–	East Pacific, West Atlantic	Froese & Pauly 2025
Dussumieria acuta	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Encrasicholina purpurea	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Engraulis mordax	Holocene	0.01	0	marine	–	North Pacific, Northwest Atlantic, Northeast Atlantic, South Africa, South South America, South Australia	Froese & Pauly 2025
Escualosa thoracata	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Etrumeus sadina	Holocene	0.01	0	marine	–	Indo-West Pacific, West Atlantic, East Pacific, North Pacific, North Pacific, Northwest Atlantic, South Africa, South Australia	Froese & Pauly 2025
Gilchristella aestuaria	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Harengula jaguana	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Herklotsichthys dispilonotus	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Hilsa kelee	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Hyperlophus vittatus	Holocene	0.01	0	euryhaline	–	South Australia	Froese & Pauly 2025
Ilisha kampeni	Holocene	0.01	0	euryhaline	–	Indo-West Pacific, West Atlantic, East Pacific	Froese & Pauly 2025

Appendix 3. — Continuation.

Living taxon	Geological age	FAD	LAD	Habitat	Fossil Locality	Geographic realm	References
Jenkinsia lamprotaenia	Holocene	0.01	0	marine	–	West Atlantic	Froese & Pauly 2025
Kneria auriculata	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Konosirus punctatus	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Lile stolifera	Holocene	0.01	0	marine	–	East Pacific	Froese & Pauly 2025
Limnothrissa miodon	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Lycengraulis grossidens	Holocene	0.01	0	euryhaline	–	West Atlantic, East Pacific	Froese & Pauly 2025
Lycothrissa crocodilus	Holocene	0.01	0	freshwater	–	Orient	Froese & Pauly 2025
Microthrissa royauxi	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Nannothrissa stewarti	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Nematalosa erebi	Holocene	0.01	0	freshwater	–	Australia	Froese & Pauly 2025
Neoopisthopterus tropicus	Holocene	0.01	0	euryhaline	–	East Pacific	Froese & Pauly 2025
Odaxothrissa losera	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Odontognathus mucronatus	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Opisthonema oglinum	Holocene	0.01	0	marine	–	West Atlantic	Froese & Pauly 2025
Opisthopterus equatorialis	Holocene	0.01	0	euryhaline	–	East Pacific	Froese & Pauly 2025
Osmerus mordax	Holocene	0.01	0	euryhaline	–	Northeast Atlantic, Northwest Atlantic, North Pacific	Froese & Pauly 2025
Pellona ditchela	Holocene	0.01	0	euryhaline	–	Indo-West Pacific, West Atlantic	Froese & Pauly 2025
Pellonula leonensis	Holocene	0.01	0	euryhaline	–	East Atlantic	Froese & Pauly 2025
Platanichthys platana	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Pliosteostoma lutipinnis	Holocene	0.01	0	marine	–	East Pacific	Froese & Pauly 2025
Potamalosa richmondia	Holocene	0.01	0	euryhaline	–	South Australia	Froese & Pauly 2025
Potamothrissa obtusirostris	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Pristigaster cayana	Holocene	0.01	0	freshwater	–	Neotropics	Froese & Pauly 2025
Pterengraulis atherinoides	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Raconda russeliana	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Rhinosardinia amazonica	Holocene	0.01	0	euryhaline	–	West Atlantic	Froese & Pauly 2025
Sardina pilchardus	Holocene	0.01	0	euryhaline	–	Northeast Atlantic	Froese & Pauly 2025
Sardinella maderensis	Holocene	0.01	0	euryhaline	–	Indo-West Pacific, East Atlantic, West Atlantic	Froese & Pauly 2025
Sardinops sagax	Holocene	0.01	0	marine	–	North Pacific, Northwest Atlantic, South Africa, South South America, South Australia	Froese & Pauly 2025
Setipinna tenuifilis	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Spratelloides delicatulus	Holocene	0.01	0	marine	–	Indo-West Pacific	Froese & Pauly 2025
Sprattus sprattus	Holocene	0.01	0	euryhaline	–	Northeast Atlantic, Ponto-Caspian system	Froese & Pauly 2025
Stolephorus indicus	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025
Stolothrissa tanganicae	Holocene	0.01	0	freshwater	–	Afrotropics	Froese & Pauly 2025
Tenualosa thibaudeaui	Holocene	0.01	0	freshwater	–	Orient	Froese & Pauly 2025
Thryssa hamiltonii	Holocene	0.01	0	euryhaline	–	Indo-West Pacific	Froese & Pauly 2025