CHAPTER 1

Progress in Clupeiform Systematics

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1.1 Introduction: the Clupeiformes, a diverse and natural group of fishes

Phylogenetic trees depicting evolutionary relationships and classifications based on these relationships are the central underpinning of research in biology (Baum and Smith 2013). Within a phylogenetic framework, it is possible to study the pattern and process of evolution of morphological, physiological and genetic traits among organisms, and it allows interpreting biogeographic patterns within an historical perspective. It also provides guidelines for conservation and management of natural resources such as fisheries.

However, it is sometimes challenging to infer reliable, fully resolved phylogenetic trees due to the effects of several processes (e.g., convergence, rapid diversification, ancestral polymorphism, incomplete lineage sorting, horizontal gene transfer, etc.) and/or methodological artifacts (e.g., inappropriate phylogenetic method, inadequate character sampling and/ or incomplete taxon sampling, etc.).

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The understanding of the phylogeny of the Clupeiformes (i.e., sardines, herrings, anchovies, sprats, wolf herrings, shads and relatives) has made important progress in the last 50 yr thanks to the efforts to search for natural groups (monophyletic groups or clades) based on shared and derived morphological and molecular characters, using comprehensive taxon sampling. The current phylogenetic hypothesis of the Clupeiformes may serve as a framework to discuss the evolution and biogeography of these fishes.

The living Clupeiformes comprise approximately 400 valid species classified into five to seven families and two suborders (Denticipitoidei and Clupeoidei) (Eschmeyer 2013, Nelson 2006). The only extant species of the suborder Denticipitoidei, *Denticeps clupeoides* occurs in the region of the Niger Delta in West Africa (Clausen 1959). A 45 million-yr-old fossil species, †*Paleodenticeps tanganikae*, has been described from East Africa (Greenwood 1960). The two denticipitid species are strictly freshwater. The suborder Clupeoidei has a worldwide distribution with marine, euryhaline and freshwater species along with tropical, subtropical and temperate species. Herrings, sardines and anchovies often are important parts of assemblages of pelagic fishes off coasts. The two-volume FAO catalog for the clupeoid fishes provides the distribution and the salinity preference for each species known at that time along with additional biological and fisheries data (Whitehead 1985a, Whitehead et al. 1988).

Most of the clupeoid species have distributions restricted to one of the world marine biogeographic provinces (Briggs and Bowen 2012). This pattern of high endemism is more accentuated in the tropical regions than in the temperate regions. Lavoué et al. (2013) compiled the distributions of all species together into a density-map to show the species richness per region (Fig. 1.1A).

Species richness is higher in tropical regions than in septentrional and meridional regions, a common distribution pattern known as the latitudinal gradient in species richness (Crame 2001, Hillebrand 2004). The Indo-West Pacific (IWP) region, a region known for its exceptional marine biodiversity (Briggs and Bowen 2012), comprises more clupeoid species than any other tropical region. This is also a general pattern of longitudinal distribution of biodiversity (Briggs 1999, Bellwood and Wainwright 2002).

Most of the clupeiforms are easily recognizable in having the following combination of external characters (Whitehead 1985a): a reduced lateral line system restricted to the head and the anterior portion of the trunk (except for *Denticeps clupeoides*), no spiny fins, no adipose fin, a short dorsal fin (absent in *Raconda*), presence of a series of abdominal scutes, which are modified scales anterior and posterior of the pelvic fins (Fig. 1.2A); sometimes the series is reduced to a single pelvic scute in front of the pelvic fins (e.g., dussumieriids, *Congothrissa gossei*, etc.) or completely absent (*Sundasalanx*).
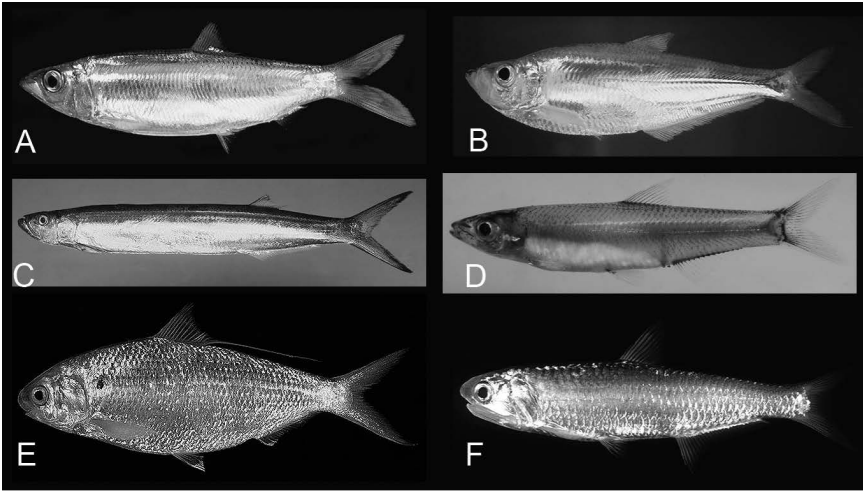
Clupeoid distribution and species richness

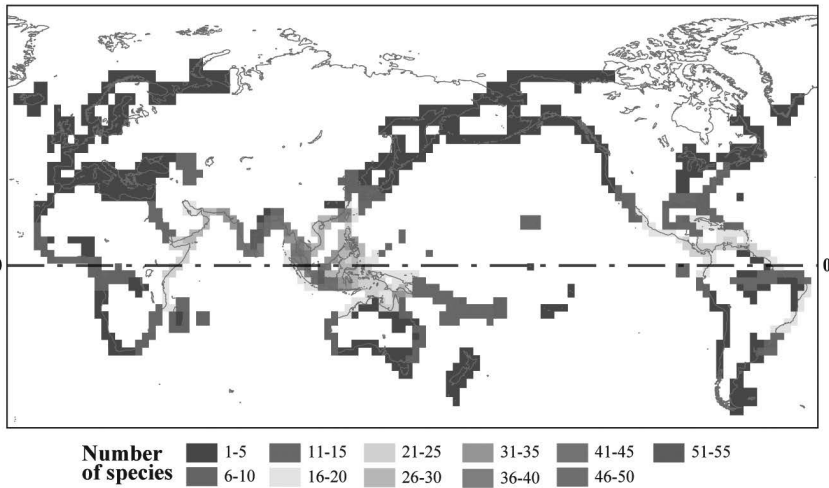| Number of species					
1-5	11-15	21-25	31-35	41-45	51-55
6-10	16-20	26-30	36-40	46-50	

Figure 1.1. Top: Live photos of representatives of Clupeoidei. A) *Dussumieria acuta* Dussumieriidae (standard length (SL) about 11 cm, photo John Randall), B) *Ilisha elongata*, Pristigasteridae (SL ~ 22 cm, photo John Randall), C) *Chirocentrus dorab*, Chirocentridae (SL ~ 34 cm, photo John Randall), D) *Sauvagella madagascariensis*, Clupeidae, Ehiravinae (SL ~ 10 cm, photo Paul V. Loiselle), E) *Nematalosa nasus*, Clupeidae, Dorosomatinae (SL ~ 16 cm, photo John Randall) and F) *Thryssa baelama*, Engraulidae (SL ~ 10 cm, photo John Randall). Bottom: Approximate distribution and species richness of Clupeoidei. Number of species per grid cell (4 degree latitude by 4 degree longitude resolution) is represented by cool (low diversity) to warm (high diversity) colours. Modified from Lavoué et al. (2013).

Color image of this figure appears in the color plate section at the end of the book.
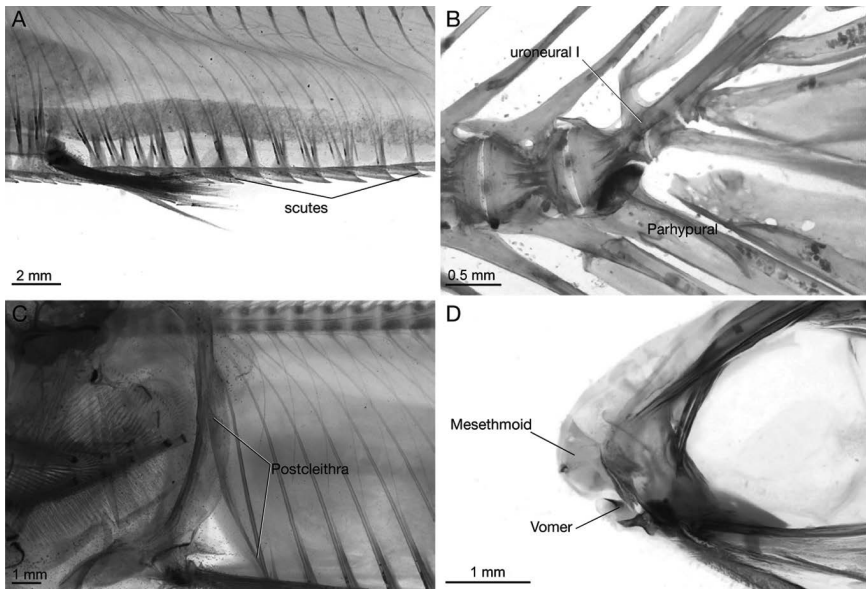
Figure 1.2. Morphological characters important in the systematics of the Clupeiformes (shown on cleared and stained specimens). A–C, *Alosa aestivalis*; D, *Anchoa mitchili*. A) abdominal (=ventral) scutes anterior and posterior of the pelvic fins. B) Fusion of the first uroneural with the first preural centrum and the autogenous parhypural. C) Pectoral girdle with two postcleithra. D) Anterior part of the head with the large mesethmoid and the vomer.

Color image of this figure appears in the color plate section at the end of the book.

The single pelvic scute in the wolf herring *Chirocentrus* is further reduced. The range in size is noteworthy: from large species (up to 1 meter standard length [SL]; species of *Chirocentrus*) to miniature species sexually mature at about 2 centimeters SL (e.g., *Thrattidion noctivagus*, *Amazonsprattus scintilla* or species of *Sundasalanx*). Anchovies genus *Coilia* have elongated tapering bodies while the two *Pristigaster* species possess rather deep bodies. Some species lack scales (e.g., *Amazonsprattus scintilla*, *Minyclupeoides dentibranchius*) or pelvic fins (e.g., several pristigasterids, *Pseudosetipinna haizhouensis*).

The extant clupeiforms, along with the extinct order †Ellimmichthyiformes and the extinct genera †*Armigatus* and †*Erichalcis*, were combined into the superorder Clupeomorpha (Grande 1985) (Fig. 1.3A).

Arratia (1997) removed the enigmatic genus †*Erichalcis* from the Clupeomorpha as it shows closer affinities with the Euteleostei. Among the living teleostean fishes, the characters that diagnose the Clupeomorpha are also diagnostic for the Clupeiformes because there is no living non-clupeiform clupeomorphs. Greenwood et al. (1966) provided the first synapomorphy-based definition of the Clupeomorpha which was
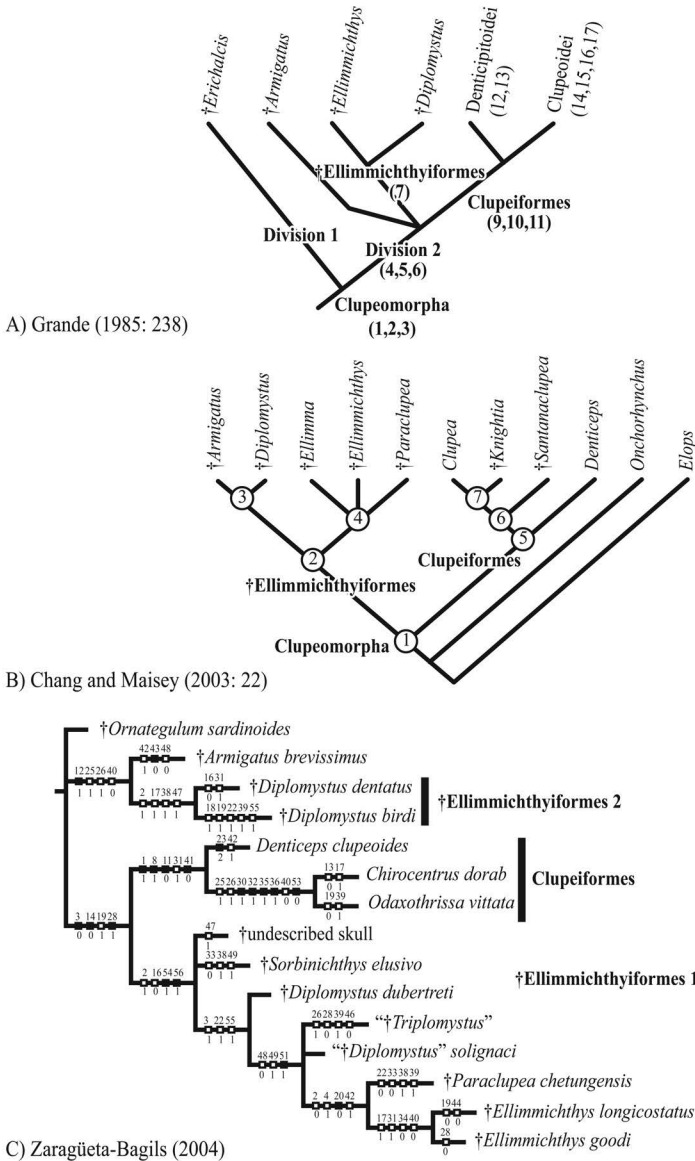
Figure 1.3. Three phylogenetic hypotheses of the Clupeomorpha. A) Modified from Grande (1985); numbers in parentheses refer to the synapomorphies as listed and discussed in Grande (1985). B) Modified from Chang and Maisey (2003); number in circle refers to clade number as discussed in Chang and Maisey (2003). C) Modified from Zaragüeta-Bagils (2004); character states are indicated by squares along the corresponding branch with numbers above referring to character numbers and numbers below referring to state numbers (both as listed in Zaragüeta-Bagils 2004). The hypothesis A includes †*Erichalcis* in the Clupeomorpha, whereas the hypotheses B and C exclude it.

subsequently critically reviewed and expanded by Patterson and Rosen (1977) and Grande (1985). There is strong evidence that the Clupeomorpha (excluding †*Erichalcis*) form a natural assemblage (Grande 1985, Chang and Maisey 2003, Forey 2004, Zaragüeta-Bagils 2004) (Fig. 1.3A, B and C).

Several major evolutionary features distinguish clupeomorphs (and extant clupeiforms) from their immediate relatives, among them [characters 1–3 in Fig. 1.4]: 1) "the extension of the gas bladder into the brain case so that it contacts the inner ear" (Patterson and Rosen 1977, Grande 1982a), 2) "the reduction of the caudal skeleton" (Patterson and Rosen 1977) (Fig. 2B) and 3) "one or more abdominal scutes, each an unpaired element that crosses ventral midline of body" (Whitehead 1963a, Patterson 1970).

The Clupeiformes have a rich fossil record (with more than 150 extinct species excavated globally) that dates the origin of this group to the Lower Cretaceous (Grande 1985, Murray et al. 2005, De Figueiredo 2009a). The first fossils assigned to the Clupeoidei date back to the mid Cretaceous and were mostly discovered from tropical marine or estuarine deposits in South America, Africa and the Tethys Sea region (Taverne 1997a,b, Forey et al.
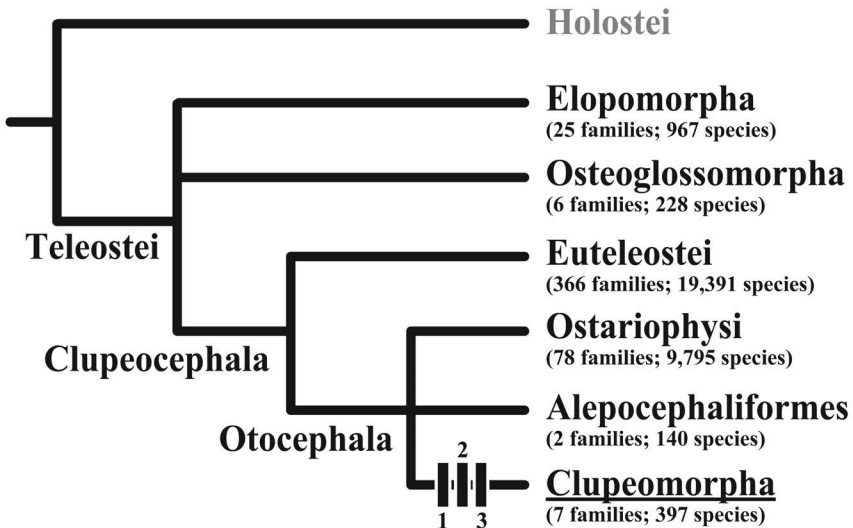

Figure 1.4. A phylogenetic hypothesis for the position of the Clupeomorpha within the Teleostei. The Holostei (bowfin and gars) are considered as the living sister group of the Teleostei. Within the Teleostei, three main lineages are recognized: the Osteoglossomorpha (bony-tongue fishes), the Elopomorpha (eels and relatives) and the Clupeocephala. The Clupeomorpha belong to the Clupeocephala, which are closely related to the Ostariophysi and Alepocephaliformes. The number of families and species for each main teleost lineage indicated in parentheses (from Eschmeyer 2013).

2003, De Figueiredo 2009a,b). During the Upper Cretaceous, clupeiforms (especially the early clupeoids) were well diversified with several primitive forms that represent ancient and extinct lineages, sometimes of uncertain affinities (Chang and Maisey 2003, De Figueiredo 2009a,b) along with more recent forms assignable to extant clupeoid lineages (Taverne 2002, 2004, 2007a,b, 2011). Altogether, these and other fossils provide relevant knowledge on the evolution of the early clupeiforms and clupeoids such as information about their paleodistribution and paleobiogeography (Chang and Maisey 2003, Cavin 2008), paleoenvironment (Newbrey et al. 2010) and character evolution (De Figueiredo 2009a).

Hereafter and unless otherwise stated, only the systematics of the living clupeomorphs, all belonging to the order Clupeiformes, will be introduced. Therefore, we indiscriminately use the names Clupeomorpha and Clupeiformes to designate them.

1.2 The phylogenetic position of the Clupeomorpha within the Teleostei

1.2.1 Strong morphological support for the monophyly of the Clupeocephala

 Modern research of the phylogenetic position of the living Clupeomorpha within the Teleostei began with the publication of Greenwood et al. (1966). Reviews of earlier works relative to the position of the Clupeomorpha can be found elsewhere (Grande 1985, Whitehead 1985b, Lecointre and Nelson 1996).

In Greenwood et al. (1966), the Clupeomorpha were considered as one of the four main lineages within the Teleostei along with the Elopomorpha (= Division I of Greenwood et al. (1966)), the Osteoglossomorpha (= Division II) and the Euteleostei (= Division III) [consult Fig. 1 in Greenwood et al. (1966)]. The phylogenetic relationships among these four groups were left unresolved but these authors suggested in their section *Provisional outline classification of the Teleostean fishes* (Greenwood et al. 1966: pages 393–394) that the Elopomorpha and the Clupeomorpha share a common ancestry. Nelson (1973) and Patterson and Rosen (1977) united the Clupeomorpha and the Euteleostei to form the cohort Clupeocephala (Fig. 1.4). Patterson and Rosen (1977) presented five morphological characters to diagnose the Clupeocephala. According to a recent series of works on the basal teleost relationships (Arratia 1997, 1999, 2010), no less than 10 synapomorphies support the monophyly of the Clupeocephala.

1.2.2 The phylogenetic position of the Clupeomorpha within the Clupeocephala

Whereas the monophyly of the Clupeocephala is well documented on the basis of several anatomical characters as well as the monophyly of the modern clupeomorphs [see the early review by Lauder and Liem (1983)], the phylogenetic position of the Clupeomorpha within the Clupeocephala was until recently uncertain because of the difficulty of diagnosing the Euteleostei. Rosen (1985) was the first author to redefine the Euteleostei based on "the presence of an adipose dorsal fin". Consequently, he excluded the esocoids from the Euteleostei, as they lack such adipose fin. The relative positions among the Clupeomorpha, Esocoidei and the Euteleostei *sensu* Rosen (1985) were left unresolved. The first molecular studies aiming to test the phylogenetic relationships among the so-called "basal" teleosts found unexpected results regarding the phylogenetic position of the Clupeomorpha.

The rapid and continuing development of molecular systematics from the end of the 1980s was catalyzed by the advances of molecular biology (e.g., the polymerase chain reaction), the development of phylogenetic reconstruction methods (e.g., parsimony and maximum likelihood) and new computing technologies (e.g., faster microprocessors). These developments made it possible to test morphology-based phylogenetic hypotheses by directly examining inherited genetic variation. Molecular markers provide additional characters that can be used to track the evolution of lineages. Morphological and molecular studies are complementary approaches to search for phylogenetic relationships and often both approaches yield similar results. Cases of strong incongruence are rare but often informative, as it requires the re-examination of the morphological and molecular evidence to document the source of the conflict.

One of the first unexpected findings in molecular fish systematics was the sister-group relationship between the Clupeiformes and the Ostariophysi (e.g., carps, catfishes, milkfishes and relatives) within the Clupeocephala (Lê et al. 1993). Since the publication of this explorative work, most of the subsequent molecular studies that have included at least one representative from each of the following five groups, Osteoglossomorpha, Elopomorpha, Clupeiformes, Ostariophysi *sensu* Fink and Fink (1981) and Euteleostei (excluding Ostariophysi), have recovered a sister-group relationship between the Clupeiformes and Ostariophysi with high statistical support (Zaragüeta-Bagils et al. 2002, Ishiguro et al. 2003, Lavoué et al. 2005, Li et al. 2008, Near et al. 2012, Chen et al. 2013).

The re-examination of the morphology of these fishes led to the discovery of five synapomorphies (Johnson and Patterson 1996, Lecointre and Nelson 1996, Arratia 1997, Wiley and Johnson 2010). This group is named Otocephala

(Johnson and Patterson 1996) [preferred] or Ostarioclupeomorpha (Arratia 1997) or Otomorpha (Wiley and Johnson 2010).

Whereas the close relationship between the Clupeiformes and Ostariophysi is now well documented, it was only more recently that the phylogenetic position of a largely overlooked group of deep-sea fishes, named the Alepocephaliformes (tubeshoulders and slickheads), was examined using molecular data (Ishiguro et al. 2003). The Alepocephaliformes comprise two to three families and about 100 species (Nelson 2006). It is generally classified within the euteleost order Argentiniformes (Begle 1992, Johnson and Patterson 1996, Nelson 2006). In Ishiguro et al. (2003) as well as in all subsequent molecular studies addressing the relationship of the Alepocephaliformes within the Teleostei, the Alepocephaliformes and the Otocephala form a strongly supported monophyletic group (Lavoué et al. 2008b, Poulsen et al. 2009, Kawaguchi et al. 2012, Near et al. 2012).

As for the relationship between the Clupeiformes and Ostariophysi, the monophyly of the Alepocephaliformes and Otocephala is an unexpected result because the Alepocephaliformes do not appear to share any progressive morphological characters with the Clupeiformes and/or Ostariophysi (Johnson and Patterson 1996, Diogo 2008). Current molecular evidence offers only moderate support for a clade formed by the Alepocephaliformes and the Ostariophysi; the Clupeiformes being the sister group of this clade (Lavoué et al. 2008b, Poulsen et al. 2009, Near et al. 2012).

1.3 Phylogeny and classification of the Clupeoidei (Clupeiformes)

1.3.1 Morphology-based phylogenetic hypotheses

The Clupeoidei is the speciose sister group of the monotypic Denticipitoidei. Several morphological characters support its monophyly (Grande 1985, Di Dario 2004, Di Dario and de Pinna 2006), among them: 1) "Fusion of the first uroneural with the first preural centrum" (Fig. 2B), 2) "reduction in relative size of the first ural centrum" (Fig. 1.2B), 3) "loss of lateral line scales" and 4) "separation of the parhypural from the first ural centrum" (Fig. 1.2B) [characters 4–7 in Fig. 1.7].

Nelson (1967, 1970b) extensively examined the gill arches anatomy of the Clupeoidei (Fig. 1.5A). He recognized four different superfamilies, each comprising only one family: Chirocentroidae (Chirocentridae), Engrauloidae (Engraulidae), Pristigasteroidae (Pristigasteridae) and Clupeoidae (Clupeidae). The interrelationships among these four superfamilies were left unresolved. Whitehead (1985a) and Grande (1985) presented a similar taxonomical arrangement with the same four families (Figs. 1.5B and C). Grande (1985) proposed a single character to support the sister group relationship between the Clupeidae and Chirocentridae (=Clupeoidae)
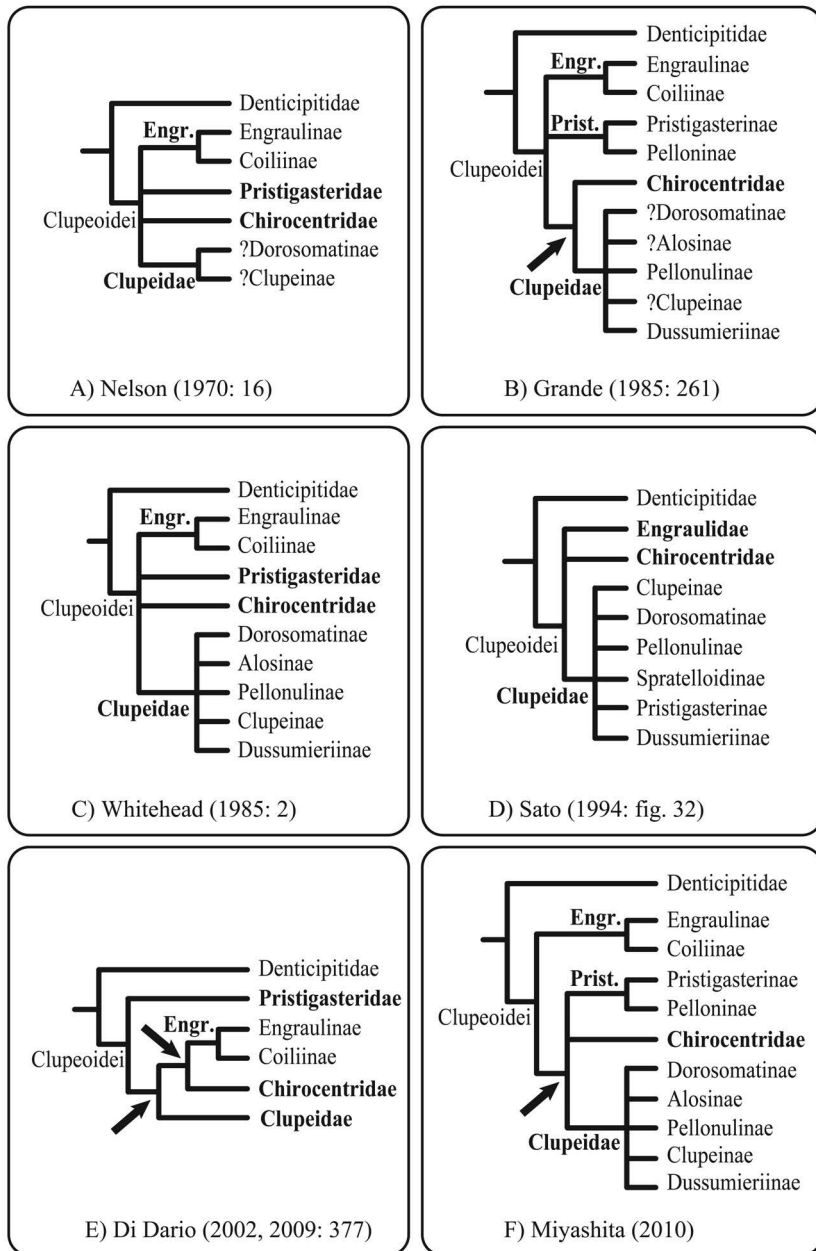
Figure 1.5. Previous family-level phylogenetic hypotheses of the Clupeoidei from Nelson (1970b) to Miyashita (2010). Arrows indicate specific relationships newly supported by the corresponding reference. Question marks indicate poorly defined groups. Abbreviations: Engr., Engraulidae; Prist., Pristigasteridae.

(Fig. 1.5B): "increase in pleural rib to preural vertebrae ratio". Patterson and Johnson (1995) suggested that this character might not be derived. Instead, Patterson and Johnson (1995) offered another character to support the monophyly of Clupeoidae: the "rib/epicentral fusion".

The classification of Sato (1994), based on the interpretation of a cladistic analysis of a morphological dataset, slightly differed from the preceding ones because it did not recognize the Pristigasteridae as a distinct family but as a clupeid subfamily (Fig. 1.5D).

Siebert (1997) identified clupeoid synapomorphies in the paedomorphic freshwater genus *Sundasalanx* (family Sundasalangidae) that was previously classified within the Osmeriformes (Roberts 1981). Siebert (1997) further hypothesized that *Sundasalanx* and the dussumieriid genus *Jenkinsia* were closely related to each other because of the similarity in their caudal skeletons. Subsequent molecular studies confirmed the placement of *Sundasalanx* within the Clupeoidei but not a close relationship to *Jenkinsia* (Ishiguro et al. 2005, Lavoué et al. 2007).

Recently, Di Dario (2002, 2009) and Miyashita (2010) re-examined the relationships among the clupeoid families using different sets of morphological characters (Fig. 1.5E and F). Di Dario (2002) identified three synapomorphies to support the sister relationship between the Clupeoidea of Grande (1985) and the Engraulidae (Engrauloidea) (Fig. 1.5E): 1) "presence of cartilage chevrons at the tips of epicentrals", 2) "posteriorly directed parapophyses of the second vertebra" and 3) "interzygapophyseal articulation" [characters 39–41 in Fig. 1.7]. The Pristigasteridae is hypothesized to be the sister group of this clade. Later, Di Dario (2009) completed his investigation in refuting the monophyly of the Clupeoidea: the Chirocentridae was more closely related to the Engraulidae (Engrauloidea) than to the Clupeidae [see Fig. 10 in Di Dario (2009), p. 377]. Seven characters support this relationship (Di Dario 2009), among them: 1) "posterodorsal margin of metapterygoid in line with the condyle of articulation of the hyomandibula with the opercle", 2) "presence of a laminar outgrowth of the anterior margin of quadrate" and 3) "endochondral portion of quadrate in the shape of an isosceles triangle" [characters 36–38 in Fig. 1.7]. Miyashita (2010) proposed a different hypothesis in which the Engraulidae is the sister group of the rest of the Clupeoidei because the pristigasterids, chirocentrids and clupeids share "a unique occipital articulation with the first vertebra" [character 35 in Fig. 1.7] (Fig. 1.5F).

The classification of the family Clupeidae is the most challenging because of the difficulty of diagnosing the Clupeidae and several of its subfamilies. Nelson (1970b) excluded the Pristigasteridae from the Clupeidae but admitted that, even without the Pristigasteridae, the Clupeidae was still weakly supported by some "tendencies toward loss of teeth, proliferation of gill rakers and development of a mediopharyngobranchial cartilage and

epibranchial organs". Grande (1985) provided one diagnostic character to define the Clupeidae of Nelson (1970b), "the presence of two long, rod-like postcleithra" (Fig. 1.2C) but, notably, this character is absent in three of the four dussumieriid genera (i.e., *Dussumieria*, *Spratelloides* and *Jenkinsia*).

Assuming that the Clupeidae minus the Pristigasteridae is monophyletic, Nelson (1970b) presented two characters to further subdivide this group into two large subfamilies (see his Fig. 11, p. 27): the Clupeinae *sensu* Nelson (1970b) having "the foramen in the fourth epibranchial" (grouping, at least, *Etrumeus*, *Jenkinsia*, *Spratelloides*, *Clupea*, *Sprattus* and *Potamalosa*) and the Dorosomatinae *sensu* Nelson (1970b) based on "the non-overlap of the gill rakers" (grouping, at least, *Sardinella*, *Opisthonema*, *Hilsa* and *Dorosoma*). Neither Whitehead (1985a,b) nor Grande (1985) followed this taxonomic arrangement, but they agreed with Nelson (1970b) that the Pristigasteridae was distinct from the Clupeidae (Fig. 1.5B and C).

Grande (1985) provided diagnoses for the Pellonulinae and Dussumieriinae but not for the Alosinae, Dorosomatinae and Clupeinae, which he merely considered to be "groups of convenience" because of the difficulty in diagnosing them (Fig. 1.5B). Grande (1985) stated: "the greatest remaining problem in clupeomorph systematics is to discover how the members of the Dorosomatinae, Clupeinae and Alosinae are interrelated within the Clupeoidei".

The consensus of all these previous morphology-based hypotheses emphasizes the following points: 1) the Clupeoidei form a natural group; 2) the families Engraulidae, Chirocentridae and Pristigasteridae are each monophyletic; 3) the most speciose family, the Clupeidae, is poorly defined, as are several of its subfamilies; 4) there is no consensus about the family-level phylogenetic relationships and 5) the family Sundasalangidae belongs to the Clupeoidei, but its phylogenetic position is uncertain.

1.3.2 Molecular evidence

Several molecular studies aiming to examine the higher level systematics of the Clupeoidei, each based on different taxonomic and character sampling (Lavoué et al. 2007, 2013, Li and Ortí 2007, Wilson et al. 2008, Bloom and Lovejoy 2012), discovered the following consistent results (summarized in Fig. 1.6): 1) the monophyly of the Clupeoidei, sister group of the Denticipitoidei, 2) the monophylies of the Pristigasteridae, Engraulidae, Engraulinae, Coiliinae, and Spratelloidinae, 3) the non-monophyly of the Clupeidae *sensu* Nelson (1970b) as well as the non-monophyly of each of the five clupeid subfamilies (i.e., Alosinae, Dorosomatinae, Pellonulinae, Dussumieriinae and Clupeinae) and 4) the identification of several major lineages of new content.

In considering the recent molecular phylogenetic results along with previous morphological evidence, we herein present and comment on a revised classification of the Clupeoidei (Table 1.1, Figs. 1.6, 1.7 and 1.8) in

Table 1.1. Revised classification of the Clupeiformes.

Order Clupeiformes

Suborder DENTICIPITOIDEI

    Family **Denticipitidae** Clausen 1959. Type genus: *Denticeps* Clausen 1959.

        Content: *Denticeps*.

Suborder CLUPEOIDEI

    Family **Engraulidae** Gill 1861. Type genus: *Engraulis* Cuvier 1816. Note: Engraulidae

        preferred to Engraulididae see Wheeler (1990).

      Subfamily **Engraulinae** Gill 1861 *sensu* Grande & Nelson 1985. Type genus: *Engraulis*

        Cuvier 1816.

        Content: *Engraulis*, *Encrasicholina*, *Stolephorus*, *Anchoa*, *Anchoviella*, *Anchovia*,

        Cetengraulis, *Jurengraulis*, *Lycengraulis*, *Pterengraulis* and *Amazonsprattus*.

      Subfamily **Coiliinae** Bleeker 1872 *sensu* Grande & Nelson 1985. Type genus:

        Coilia Gray 1830.

        Content: *Coilia*, *Lycothrissa*, *Papuengraulis*, *Setipinna*, *Thryssa* (including

        Thrissina) and *Pseudosetipinna*.

    Family **Chirocentridae** Bleeker 1849 . Type genus: *Chirocentrus* Cuvier 1816.

        Content: *Chirocentrus*.

    Family **Pristigasteridae** Bleeker 1872. Type genus *Pristigaster* Cuvier 1816.

      Subfamily **Pristigasterinae** Bleeker 1872 *sensu* Grande 1985. Type genus:

        Pristigaster Cuvier 1816.

        Content: *Pristigaster*, *Odontognathus*, *Raconda*, *Opisthopterus* and *Ilisha*

        africana.

      Subfamily ?**Pelloninae** Gill 1861 *sensu* Nelson 2006. Type genus *Pellona* Valenciennes

        1847.

        Content: *Pellona*, *Pliosteostoma*, *Chirocentrodon*, *Neoopisthopterus* and *Ilisha*

        (but not *Ilisha africana*).

Table 1.1. contd....

Table 1.1. contd.

Family ?**Dussumieriidae** Gill 1861. Type genus: *Dussumieria* Valenciennes 1847.

Subfamily **Spratelloidinae** Jordan 1925 [part of Lineage 5 in Lavoué et al. (2013)].

Type genus: *Spratelloides* Bleeker 1851.

Content: *Spratelloides* and *Jenkinsia*.

Subfamily **Dussumieriinae** Gill 1861. Type genus: *Dussumieria* Valenciennes 1847.

Content: *Dussumieria* and *Etrumeus*.

Note: a paedomorphic taxon, not yet described and classified, is the sister group of the

Spratelloidinae (see Lavoué et al. 2008).

Family ?**Clupeidae** Cuvier 1816. Type genus: *Clupea* Linnaeus 1758.

Subfamily **Clupeinae** Cuvier 1816 *new usage* [Lineage 4 in Lavoué et al. (2013)].

Type genus: *Clupea* Linnaeus 1758.

Content: *Clupea, Sprattus, Strangomera, Ramnogaster, Potamalosa, Hyperlophus*
and *Ethmidium*.

Subfamily **Ehiravinae** Deraniyagala 1929 *new usage* [Lineage 3 in Lavoué et al.

(2013)]. Type genus: *Ehirava* Deraniyagala 1929.

Content: *Ehirava, Sundasalanx, Clupeichthys, Clupeoides, Minyclupeoides,*

Corica, Gilchristella, Clupeonella, Sauvagella, Spratellomorpha and *Dayela*.

Subfamily **Alosinae** Svetovidov 1952 *new usage* [Lineage 2 in Lavoué et al. (2013)].

Type genus: *Alosa* Linck 1790.

Content: *Alosa, Brevoortia, Sardinops* and *Sardina*.

Subfamily **Dorosomatinae** Gill 1861 *new usage* [Lineage 1 in Lavoué et al. (2013)].

Type genus: *Dorosoma* Rafinesque 1820.

Content: *Dorosoma, Hilsa, Ethmalosa, Tenualosa, Gudusia, Gonialosa,*

Konosirus, Clupanodon, Nematalosa, Anodontostoma, Herklotsichthys,

Opisthonema, Harengula, Amblygaster, Sardinella, Escualosa, Rhinosardinia,

Pellonula, Odaxothrissa, Nannothrissa, Microthrissa, Potamothrissa, Stolothrissa,

Limnothrissa, Sierrathrissa, Thrattidion, Laeviscutella, Congothrissa, Lile and
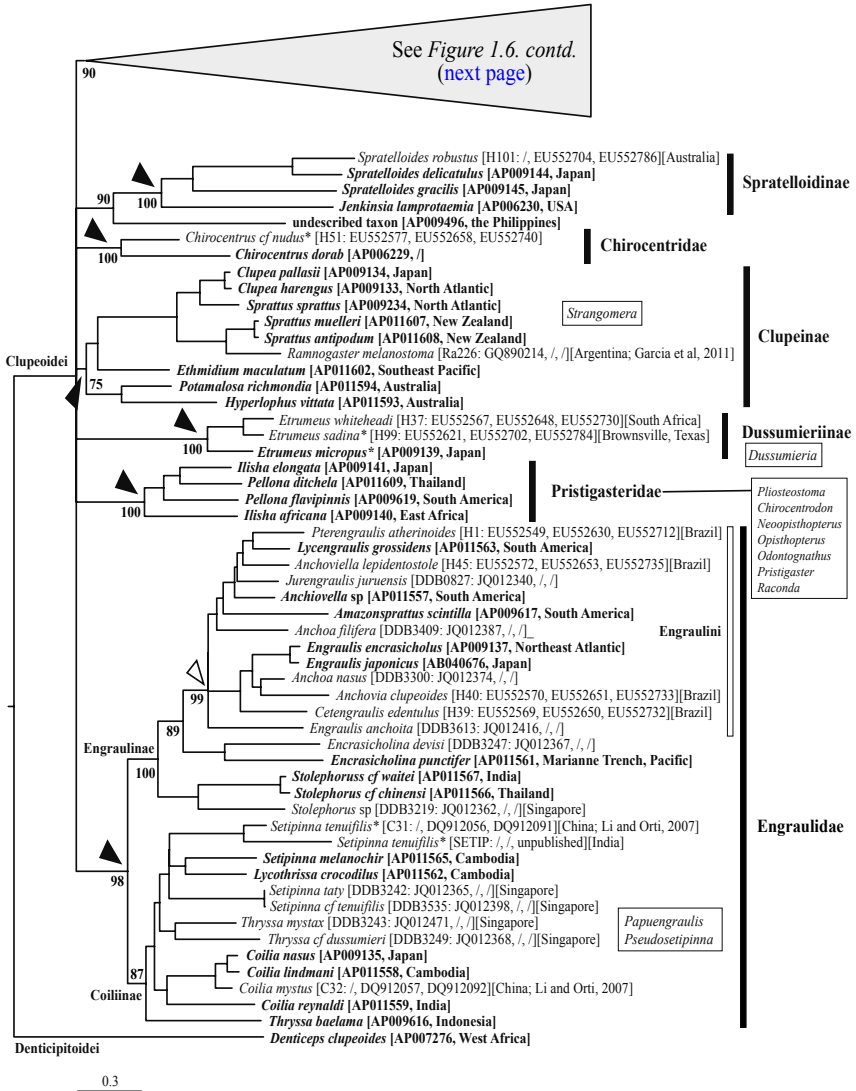
Platanichthys (*ad interim*).

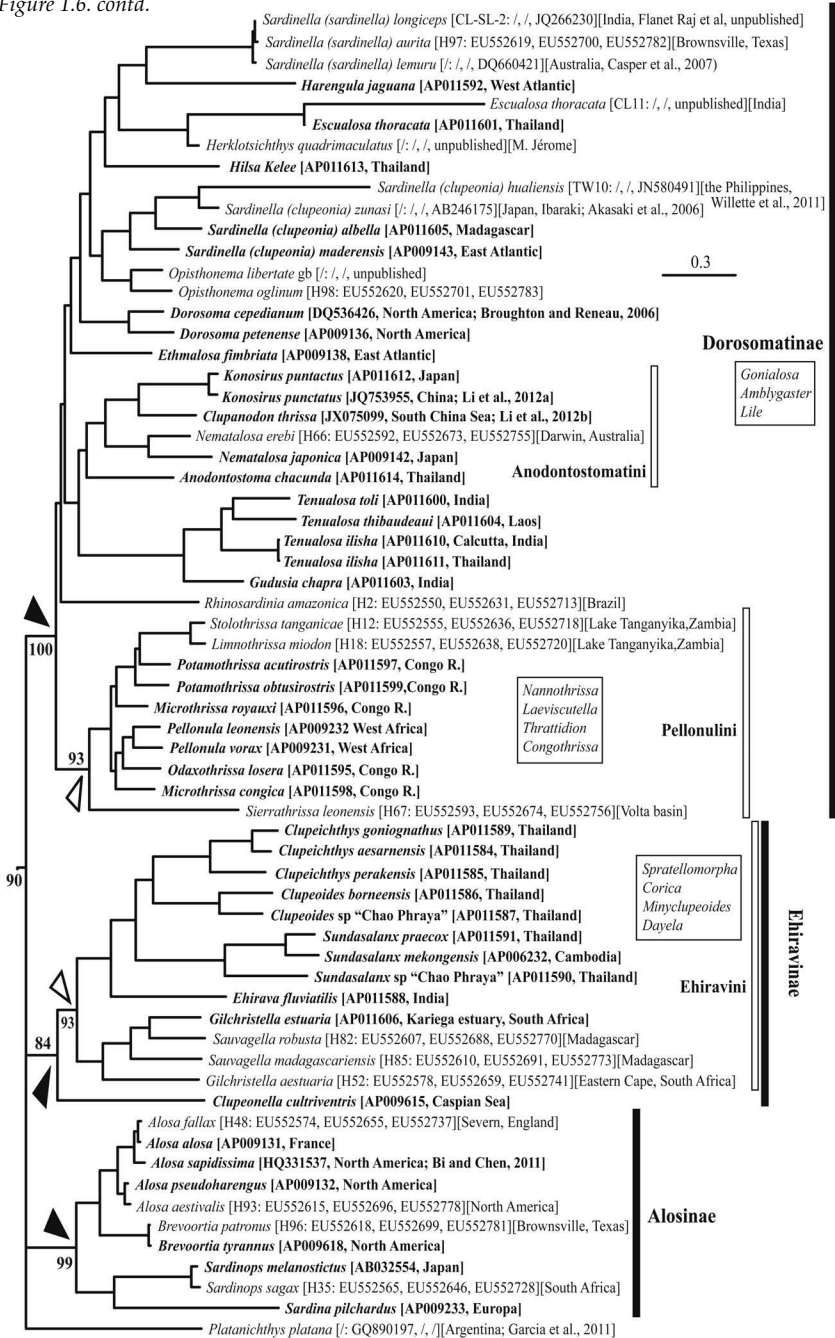Figure 1.6. contd....

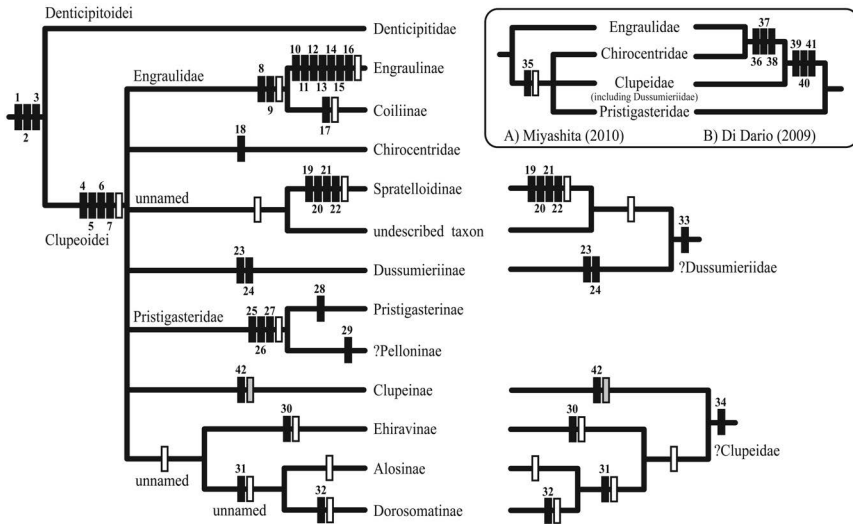*Figure 1.6. contd.*

Figure 1.6. contd....

Figure 1.7. Simplified clupeoid family-level phylogenetic tree (left side) indicating molecular (white bars) and morphological (black bars) synapomorphies. The gray bar indicates only overall genetic support for the monophyly of the Clupeinae *new usage*. Each morphological character (from 1 to 42) is described in the text. Molecular characters are from the mitogenome and are listed in Table 1.2. On the top right side, Miyashita (2010) and Di Dario (2009)'s morphology-based hypotheses are shown with characters supporting each hypothesis (see text for explanation). On the right side, Dussumieriidae and Clupeidae *new usage* clades are shown with their current morphological support. A question mark before the family-level name indicates current weak or ambiguous support for the corresponding family-level group monophyly.

Figure 6.4. contd.

Figure 1.6. The molecular phylogenetic tree of the Clupeoidei. The mitogenomic dataset of Lavoué et al. (2013) was used as the backbone to construct this tree. Additional taxa with incomplete mitochondrial sequences (cytochrome b and/or 12S and 16S rRNAs) were principally compiled from Li and Ortí (2007) (code of the individual starting with "C"), Wilson et al. (2008) (code of the individual starting with "H") and Bloom and Lovejoy (2012) (code of the individual starting with "DDB"). Other sequence sources are indicated after the corresponding sequence name. *Denticeps clupeoides* is used as the outgroup. This is the maximum likelihood tree obtained using the software RAxML (Stamatakis 2006) and the GTRGAMMA model of sequence evolution. The mitogenomic sequences are indicated in bold characters and, for each of them, the corresponding GenBank accession number and the origin of the individuals are indicated in brackets. Taxa with incomplete sequences are indicated in regular characters; the code of the individual, the GenBank accession number for the cytochrome b, 12S and 16S rRNA sequences (individual missing sequences are indicated with "/"), the geographic origin of the samples and the source reference, are successively indicated within brackets.
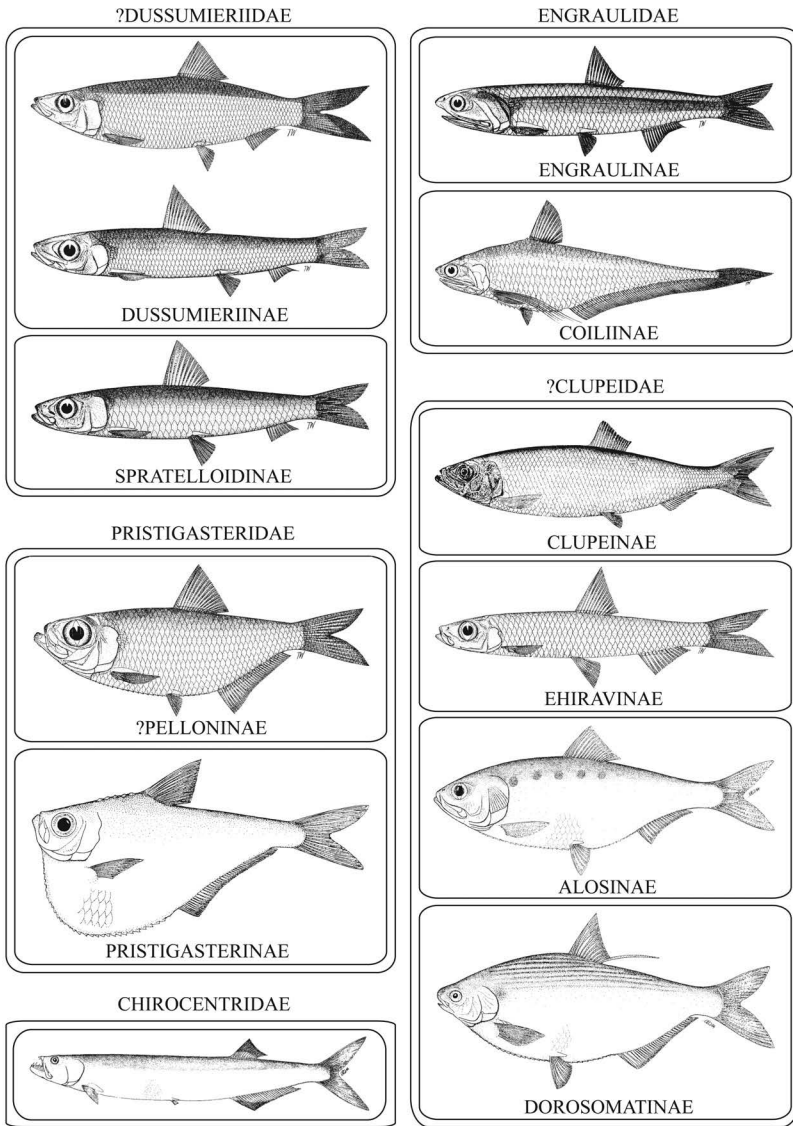
Figure 1.8. Illustrations of representatives for familial and subfamilial groups of Clupeoidei. Drawings reproduced from Whitehead (1985a) and Whitehead et al. (1988).

which 15 family-level groups are identified forming seven to five major lineages of unresolved positions (Fig. 1.7). The branching pattern among these lineages is left unresolved in the absence of unambiguous signal. This classification differs from the previous ones as it questions the monophyly

Table 1.2. Mitogenomic synapomorphies for family-level clupeoid groups. Abbreviations: subst., nucleotide substitution; AcA, amino acid substitution; pos., position; COI, cytochrome oxidase I gene; COII; cytochrome oxidase II; ND1, NADH dehydrogenase 1; ND2, NADH dehydrogenase 2; ND4, NADH dehydrogenase 4; ND4L, NADH dehydrogenase 4L; ND5, NADH dehydrogenase 5; ATP6, ATP synthase 6; ATP8, ATP synthase 8, Cytb, Cytochrome b. Amino Acid abbreviations in the standard IUB/IUPAC 3-letter amino acid codes.

Family-level groups:	Total:	Mitogenomic synapomorphies:
Engraulidae	15 AcA, 19 subst.	COII: pos.21 Leu→Ileu and pos.48 Thr→Ileu; ND2: pos.22 Ala→Met and pos.267 Leu→Ileu; ND4: pos.323 Val→Thr, pos.393 Thr→Ser and pos.426 Gly→Ala; ND5: pos.196 Asn→Lys, pos.218 Leu→Ala and pos.481 Lys→Asn; ATP6: pos.54 Phe→Leu; COI: pos.391 Met→Val and pos.253 Met→Ileu; ATP8: pos.15 Phe→Leu and pos.19 Ileu→Thr; tRNAs: 4 transversions and 6 transitions; 16S rRNA: 1 transversion and 7 transitions; 12S rRNA: 1 transition.
Engraulinae	1 AcA, 2 subst.	Cytb: pos.315 Leu → Ileu; tRNAs: 1 transversion and 1 transition.
Coiliinae	2 AcA, 1 subst.	ND4: pos.257 Glu→Asp; ND5: pos.59 Leu→Met; tRNAs: 1 transition.
Pristigasteridae	14 AcA, 22 subst.	ND1: pos.161 Val→Ala, pos.246 Ileu→Thr and pos.315 Val→Met; ND2: pos.41 Ileu→Ala; ND4: pos.414 Met→Thr; ATP6: pos.37 Arg→Gln; COI: pos.29 Val→Ala, pos.73 Ileu→Met, pos.122 Ala→Val, pos.491 Thr→Met, pos.253 Met→Leu and pos.484 Ala→Thr; ATP8: pos.11 Ala→Leu and pos.40 Val→Thr; tRNAs: 1 transversion and 4 transitions; 16S rRNA: 6 transversions and 7 transitions; 12S rRNA: 3 transversions and 1 transitions.
Spratelloidinae	9 AcA, 10 subst.	ND1: pos.259 Glu→Trp, pos.275 Val→Gly, and pos.158 Ser→Ala; ND2: pos.64 Ala→Ser and pos.140 Ala→Ser; ATP6: pos. 12 Pro→Ser and pos.148 Ileu→Val; ND4L: pos.63 Leu→Met; ATP8: pos.43 Glu→Gln; tRNAs: 4 transversions and 1 transition; 16S rRNA: 2 transversions and 1 transition; 12S rRNA: 2 transitions.
Spratelloidinae plus undesc. taxon	2 AcA, 2 subst.	ND1: pos.303 Thr→Ala; ATP8: pos.48 Glu→Asp; 16S rRNA: 1 transversion; 12S rRNA: 1 transition.
Ehiravinae	2 AcA, 1 subst.	COII: pos.5 Ser→Ala; ATP6: pos.124 Ala→His; 12S rRNA: 1 transition (convergent in the clade *Encrasicholina* but *Anchiovella* sp.).
Alosinae	2 AcA	Cytb: pos.262 Leu→Met (convergent in the clade *Gilchristella*); COII: pos.67 Ileu→Val (convergent in *Spratelloides delicatulus* and *Tenualosa* spp.).
Dorosomatinae	3 AcA	COII: pos.36 Thr→Val (further derived Val→Met in the clade (*Tenualosa*, *Gudusia*)); ND5: pos.273 Gln→His and pos.325 Asn→Asp.

Table 1.2. contd....

Table 1.2. contd.

Family-level groups:	Total:	Mitogenomic synapomorphies:
Alosinae plus Dorosomatinae	1 AcA	COII: pos.52 Asn→Asp (convergent in *Chirocentrus*).
Alosinae plus Dorosomatinae plus Ehiravinae	3 AcA, 1 subst.	ND1: pos.158 Ser→Cys (reversion in the clade *Ehirava*) and *Hilsa kelee*; ND4: pos.454 Leu→Phe (convergent in *Ethmidium*, *Chirocentrus* and reversion in *Sundasalanx* sp1); ND5: pos.332 Leu→Phe; 12S rRNA: 1 transition.
Clupeoidei excluding Engraulidae	3 AcA, 4 subst.	ND1: pos.313 Ileu→Leu; ND2: pos.89 Met→Leu (reversion in *Etrumeus*, *Spratelloides* and the clade *Ehirava*); ND5: pos.432 Ileu→Val (reversion in undescr. taxon); tRNAs: 1 transition; 16S rRNA: 1 transition (reversion in *Jenkinsia*); 12S rRNA: 2 transitions.

of the Dussumieriidae and Clupeidae but it improves the situation within the "Clupeidae" in recovering monophyletic subfamilies.

1.3.3 Comments on a revised classification of the Clupeoidei (Clupeiformes)

The family Engraulidae [not Engraulididae, see Wheeler (1990) and van der Laan et al. (2013)] currently includes about 144 species in 17 genera (Eschmeyer 2013). Species of the genus *Engraulis* are of incomparable economic importance and the Peruvian anchovy, *Engraulis ringens*, is by far the most harvested fish species in the world (FAO Fisheries Department 2011). The Engraulidae has long been perceived as a natural group because of the particular snout morphology of most of its representatives (Nelson 1984b, Stephens 2010). Grande and Nelson (1985) identified two morphological characters to support the monophyly of the Engraulidae: 1) "the oblique inclination of the suspensorium" and 2) "the mesethmoid bone projects in advance of the vomer and supports a paired rostral organ" (Fig. 1.2D) [characters 8–9 in Fig. 1.7]. Molecular markers have confirmed the monophyly of this family (Lavoué et al. 2010, Bloom and Lovejoy 2012). The mitogenome provides 34 unique amino acid and nucleotide substitutions (Table 1.2).

Morphological (Grande and Nelson 1985) and molecular variation (Lavoué et al. 2010, Bloom and Lovejoy 2012) also concur to divide the Engraulidae into two subfamilies. The Engraulinae comprises the New World anchovies, including *Amazonsprattus*, along with the worldwide-distributed genus *Engraulis*, and the Indo-West Pacific genera *Stolephorus* and *Encrasicholina* on the basis of seven characters (Grande and Nelson 1985)

[characters 10–16 in Fig. 1.7]. The mitogenome provides three additional characters (Table 1.2). The Coiliinae comprises the Indo-West Pacific genera *Coilia*, *Lycothrissa, Papuengraulis, Setipinna, Pseudosetipinna*, and *Thryssa* (including *Thrissina*) as these fishes have "lost the peg on the proximal end of the upper most ray of the lower caudal lobe" (Grande and Nelson 1985) [character 17 in Fig. 1.7] and share two unique amino acid substitutions (Table 1.2).

The relationships within the Engraulinae have been studied both using morphology (Nelson 1983, 1984a, 1986, Grande and Nelson 1985) and molecular markers (Grant et al. 2010, Bloom and Lovejoy 2012) leading to different results. In the most taxon-rich molecular study, Bloom and Lovejoy (2012) found that several genera of New World anchovies as well as *Engraulis* are not monophyletic. The relationships within the Coiliinae are mostly unstudied.

The family Chirocentridae (wolf herrings) currently includes only two morphologically similar species from the Indo-West Pacific, *Chirocentrus dorab* and *C. nudus* (Luther 1985, Whitehead 1985a). These large piscivorous fishes are readily distinguishable by their compressed and elongated body, with only the pelvic scute present but reduced. The phylogenetic position of the wolf herrings within the Clupeoidei is not yet established (Grande 1985, Di Dario 2009, Lavoué et al. 2013) (Fig. 1.7).

As redefined by Nelson (1970b) and Whitehead (1972), the Dussumieriidae [round herrings (Nelson 2006)] comprises only four marine genera (*Dussumieria*, *Etrumeus*, *Spratelloides* and *Jenkinsia*) that share "an unkeeled and W-shaped pelvic scute immediately anterior to the pelvic fins along with the absence of any other scute" (Whitehead 1962a) [character 33 in Fig. 1.7]. Recent molecular investigations that included three of the four genera found that the Dussumieriidae were not monophyletic (Lavoué et al. 2007, 2013, Li and Ortí 2007, Wilson et al. 2008) (Fig. 1.6). In his talk given at the 1968 ASIH meeting, William Eschmeyer (pers. comm.) suggested that *Spratelloides* and *Jenkinsia* are more closely related to Clupeidae than to *Dussumieria* and *Etrumeus* based on morphological evidence (check also van der Laan et al. 2013). However, we temporarily retain the Dussumieriidae sensu Nelson (1970b) in our classification in the absence of a supported alternative hypothesis.

Grande (1985) showed the Dussumieriidae were divisible into two subfamilies. The Spratelloidinae (=tribe Spratelloidini of Grande 1985) comprises *Spratelloides* and *Jenkinsia*. It is supported by four morphological characters (characters 19–22 in Fig. 1.7) among which are 1) "the reduction of number of epurals to 1" and 2) "the fusion of the first ural centrum to the first preural centrum" and 19 molecular characters (Table 1.2). An undescribed paedomorphic taxon is likely the sister group of the Spratelloidinae as evidenced by the sharing of two unique amino acid residues and two

nucleotide substitutions (Lavoué et al. 2008a) (Table 1.2). The Dussumieriinae (=tribe Dussumieriini of Grande 1985) comprises *Dussumieria* plus *Etrumeus*. Two morphological characters support its monophyly (Grande 1985): 1) "an extremely high number of branchiostegal rays" and 2) "the parhypural fused with the first preural centrum" (characters 23–24 in Fig. 1.7).

Recently, the two most ancient (about 74 millions yr old) members assigned to the Dussumieriidae were described (Taverne 2002, 2007b). †*Portoselvaggioclupea whiteheadi* is only known by one caudal skeleton while the skeleton of †*Nardoclupea grandei* is more complete. The caudal skeletons of these two fossils bear strong resemblance with those of the living dussumieriids, especially with *Dussumieria* and *Etrumeus* (Dussumieriinae), in having the "parhypural fused with the first preural centrum" (Taverne 2002, 2007b). †*Nardoclupea grandei*, however, does not exhibit the only truly dussumieriid character, the unkeeled and W-shaped pelvic scute (character not observable in †*Portoselvaggioclupea whiteheadi*). The oldest member of the Dussumieriidae with this character is an undescribed taxon known from the Eocene (52 millions yr ago, MYA) of the Monte Bolca Formation in Italy (Grande 1985).

The family Pristigasteridae (longfin herrings) includes nine genera and about 40 species distributed worldwide in tropical waters (Eschmeyer 2013). Some pristigasterids are of significant local economic value (Blaber et al. 1998, Zhang et al. 2009). At least three unique morphological characters support the monophyly of the living Pristigasteridae: 1) "Predorsal bones oriented either vertically or inclined anterodorsally", 2) "loss of interlobar notch in third hypural of caudal skeleton" and 3) "prominent basibranchial dentition, including separate toothplates fused with B2 and one or more pairs of hypobranchials" (Nelson 1967, p. 392) [characters 25–27 in Fig. 1.7]. The mitogenome provides 36 additional diagnostic characters (Table 1.2). The Santonian (83.5–85.8 MYA) †*Gasteroclupea branisai* of Bolivia is currently identified as the oldest pristigasterid (Grande 1982a, 1985). Because †*Gasteroclupea branisai* lacks one morphological synapomorphy of the living pristigasterids, this fossil is considered to be a stem pristigasterid and provides a corresponding minimum age for the stem group Pristigasteridae.

The phylogeny of Pristigasteridae has not yet been comprehensively examined. Grande (1985) recognized three groups: 1) the Pristigasterinae (= Grande's Pristigasteridae) supported by the "presence of a bony process on the first pleural rib which articulates with the shoulder girdle" (character 28 in Fig. 1.7), 2) the Pelloninae (= Grande's Pellonidae) supported by the "maxillary-premaxillary gap covered by bone" (character 29 in Fig. 1.7) and 3) the genus *Ilisha* (minus "*Ilisha*" *africana* that was placed within the Pristigasterinae). According to de Pinna and Di Dario (2003), *Ilisha* and *Pellona* may not be reciprocally monophyletic, leading Nelson (2006) to

include *Ilisha* within the Pelloninae. We tentatively follow Nelson's (2006) classification.

There is no molecular support for the monophyly of the Clupeidae *sensu* Nelson (1970b) and Grande (1985). It seems, however, possible to define a more restricted group from which the Dussumieriidae is excluded but the Sundasalangidae is included (see Lavoué et al. 2013). We retain the diagnostic character "presence of two long, rod-like postcleithra" (Fig. 1.2C) for the more restrictive family Clupeidae *new usage* (character 34 in Fig. 1.7). The phylogenetic position of *Etrumeus*, which possesses this character, needs to be further investigated and the condition in *Sundasalanx* needs to be examined. The family Clupeidae is further dividable into four monophyletic subfamilies, discussed later.

The composition of the subfamily Clupeinae *new usage* is limited to the temperate genera *Clupea* (two species), *Sprattus* (five species), *Strangomera* (one species)*, Ramnogaster* (two species), *Ethmidium* (one species)*, Hyperlophus* (two species) and *Potamalosa* (one species). Evidence for the monophyly of this group is moderate as there are no unique morphological and molecular characters to diagnose it (Fig. 1.7). This subfamily includes species of prime economic importance such as the European herring (*Clupea harengus*), the Araucanian herring (*Strangomera bentincki*) and the European sprat (*Sprattus sprattus*). In 2009, these three species were placed amongst the top 15 of the world principal fish species for capture production (FAO Fisheries Department 2011).

Ethmidium, *Hyperlophus* and *Potamalosa* share the particularity of having complete dorsal series of scutes, from the occiput to the dorsal fin origin, a unique character within the living clupeoids otherwise known in some fossils. Despite this character, *Ethmidium* was frequently classified within the Alosinae whereas *Hyperlophus* and *Potamalosa* were placed within the Pellonulinae (Grande 1982a, Whitehead 1985a). The complete series of dorsal scutes observed in these three genera may have a unique evolutionary origin. If correct, this character is a synapomorphy of the Clupeinae *new usage*, secondarily lost in the *Clupea/Sprattus* lineage (character 42 in Fig. 1.7). This also may have important implications for the phylogenetic positions of some "double-armored" fossil genera such as the Paleocene/Eocene †*Knightia* (Grande 1982b).

The subfamily Ehiravinae *new usage* comprises the tribe Ehiravini of Grande (1985) (i.e., *Ehirava* plus *Dayela*, *Spratellomorpha* plus *Sauvagella*, *Gilschritella*, *Clupeichthys* and *Corica*) plus the genera *Clupeoides* and *Minyclupeoides*, *Sundasalanx* (previously classified within the Sundasalangidae) and *Clupeonella* (previously classified within the Clupeinae). Except for some *Clupeonella* species reaching up to 20 cm SL, all other ehiravin species are small (less than 9cm SL) and most of them

are confined to freshwater and estuarine habitats bordering the Indo-West Pacific region. *Clupeonella* spp. catches in the Caspian Sea are significant (Mamedov 2006) while only a few other species of this subfamily may have a non-negligible local economic value, such as *Sundasalanx* spp. in Borneo (Kottelat and Widjanarti 2005) and *Corica soborna* in Bangladesh (Hossain et al. 2008).

A possible derived morphological character (not unique) supporting the monophyly of the Ehiravinae is the "fusion of the first ural centrum with the first preural centrum" (Grande 1985) [character 30 in Fig. 1.7]. This character is also observed in *Sundasalanx* (Siebert 1997). Only the genus *Clupeoides* lacks this character (Grande 1985), and we interpret its absence in *Clupeoides* as a secondary loss. According to Grande (1985), this character evolved at least three more times within the Clupeoidei: 1) within the Spratelloidinae, 2) within the tribe Pellonulini (herein classified within the Dorosomatinae), and 3) within the Engraulinae. Three molecular characters support the monophyly of the Ehiravinae (Fig. 1.7, Table 1.2).

Recently, Taverne (2011) described the clupeid fossil †*Leccleclupea ehiravaensis* that he assigned to the tribe Ehiravini *sensu* Grande (1985). This discovery is remarkable because †*Leccleclupea ehiravaensis* represents the oldest known ehiravin fossil (74 millions yr old), significantly extending the temporal occurrence of this lineage.

The subfamily Alosinae *new usage* (shads, alewives, menhadens and true sardines) is here restricted to only four temperate genera, all economically important (FAO Fisheries Department 2011): *Alosa*, *Brevoortia*, *Sardinops* and *Sardina*. Only two unique molecular characters support its monophyly (Table 1.2). *Sardina pilchardus* is the sister group of *Sardinops* (Nelson 1967). The genus *Sardinops* comprises several (up to five) genetically closely related species or populations (Bowen and Grant 1997). *Brevoortia* is the sister group of *Alosa*. These two genera share more ecological similarities than with their sister group (*Sardina*, *Sardinops*) such as a greater tolerance to low salinity with several euryhaline/anadromous species (e.g., *Brevoortia patronus*, *Alosa pseudoharengus*), and with some populations/species landlocked in freshwaters in Europe and North America. Faria et al. (2006) and Bowen et al. (2008) examined the phylogeny of the North American and West European species of *Alosa*. The 15 or so *Alosa* species occurring in the Caspian Sea system, previously classified within the genus *Caspialosa*, are in need of revision (Kottelat and Freyhof 2007). Anderson (2007) examined the systematics of the North American menhadens (four species) and García et al. (2008) examined the phylogeny of the South American *Brevoortia* species.

The oldest fossil (74 millions yr old) assigned to the subfamily Alosinae is †*Pugliaclupea nolardi* because of its overall similarity with the extant alosins (Taverne 2004, 2007b). Several fossils are assigned to the genus *Alosa* from Cenozoic deposits of North America, Europe and North Africa (Grande 1985), but their taxonomic revisions will likely demonstrate that they do not belong to *Alosa* (Zaragüeta-Bagils 2001).

The subfamily Dorosomatinae *new usage* includes about 110 tropical or subtropical species from about 30 genera. Nelson (1970b) suggested "a very real possibility that some genera currently classified with *Clupea* (e.g., *Sardinela*, *Opisthonema*, and possibly *Harengula* and *Herklotsichthys*) will eventually be shown to be related to the Dorosomatinae and classified with them". Later, Nelson (1970b) wrote: "It is interesting to note also that the genera *Hilsa* (including *Tenualosa*), *Gudusia*, and *Ethmalosa* (as well as *Sardinella*, *Opisthonema*, *Harengula*, and *Herklotsichthys*) have the same, moderately advanced pattern of rays as *Dorosoma* and *Konosirus*".

According to Nelson (1970b) the "non-overlap of the gill rakers" may represent a derived feature for this group (character 32 in Fig. 1.7). Probably the most salient difference between the Dorosomatinae presented herein and the hypothesis of Nelson (1970b) is the inclusion of the tribe Pellonulini (previously classified within the subfamily Pellonulinae): the gill rakers in this group are reported as non-overlapping leading to the conclusion that either this character may have been secondarily lost in the Pellonulini or this character evolved after the divergence between the Pellonulini and the rest of Dorosomatinae, if they are sister groups (Fig. 1.6B).

Only a few dorosomatin species have been examined so far in molecular studies, which precludes the establishment of a phylogenetic hypothesis for the whole subfamily. Only a few lines can be drawn at present (Fig. 1.6B): 1) the West-Central African freshwater tribe Pellonulini is monophyletic (Wilson et al. 2008) [the position of the idiosyncratic *Congothrissa* still needs to be investigated because this genus is sometimes recognized as a distinct family (Taverne 1977)]; 2) the Indo-West Pacific "alosins" (i.e., *Tenualosa* and *Gudusia*) form a monophyletic group; 3) the non-monophyly of the speciose genus *Sardinella* and the non-monophyly of the gizzard shads of Nelson and Rothman (1973); 4) based on morphological and molecular evidence, a monophyletic group comprises the Indo-West Pacific genera *Konosirus*, *Clupanodon* and *Nematalosa*, which exhibit a long dorsal fin ray (Whitehead 1962b, Lavoué et al. 2013), and 5) there is no evidence that species of *Harengula*, *Opisthonema*, *Herklotsichthys*, *Amblygaster*, and *Sardinella* are more closely related to each other than to other Dorosomatinae (Stephens 1996). The genus *Sardinella* (false sardines) is the subject of most of the species/ population level studies (e.g., Kumar et al. 1997, Samonte et al. 2009, Quilang et al. 2011, Willette et al. 2011, Ying et al. 2011).

1.4 Character evolution and biogeography

1.4.1 The evolution of abdominal scutes in the Clupeoidei

One of the distinctive features of the Clupeiformes and in particular Clupeoidei is the presence of abdominal scutes. Most of the clupeoids have a median ventral row of scutes that usually have sharp points towards the rear. The series is said to be complete when it extends from the isthmus to the anus. In some taxa, the series is reduced to as few as a single pelvic scute positioned just anterior to the bases of the pelvic finrays. The functional significance of the abdominal scutes is still not well understood (Whitehead 1985b). Most scutes are modified scales. Only the pelvic scute may have a different origin, and Whitehead (1963a) proposed that it derives from paired pelvic splints instead of scales, but its anatomy should have evolved in concert with the other abdominal scutes.

Because the organization of the abdominal scutes is variable within the Clupeoidei, the evolution of scutes has been of substantial interest (Whitehead 1963a,b, Nelson 1970a, Grande 1985). The debate focused in particular on determining whether the most recent common ancestor of the Clupeoidei had a fully developed series of abdominal scutes because the Dussumieriidae, which have only a W-shaped pelvic scute, were considered as "basal". Whitehead (1963b) wrote "it seems more likely on present evidence that the round herrings are modern representatives of an early non-scuted herring".

We explored the evolution of the abdominal scute organization of the Clupeoidei on a simplified molecular phylogenetic tree by searching for the most parsimonious reconstruction of "scute" character states using the software application Mesquite (Maddison and Maddison 2009). For the sake of simplicity, we collapsed clades of single genus that were found to be monomorphic with respect to scute anatomy into single terminals (e.g., the clade of *Clupeichthys* species).

Three major types of abdominal scute organization among the clupeoid species are defined relative to their completeness. The three types are illustrated in Fig. 1.9.

Type 0 morphology, found in most of the genera, is said to be complete when the series extends from the isthmus to the anus (usually the series contains more than 15 scutes). The scutes are typically (but not always, e.g., *Sierrathrissa*) strongly keeled with ascending arms forming a keel (see drawings for *Dorosoma* and *Thryssa* in Fig. 1.9). **Type 1** morphology, found in some ehiravins and engraulins, lacks post-pelvic scutes and the number of pre-pelvic scutes is less than nine (*Gilchristella* and *Stolephorus* conditions shown in Fig. 1.9). **Type 2** morphology, found in some ehiravins
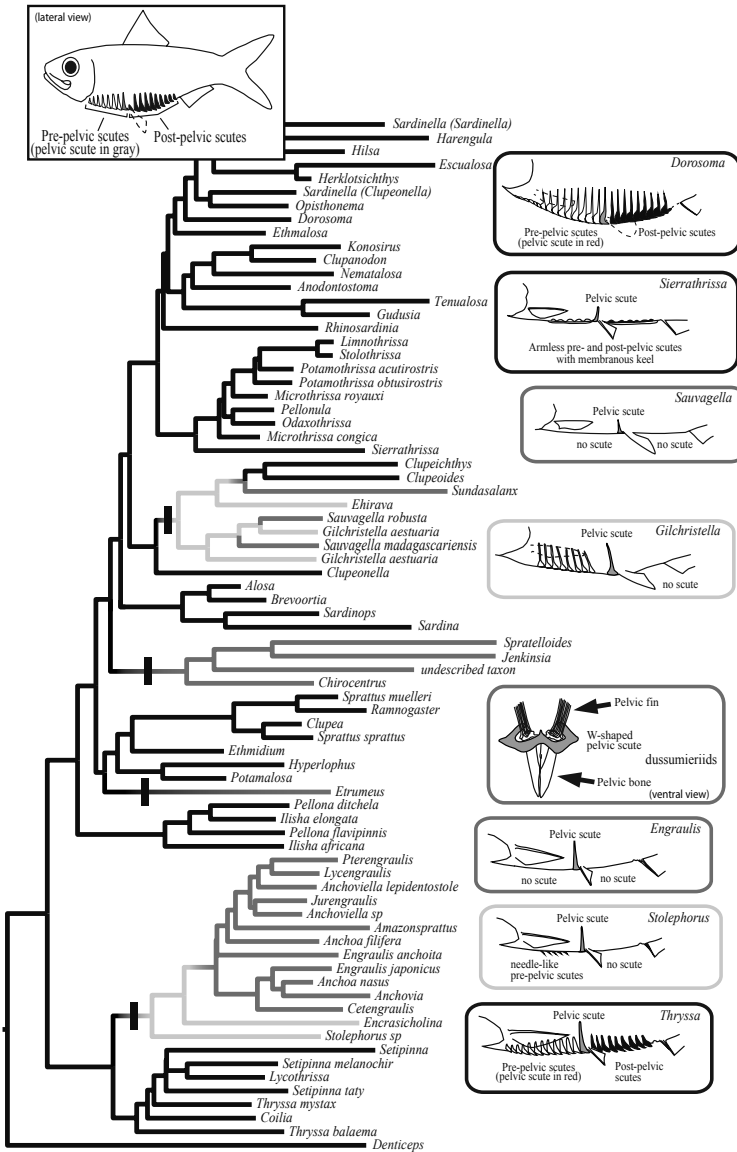
Figure 1.9. The most parsimonious reconstruction of scute evolution within the clupeoid fishes. Simplified molecular phylogenetic tree used as support (mitogenomic backbone from Lavoué et al. 2013; outgroups omitted). **Type 0** (black): full series of abdominal scutes (e.g., *Dorosoma*), sometimes scutes are reduced (e.g., *Sierrathrissa*); **Type 1** (light gray): abdominal post-pelvic scutes absent (e.g., *Gilchristella*, *Stolephorus*); **Type 2** (deep gray): all abdominal scutes absent but the pelvic scute (e.g., *Sauvagella*, *Engraulis*). Note that *Sundasalanx*, which lacks all abdominal scutes, is assigned to this category. Character optimization using parsimony and the software Mesquite (Maddison and Maddison 2009). Black bars indicate four independent events of scute reduction. Drawings modified from Whitehead (1985a) and Whitehead et al. (1988).

and engraulins, a few pellonulins and all dussumieriids, lacks all pre- and post-pelvic scutes (*Sauvagella*, dussumieriids and *Engraulis* shown in Fig. 1.9). Although *Sundasalanx* lacks all scutes, we assigned it to Type 2 for simplification purposes.

The reconstruction shown in Fig. 1.9 establishes that the most recent common ancestor of the Clupeoidei had a complete series of abdominal scutes (**Type 0**). This result is congruent with the presence of a complete series of abdominal scutes in the immediate extant sister group of the Clupeoidei, *Denticeps clupeoides*, and other non-clupeoid clupeiforms (Grande 1985, Chang and Maisey 2003, Forey 2004, Zaragüeta-Bagils 2004). Therefore, **Types 1** and **2** are derived conditions within the Clupeoidei. Furthermore, the reconstruction shows at least four independent evolutionary events of reduction of the abdominal scute series in the Clupeoidei (depending on the phylogenetic resolution of the base of the tree). As the taxonomic sampling lacks taxa with incomplete series (e.g., *Papuengraulis*, some species of *Thryssa* and *Coilia* or *Congothrissa*), the total number of reductions will likely be more. Here, an incomplete series of scutes originated within the Ehiravinae, Dussumieriinae, the clade (Spratelloidinae, Chirocentridae) and Engraulinae. Of these evolutionary events of reduction of the abdominal scute series, that within the tribe Ehiravinae is distinct as it is necessary to postulate the reappearance of a complete series (although reduced in number) of abdominal scutes in the ancestor of the clade (*Clupeoides*, *Clupeichthys*). Although a secondarily reappearance of such a character seems often less likely, other cases have been reported.

1.4.2 Evolutionary habitat transitions

Over short or long (geological) periods of time, organisms tend to retain their ancestral ecology (i.e., niche conservatism) (Crisp et al. 2009). Therefore, evolutionary transitions between environments (e.g., between marine and freshwater environments or between tropical and temperate environments) are perceived as important evolutionary events (Blaber et al. 1999, Vermeij and Dudley 2000, Bloom and Lovejoy 2012). Such transitions may deeply affect speciation and diversification rates and morphological evolution. Until recently, the Clupeiformes was seen as a counter example of such tendency to retain ancestral ecology regarding salinity and water temperature, as many taxa within a lineage co-occurred in fresh and marine waters and in temperate and tropical areas. Niche lability regarding water temperature and salinity in Clupeiformes was seen as the normal case and these two environmental parameters as poor dispersal barriers.

An emblematic case of such apparent niche lability in Clupeiformes was that of the New World anchovies. The New World anchovies (Engraulini) is a large group comprising more than 80 species classified in nine genera.

Most of these species are marine and planktonivorous. About 12 species are freshwater living in the river systems of South America. Although less abundant than marine species, these freshwater species exhibit larger trophic diversification and size range (Bloom and Lovejoy 2012). Traditionally, the freshwater species were classified in different genera along with marine species, therefore suggesting several marine to freshwater transitions. A recent molecular systematic work, however, found that freshwater anchovies are, indeed, closely related, and they were the product of a single transition from marine to freshwater environment (Bloom and Lovejoy 2012) (Fig. 1.10). Therefore and contrary to what it was previously supposed, the New World anchovies group represents a case of niche conservatism in which species tend to retain the ecological conditions of their ancestors.

At a larger taxonomic scale within the Clupeoidei, the observation of the environmental preferences of some taxa within several traditional lineages suggests that neither salinity nor temperature is perceived as strong barriers of dispersion and colonization in these fishes. Therefore, it is usually assumed that these fishes possess inherited physiological capacities to adapt to a large range of salinity and temperature conditions (Samonte et al. 2000, Palkovacs et al. 2008). In a work aiming to infer the evolution of habitat preference in the Clupeoidei, Lavoué et al. (2013) found at least 11 independent transitions from marine to freshwater environments. All these transitions occurred late in the evolution of Clupeoidei and the early clupeoids were confined to marine habitats, at least, until the end of the Cretaceous. Water temperature preference appears to represent a stronger dispersal barrier for the clupeoids with only five transitions from a tropical to temperate habitat (Lavoué et al. 2013). Two or three of these transitions occurred at the end of the Cretaceous or early in the Cenozoic, at a time of irregular global cooling (Hallam 1985).

In conclusion, clupeoids tend to be, in general, more labile regarding salinity than temperature conditions, although some clupeoid subgroups, such as the New World anchovies, exhibit strong salinity preference and few habitat shifts.

1.4.3 Early historical biogeography of Clupeoidei

The Indo-West Pacific (IWP) region forms the largest tropical region and is well known for its remarkable species richness including more than 4,000 species of fishes, most of them endemic and coral reef associated (Briggs 1999, Briggs and Bowen 2012). This number of species far exceeds the number of species in any other marine, tropical and non-tropical, region of the world. The regional species richness pattern of the Clupeoidei (Fig. 1.1) parallels that of several tropical marine organism groups in reaching its maximum within the central part of the IWP region (Briggs 1999) (Figs.
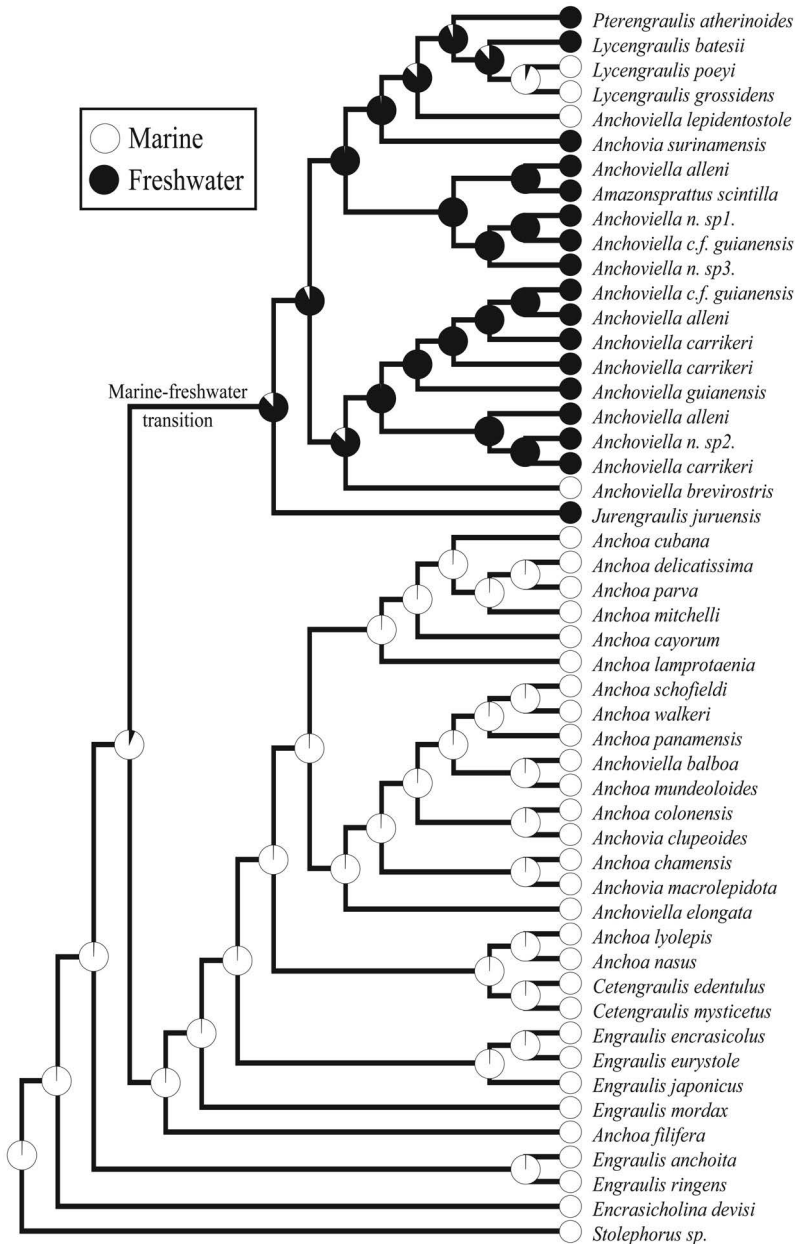
Figure 1.10. Reconstruction of the evolution of salinity preference within the New World anchovies (subfamily Engraulinae) (Modified from Bloom and Lovejoy 2012). Ancestral habitats [marine (white) and freshwater (black)] at nodes reconstructed using a maximum likelihood method of ancestral character inference. Pie charts show likelihood support for ancestral habitat states (sum=1) for the corresponding nodes.

1.1 and 1.11A). This region contains almost half of all known clupeoids (187 species), with more than 95 percent of the clupeoid species living in the IWP region being endemic (180 species). Recently, a study aiming to reconstruct ancestral area on a time-calibrated phylogenetic hypothesis suggests that the tropical marine IWP region is not only the region of highest diversity of the Clupeoidei but also their region of origin and early diversification during the Cretaceous (Lavoué et al. 2013) (Fig. 1.11).

It has been proposed that the precursor of the IWP region during the Cretaceous and Paleogene was the eastern Tethys Sea region in which several tropical marine IWP taxa originated (Bellwood and Wainwright 2002, Streelman et al. 2002, Westneat and Alfaro 2005). Among other evidence, fossil-rich Cretaceous and Early Cenozoic marine sediments from the eastern Tethys Sea support the hypothesis of the early evolution of tropical fish communities in this region, at that period (Bellwood and Wainwright 2002, Taverne 2002, 2007a,b, 2011), in particular for Clupeoidei. Among more than 300 fossil fish species already described from these sediments, about 20 species are clupeoid species (Grande 1985, Taverne 2002, 2007a,b, 2011). This large number of clupeoid species supports the hypothesis that the clupeoids were already significantly diversified in the eastern Tethys Sea region. This is consistent that the eastern Tethys Sea was the place where the early diversification of the Clupeoidei occurred.

1.5 Conclusions

In this chapter, we provide a historical perspective on the systematics and biogeography of clupeiform fishes, focusing particularly on literature about the suborder Clupeoidei that has appeared during the last 50 yr. The current hypothesis posits 1) the monophyly of the Clupeiformes, 2) the close relationship of Clupeiformes with Ostariophysi and a deep-sea fishes group, the Alepocephaliformes, and 3) a revised classification of the Clupeoidei in which 15 family-level groups are diagnosed: Engraulidae, Engraulinae, Coiliinae, Chirocentridae, Pristigasteridae, Pristigasterinae, Pelloninae, Clupeidae *new usage*, Clupeinae *new usage*, Ehiravinae *new usage*, Dorosomatinae *new usage*, Alosinae *new usage*, Dussumieriidae, Dussumieriinae, and Spratelloidinae. The Clupeidae, as redefined herein, excludes the Pristigasteridae and Dussumieriidae and comprises four main lineages: the Clupeinae *new usage*, Alosinae *new usage*, Dorosomatinae *new usage* and Ehiravinae *new usage* (including *Sundasalanx*). The last three subfamilies form a monophyletic group. The monophylies of the Clupeidae *new usage*, Dussumieriidae and Pelloninae need to be further tested. The inter-familial relationships at the base of the Clupeoidei tree are still mostly unresolved and their study represents a major venture in the systematics of Clupeiformes.
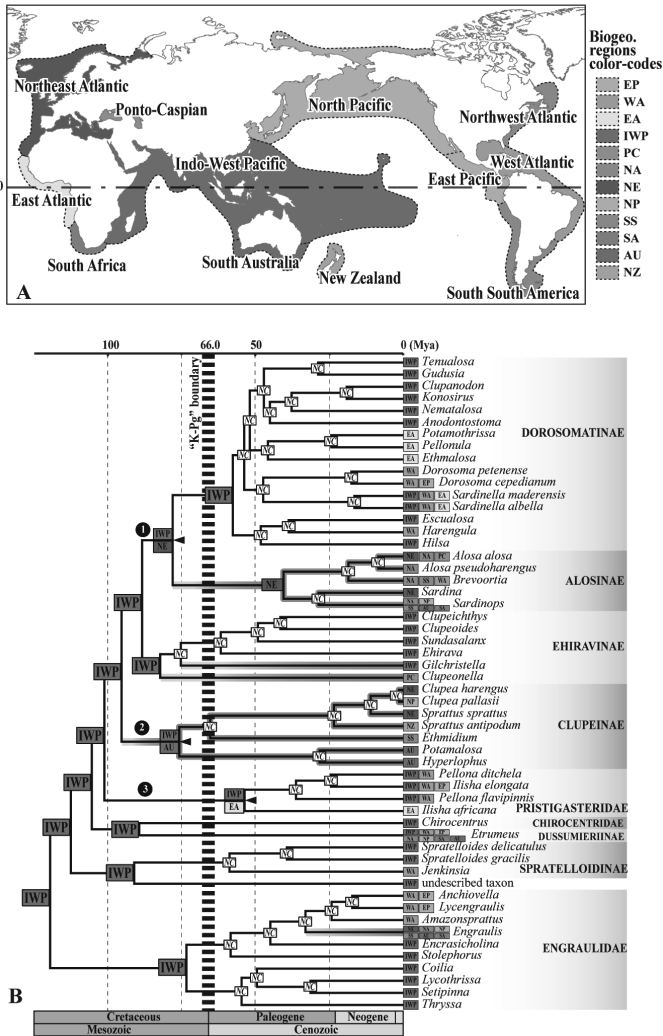
Figure 1.11. Ancestral range reconstruction of the Clupeoidei during the Cretaceous. A) Biogeographic regions as delimited based on geographical barriers, surface seawater temperature and endemism level (Modified from Lavoué et al. 2013). B) Ancestral range reconstruction using the "dispersal–extinction–cladogenesis" model (Ree and Smith 2008) on a phylogenetic chronogram. Outgroups are not shown. Within each family level group, reconstructions at nodes are not estimated ("*NC*"). Horizontal timescale in million yr ago [MYA]. Most likely ancestral range reconstructions at nodes indicated by code-color boxes (see Fig. 1.11A for correspondence between regions and two or three-letter codes and colors). Black-circled numbers indicate the three dispersal events possibly predating the Cretaceous/ Paleogene ("K-Pg") boundary. Black arrowheads at nodes indicate vicariant events. Temperate lineages are highlighted in blue (modified from Lavoué et al. 2013).

Color image of this figure appears in the color plate section at the end of the book.

The molecular phylogeny of clupeoid species, fossil and molecular clock dating of the nodes in this phylogeny and the geographic distributions of extant species show the importance of the eastern Tethys Sea in producing the high species diversity in the Indo-Pacific Region.

Acknowledgements

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