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The Fossil Record of Gonorynchiformes

Emmanuel Fara¹, Mireille Gayet² and Louis Taverne³

Abstract

The fossil record of gonorynchiform fishes provides key information on the diversity, palaeobiogeography, and phylogeny of the group. The first mention of fossil Gonorynchiformes dates back to Cuvier in the early 19th century, and there is still a need for a critical review of the earliest descriptions and of some key taxa today.

Fossil gonorynchiform fishes are known from the earliest Cretaceous (Berriasian-Valanginian) to the earliest Miocene, and the clade has several extant representatives. To date, the fossil record has yielded only about 18 genera and 35 species of Gonorynchiformes. With only 46 known localities, their fossil record is relatively poor compared to that of other groups of Ostariophysi. The distribution of these localities is heterogeneous in both space and time.

Debates on the phylogenetic status of Gonorynchiformes have mainly focused on the identity of the basal-most members of the clade and on its sister group. Unfortunately, very few large-scale phylogenetic studies have included the fossil representatives of the clade.

¹ Biogéosciences (CNRS/uB), Université de Bourgogne, 6 Boulevard Gabriel, 21000 Dijon, France. e-mail: emmanuel.fara@u-bourgogne.fr

² 18 rue Vauban, 69006 Lyon, France. e-mail: gayet.mireille@free.fr

³ Résidence "Les Platanes", Bd du Souverain, 142 (Boîte 8), B-1170 Bruxelles, Belgique. e-mail: louis.taverne@gmail.com

Using known fossil occurrences and several phylogenetic proposals, we conducted an exploratory diversity analysis. A traditional taxic approach shows that gonorynchiform diversity rose steadily during the Early Cretaceous and reached a peak in the Aptian-Cenomanian interval. It then declined slightly towards the end of the Cretaceous and it decreased further at the dawn of the Cenozoic. This apparent low diversity level is only interrupted by relative diversity peaks in the first half of the Eocene and in the Oligocene. In the absence of fossils after the earliest Miocene, diversity estimates are conjectural for most of the Neogene.

We found a close similarity of the estimates obtained with alternative phylogenetic hypotheses, meaning that the differences among these phylogenies have virtually no impact on inferred diversity patterns. Our diversity analysis points to some major gaps in the known fossil record, and it calls for the integration of most (if not all) fossil taxa in phylogenetic analyses.

Introduction

Fossil Gonorynchiformes have been known for a long time. Cuvier (in Cuvier and Brongniard 1822) first recognized the similarity between some fossil bones from the Paris Basin (Tertiary of France) and the living *Gonorynchus*, described by Gronovius in 1763 (non-available name after Nelson 1994). After the recognition of Gonorynchiformes as a taxonomic entity (Gosline 1960, Greenwood *et al.* 1966), one of the most important published works was certainly that of Rosen and Greenwood (1970), who moved Gonorynchiformes from Clupeiformes to Otophysi.

The monophyly of the order Gonorynchiformes is now well established (Fink and Fink 1981, 1996, Blum 1991a, Poyato-Ariza 1996a, Grande and Poyato-Ariza 1999, Lavoué *et al.* 2005), but the phylogenetic position of many fossil forms remains unclear. This is because some recently described taxa have not been included in a cladistic analysis yet, and also because a critical review of the earliest descriptions is still awaited.

Here we review all taxa that have been assigned to Gonorynchiformes, and we discuss their occurrence and validity. Because there is no consensus about the systematic position of several gonorynchiform species, we have chosen to present the type genus first, and then other genera in alphabetical order. The same choice was made for the species within each genus. Recent species are just listed and briefly commented on. This review is not exhaustive and it does not include all published accounts on fossil Gonorynchiformes. Instead, we selected some major studies dealing with the anatomy and/or phylogeny of the group. In the same way, synonymy lists are limited to contrasting opinions.

In a second part, we present the spatio-temporal distribution of fossil gonorynchiforms, we review some major phylogenetic proposals, and we provide an exploratory diversity analysis.

Systematic Review

GONORYNCHUS Scopoli, 1777

type genus

There is no fossil record of this genus. According to Grande (1999b), five extant species of the marine genus *Gonorynchus* are valid. They are *Gonorynchus gonorynchus* (Linnaeus 1766), Indo-Pacific; *Gonorynchus forsteri* (Ogilby 1911), New Zealand; *Gonorynchus greyi* (Richardson 1845), Hawaii; *Gonorynchus abbreviatus* (Temminck and Schlegel 1846), Japan and Taiwan; and *Gonorynchus moseleyi* (Jordan and Snyder 1923), Hawaii.

†*AETHALIONOPSIS* Gaudant, 1966

†*Anaethalion robustus* Traquair, 1911

type and only species

1911 †*Anaethalion robustus*: R.H. Traquair, p. 50; figs. 19 and 20; table XI.

1966 †*Aethalionopsis robustus* (Traquair, 1911): J. Gaudant, p. 309, fig. 2.

A single species belongs to this genus, †*Aethalionopsis robustus* (Traquair 1911). It comes from the famous dinosaur-bearing locality of Bernissart (Belgium). The age of the fossils is middle Barremian to earliest Aptian, as estimated from angiosperm pollens (Yans *et al.* 2005, 2006).

Gaudant (1966) erected the genus †*Aethalionopsis*, which he considered close to †*Anaethalion* (within *Anaethalionidae*), the taxon to which the Bernissart specimens were first assigned. †*Aethalionopsis robustus* is known from numerous complete specimens, reaching 10 to 40 cm in standard length.

According to Gaudant (1968), this genus is represented by at least two other species. Indeed, Bassani and Erasmo (1912) and Erasmo (1915) assigned to †*Anaethalion robustus* several specimens from the Aptian-Albian (Early Cretaceous) of Castellamare and Pietraroia (Italy). However, these fossils differ from the type-species by the composition of their dorsal and anal fins, and they represent another, yet unnamed, species of †*Aethalionopsis* (Gaudant 1968). The third species, †*A. valdensis*, was described by Woodward (1907) from the Berriasian-Hauterivian of Sussex, England.

Taverne (1981) revised the anatomy of †*Aethalionopsis robustus* and he designated a lectotype. This author first emphasized its similarities with some *Gonorynchiformes*, such as †*Dastilbe*, †*Tharrhias* and †*Parachanos*. However, he did not mention the Italian and English occurrences. For Taverne (1981), †*Aethalionopsis* differs from all other *gonorynchiformes* by some plesiomorphic characters, such as the shortened mandible and the lack of fusion of the third and fourth infraorbitals.

The palaeoenvironment in Bernissart was most probably fresh water with episodic connections to the sea (Marliere and Robaszynski 1975, Martin and Bultynck 1990, Grande and Bemis 1998). Grande (1999a) suggested that †*Aethalionopsis* may have been an euryhaline taxon with a wide salinity tolerance. Because †*Aethalionopsis* was found within a mixed marine and freshwater fauna, isotopic analyses would be necessary to infer the habitat of this taxon.

†*APULICHTHYS* Taverne, 1997

†*Apulichthys gayeti* Taverne, 1997

type and only species

1980 Elopiforme: F. Medizza and L. Sorbini, p. 133, fig.

1997 †*Apulichthys gayeti*: L. Taverne, p. 403; figs. 1 to 13, table.

†*Apulichthys gayeti* is a small (less than 12 cm in total length) marine gonorynchiform from the late Campanian–early Maastrichtian of Porto Selvaggio, near Nardo, Apulia, southern Italy. The age of the fossil locality was determined by nannofossils, and the ichthyofauna suggests a shallow platform environment (Sorbini 1978, Medizza and Sorbini 1980). Only four more or less complete specimens are currently known. The family †Apulichthyidae was erected for this monospecific genus, which is regarded as the sister taxon of all other fossil and modern gonorynchoids (Taverne 1997).

†*CHANOIDES* Woodward, 1901

†*Chanoides* was named for †*Clupea macropoma* Agassiz, 1839/44, a fossil found in the famous Eocene site of Monte Bolca, Italy (Woodward 1901). Because of some anatomical similarities with the extant *Chanos*, Woodward (1901) placed both †*Chanoides* and *Chanos* in the family Albulidae. Patterson (1984a) showed that †*Chanoides macropoma* is neither an albulid nor a chanid, but an ostariophysan fish. A second species of †*Chanoides* has been described recently as †*Chanoides chardonii* (Taverne 2005). It comes from the late Campanian–early Maastrichtian of Nardo, Apulia, southern Italy. The species †*Chanoides striata*, originally described by Weiler (1920), was moved to †*Neohalecopsis* by Weiler (1928), whereas †*Chanoides leptostea* was transferred to †*Coelogaster* (see below). A yet older species of †*Chanoides* from the Santonian of southern Italy (Apricena) is currently under study by Taverne and De Cosmo.

†*CHANOPSIS* Casier, 1961

†*Chanopsis lombardi* Casier, 1961

type and only species

1961 †*Chanopsis lombardi*: E. Casier, p. 60; figs. 17 and 18; table 10, figs. 1 and 2; table 11, figs. 1 to 4; table 12, figs. 1 to 6.

Casier (1961) described †*Chanopsis lombardi* based on some isolated bones of a single individual that was about one metre long. The fossils were found in the Wealdian (perhaps Albian according to Taverne 1984) Loia strata, Democratic Republic of Congo. This species was tentatively assigned to the family Chanidae by Casier (1961), but Taverne (1984) showed that it belongs in Osteoglossidae, on the basis of the peculiar enlarged shape of the frontals, the large opercle, the small or absent subopercle, and the anterior position of the autosphenotic, among other characters. Poyato-Ariza (1996a) agreed with the conclusions of Taverne (1984).

CHANOS Lacepède, 1803

Chanos is the only Recent gonorynchiform genus known also from the fossil record. It lives in tropical and sub-tropical areas of the Indian and Pacific oceans, mainly in coastal and brackish waters that enter estuaries and rivers (Riede 2004). Adults spawn in fully saline water, whereas larvae occasionally enter freshwater lakes (Bagarinao 1994). A single extant species is known, and it is the type species: *Chanos chanos* Forsskål, 1775.

†*Chanos brevis* (Heckel, 1854)

1854 †*Albula brevis*: J.J. Heckel, p. 132.

1863 †*Chanos brevis* (Heckel): R. Kner and F. Steindachner, p. 19; table I.

Several articulated specimens of †*Chanos brevis* are known from the Oligocene beds of Chiavon (Vicentin, Italy). With its 40 vertebrae, †*C. brevis* has an intermediate number of vertebrae compared to †*C. zignoi* (35 vertebrae) and †*C. forcipatus* (45 vertebrae). According to Arambourg and Schneegans (1935a), †*C. brevis*, †*C. zignoi* and †*C. forcipatus* are so close to each other that they may simply represent the geographical variation of a single species. These three species, for which the latest description dates back to the 19th century, clearly need a systematic revision. The palaeoenvironment of †*Chanos brevis* was probably a lagoon with more or less brackish waters (Sorbini 1980).

†*Chanos compressus* Stinton, 1977

1977 †*Chanos compressus*: F.C. Stinton, p. 69; table 5, figs. 5, 6.

Gonorynchiform otoliths are rare. Five specimens from the Wittering Formation (late Ypresian, Early Eocene) in Hampshire, England, have been assigned to *Chanos* by Stinton (1977).

†*Chanos forcipatus* Kner and Steindachner, 1863

1854 †*Megalops forcipatus*: J.J. Heckel, p. 132. listed.

1863 †*Chanos forcipatus*: R. Kner and F. Steindachner, p. 21; table 3.

This species comes from the marine beds of the Monte Postale, Bolca, in Italy. The age is late Lutetian-early Bartonian (Middle Eocene). Kner and Steindachner (1863) moved this species to the genus *Chanos*. According to Blot (1980), another new, but unnamed, species is also present in the same locality. Unfortunately, there is no recent study on this material.

†*Caesus leopoldi* (Costa, 1860)

1857 †*Caesus* sp.: O.G. Costa, p. 235; table.

1860 †*Caesus Leopoldi*: O.G. Costa, p. 45; table 4.

1879 †*Prochanos rectifrons*: F. Bassani, p. 163, listed.

1882 †*Prochanos rectifrons* Bassani: F. Bassani, p. 218; table 13; table 14, fig. 1; table 15.

1915 †*Chanos Leopoldi* (Costa): G. d'Erasmus, p. 35; figs. 32 and 33; table 6, fig. 1.

†*Chanos leopoldi* is known from a single specimen found in Pietraroia, Benevento, Italy. Catenacci and Manfredini (1963) gave a Barremian-Albian age for the "calcari a ittioliti" of Pietraroia, which could be Aptian (Argenio 1963, Scorziello 1980). Erasmus (1915) regarded †*Prochanos rectifrons* (Bassani 1882) as a possible synonym of †*Chanos leopoldi*.

†*Chanos torosus* Danil'chenko, 1968

1968 †*Chanos torosus*: P.G. Danil'chenko, p. 119, fig. 4, table 25, figs. 1–4.

This species was attributed to the genus *Chanos* by Danil'chenko (1968) after comparison with other fossil and extant species of *Chanos*. The fossils come from the Danatinsk Formation, Kopetdag, Turkmenia. Danil'chenko (1968) noticed that this Thanetian (Late Paleocene) fish fauna is similar to several Eocene marine faunas, especially that of Monte Bolca. The palaeoenvironment probably corresponds to an open marine basin with a normal salinity under a warm climate (Danil'chenko 1980, A.F. Bannikov, personal communication to M. Gayet, 2005).

†*Chanos zignoi* Kner and F. Steindachner, 1863

1854 †*Albula de zignii*: J.J. Heckel, p. 129, listed

1854 †*Albula lata*: J.J. Heckel, p. 131.

1863 †*Chanos Zignii* (Heckel): R. Kner and F. Steindachner, p. 20; table 2.

This species is from the Oligocene of Chiavon, Vicenza, Italy. It has not been revised since the works by Kner and Steindachner (1863) and Bassani (1889a, b). According to Bassani (1889a), †*C. zignoi* differs from †*C. forcipatus* mostly by its lower number of vertebrae (only 35 vertebrae *versus* 45 or 46 for †*C. forcipatus*).

†*CHARITOPSIS* Gayet, 1993a

†*Charitopsis spinosus* Gayet, 1993a

type and only species

1993a †*Charitopsis spinosus*: M. Gayet, p. 259; figs. 1 to 4.

†*Charitopsis* was erected on the basis of several fossils found in early Cenomanian marine deposits at Haqil, Lebanon (Gayet 1993a, b). It is close to †*Charitosomus*, another gonorynchiform fish from the same locality (Gayet 1993a), and Grande and Grande (1999) suggested that †*Charitopsis spinosus* may belong to this later genus. However, †*Charitopsis* shares with †*Notogoneus* and *Gonorynchus* the lengthening of the preopercular branch (and/or the shortening of the upper branch), as well as the separation between the dentary and the angular, two characters absent in †*Charitosomus*. In addition, it is the only gonorynchiform with a flat premaxilla and an opercle whose posterior border is strongly spinous.

In the Late Cretaceous, the Haqil site was probably located near the shore, as attested by the associated macro- and microfauna. Marine algae (Basson and Edgell 1971, Basson 1981), varanoid dolichosaurs and ophiomorph reptiles (Dal Sasso and Renesto 1999) are found, together with terrestrial plant remains (Hückel 1970).

†*CHARITOSOMUS* von der Marck, 1885

†*Charitosomus formosus* von der Marck, 1885

type species

1885 †*Charitosomus formosus*: W. von der Marck, p. 257; table 24, fig. 1.

1954 †*Charitosomus formosus* Marck: P. Siegfried, p. 14; table 5, fig. 3.

1954 †*Charitosomus* (?) cf. *formosus*: P. Siegfried, p. 14; table 5, figs. 4 and 5.

†*Charitosomus formosus*, the type species of the genus, was originally created by von der Marck (1885) for German fossils from the Late Senonian (late Campanian–Maastrichtian) of Baumberg, Westphalia. Only two large specimens are known, and the total length of each is about 26 cm. The anatomy was described by von der Marck (1885) and Woodward (1901). Gayet (1993b) noticed that the subopercle of †*C. formosus* presents a large dorsal spine (as all other †*Charitosomus* species), a character that is absent in †*Hakeliosomus*. Gayet (1993b) proposed the new family †Charitosomidae to accommodate †*Charitosomus*, †*Hakeliosomus* and †*Charitopsis*.

As for all other Lebanese fossil species, the palaeoenvironment was marine (Hückel 1970, Cappetta 1980).

†*Charitosomus* aff. †*C. formosus*

- 1885 †*Mesogaster cretaceus*: W. von der Marck, p. 247; table 22, fig. 2.
1894 †*Spaniodon lepturus*: W. von der Marck, p. 46; table 5, fig. 5.
1954 †*Charitosomus* (?) cf. *formosus*: P. Siegfried, p. 14, pl. 5, figs. 4 and 5.

Siegfried (1954) tentatively assigned to †*Charitosomus* aff. †*C. formosus* two specimens from the Late Senonian (late Campanian–Maastrichtian) of Baumberg, Westphalia, which were originally described as †*Mesogaster cretaceus* (von der Marck 1885) and †*Spaniodon lepturus* (von der Marck 1894).

†*Charitosomus hermani* Taverne, 1976a

This species was created on the basis of late Albian to middle Cenomanian fossils from Kipala, Kwango, Democratic Republic of Congo. The material is now identified as belonging to an undetermined species of Gonorynchidae.

†*Solenognathus lineolatus* Pictet and Humbert, 1866

- 1866 †*Solenognathus lineolatus*: F.J. Pictet and A. Humbert, p. 56; table 4, figs. 4 to 7.
1901 †*Charitosomus lineolatus* (Pictet and Humbert): A.S. Woodward, p. 274; table 15, fig. 4.

This eel-shaped species has been reported from Santonian marine strata at Sahel Alma, Lebanon. It is the smallest known †*Charitosomus*, with a maximal total length of about 8 cm. As for all fish from Sahel Alma, anatomical study is rather difficult due to their state of preservation (Pictet and Humbert 1866, Woodward 1901), but this species was redescribed recently (Gayet 1993b) on the basis of numerous specimens and acid preparation. This author noticed the possible presence of a supraneural 1 in †*Charitosomus lineolatus*, as observed in †*Hakeliosomus* and †*Chanoides chardonni* (Gayet 1993b, Taverne 2005). This could be interesting to investigate because the

absence of supraneural 1 is the rule among all other Ostariophysii (Fink and Fink 1981).

†*Charitosomus major* Woodward, 1901

1901 †*Charitosomus major*: A.S. Woodward, p. 272; table 15, fig. 3.

This large †*Charitosomus* species, also from the Santonian Sahel Alma locality in Lebanon, can reach a total length of 20 cm. Only five specimens are presently known and described (Gayet 1993b). Like †*Charitosomus lineolatus*, two body shapes are present and they could represent a case of sexual dimorphism.

Most Middle East †*Charitosomus* species (including †*Hakeliosomus hakelensis*) are known from Lebanon only, although an occurrence from Syria was mentioned by Grande and Grande (1999).

†*COELOGASTER* Eastman, 1905

†*Chanoides leptostea* Eastman, 1905

type species

- 1835 †*Clupea leptostea*: L. Agassiz, p. 306, listed.
1835 †*Coelogaster analis*: L. Agassiz, p. 304, listed.
1844 †*Clupea leptostea*: L. Agassiz, p. 170, listed.
1844 †*Coelogaster analis*: L. Agassiz, t. V, pt II, p. 106, listed.
1905 †*Chanoides leptostea*: C.R. Eastman, p. 11; table 1, fig. 1.
1905 †*Coelogaster analis*: C.R. Eastman, p. 12; table 1, fig. 2.
1984b ? †*Coelogaster leptostea* (Eastman): C. Patterson, p. 448.

This species from Monte Bolca (late Ypresian–early Lutetian marine deposit, Italy) was based on a rather poorly preserved holotype, the only known specimen. According to Patterson (1984b), †*Coelogaster leptostea* may be a chanid. He discussed the taxonomic status of †*Coelogaster leptostea* and rejected the possibility that this species could belong to †*Chanoides*. Patterson (1984b) also suggested the possible conspecificity with †*Coelogaster analis* Eastman, 1905, from the same locality. We agree with this interpretation and the chanoid affinities based on the similarity of the caudal skeleton with that of †*Chanos*. Consequently, we regard †*Coelogaster leptostea* (Eastman, 1905) as the valid name for the species.

CROMERIA Boulenger, 1901

No fossil has been assigned to this genus. The two Recent subspecies, *Cromeria nilotica nilotica* Boulenger, 1901, and *Cromeria nilotica occidentalis* Daget, 1954, occur in the Nile, Niger, Volta and Chad basins.

†*DASTILBE* Jordan, 1910

Several authors have studied †*Dastilbe* and its various species, but opinions differ about possible synonymies. Four species have been described so far.

†*Dastilbe crandalli* Jordan, 1910

type species

1910 †*Dastilbe crandalli*: D.S. Jordan, p. 30; table 9, figs. 9 to 13.

Type species for the genus and the only valid species of †*Dastilbe* according to Davis and Martill (1999) and Brito and Amaral (2008). It has been reported from black shales in the Aptian Muribeca Formation of Riacho Doce, Sergipe-Alagoas Basin, northeastern Brazil. Santos (1990) cited †*Dastilbe crandalli* in the Aptian Cabo Formation (Brazil). Because he differentiated †*D. crandalli* from †*D. elongatus* by the number of pectoral fin rays, Blum (1991a) reported the former species from the Crato Formation, Araripe Basin, Brazil. Davis and Martill (1999) analysed the very abundant specimens of †*Dastilbe* from the Nova Olinda Member of this formation. Berthou (1990) suggested a latest Aptian to early Albian age for the sequence containing the Nova Olinda Member.

Numerous specimens are known, and they range up to 7 cm in total length. Otoliths rarely occur *in situ* but can be abundant as isolated microfossils (Davis and Martill 1999). In contrast with Blum (1991a) and Martill (1993), who suggested that †*Dastilbe* was a non-marine fish, Davis and Martill (1999) speculated that †*D. crandalli* was an anadromous fish tolerant to hypersalinity.

†*Dastilbe batai* Gayet, 1989

1989 *Dastilbe batai*: M. Gayet, p. 22; table 1, fig. 1.

This species was erected by Gayet (1989) on the basis of a single, complete specimen from the Aptian-Albian beds of Río Benito, south of Bata, Equatorial Guinea. It was distinguished from †*D. crandalli* by the anterior position of the pelvics, with only seven lepidotriches, and by anal fins with eight lepidotriches. Poyato-Ariza (1996a), followed by Davis and Martill (1999), considered the diagnostic characters of this species not convincing, and the later authors considered it synonymous with †*D. crandalli*. The position of the pelvic fins relative to the dorsal fin is a variable feature of little diagnostic value, and the fin ray counts overlap with the variation observed among the Brazilian specimens of †*D. crandalli*. Some of the numerous isolated bones surrounding the holotype may belong to this species, but the poor state of

preservation may hamper any robust taxonomic decisions (Brito and Amaral 2008). In any case, the specimen from Bata currently represents the only occurrence of †*Dastilbe* in Africa (but see Dietze 2007).

†*Dastilbe batai* was found in black shales. The same level yielded two clupeomorphs, †*Ellimma goodi* (referred to the marine †*Ellimmichthys* by Chang and Grande 1997) and †*Clupavichthys dufouri* (Gayet 1989). Clupavidae seem to be marine [for example, *Clupavus* is known in marine deposits in Portugal and Morocco (Gayet 1981, Taverne 1977)]. Other fossil fish, including †*Parachanos*, also occur in bituminous shales in several fossil localities close to Rio Benito (Casier and Taverne 1971). They are mostly marine, and the palaeoenvironment corresponds to a calm bay temporarily lagoonal (Weiler 1922).

†*Dastilbe elongatus* Santos, 1947

1947 †*Dastilbe elongatus*: R. da Silva Santos, p. 2; table I, figs. 1 and 2; table 2, fig. 1.

1968 †*Dastilbe elongatus* Santos: R. da Silva Santos and L. G. Valença, p. 349, fig. 6.

†*Dastilbe elongatus* was first reported in an oral communication about some specimens from the Codó Formation of the Parnaíba Basin, Maranhão State, northeastern Brazil (Santos 1947, Duarte and Santos 1993), and in a manuscript that remained unpublished. Santos (1947) described and figured this species on the basis of five specimens from the laminated limestone of the Aptian Crato Member, Santana Formation, Araripe Basin, northeastern Brazil. However, he did not provide any diagnostic character. These specimens seem to be lost (Davis and Martill 1999). †*Dastilbe elongatus* was also listed in a review of the Araripe fish fauna (Santos and Valença 1968).

Blum (1991a) distinguished †*D. elongatus* and †*D. crandalli* on the basis of the count of pectoral fin rays and of total length (respectively 13 rays and TL up to 20 cm for †*D. elongatus*, and 10 rays and TL up to 6 cm for †*D. crandalli*). These characters were criticized by Poyato-Ariza (1996a) and Davis and Martill (1999). Taverne (1981) hypothesized that †*Dastilbe crandalli* and †*D. elongatus* may represent distinct populations of a single species. Davis and Martill (1999), Dietze (2007) and Brito and Amaral (2008) found no skeletal criterion for distinguishing these two species and they regard †*D. elongatus* as a junior synonym of †*D. crandalli*, an opinion that we follow here. Poyato-Ariza (1996a) considered the specimens of †*Dastilbe crandalli* from Riacho Doce and specimens from the Crato member as a distinct species, based on their absence of distema in the caudal skeleton.

†“*Dastilbe minor*” Santos, 1975

- 1975 †*Dastilbe minor*: R. da Silva Santos, unpublished doctoral thesis.
1990 †*Dastilbe minor* Santos, 1975: R. da Silva Santos, p. 267, listed
1996a †*Dastilbe minor*?: F. J. Poyato-Ariza, p. 43, listed.

In his unpublished doctoral thesis, Santos (1975) proposed under the name †*Dastilbe minor* a new species from the Marizal Formation (Lower Cretaceous), Bahia State, Brazil. He quoted this name again many years later in another paper (Santos 1990). Unfortunately, that species has never been diagnosed or described, only listed, so that it can be regarded as *nomen nudum* (Brito and Amaral 2008).

†*Dastilbe moraesii* Santos, 1955

- 1955 †*Dastilbe moraesii*: R. da Silva Santos, p. 19; tables 1 and 2.

Santos (1955) reported this species from the Aptian (or late Barremian–early Aptian, see Brito and Amaral, 2008) of the Areado Formation, Presidente Olegario, State of Minas Gerais, Brazil. Some cranial characters seem to relate this species more closely to †*Tharrhias* than to †*Dastilbe* (Poyato-Ariza 1996a), but the count of vertebrae differs between these two genera (respectively 50 and 36 for the single specimen examined by this author). Davis and Martill (1999) agreed with Poyato-Ariza (1996a) by considering this taxon valid, awaiting a more complete study, whereas Brito and Amaral (2008) consider it as a junior synonym of †*D. crandalli*.

†*Dastilbe* sp.

Malabarba *et al.* (2002) reported †*Dastilbe* from the Aptian/Albian outcrops of the Maceió Formation, Alagoas Basin, northeastern Brazil, and Soares and Calheiros (1991) reported †*Dastilbe* sp. from Aptian-Albian bituminous shales at Rio Largo, Muribeca Formation, in levels younger than those in which †*D. crandalli* was found. According to Soares and Calheiros (1991), these bituminous shales were formed in a paralic flysch depositional environment.

†*ECTASIS* Jordan and Gilbert, 1919

†*Ectasis proriger* Jordan and Gilbert, 1919

type and only species

- 1919 †*Ectasis proriger*: Jordan and Gilbert (*in* Jordan), p. 62; pl. 22.

A single specimen from the Pliocene of the Los Angeles clay shale, at the Third Street Tunnel, was first assigned with doubts to the family

Gonorynchidae by Jordan and Gilbert (*in* Jordan 1919). Later on, Jordan (1921a) placed †*Ectasis* in Elopidae, close to *Elops*.

Gonorynchiformes? incertae sedis

A single articulated skeleton from the Early Cretaceous freshwater deposits of Kyushu, Japan, was reported and figured by Yabumoto (1994) as “Gonorynchiformes? *incertae sedis*” (probably meaning “Gonorynchiformes? indet.”). According to Grande and Grande (1999), based on the specimen figured by Yabumoto, the form of the body is gonorynchid-like.

Gonorynchidae indet.

- 1965 *Incertae sedis*: E. Casier, p. 47; table 15, fig. 7.
1976a †*Charitosomus hermani*: L. Taverne, p. 36; fig. 20.
1976b †*Charitosomus hermani*: L. Taverne, p. 762, listed.

The posterior part of an individual with 23 vertebrae and the caudal skeleton, from the late Albian to middle Cenomanian of Kipala, Kwango, Democratic Republic of Congo, was assigned to a new species of †*Charitosomus*, †*C. hermani* by Taverne (1976a). However, it seems more appropriate to attribute this caudal skeleton to an indeterminate gonorynchid fish. Even if close to fossil genera from the Middle East, it differs by the fusion of the hypural 1 and 2, both attached to the terminal centrum. In all studied specimens of †*Hakeliosomus*, †*Charitosomus* and †*Charitopsis*, the first hypural is free from the second, and it articulates with the terminal centrum. The whole fauna from Kipala suggests a lagoonal palaeoenvironment (Taverne 1976a).

†GORDICHTHYS Poyato-Ariza, 1994

†*Gordichthys conquensis* Poyato-Ariza, 1994

type and only species

- 1988 Undetermined teleost: J.L. Sanz *et al.*, p. 622.
1990 Teleost *incertae sedis* “Tipo B”: F.J. Poyato-Ariza and S. Wenz, p. 307, fig. 4C.
1994 †*Gordichthys conquensis*: F.J. Poyato-Ariza, p. 5; figs. 1 and 3; table 1.

First mentioned as an undetermined teleost close to †*Ascalabos* (*Leptolepis*) *voithi* (Sanz *et al.* 1988), and as a teleost *incertae sedis* (Poyato-Ariza and Wenz 1990), this small fish was recognized as a chanid and described in detail by Poyato-Ariza (1994). It comes from the freshwater late

Hauterivian–early Barremian beds of Las Hoyas, Cuenca Province, Spain (Poyato-Ariza 1994, Poyato-Ariza *et al.* 1998). After his cladistic analysis of chanids, Poyato-Ariza (1996a, b) arranged †*Gordichthys* and †*Rubiesichthys* in the new subfamily †Rubiesichthyinae. This result is based on five synapomorphies, including two unique derived characters (acute angle between the preopercular limbs in adults and presence of the posterior process of the first supraneural). The numerous specimens currently known are all less than 4 cm in standard length.

GRASSEICHTHYS Géry, 1964

Only one Recent species, *Grasseichthys gabonensis* Géry, 1964, is reported from the Cuvette Centrale, Democratic Republic of Congo and from the Ivindo Basin, Gabon (Roberts 1972). No fossil species is known for this genus.

†**HAKELIOSOMUS** Gayet, 1993b

†*Spaniodon hakelensis* Davis, 1887

type and only species

- 1887 †*Spaniodon hakelensis*: J. W. Davis, p. 591; table 34, fig. 4.
1898 †*Charitosomus hakelensis* (Davis): A. S. Woodward, p. 412.
1993b †*Hakeliosomus hakelensis* (Davis): M. Gayet, p. 19; figs. 1 to 18; tables 1 to 3.

†*Hakeliosomus hakelensis* has been reported from the marine early Cenomanian strata of Haqil, Lebanon. The species has long been considered as belonging to †*Charitosomus* (Davis 1887, Woodward 1898, 1901, Patterson 1970). However, acid preparation of numerous specimens allowed a re-description of the species and its transfer into the monospecific genus †*Hakeliosomus* (Gayet 1993b). Grande and Poyato-Ariza (1999) found no justification for this taxonomic choice. Phylogenetically, †*Hakeliosomus* is close to †*Charitosomus* and †*Charitopsis*. However, it differs from all species of †*Charitosomus* and from †*Charitopsis* by the smooth border of its subopercle (that is spinous in these two genera). Also, a supraneural 1 seems to be present, as in some species of †*Charitosomus* (e.g., †*C. lineolatus*). For these reasons, we believe that it represents a valid genus, although Grande and Grande (2008) argued that it is a synonym of †*Ramallichthys*.

†*HALECOPSIS* Woodward, 1901

†*Osmeroides insignis* Delvaux and Ortlieb, 1888

type and only species

- 1844 †*Halecopsis laevis*: L. Agassiz, p. 139 (*nomen nudum*).
1887 †*Osmeroides insignis*: E. Delvaux, p. 74; table 3, figs. 2 to 7, 10 and 11 (not described).
1888 †*Osmeroides insignis*: E. Delvaux and J. Ortlieb, p. 60; tables 1 and 2.
1901 †*Halecopsis insignis* (Delvaux and Ortlieb): A.S. Woodward, p. 134.

This species was reported from the marine Ypresian London Clay (southeast England), from the “Argile des Flandres” (Belgium), from the Clay of Hemmoor (northwest Germany), and from northern France. Its osteology was studied by Delvaux and Ortlieb (1888), Woodward (1901), and especially Casier (1946, 1966). Jordan (1910) suspected some relationship with the chanid †*Dastilbe*, but Schaeffer (1947) questioned this affinity. Casier (1966) was the first to suggest gonorynchid affinities. For Patterson (1984b), †*Halecopsis* and †*Neohalecopsis* (see below) are chanids rather than members of the family †Halecopsidae, which is not well defined. Because the specimens of these two genera are poorly preserved, they were not included into the phylogenetic analysis by Poyato-Ariza (1996a). However, because they lack two chanid synapomorphies (wide frontals and expanded operculum), that author suspected that they may be closer to *Gonorynchus* than to *Chanos*. Neither Grande (1999a) nor Grande and Grande (1999) mentioned this teleost. Taverne and Gayet (2006) confirmed the gonorynchoid status of †*Halecopsis insignis*, and they placed it between †*Apulichthys* and the other families of the suborder.

†*JUDEICHTHYS* Gayet, 1985

†*Judeichthys haasi* Gayet, 1985

type and only species

- 1985 †*Judeichthys haasi*: M. Gayet, p. 67; figs. 1 to 8; table 1, figs. 1 to 3; table 2, fig. 1.

Only one specimen from the marine early Cenomanian of Ramallah, Judea Mounts, Israel, is presently known. A new family, †Judeichthidae, was erected for this taxon (Gayet 1985). Grande (1996) rejected the validity of both this family and this genus. This author included both †*Judeichthys* and †*Ramallichthys* into †*Charitosomus*. More recently, Grande and Grande (2008) argued that †*Judeichthys* should be synonymized with †*Ramallichthys*.

There is a controversy for the identity of the two posterior pharyngeal patches of conical teeth. For Grande (1996), these teeth belong to the entopterygoid and to the basibranchials, as in all gonorynchiforms. However, the specimen of †*Judeichthys* was apparently not subject to post-mortem displacement because the two mandibles are nearly superposed. It is therefore difficult to imagine how the right entopterygoid only could have been turned out in a movement placing the patch of teeth at a level as low as the second basibranchial. In addition, two teeth belonging to the upper patch are placed outside the entopterygoid (Gayet 1985).

Gonorynchus and †*Notogoneus* have elongated skull, and Grande (1996) argued that the shortness of the anterior part of the skull of †*Judeichthys* is similar to the 'derived' *Phractolaemus*. However, there was no direct evidence of a relationship between these two taxa.

Although it would be out of place to discuss all the characters of †*Judeichthys* here, we propose not to maintain the family †Judeichthyidae, but we do maintain the generic status of †*Judeichthys*.

***KNERIA* Steindachner, 1866**

This freshwater taxon comprises 13 extant species distributed in East, West and Central Africa. These are: *K. angolensis* (Steindachner 1866), *K. ansorgii* (Boulenger 1910), *K. auriculata* (Pellegrin 1905), *K. katangae* (Poll 1976), *K. maydelli* (Ladiges and Voelker 1961), *K. paucisquamata* (Poll and Stewart 1975), *K. polli* (Trewavas 1936), *K. ruaha* (Seegers 1995), *K. rukwaensis* (Seegers 1995), *K. sjolandarsi* (Poll 1967), *K. stappersii* (Boulenger 1915), *K. uluguru* (Seegers 1995), and *K. wittei* (Poll 1944). See Poll (1965) and Roberts (1975) for a detailed account on the distribution of these species.

Kneria mashkova (Karatajute-Talimaa 1997) from Spain is a chondrichthyan and it was renamed †*Knerialepis mashkova* (Hanke and Karatajute-Talimaa 2002).

†*LECCEICHTHYS* Taverne, 1998

†*Lecceichthys wautyi* Taverne, 1998

type and only species

1998 †*Lecceichthys wautyi*: L. Taverne, p. 292; figs. 1 to 6; table.

One near complete specimen from late Campanian–early Maastrichtian marine deposits in Nardo, Apulia, Southern Italy, was named †*Lecceichthys wautyi* by Taverne (1998). Close to †*Notogoneus* and *Gonorynchus*, it was placed in the Gonorynchidae, as the basal sister group of these two genera.

†*NEOHALECOPSIS* Weiler, 1928.

†*Neohalecopsis striatus* (Weiler, 1920)

type and only species

1920 †*Chanoides striata*: W. Weiler, p. 4.

1928 †*Neohalecopsis striatus* (Weiler): W. Weiler, p. 14; table 4, figs. 3 to 5; table 6, fig. 2.

This taxon is based on a single specimen from the Oligocene Septarientones, Flörsheim, Rheinhessen (Germany). The fossil was first described as †*Chanoides striata* by Weiler (1920), and it was later assigned to a new monospecific genus, †*Neohalecopsis*, supposed close to †*Halecopsis*. Casier (1946) erected the family †Halecopsidae for these two genera (see †*Halecopsis*). However, the skull and the general morphology of †*Neohalecopsis* greatly differ from †*Halecopsis*, and they seem to indicate chanid affinities instead (Taverne and Gayet 2006).

†*NOTOGONEUS* Cope, 1885

†*Notogoneus osculus* Cope, 1886

type species

1885 †*Notogoneus osculus*: E.D. Cope, p. 1091, listed.

1886 †*Notogoneus osculus* Cope: E.D. Cope, p. 163; figs. 4 and 5.

1890 †*Protocatostomus constablei*: R.P. Whitfield, p. 117; pl. 4.

1984 †*Notogoneus osculus* Cope 1885: L. Grande, p. 104.

Type species of the genus, †*Notogoneus osculus* was first reported from the early Eocene of Wyoming (Green River Formation and Bridger Formation). †*Notogoneus osculus* was apparently not common in Eocene lake faunas, and it was not a near-shore species (Grande 1999a). Hundreds of nearly complete specimens are known. This species has been described by several authors, including Cope (1885), Whitfield (1890), Perkins (1970) and Grande (1984). The known representatives of †*Notogoneus osculus* are between 20 and 80 cm long.

Isolated scale fragments from the early Eocene freshwater deposits of the Coalmon Formation, northern Colorado, have been assigned to †*Notogoneus* sp. cf. *N. osculus* (Wilson 1981).

†*Notogoneus alsheimensis* (Weiler, 1942)

- 1942 † *Otolithus* (? *Coregonidarum*) *alsheimensis*: W. Weiler, p. 18, pl. 1, fig. 14–19.
1963 † *Notogoneus alsheimensis* Weiler: W. Weiler, p. 19.

This species was found in the Hydrobia marl (early Miocene, Aquitanian) of Alsheim, middle Rhein Valley, Germany. According to W. Schwarzhans (personal communication to M. Gayet, 2005), it lived in a brackish to freshwater environment.

†*Notogoneus brevirostris* Schwarzhans, 1974

- 1974 †*Notogoneus brevirostris*: W. Schwarzhans, p. 95; figs. 77 and 78; pl. 3, fig. 20.

Otoliths from the late Oligocene of Niederrhein, Germany, have been reported as a species of †*Notogoneus* by Schwarzhans (1974). Nolf (1985) first agreed with this determination, but further research indicates that these otoliths now appear to belong to a perciform fish from the family Acropomatidae (D. Nolf, personal communication to L. Taverne, 2004).

†*Sphenolepis cuvieri* Agassiz, 1844

- 1818 †*Anormurus macrolepidotus*: H.D. de Blainville, p. 374.
1822 †“Gonorynque”: G. Cuvier, p. 346; table 77, figs. 9, 11, 12, 13 and 15.
1844 †*Sphenolepis cuvieri*: L. Agassiz, part 1, p. 13; part 2, p. 89; table 44, figs. 1, 2, 4 to 9 and 11.
1895 †*Notogoneus cuvieri* (Agassiz): A.S. Woodward, p. 503.
1900 †*Notogoneus* sp.: F. Priem, p. 849; table 15, figs. 2 to 5.
1908 †*Notogoneus janeti*: F. Priem, p. 133; pl. 3, figs. 2 and 3.
1911 †*Notogoneus* aff. *squammosseus* (Blainville): F. Priem, p. 34.
1931 †*Phalacropholis centumnucesianus* (Chabanaud): P. Chabanaud, p. 502; table 22, fig. 2.
1934 †*Colcopholis centumnucesianus* (Chabanaud): P. Chabanaud, p. 9.
1981a †*Notogoneus cuvieri* (Agassiz): J. Gaudant, p. 63; pl. 3.

†*Notogoneus cuvieri* was reported from the late Oligocene gypsum deposits of Montmartre, Paris, France. According to Gaudant (1981a), these layers were deposited in the slightly brackish waters of a lagoon that had some connection to the sea. Only two imperfect articulated skeletons and some isolated bones are known.

Gaudant and Burkhardt (1984) also reported †*Notogoneus* cf. *cuvieri* from the “marnes grises” (grey marls) at Altkirch (Haut-Rhin, France), a site dated as early Oligocene (Sittler 1965, 1972). These †*Notogoneus* specimens represent about two thirds of the ichthyofauna at this locality. The skeletons

are more or less fragmentary, but the bones are usually found in connection. The fish fauna, the invertebrates, the plant remains, as well as some isotopic analyses suggest a low salinity for the palaeowater at Altkirch (Gaudant and Burkhardt 1984).

†*Notogoneus fusiformis* Schwarzahns, 1994

1994 †*Notogoneus fusiformis*: W. Schwarzahns, p. 57; fig. 40.

Schwarzahns (1994) described this species from the late Oligocene (Chattian) of Niederrhein (Germany), based on isolated otoliths. The generic determination seems correct (D. Nolf, personal communication to L. Taverne, 2004). Interestingly, Schwarzahns (1994) described the palaeoenvironment as “a shallow marine setting”.

†*Notogoneus gracilis*, Sytchevskaya, 1986

1986 †*Notogoneus gracilis*: E.K. Sytchevskaya, p. 51; figs. 15 and 16; tables 8 and 9.

Sytchevskaya (1986) described a new species of a small †*Notogoneus* from the late Paleocene or early Eocene Boltyska Basin, Ukraine. This taxon is represented by numerous partial or complete specimens of small size, between 5 and 9 cm (Grande and Grande 1999). †*Notogoneus gracilis* is the oldest record of the genus in Europe.

†*Notogoneus janeti* Priem, 1908

1908 †*Notogoneus janeti*: F. Priem, p. 133; pl. 3, figs. 2 and 3.

This species was erected for a single specimen from the late Eocene or early Oligocene “Marnes bleues supragypseuses” of the Paris Basin, France. It was described and figured by Signeux (1961). †*Notogoneus janeti* was regarded as a junior synonym of †*Notogoneus cuvieri* by Gaudant (1981a).

†*Cobitis longiceps* (von Meyer, 1848)

1844 †*Cobitis longiceps*: L. Agassiz, part I, p. 10 (listed)

1848 †*Cobitis longiceps*: H. von Meyer, p. 151; table 20, fig. 2.

1901 †*Notogoneus longiceps* (von Meyer): A.S. Woodward, p. 278; table 20, fig. 2.

Numerous complete specimens from the early Miocene (Aquitanian) freshwater “Hydrobienschichten” deposits in Germany were assigned to †*Notogoneus longiceps* by Weiler (1963). This species is also present at Godrastein-bei-Landau (Palatinat, Germany), in the lower part of the Hydrobienschichten layers (Brelie *et al.* 1973). According to Gaudant (1981b),

isolated otoliths from the same areas were also attributed to this species by these authors and by Malz (1978a, b).

Despite the presence of the amphibians *Rana*, †*Palaeobatrachus* and *Salamandra*, as well as of freshwater gastropods (Planorbidae and Lymnaeidae), Gaudant (1981b) argued for oligohaline conditions during the formation of the Hydrobienschichten deposits, because strictly marine fishes are absent.

†*Notogoneus montanensis* Grande and Grande, 1999

1999 †*Notogoneus montanensis*: L. Grande and T. Grande, p. 614; figs. 1 to 4; table 1.

Grande and Grande (1999) described this new species of †*Notogoneus* from the Campanian Two Medicine Formation, northwestern Montana (USA). It is based primarily on a single skeleton that is less than 5 cm in total length and that is missing much of the skull. It represents the earliest ascertained occurrence of †*Notogoneus* in North America, and the earliest known freshwater gonorynchiform from this continent. The palaeoenvironment is described as a small lacustrine or waterhole environment by Varrichio and Horner (1993).

†*Notogoneus parvus* Hills, 1934

1934 †*Notogoneus parvus*: E.S. Hills, p. 164; figs. 8 and 9; pl. 20.

This species, about 20 cm in total length, is known from late Eocene or early Oligocene freshwater deposits of Redbank Plains, southern Queensland, Australia. It was first described by Hills (1934) on the basis on five nearly complete specimens preserved as moulds in a limonitic mudstone. However, the absence of denticles on the scales suggests that the Australian specimens may belong to another genus.

†*Cyprinus squamosseus* Blainville, 1818

1818 †*Cyprinus squamosseus*: H.D. de Blainville, p. 371.

1844 †*Sphenolepis squamosseus*: L. Agassiz, part 1, p. 13; part 2, p. 87; table 65.

1896 †*Notogoneus squamosseus* (Blainville): A.S. Woodward, p. 502; table 18, figs. 3 and 4.

†*Notogoneus squamosseus*, from the late Oligocene gypsum quarry of Aix-en-Provence (southern France), is known from several complete specimens up to 77 cm in total length. They were re-described by Gaudant (1981c), who suggested a brackish palaeoenvironment for the deposits, based on the fish assemblage.

†*Notogoneus* sp.

Numerous specimens, lacking specific diagnostic characters, have been assigned to †*Notogoneus* sp. These specimens come from the late Paleocene freshwater deposits of Alberta (Paskapoo Formation), Canada (Wilson 1980); from the middle Eocene (Lutetian) of Brasles, Aisne Departement, France (subopercle and scales, Gaudant 1981b); from the early Oligocene potassic basin of Alsace, France (caudal skeleton associated with the cyprinodontid †*Prolebias*, Gaudant 1981d); from the early Oligocene of the Isle of Wight, England (Gaudant 1981b); and from the early Oligocene of Hoeleden, Brabant, in Belgium (Nolf 1977, Gaudant 1981b).

? †*Notogoneus*

1996 Undescribed gonorynchidae: S.P. Applegate, p. 534; fig. 5.

A new, undescribed genus, based on two specimens, was reported by Applegate (1996) from the middle-late Albian Tlayúa quarry, near Tepexi de Rodríguez, Puebla, Mexico. There is currently no information about the morphology of the fossil specimens, and only size and body shape were used to tentatively assign it to †*Notogoneus*. The co-occurrence of coral reef, freshwater and open ocean taxa suggests that the paleoenvironment was a lagoon protected behind a reef barrier (Espinosa-Arrubarrena and Applegate 1996). If the specimens really belong to †*Notogoneus*, they would represent the earliest occurrence of the genus.

? †*Notogoneus*

1999 Gonorynchidae: L. Grande and T. Grande, p. 620.

1999a ? †*Notogoneus*: T. Grande, p. 437.

Some isolated bones from late Paleocene to middle Eocene freshwater oilshale deposits in Longkou county (Shandong Province, China) have been attributed to a gonorynchiform by Grande and Grande (1999). The material, still to be studied in detail, probably represents a species of †*Notogoneus* (Grande 1999a). Such an occurrence is not unexpected, given the wide geographic and temporal distribution of †*Notogoneus*.

†*PARACHANOS* Arambourg and Schneegans, 1935a.

†*Leptosomus aethiopicus* Weiler, 1922

type and only species

1922 †*Leptosomus aethiopicus*: W. Weiler, p. 154; figs. 3 to 5.

1935a †*Parachanos aethiopicus* (Weiler): C. Arambourg and D. Schneegans, p. 141; table 1, figs. 1 and 2; table 2, figs. 1, 2 and 4; table 3, figs. 1, 5 and 7.

1935b †*Parachanos aethiopicus* (Weiler): C. Arambourg and D. Schneegans, p. 1934, listed.

Weiler (1922) described four small complete specimens from the Aptian/Albian bituminous shales of Rio San Benito, south of Bata, Equatorial Guinea. This fossil material led Weiler (1922) to erect a new species: †*Leptosomus aethiopicus*. Arambourg and Schneegans (1935a, b) later removed this species from the genus †*Leptosomus* because they regarded the Rio Benito specimens as juveniles of a new genus they just discovered in Gabon: †*Parachanos*. This taxon was found in the sub-littoral sandstones of the Cocobeach series, Gabon. Like *Chanos*, †*Parachanos* was placed among the clupeiforms at that time (Arambourg and Schneegans 1935a). Later recognized as a chanid, †*Parachanos* then became the focus of another debate: its similarity with †*Dastilbe*.

In contrast with Arambourg and Schneegans (1935a), Santos (1947) suggested a synonymy between †*Parachanos* and †*Dastilbe* because the anatomical differences (vertebral counts and persistence of a notochordal canal in †*Dastilbe*) were not regarded as taxonomically significant. Taverne (1974) first questioned this synonymy, but he later suggested that †*Dastilbe* (†*D. crandalli* and †*D. elongatus*) and †*Parachanos* represent separate populations of a single species, †*D. crandalli* (Taverne 1981). After a study of the type species of †*Parachanos* (†*P. aethiopicus*) and of †*Dastilbe* species, Gayet (1989) disagreed with this synonymy. Blum (1991a), who regarded both †*D. crandalli* and †*D. elongatus* as valid species (although he did not mention †*D. batai*), considered that the validity of †*Parachanos* remains to be tested. Finally, recent cladistic analyses have considered †*Parachanos* and †*Dastilbe* (on the basis of †*D. crandalli* and †*D. elongatus*) distinct genera (Poyato-Ariza 1996a, Grande and Poyato-Ariza 1999).

†*Parachanos* sp.

Erasmus (1952) figured six specimens from the Late Cretaceous at Redipuglia, Carso Triestino, Komen, in Croatia and he attributed them to †*Parachanos* sp. According to Radovic (1975), the beds these fish come from may range from Cenomanian to Maastrichtian in age. Gayet (1993a) placed it erroneously in synonymy with †*Dastilbe*, as noted by Poyato-Ariza (1996a).

Nardon (1990) also reported on †*Parachanos* sp. from the Coniacian-Santonian of Palazzo, Carso Goriziano, Italy.

PARAKNERIA Poll, 1965

No fossil is known for this extant freshwater genus. Fourteen stream-dwelling species of *Parakneria* are known from East, West and Central Africa (see Poll 1965 and Roberts 1975 for details). These are: *Parakneria abbreviata*

(Pellegrin, 1931), *P. cameronensis* (Boulenger, 1909), *P. damasi* Poll, 1965, *P. fortuita* Penrith, 1973, *P. kissi* Poll, 1969, *P. ladigesi* Poll, 1967, *P. lufirae* Poll, 1965, *P. malaissei* Poll, 1969, *P. marmorata* (Norman, 1923), *P. mossambica* Jubb and Bell-Cross, 1974, *P. spekii* (Günther, 1868), *P. tanzaniae* Poll, 1984, *P. thysi* Poll, 1965, and *P. vilhenae* Poll, 1965.

PHRACTOLAEMUS Boulenger, 1901

A single Recent species, *Phractolaemus ansorgii*, is known for this genus. There are two subspecies, *P. ansorgii ansorgei* Boulenger, 1901, and *P. ansorgii spinosus* Pellegrin, 1925, that are found respectively in Niger and in the central basin of the Democratic Republic of Congo (Thys van den Audenaerde 1961). No fossil is known for this genus.

†**PROCHANOS** Bassani, 1882

†*Prochanos rectifrons* Bassani, 1882

type and only species

1879 †*Prochanos rectifrons*: F. Bassani, p. 163, listed.

1882 †*Prochanos rectifrons* Bassani: F. Bassani, p. 218; table 13; table 14, fig. 1; table 15.

This large fish (54 cm in total length) was described from the Late Cretaceous of Lesina Island, Hvar, Dalmatia (Croatia). It is probably a junior synonym of †*Chanos leopoldi* (Erasmio, 1915). The limestones from this area are regarded as Turonian to Maastrichtian in age (Radovic 1975).

†*Prochanos* ? sp.

Bassani (1882) listed †*Prochanos* ? sp. in the early Cenomanian of Haqil, Lebanon. Later, Woodward (1901) reidentified the specimen as †*Chirocentrites libanicus* Pictet and Humbert, 1866, an ichthyodectid fish found in the same beds. In fact, Woodward (1901) transferred that species into the genus †*Ichthyodectes*. Two years later, Hay (1903) erected the new genus †*Eubiodectes* for that species. Clearly, †*Eubiodectes libanicus* does not belong to the Gonorynchiformes. Thus, there is currently no evidence for the presence of †*Prochanos* in the Cretaceous of Lebanon.

†**RAMALLICHTHYS** Gayet, 1982

†*Ramallichthys orientalis* Gayet, 1982

type and only species

1982 †*Ramallichthys orientalis*: M. Gayet, p. 405; fig. p. 406.

Gayet (1982) created this taxon for seven specimens found in the marine Beit-Mer Formation (early Cenomanian) at Ein-Yabrud, near Ramallah, Judea Mounts, Israel. As for †*Judeichthys*, Grande (1996) rejected the validity of the genus and suggested that †*Ramallichthys orientalis* may be a junior synonym of †*Charitosomus hakelensis*. In fact, the study of the type species †*Charitosomus formosus* led Gayet (1993b) to argue that †*Charitosomus hakelensis* is certainly not a †*Charitosomus* (see †*Hakeliosomus hakelensis* above). In addition, the validity of †*Ramallichthys orientalis* is supported by several characters, such as the parhypural and hypural 1 being unfused to the centrum complex, and the strong modification of the anteriormost vertebrae, as figured by Gayet (1986). As for †*Judeichthys*, the detailed controversy about †*Ramallichthys* is well beyond the scope of this paper. However, it is certain that the phylogenetic status of this taxon poses an interesting problem of character distribution among Ostariophysii. Recently, Grande and Grande (2008) proposed to synonymize †*Judeichthys* and †*Hakeliosomus* with †*Ramallichthys*.

†**RUBIESICHTHYS** Wenz, 1984

†*Rubiesichthys gregalis* Wenz, 1984

type and only species

1984 †*Rubiesichthys gregalis*: S. Wenz, p. 276; figs. 1 and 2.

Wenz (1984, 1991) described this taxon on the basis of 10 complete specimens (each less than 5 cm in standard length) from the Berriasian-Valanginian (Early Cretaceous) lithographic limestones of Serra del Montsec, Lérida Province, Spain. Abundant specimens (more than 400) of †*Rubiesichthys gregalis* have been reported from both this locality and the late Hauterivian–early Barremian site of Las Hoyas, Cuenca Province, Spain (Sanz *et al.* 1988, Poyato-Ariza 1996c). Poyato-Ariza (1996a, c) provided a detailed account on this channid species and found many similarities with †*Gordichthys conquensis*.

†**THARRHIAS** Jordan and Branner, 1908

From Arambourg and Schneegans (1935a, b) onwards, most authors have included †*Tharrhias* species within Chanidae, but Patterson (1984b), followed by Brito and Wenz (1990), Blum (1991b) and Gayet (1993c), treated †*Aethalionopsis*, †*Tharrhias*, †*Dastilbe*, †*Parachanos*, and occasionally †*Rubiesichthys* as stem group gonorynchiforms (or gonorynchoids).

†*Tharrhias araripis* Jordan and Branner, 1908

type species

1908 †*Tharrhias araripis*: D. S. Jordan and J. C. Branner, p. 14; pl. II

Type species of the genus, †*Tharrhias araripis* was erected based on specimens from the Aptian/Albian Romualdo Member of the Santana Formation, Araripe Basin, northeastern Brazil. †*Tharrhias* is the most abundant taxon in the fish assemblages found in the lower part of these deposits, where it typically occurs in early diagenetic carbonate concretions (Fara *et al.* 2005). According to Poyato-Ariza (1996a), †*T. araripis* is currently the only valid species of the genus.

†*Tharrhias castellanoi* Santos and Duarte, 1962

1962 †*Tharrhias castellanoi*: R. da Silva Santos and L. Duarte, pl. 3, figs. 3 and 4.

Santos and Duarte (1962) created this species based on imprints of isolated scales found in the Turonian Açú Sandstones in Rio Grande do Norte, Brazil. Brito and Wenz (1990) first pointed out that the very poor material does not support the creation of a new taxon, and †*T. castellanoi* is certainly not a valid species.

†*Tharrhias feruglioi* (Bordas, 1942)

1942 †*Tharrhias feruglioi*: A. Bordas, p. 316; fig. 1.

1949 †*Tharriasis shamani*: M. Dolgopol de Sáez, p. 445; fig. 1.

1949 †*Leptolepis leanzai*: M. Dolgopol de Sáez, p. 447; fig. 2.

1978 †*Leptolepis feruglioi* Bordas, 1942: A. Bocchino, p. 303; figs. 1 and 2, pl. 1.

1987 “†*Tharrhias*” *feruglioi* Bordas, 1942: A.L. Cione and S.M. Pereira, p. 290; table 3 and table 5, fig. C.

2001 †new genus *feruglioi* (Bordas): G. Arratia and A. Lopez-Arbarello, p. 5.

Bordas (1942) erected the species †*Tharrhias feruglioi* for specimens found in the vicinity of Cerro C ndor, Rio Chubut, Argentina. This taxonomic choice may have been influenced by both the age of the sediments (thought to be Early Cretaceous at that time, but actually Jurassic [Arratia and Lopez-Arbarello, 2001]) and by the overall similarity with †*Tharrhias araripis*. Bocchino (1978) moved this species to genus †*Leptolepis* (*sensu* Nybelin 1974). Cione and Pereira (1987) later suggested that †*T. shamani* Dolgopol de S ez, 1949 and †*Leptolepis leanzai* Dolgopol de S ez, 1949 are synonyms of †"*Tharrhias*" *feruglioi*. Poyato-Ariza (1996a: 42) first suggested that this species can be removed from the genus †*Tharrhias* and from the clade Ostariophysii. More recently, Arratia and Lopez-Arbarello (2001) provided a wealth of anatomical detail based on abundant new material for this taxon. Because of its generalized morphology, these authors also concluded that †"*Tharrhias*" *feruglioi* can be removed from the genus †*Tharrhias* as a yet unnamed species of Teleostei *incertae sedis*.

†*Cearana rochae* Jordan and Branner, 1908

- 1908 †*Cearana rochae*: D.S. Jordan and J.C. Branner, p. 27; pl. VIII, fig. 2.
- 1921b †*Tharrhias rochae* (Jordan and Branner): D.S. Jordan, p. 28; pl. VII, fig. 4.
- 1938 †*Tharrhias Rochai* (Jordan and Branner): G. d'Erasmus, p. 19; pl. III, figs. 1–3; pl. IV, fig. 1.
- 1991b †*Tharrhias araripis* Jordan and Branner: S. Blum, p. 287; figs. and pl. pp. 286–293.

Based on specimens from the Aptian/Albian Romualdo Member of the Santana Formation (northeastern Brazil), Jordan and Branner (1908) erected two genera, †*Tharrhias* (†*T. araripis*) and †*Cearana* (†*C. rochae*). They assigned them to the families †Leptolepididae and Osteoglossidae, respectively. Later, Jordan (1921b) moved the two type species to the genus †*Tharrhias* (considered to be a †Leptolepididae at that time). This author regarded †*T. araripis* and †*T. rochae* as valid species that could be distinguished by the body shape, and Erasmus (1938) acknowledged the taxonomic status of the two forms. Taverne (1975) did not discuss the synonymy of the genera †*Tharrhias* and †*Cearana*, but he assigned both taxa to the Gonorynchiformes. The study by Oliveira (1978) provided six anatomical features that discriminate †*T. araripis* and †*T. rochae*. Patterson (1984a) listed the two species, but he only discussed and figured †*T. araripis*. Finally, Blum (1991b) was the first to check for a possible synonymy between †*T. araripis* and †*T. rochae*. He concluded that †*T. rochae* must be regarded as a junior synonym of †*T. araripis*, a suggestion with which Poyato-Ariza (1996a) agreed.

†*Tharrhias shamani* Dolgopol de Sáez, 1949

- 1949 †*Tharrhias shamani*: M. Dolgopol de Sáez, p. 445; fig. 1.
1949 †*Leptolepis leanzai*: M. Dolgopol de Sáez, p. 447; fig. 2.
1987 “†*Tharrhias*” *feruglioi* Bordas, 1942: A.L. Cione and S.M. Pereira, p. 290; tables 3 and 5, fig. C.

Junior synonym of †*Tharrhias feruglioi*.

Discussion

From the review above, and considering the conflicts among taxonomic opinions, the following list of valid gonorynchiform fossil species is proposed:

- Aethalionopsis robustus* (Traquair, 1911)
Apulichthys gayeti Taverne, 1997
Chanos brevis Heckel, 1854
Chanos compressus Stinton, 1977
Chanos forcipatus Kner and Steindachner, 1863
Chanos leopoldi (Costa, 1860)
Chanos torosus Danil’chenko, 1968
Chanos zignoi Kner and Steindachner, 1863
Charitopsis spinosus Gayet, 1993a
Charitosomus formosus von der Marck, 1885
Charitosomus lineolatus (Pictet and Humbert, 1866)
Charitosomus major Woodward, 1901
Coelogaster leptostea (Eastman, 1905)
Dastilbe crandalli Jordan, 1910
Dastilbe moraesi Santos, 1955
Gordichthys conquensis Poyato-Ariza, 1994
Hakeliosomus hakelensis (Davis, 1887)
Halecopsis insignis (Delvaux and Ortlieb, 1888)
Judeichthys haasi Gayet, 1985
Lecceichthys wautyi Taverne, 1998
Neohalecopsis striatus (Weiler, 1920)
Notogoneus alsheimensis (Weiler, 1942)
Notogoneus cuvieri (Agassiz, 1844)
Notogoneus fusiformis Schwarzhans, 1994
Notogoneus gracilis Sytchevskaya, 1986
Notogoneus longiceps (Meyer, 1848)
Notogoneus montanensis Grande and Grande, 1999
Notogoneus osculus Cope, 1886
Notogoneus parvus Hills, 1934
Notogoneus squamosseus (Blainville, 1818)

Parachanos aethiopicus (Weiler, 1922)
Ramallichthys orientalis Gayet, 1982
Rubiesichthys gregalis Wenz, 1984
Tharrhias araripis Jordan and Branner, 1908

Fossil Distribution

Fossil gonorynchiform fishes are known from the earliest Cretaceous (Berriasian-Valanginian) to the earliest Miocene, and the clade has several extant representatives. With only 46 known localities, their fossil record is relatively poor compared to that of other groups of Ostariophysii. For example, Siluriformes are present in more than 500 fossil sites (Gayet and Meunier 2003), despite their first appearance in the Late Cretaceous. The paucity of the fossil record of Gonorynchiformes might reflect the actual low diversity of the group through geological time, but this apparent poor diversity is certainly accentuated by some biasing factors, such as the low frequency of diagnostic specimens.

The distribution of gonorynchiform-bearing localities is heterogeneous in both space and time. More than half the localities are Cretaceous in age (16 in the Early Cretaceous and nine in the Late Cretaceous), and there are only three sites known from the Palaeocene, seven from the Eocene, 10 from the Oligocene, and one from the earliest Miocene (Aquitanian). There are no fossil sites with gonorynchiform fossils between the Miocene and the Recent, and the clade could therefore be qualified as a “Lazarus taxon” for that time interval.

The spatial distribution of localities is also unbalanced (see also Grande 1999a and Fara *et al.* 2007 for summary maps). More than half the sites are located in Europe, and this is accompanied by a higher taxonomic diversity, because the majority of fossil genera and species are European (Figs. 6.1 and 6.2). The oldest representative of the group (†*Rubiesichthys*) is known from Europe, as well as the most basal taxa. The Italian taxon †*Chanos leopoldi* is currently the oldest known record of *Chanos*, which is the only extant gonorynchiform genus with fossil representatives. All fossil *Chanos* species are restricted to Europe (although the extant *Chanos* is Indo-Pacific), and they range apparently from the Early Cretaceous to the Oligocene.

Only three fossil genera and three species have been reported from Africa (Fig. 6.3), but their precise taxonomic status remains unresolved (†*Parachanos*, †*Dastilbe*, and †*Charitosomus*). Therefore, gonorynchiform fish are undoubtedly present in Africa since Aptian-Albian times, but the exact nature of the taxa is open to debate. Nothing is known about the origin of the two living African families, Kneriidae and Phractolaemidae, which lack a fossil record.

Occurrences in the Middle East (Fig. 6.3) suggest that gonorynchiform diversity was apparently higher than in Africa, and they provide important information on the Tethyan biogeography in the early Late Cretaceous.

		Europe	
QUATERNARY			
NEOGENE	PLIOCENE	Piacenzian	
		Zanclean	
	MIOCENE	Messinian Tortonian	
		Serravallian Langhian	
		Burdigalian Aquitanian	
PALEOGENE	OLIGOCENE	Chattian	
		Rupelian	
	EOCENE	Priabonian	
		Bartonian	
		Lutetian	
		Ypresian	
	PALEOCENE	Thanetian	
		Selandian	
Danian			
CRETACEOUS	UPPER	Maastrichtian	
		Campanian	
		Santonian Coniacian Turonian	
		Cenomanian	
	LOWER	Albian	
		Aptian	
		Barremian	
		Hauterivian	
		Valanginian	
		Berriasian	

Fig. 6.1 Stratigraphic distribution of Gonorynchiformes in the Cretaceous of Europe. Because there is some uncertainty about the precise age of several localities, the stratigraphic ranges given in Figs. 6.1 to 6.6 provide the maximum possible age for each taxon. Thin bars represent the inferred presence of taxa in the fossil record.

	Europe
Quaternary	
Piacenzian	
Zanclean	
Messinian Tortonian	
Serravallian Langhian	
Burdigalian	
Aquitanian	
Chattian	
Rupelian	
Priabonian	
Bartonian	
Lutetian	
Ypresian	
Thanetian	
Selandian	
Danian	
Maastrichtian	
Campanian	
Santonian Coniacian Turonian	
Cenomanian	
Albian	
Aptian	
Barremian	
Hauterivian	
Valanginian	
Berriasian	

The chart displays the stratigraphic distribution of post-Cretaceous Gonorynchiformes in Europe. The vertical axis represents geological stages from the Berriasian at the bottom to the Quaternary at the top. The horizontal axis represents the duration of various species. Vertical bars indicate the stratigraphic range of each species. The species and their approximate stratigraphic ranges are as follows:

- Chanos torosus* (Turkmenia): Danian to Thanetian
- Halecopsis insignis* (England): Thanetian to Ypresian
- Chanos compressus** (England): Thanetian to Ypresian
- Coelogaster leptostea* (Italy): Ypresian to Lutetian
- Chanos forcipatus* (Italy): Lutetian to Bartonian
- Notogoneus sp.* (France): Bartonian to Rupelian
- Notogoneus cf. cuvieri* (France): Rupelian to Priabonian
- Notogoneus spp.* (Belgium, England): Bartonian to Rupelian
- Chanos brevis* (Italy): Chattian to Rupelian
- Chanos zignoi* (Italy): Chattian to Rupelian
- Neohalecopsis sirriatus* (Germany): Chattian to Rupelian
- Notogoneus squamosseus* (France): Chattian to Rupelian
- Notogoneus cuvieri* (France): Chattian to Rupelian
- Notogoneus fusiformis* (Germany): Chattian to Rupelian
- Notogoneus longiceps* (Germany): Aquitanian to Chattian

Fig. 6.2 Stratigraphic distribution of post-Cretaceous Gonorynchiformes in Europe.

The most remarkable feature of the gonorynchiform fossil record in North and Central America is that it documents only a few species of a single genus, †*Notogoneus* (Fig. 6.4), unless the yet undescribed *Notogoneus*-like form from Mexico represents another genus. Given the size of the continent, the well-known geology, the intensive sampling and the numerous fossil fish localities, this very low gonorynchiform diversity is puzzling, but it certainly represents a real biological pattern.

		Africa	Middle East	
QUATERNARY				
NEOGENE	PLIOCENE	Piacenzian		
		Zanclean		
	MIOCENE	Messinian Tortonian		
		Serravallian Langhian		
		Burdigalian		
		Aquitanian		
PALEOGENE	OLIGOCENE	Chattian		
		Rupelian		
	EOCENE	Priabonian	<i>Parachanos aethiopicus</i> (Equatorial Guinea)	
		Bartonian		
		Lutetian		
		Ypresian	<i>Dastilbe batai</i> (Equatorial Guinea)	
	PALEOCENE	Thanetian	<i>Charitosomus hermani</i> (Democratic Republic of Congo)	
		Selandian		
		Danian		
	CRETACEOUS	UPPER	Maastrichtian	
Campanian			<i>Parachanos aethiopicus</i> (Equatorial Guinea)	<i>Judeichthys haasi</i> (Israel)
Santonian Coniacian Turonian			<i>Dastilbe batai</i> (Equatorial Guinea)	<i>Ramallichthys orientalis</i> (Israel)
			<i>Charitosomus hermani</i> (Democratic Republic of Congo)	<i>Hakeiosomus hakei</i> (Lebanon)
				<i>Charitopsis spinosus</i> (Lebanon)
LOWER		Cenomanian		<i>Charitosomus lineolatus</i> (Lebanon)
				<i>Charitosomus major</i> (Lebanon)
		Albian		
		Aptian		
		Barremian		
		Hauterivian		
		Valanginian Berriasian		

Fig. 6.3 Stratigraphic distribution of Gonorynchiformes in Africa and in the Middle East.

Asia and Australia have very poor but interesting gonorynchiform fossil records (Fig. 6.4). For example, the oldest known occurrence of the group may be a gonorynchid-like specimen from the earliest Cretaceous (Berriasian-Valanginian) of Japan. Also, there is currently no palaeobiogeographic model to explain the presence of an Eocene/Oligocene freshwater †*Notogoneus* in Australia. In turn, there is no doubt that more Asian and Australian fossils would provide key phylogenetic and palaeobiogeographic information for the group.

The fossil record of Gonorynchiformes in South America (Fig. 6.5) is limited taxonomically (only two genera, †*Dastilbe* and †*Tharrhias*), spatially

		North and Central America	Asia	Aust.	
QUATERNARY					
NEOGENE	PLIOCENE	Piacenzien			
		Zanclean			
	MIOCENE	Messinian			
		Tortonian			
		Serravallian			
PALEOGENE	OLIGOCENE	Langhian			
		Burdigalian			
CRETACEOUS	Eocene	Aquitanian			
		EOCENE	Chattian		
			Rupelian		
			Priabonian		
	Bartonian				
	PALEOCENE	PALEOCENE	Lutetian		
			Ypresian		
		Thanetian			
		Selandian			
		Danian			
UPPER		UPPER	Maastrichtian		
	Campanian				
	Santonian				
	Coniacian				
	LOWER	LOWER	Turonian		
			Cenomanian		
			Albian		
			Aptian		
CRETACEOUS	LOWER	Barremian			
		Hauterivian			
		Valanginian			
		Berriasian			

Fig. 6.4 Stratigraphic distribution of Gonorynchiformes in North and Central America, Asia and Australia (Aust.).

(most records are from northeastern Brazil), and temporally (Aptian-Albian). The distribution of †*Dastilbe* seems to be linked with regional events during the opening of the South Atlantic Ocean. However, the precise palaeobiogeographical history of †*Dastilbe* awaits a better understanding of the relationships among its various species (Maisey 2000).

The synoptic range-chart in Fig. 6.6 summarizes the temporal distribution of all fossil genera considered valid in this work.

		South America		
QUATERNARY				
NEOGENE	PLIOCENE	Piacenzian		
		Zanclean		
	MIOCENE	Messinian		
		Tortonian		
		Serravallian		
PALEOGENE	OLIGOCENE	Langhian		
		Burdigalian		
	EOCENE	Aquitanian		
		Chatthian		
		Rupelian		
		Priabonian		
	CRETACEOUS	UPPER	Bartonian	
			Lutetian	
			Ypresian	
			Thanetian	
PALEOCENE		Selandian		
		Danian		
LOWER	UPPER	Maastrichtian		
		Campanian	<i>Dastilbe moraesii</i> (Brazil)	
		Santonian	<i>Dastilbe elongatus</i> (Brazil)	
		Coniacian	<i>Dastilbe crandalli</i> (Brazil)	
	LOWER	Turonian	<i>Dastilbe</i> sp. (Brazil)	
		Cenomanian	<i>Tharrhias araripis</i> (Brazil)	
		Albian		
		Aptian		
		Barremian		
		Hauterivian		
		Valanginian		
Berriasian				

Fig. 6.5 Stratigraphic distribution of Gonorynchiformes in South America.

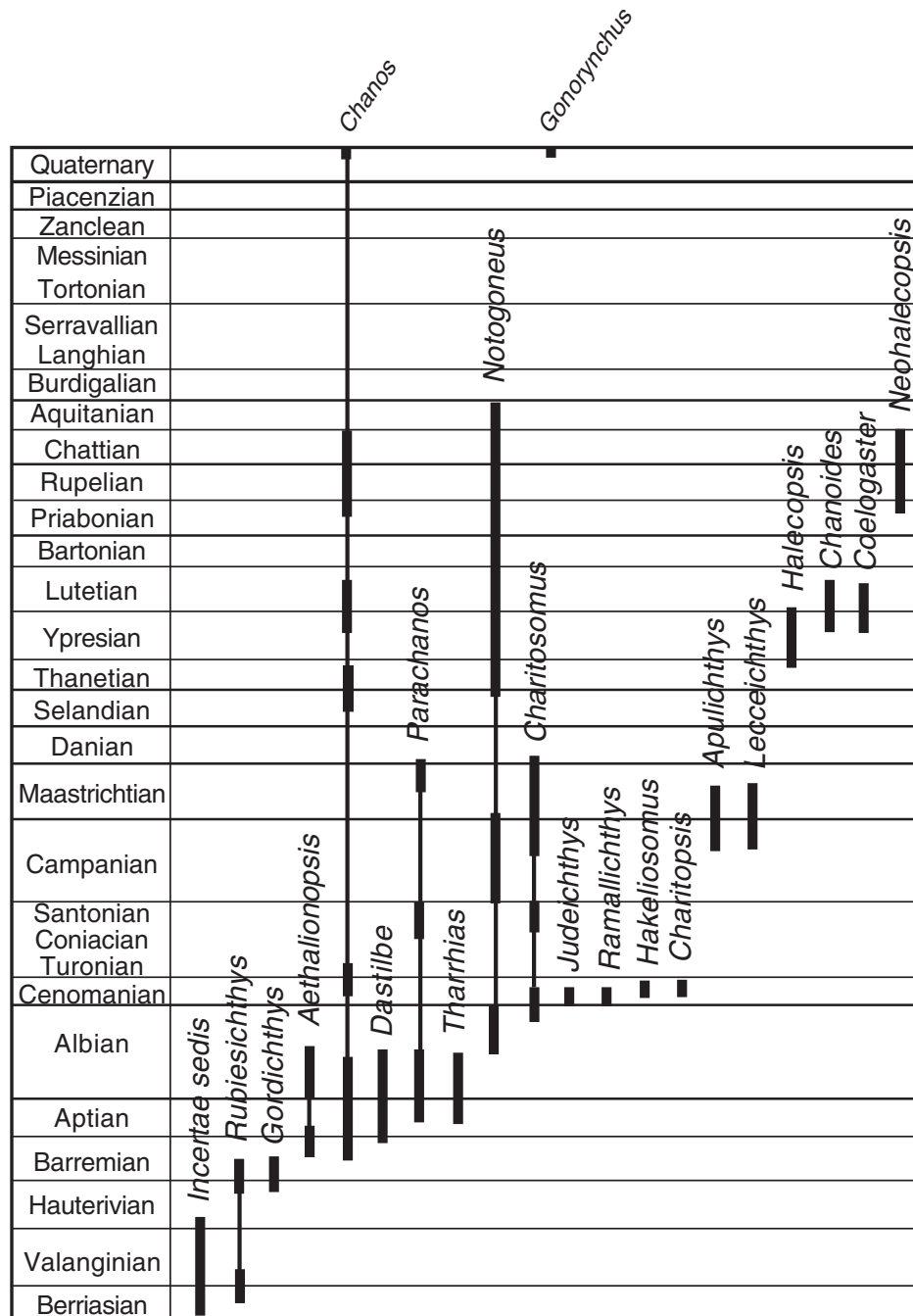


Fig. 6.6 Summary range-chart of the gonorynchiform genera considered valid in this chapter.

Phylogenetic Relationships

In recent years, debates on the phylogenetic status of gonorynchiforms have mainly focused on the identity of the basal-most members of the clade and on its sister group (e.g. Grande and Poyato-Ariza 1999, Lavoué *et al.* 2005). We shall briefly review the main phylogenetic hypotheses in order to test whether conflicting proposals affect diversity patterns inferred from the fossil record.

Very few large-scale phylogenetic studies have included the fossil representatives of Gonorynchiformes. The hypothesis by Gayet (1993c) needed to be updated after the discovery of new taxa such as †*Gordichthys*

(Poyato-Ariza 1994), †*Apulichthys* and †*Lecceichthys* (Taverne 1997, 1998). Grande and Poyato-Ariza (1999) provided the most comprehensive phylogenetic analysis of fossil and extant Gonorynchiformes, although †*Apulichthys* and †*Lecceichthys* could not be included at that time. We summarize below these three proposals as indented lists, and we present the corresponding phylogenetic trees (phylogenetic hypotheses projected on a time scale) in Figs. 6.7–6.9. Poyato-Ariza (1996a) first provided a cladistic analysis of extant and fossil Gonorynchiformes, but it is not included here because it focused primarily on Chanidae and was later updated in Grande and Poyato-Ariza (1999).

Gayet (1993c) first proposed a sister-group relationship between *Gonorynchus* and †*Notogoneus*, and she was followed by subsequent workers

Superorder Ostariophysi *sensu* Rosen and Greenwood 1970
 Series Anatophysyi *sensu* Rosen and Greenwood 1970
 Order Gonorynchiformes *sensu* Rosen and Greenwood 1970

Gayet 1993c (Fig. 7)	Taverne 1997 and 1998 (Fig. 8)	Grande and Poyato-Ariza 1999 (Fig. 9)
† <i>Aethalionopsis</i>	Suborder Chanoidei	Suborder Chanoidei
"† <i>Tharrhias</i> group"	Family Chanidae	† <i>Aethalionopsis</i>
† <i>Rubiesichthys</i>	Subfamily	Family Chanidae
† <i>Tharrhias</i>	Rubiesichthyinae	Subfamily Chaninae
† <i>Dastilbe</i>	† <i>Rubiesichthys</i>	† <i>Dastilbe</i>
† <i>Parachanos</i>	† <i>Gordichthys</i>	† <i>Parachanos</i>
unnamed clade	Subfamily Chaninae	<i>Chanos</i>
<i>Chanos</i>	† <i>Aethalionopsis</i>	† <i>Tharrhias</i>
Kneriidae	<i>Chanos</i>	Subfamily
Phractolaemidae	† <i>Dastilbe</i>	†Rubiesichthyinae
Suborder	† <i>Parachanos</i>	† <i>Gordichthys</i>
Gonorynchoidei	† <i>Prochanos</i>	† <i>Rubiesichthys</i>
† <i>Ramallichthys</i>	† <i>Tharrhias</i>	Suborder Gonorynchoidei
Family	Suborder Gonorynchoidei	Family Gonorynchidae
Judeichthyidae	Family Apulichthyidae	Subfamily
† <i>Judeichthys</i>	† <i>Apulichthys</i>	Gonorynchinae
Family	Family Halecopsidae	<i>Gonorynchus</i>
Charitosomidae	† <i>Halecopsis</i>	† <i>Notogoneus</i>
† <i>Hakeliosomus</i>	Family	† <i>Charitosomus</i>
† <i>Charitosomus</i>	Phractolaemidae	† <i>Ramallichthys</i>
† <i>Charitopsis</i>	Family Kneriidae	† <i>Judeichthys</i>
Family	Family	† <i>Charitopsis</i>
Gonorynchidae	Gonorynchidae	Family Kneriidae
† <i>Notogoneus</i>	† <i>Ramallichthys</i>	Subfamily
<i>Gonorynchus</i>	† <i>Judeichthys</i>	Phractolaeminae
	† <i>Hakeliosomus</i>	<i>Phractolaemus</i>
	† <i>Charitosomus</i>	Subfamily Kneriinae
	† <i>Charitopsis</i>	Tribe Cromerini
	† <i>Lecceichthys</i>	<i>Cromeria</i>
	† <i>Notogoneus</i>	<i>Grasseichthys</i>
	<i>Gonorynchus</i>	Tribe Kneriini
		<i>Kneria</i>
		<i>Parakneria</i>

(but see Grande and Grande 2008 for an alternative opinion). The family Gonorynchidae, as defined by Grande and Poyato-Ariza (1999), includes *Gonorynchus* and †*Notogoneus* plus the Middle East Cretaceous taxa †*Ramallichthys*, †*Judeichthys*, †*Charitosomus*, and †*Charitopsis*. In turn, this family is similar in content to what Gayet (1993b) named the Gonorynchoidei in her taxonomic scheme, with the exception of †*Hakeliosomus*, which was not considered a valid taxon by Grande and Poyato-Ariza (1999). The family names †Judeichthyidae and †Charitosomidae have no more reason to exist, as observed by Grande and Grande (1999). Another similarity between the hypotheses of Gayet (1993c) and Grande and Poyato-Ariza (1999) is the sister-group relationship between *Gonorynchus*, †*Notogoneus* and the Middle East taxa on the one hand and the extant Kneriinae and Phractolaeminae on the other hand.

The monophyly of the clade including all these extant African freshwater taxa is well supported by osteological, myological, and molecular data (Howes 1985, Gayet 1993c, Fink and Fink 1996, Grande and Poyato-Ariza 1999, Lavoué *et al.* 2005). Within this clade, however, there is some disagreement between the results of osteological studies (Grande 1996, Grande and Poyato-Ariza 1999) and those of a recent study based on whole mitogenome sequences (Lavoué *et al.* 2005), in which *Grasseichthys* and *Cromeria* are regarded as sequenced sister groups to the clade (*Kneria*+*Parakneria*). Such a conflict has a great heuristic value in the systematics of Gonorynchiformes.

Taverne's (1997, 1998) definition of Gonorynchoidei was similar to that of Gayet (1993c) and Grande and Poyato-Ariza (1999), but he added †*Lecceichthys*, †*Apulichthys* and †*Halecopsis* to that group. His definition of Chanoidei made this clade paraphyletic.

The identity of the basal-most members of Gonorynchiformes is a recurrent debate. Poyato-Ariza (1996a) and Taverne (1997, 1998) placed †*Aethalionopsis* among the Chaninae, but the analysis of Grande and Poyato-Ariza (1999) excluded this taxon from the Chanidae, a result in accordance with Gayet's (1993c) early hypothesis. The relationships of †*Tharrhias*, †*Dastilbe*, and †*Parachanos* are similar in the three phylogenetic schemes reviewed here. Although Gayet (1993c) placed *Chanos* outside the "†*Tharrhias* group", this genus certainly belongs to the clade composed of †*Dastilbe*, †*Parachanos*, †*Prochanos*, and †*Tharrhias* (Taverne 1997, 1998, Grande and Poyato-Ariza 1999). A vast majority of osteological studies (Fink and Fink 1981, Gayet 1993c, Poyato-Ariza 1996a, Taverne 1997, 1998, Grande and Poyato-Ariza 1999) agree on the relationships of extant forms, with the structure {*Chanos*[*Gonorynchus*(Phractolaemidae+Kneriidae)]}. However, this configuration has been challenged recently by the mitogenomic study of Lavoué *et al.* (2005), in which the arrangement {*Gonorynchus*[*Chanos*(Phractolaemidae+Kneriidae)]} was found.

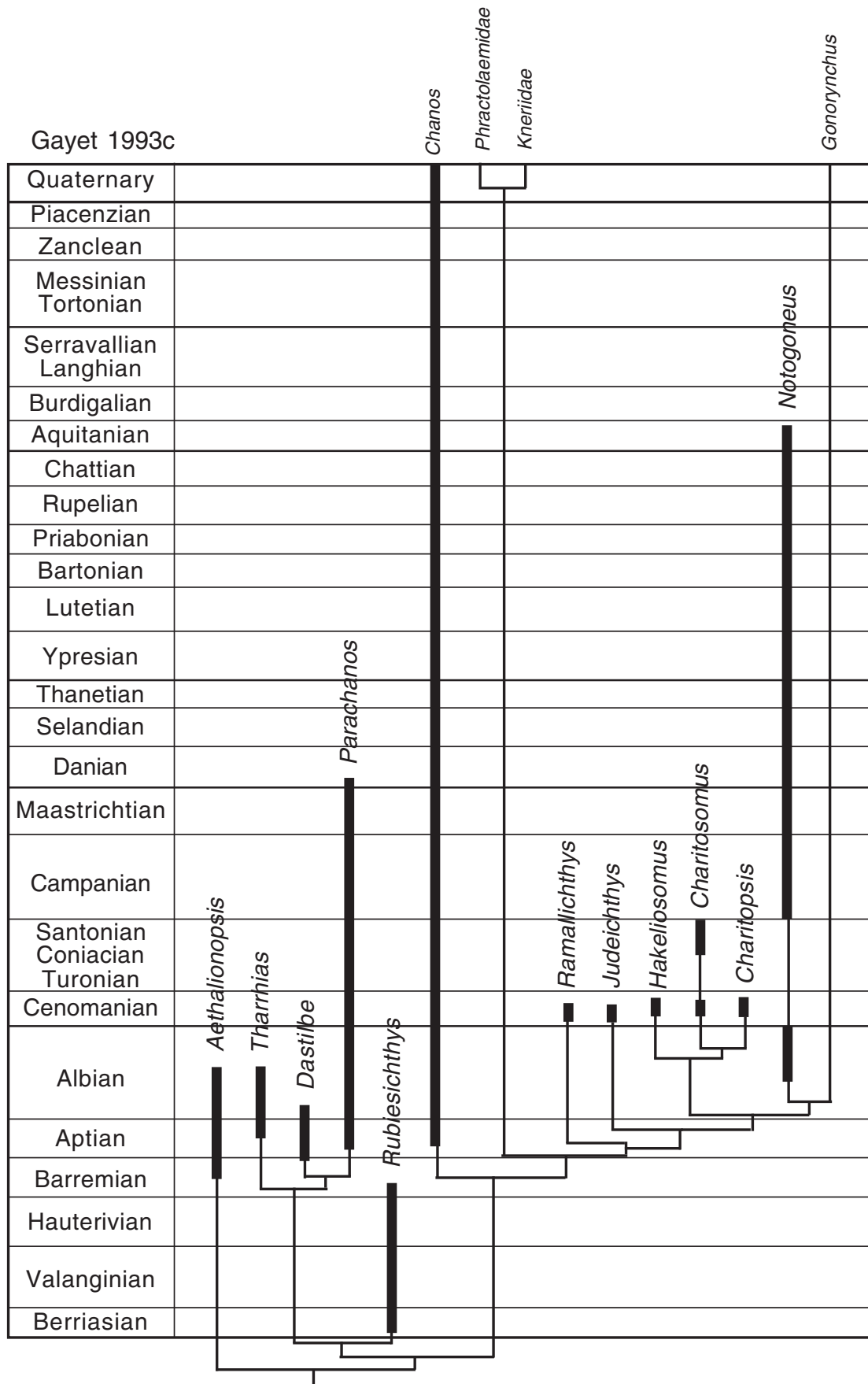


Fig. 6.7 Phylogenetic tree obtained according to the phylogenetic hypothesis by Gayet (1993c).

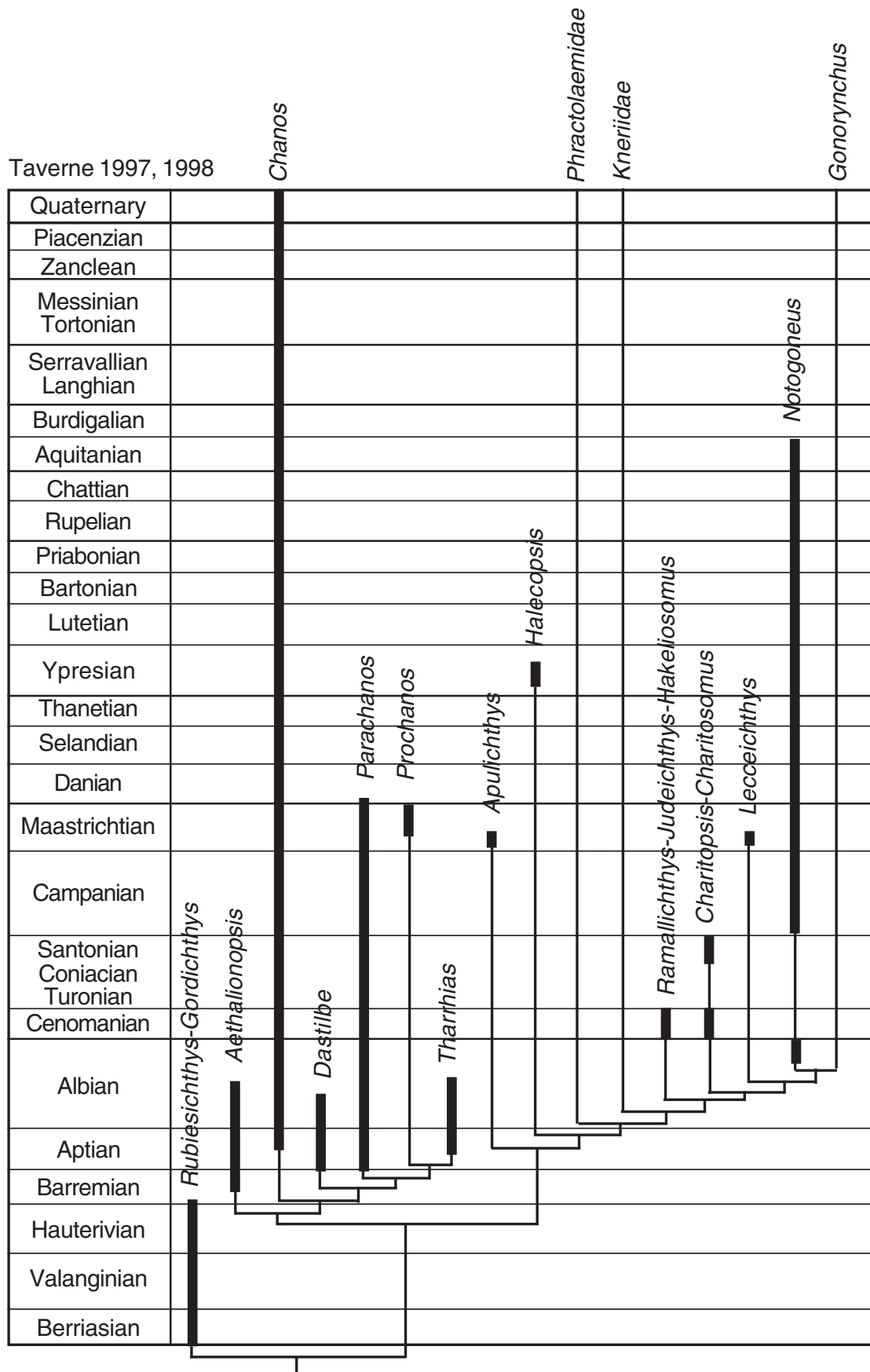


Fig. 6.8 Phylogenetic tree derived from the phylogenetic hypotheses by Taverne (1997, 1998).

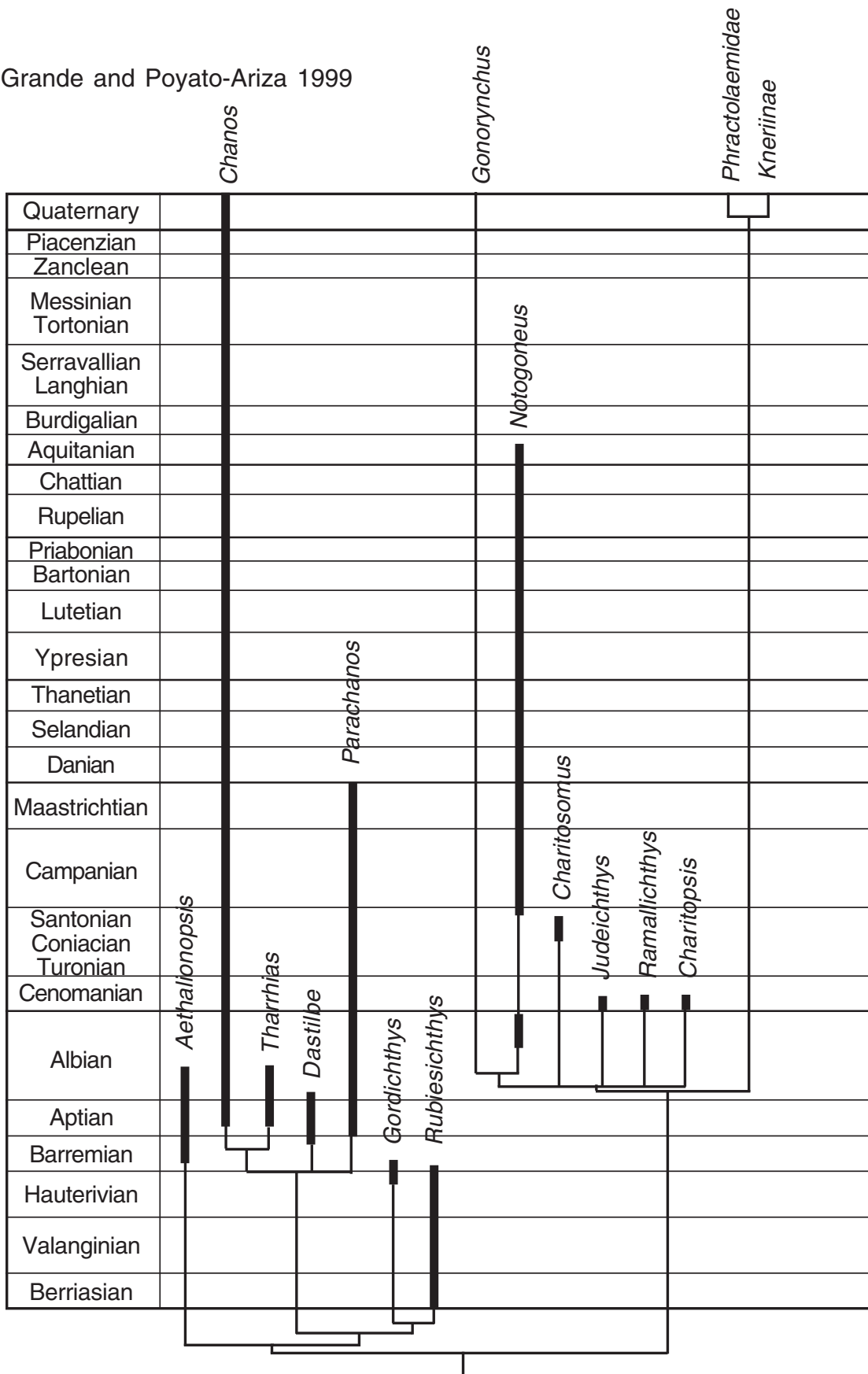


Fig. 6.9 Phylogenetic tree obtained according to the phylogenetic hypothesis by Grande and Poyato-Ariza (1999).

Interestingly, such a structure is in accordance with the early osteology-based study by Greenwood *et al.* (1966).

Diversity Dynamics

From the problems outlined above, it is clear that both the fossil record of Gonorynchiformes and our understanding of their phylogenetic relationships are not yet ripe for carrying out a robust diversity study. The following attempt should be regarded as an exploratory analysis and a base for future work.

In this review, we count 18 genera and 35 valid species of fossil gonorynchiforms between the Early Cretaceous and the Miocene. Diversity dynamics was estimated by different techniques at the species and generic levels. First, we assessed diversity by simply counting observed ranges within each stratigraphic stage. This traditional “taxic approach” (Levinton 1988) yields a raw diversity estimate. The latter was corrected for the “Lazarus effect” (Jablonski 1986, Fara 2001), that is, a taxon is counted as present between its first and last occurrence even if no fossil record is actually known in the intervening stages. Taxa whose estimated ages cross a boundary between two time intervals were counted as present in both intervals.

Second, we used the “phylogenetic approach” (Smith 1994). This method extends the observed stratigraphic ranges of taxa with the “ghost lineages” in order to confirm the predictions of a phylogenetic hypothesis (Smith 1988, 1994, Norell 1993). It supposes that sister taxa originate at the same time. We have applied this approach to the phylogenetic hypotheses by Gayet (1993c), Taverne (1997, 1998), and Grande and Poyato-Ariza (1999) to see how these different proposals affect inferred diversity patterns. For comparison purposes, only taxa common to these three phylogenetic schemes were retained in the analysis. The lack of resolution in some parts of Grande and Poyato-Ariza’s (1999) cladogram did not affect the calculations because it concerns a series of either Aptian or mostly Cenomanian taxa.

Third, we computed minimal species diversity of Gonorynchiformes with the method described by Fara (2004). This approach is an intermediate between the taxic and the phylogenetic approaches.

Figure 6.10 shows the raw species and genus diversity estimated with the taxic approach. These two estimates are very similar because most genera have only one species represented in each stratigraphic stage. Gonorynchiform diversity rose steadily during the Early Cretaceous and reached a peak in the Aptian–Cenomanian interval. The high diversity level in the Aptian occurred both in Gondwana (†*Dastilbe*, †*Parachanos*, †*Tharrhias*) and in southern Europe (†*Rubiesichthys*, †*Gordichthys*, †*Aethalionopsis*, *Chanos*), whereas the Cenomanian diversity maximum is dominated by

Tethyan forms (†*Ramallichthys*, †*Judeichthys*, †*Hakeliosomus*, †*Charitopsis*, †*Charitosomus*). Gonorynchiform diversity then declined slightly towards the end of the Cretaceous and dropped at the beginning of the Cenozoic. This apparent low diversity level is only interrupted by relative peaks in the first half of the Eocene (*Chanos*, †*Notogoneus*, †*Halecopsis*, †*Coelogaster*) and, to a lesser extent, in the Oligocene (*Chanos*, †*Notogoneus*, †*Neohalecopsis*). This uneven Cenozoic diversity pattern occurred in Europe, North America, and Asia. After the last record of †*Notogoneus* in the Aquitanian (earliest Miocene) gonorynchiform diversity dropped to a minimum for the rest of the Neogene (Fig. 6.10).

This literal reading of the fossil record cannot be taken at face value, however. It is always possible that gonorynchiform diversity stabilized or decreased in a more or less regular pattern since the Cenomanian, and that new taxa wait to be discovered in Palaeocene, late Eocene, and Mio-Pleistocene deposits.

Figure 6.11 shows the diversity estimates computed with the phylogenetic approach based on the three phylogenetic hypotheses mentioned above (curves), together with the raw diversity of the genera common to these phylogenetic proposals (histogram). The diversity level is of course higher in the curves derived from the phylogenetic approach because of the addition of range extensions. The most remarkable feature is the similarity of the three estimates (Fig. 6.11), meaning that the differences across the studied phylogenies have virtually no impact on inferred diversity patterns. The same is true for the estimates of minimal species diversity (not shown here).

Figure 6.11 also shows a limit of the phylogenetic approach in the case of the Gonorynchiformes. The post-Cenomanian diversity level is remarkably low because several taxa were not included in most phylogenetic analyses (e.g., †*Coelogaster*, †*Apulichthys*, †*Halecopsis*, †*Chanoides*). Updated and comprehensive phylogenetic analyses will certainly help to resolve this issue (see Poyato-Ariza *et al.*, this volume).

This brief overview of diversity is limited by the low number of fossil taxa currently known, and it calls for caution when analysing fossil diversity patterns for Gonorynchiformes. These fossil diversity patterns strongly contrast with the relatively high diversity observed among modern gonorynchiform fishes. Unless most of these extant forms have originated in a sub-Recent radiation, this pattern is suggestive of a bias in the fossil record, especially for the Neogene (see also Fara *et al.* 2007).

Historical Biogeography

The historical biogeography and associated palaeoenvironments of Gonorynchiformes have been recently studied in detail by Grande (1999a),

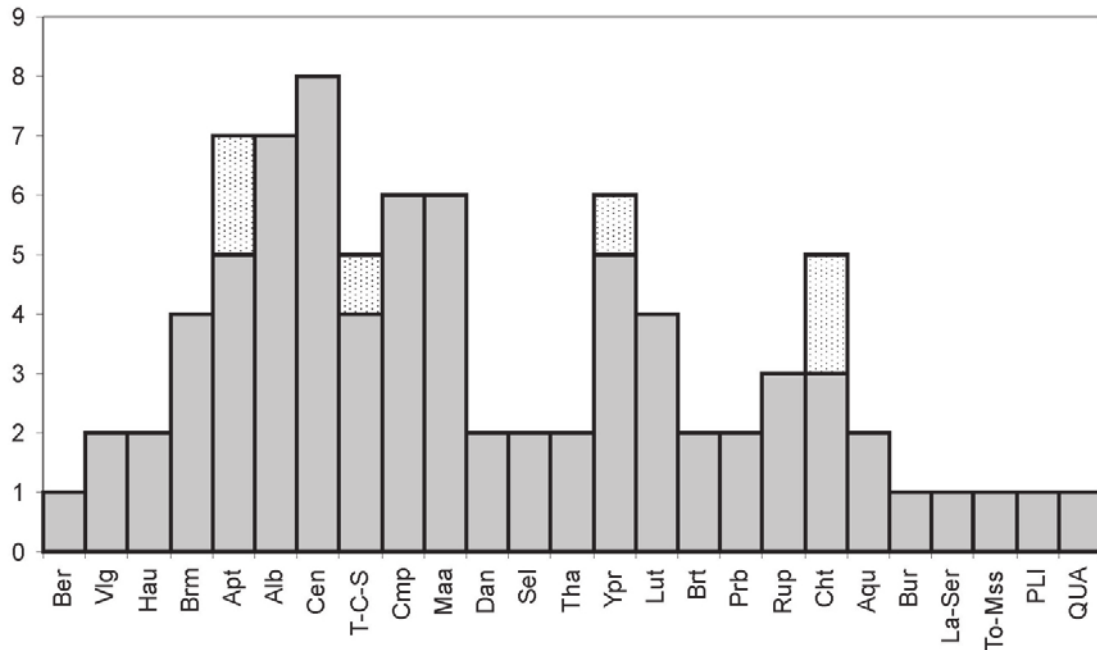


Fig. 6.10 Diversity dynamics of Gonorynchiformes during geological times as assessed by the taxic approach. The histogram represents the total raw diversity at the genus level (gray bars) and species level (dotted bars). The minimal species diversity patterns (not shown here) are virtually identical. Abbreviations of international stratigraphic stages (x-axis) are from Harland *et al.* (1990), except T-C-S, Turonian-Coniacian-Santonian; La-Ser, Langhian-Serravallian; To-Mss, Tortonian-Messinian; PLI, Pliocene; QUA, Quaternary.

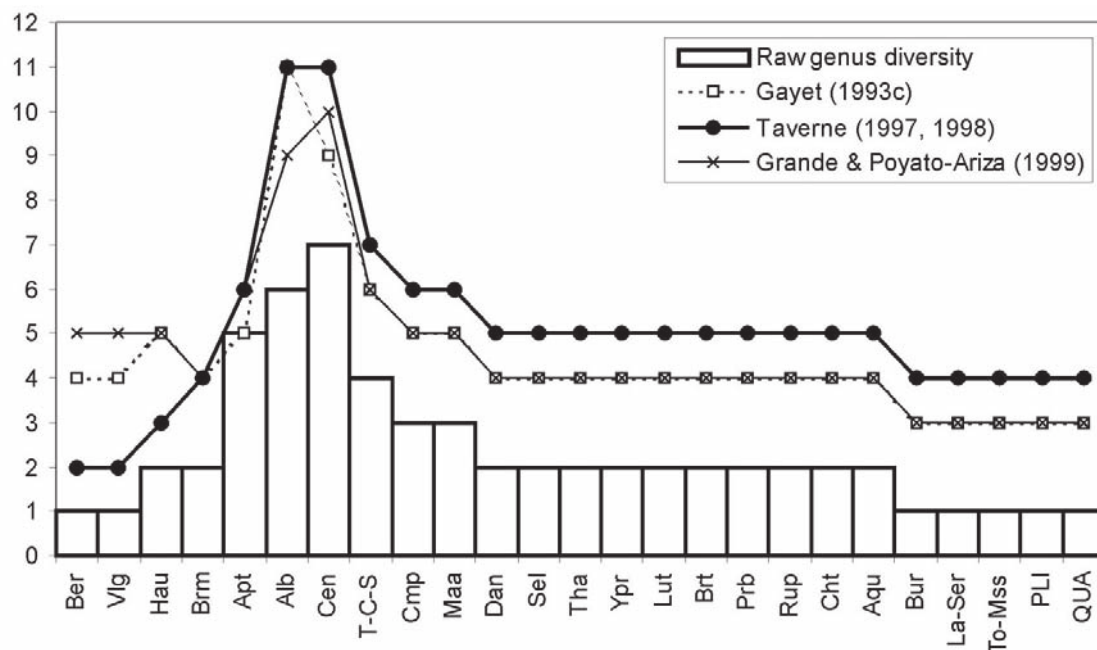


Fig. 6.11 Phylogenetic hypotheses and diversity estimates. The histogram represents the raw diversity of the genera common to the phylogenetic studies of Gayet (1993c), Taverne (1997, 1998), and Grande and Poyato-Ariza (1999). The curves correspond to the diversity estimated from these three phylogenetic proposals using the phylogenetic approach. Note the similarity of these estimates, regardless of the selected phylogenetic scheme. Abbreviations as in Fig. 6.10.

and we shall not duplicate this work here. She used cladistic vicariance biogeography on available fossil data based on the phylogenetic hypothesis by Grande and Poyato-Ariza (1999). She found that the historical biogeography of Gonorynchiformes is complex and probably results from various episodes of vicariance and dispersal (Grande 1999a).

Conclusions

Although they are known since Cuvier, gonorynchiform fishes have still many secrets to unveil. Their fossil record is crucial to this endeavour, and it certainly provides key information that complements recent advances in molecular and developmental biology. However, our current knowledge of Gonorynchiformes makes it difficult to quantify precisely several aspects of their evolutionary history. Whether for biogeography or diversity analysis, the known fossil record and the understanding of their phylogenetic relationships are still insufficient to draw robust inferences and models. In particular, our diversity analysis calls for a special effort in sampling several parts of the fossil record, and it pleads for the integration of most (if not all) fossil gonorynchiform taxa in the phylogenetic analyses of the order.

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