Temporal and latitudinal trends in the biodiversity of European Atlantic Cenozoic gastropod (Mollusca) faunas. A base for the history of biogeographic provinces

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Abstract: A general overview of the biodiversity of the marine fauna during the Tertiary period is developed in the context of the biogeographical evolution of the European realm. This study combines a reappraisal of the literature with a unique first-hand source of data on the richest marine group (the gastropods) from over a 25 million year period (Early Oligocene to Late Miocene). In total the French deposits have yielded more than 10,000 species from the Eocene to the Upper Miocene. Evidence of significant bias in the fossil record is pointed out for the Palaeocene (Danian) and Upper Eocene (Priabonian). For the period considered (Palaeocene to Late Miocene, ca 50 million years) the second highest diversity is reported in the Late Oligocene. This study reveals also the importance of pre-Miocene extinctions of genera. The Oligocene was when the latitudinal differentiation of the faunas was greatest. The local generic gastropod richness ranges from 59 (Rupelian of Belgium) to 494 (Chattian of Aquitaine). A clear trend towards homogenization appears in the Late Oligocene which leads to the development of a vast biogeographical region named Euro-West Africa. This faunal evolutionary pattern has never been demonstrated before and is a novel feature of the biogeography of the Eastern-Atlantic region.

Key Words: Biogeography; Tethys; extinction; France; Paleogene; Miocene; molluscs.

Résumé : ***Évolution temporelle et latitudinale de la biodiversité des faunes de gastéropodes (Mollusca) du Cénozoique atlantique européen. Une base pour l'histoire des provinces biogéographiques.-*** Une revue globale de la biodiversité des faunes marines du tertiaire est proposée dans le cadre de l'évolution biogéographique du domaine européen. Cette étude est fondée sur une revue critique de la littérature et une source unique de données sur le groupe marin le plus riche (les gastéropodes) examinés durant une période de 25 millions d'années (Oligocène inférieur à Miocène supérieur). Au total, les dépôts français renferment plus de 10 000 espèces dans l'intervalle Éocène à Miocène supérieur. Des biais importants dans les archives fossiles sont soulignés pour le Paléocène (Danien) et l'Éocène supérieur (Priabonien). La richesse générique locale s'étire de 59 genres (Rupélien de Belgique) à 494 genres (Chattien d'Aquitaine). Pour la période considérée (Paleocène à Moicène supérieur, environ 50 Ma), la seconde plus grande diversité (richesse spécifique) est relevée pour l'Oligocène supérieur. L'Oligocène inférieur est la période durant laquelle la différentiation latitudinale des faunes est la plus grande. Une nouvelle tendance apparaît à l'Oligocène supérieur qui conduit à la formation d'une vaste région biogéographique nommée Euro-Ouest Africaine. Cette évolution faunistique n'avait jamais été démontrée avant et apparaît comme un nouveau schéma dans la biogéographie des faunes Est-Atlantiques.

Mots-clefs : Biogéographie ; Téthys ; extinction ; France ; Paléogene ; Miocène ; mollusques.

Introduction

Located where the North Sea and tropical Tethyan faunas converge, the French Atlantic Cenozoic domain outranks all others in Europe with its particularly rich molluscan faunas. The preservation of fossil molluscs is also exceptional, being the finest in the World for the Eocene (the famous Lutetian malacofauna of the Paris Basin), the best in the Tethyan realm for the Lower Oligocene (Rupelian = Stampian stage) and the Upper Oligocene (Chattian stage), and one of the best for the Lower and Middle Miocene.

Because molluscs dominate Cenozoic marine fossils (KOWALEWSKI *et al.*, 2002) and outnumber all other macro-invertebrate taxonomic groups,

they provide one of the prime sources of information on the history of the biosphere. Paradoxically we do not know how many species of molluscs occurred in the Cenozoic of the French Atlantic. Therefore, I propose estimates based on two approaches. The first is for Eocene deposits and is founded principally on revised bibliographic data but includes new data and personal research. The second, a more detailed approach, is for the Oligocene and Miocene deposits, with a new generic and species synthesis based on a huge quantity of partly unpublished material collected in the Aquitaine, Loire and Paris basins (LOZOUET, 1997). Finally, a comparison of families' specific richness should provide insight into the global evolution of the malacofauna.

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The paleobiogeography (provincialism) of French Atlantic Cenozoic molluscan faunas was based on qualitative observations (CAVELIER, 1979; BRÉBION, 1974, 1988), using restricted sources of data. This new review is the first general overview on the basis of a larger collection of data personally verified (Appendix Table 3) using a multivariate analysis at the generic level. Several questions may then be addressed: How much have the faunas changed after the eastward closure of the Tethys Sea? Was the latitudinal gradient of specific richness reinforced after the closure? Did the faunas affected by long-term global cooling evolve towards more marked provincialism?

Study area, geological and palaeobiogeographic setting

The geographical area taken into account includes the Paris Basin, the Aquitaine Basin and the Loire, Brittany, and Cotentin (Normandy) in France and the southern North Sea Basin (Belgium, Denmark and Germany), the Late Burdigalian/Middle Miocene of the Netherlands, and the Upper Oligocene of Hungary (Paratethys extension) (Fig. 1).

For the comparison of global species richness we used data from the Palaeocene and Paleogene (Eocene and Oligocene) of the Paris Basin, Miocene of the Loire Basin and Oligocene and Miocene of the Aquitaine Basin (Fig. 1). On the other hand the paleobiogeographic reconstructions for the Oligocene and the Miocene are based on the generic distribution and are limited to malacofaunas from the Lower Oligocene of Belgian and Germany, the Upper Oligocene of Belgian, Germany and Hungary and the Middle Miocene of the Netherlands.
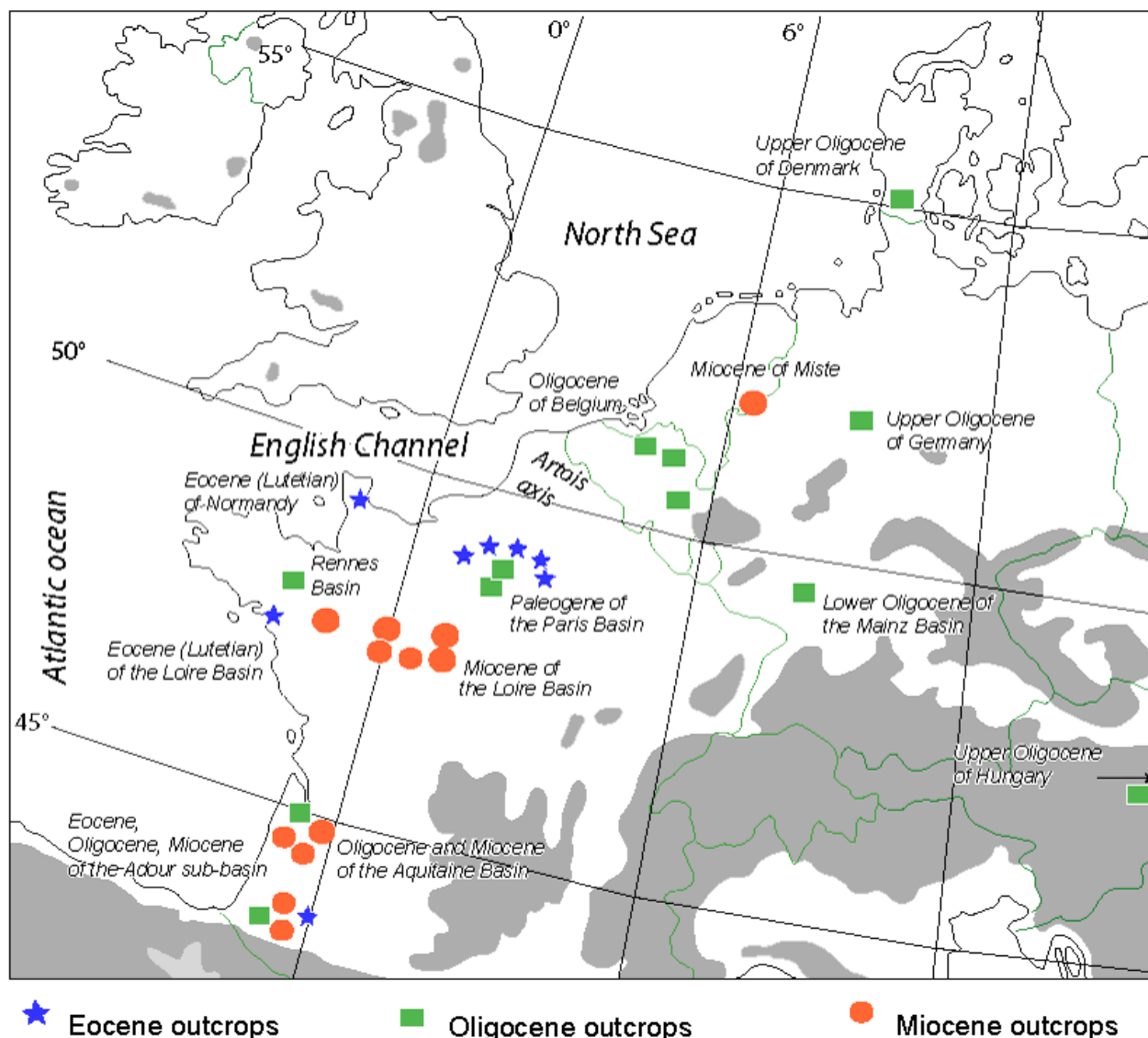

Figure 1: Locations of the faunas analyzed in the Cenozoic of the Eastern Atlantic coast basins and its North Sea extension.

Global palaeobiogeography

During the Palaeogene, the composition of marine molluscan faunas of the Atlantic coasts is determined mainly by the influences of the Nordic realm (warm temperate waters) and the Tethyan realm (tropical and subtropical). The presence or absence of an isthmus between the North Sea Basin and the Paris Basin plays a major role in local biogeographic changes. The Middle Lutetian uplift of the Artois axis interrupted communication between the London-Belgian basins and the Atlantic. The Artois isthmus reopened only much later, after the Miocene, when exchange was again possible via the English Channel. Meanwhile, we called the sudden invasion of the Paris Basin of molluscs of southern Tethyan origin a "Mesogean bubble" (LOZOUET, 2012). The best example is provided by the upper part of the Paris Basin Stampian (Lower Oligocene, Rupelian Stage) where a significant part of the Pierrefitte Sands fauna, beforehand known only in the latitude of the Aquitaine Basin, appeared suddenly (ca. 30 Ma).

Much later, in the latest Oligocene (Chattian) to Middle Miocene (Langhian and Badenian ages), the progressive closure of the eastern Tethyan seaway and its brief re-opening were the main palaeogeographical events. According to PILLER et al. (2007) this intermittent connection was definitively sealed during the middle Badenian (approx. 14-15 Ma).

The severe cooling during middle Miocene time (Serravallian age) is the first reliable evidence of a global change in the climate, suggested to be an incipient glaciation. The "greenhouse period" was definitely over (PROTHERO, 1994). However, before this time, a significant change occurred: the appearance and development of a new Eastern Atlantic faunistic province, during the Early Neogene (BRÉBION, 1983, 1988). DOLLFUS (1888, 1909) first pointed out the similarity between European Neogene molluscan faunas and modern faunas of the West African biogeographical province. He considered that the changes were caused by an invasion of West-African species during the Early Miocene. In fact, this suggestion is speculative as DOLLFUS (1888, 1909) did not have access to a body of data that was adequate to address the relationships of Oligocene–Upper Miocene faunas of the French basins to their North Sea domain European counterparts. Only selected genera or species have been considered.

With respect to terminology we should note that the terms Boreal province (see KOWALEWSKI et al., 2002), Nordic realm, Northern province (e.g., CAVELIER, 1979), Atlantic-Boreal Bioprovince (RÖGL & STEININGER, 1984), Boreal-Celtic province (SILVA & LANDAU, 2007) and North Sea Basin designate roughly the same geographic and palaeogeographic area. Nevertheless, palaeoclimatological ambiguity exists in that the subtropical Boreal Miocene province is not equivalent to the modern cool-temperate Boreal-

Celtic province. In contrast, the Mesogean realm (for example CAVELIER, 1979) is strictly equivalent to Tethyan realm. In fact Mesogean is routinely used in French geology as equivalent to Mediterranean or Tethyan.

Material and methods

The main taxonomic dataset used is the species-level data derived from material collected by the author. For basins for which I have little of my own data, the data result from a critical compilation from the literature (Appendix S1). Over the course of 25 years I (alone or with collaborators) have described about 300 new species, but 500-1000 or more, principally of small size, are still undescribed. In the database these species are labelled as "sp.". From a taxonomic point of view these "sp." can be considered as "morphospecies" or "Operational Taxonomic Units" (OTUs). These informal units are here taken to represent specific-level taxa, equivalent to formal "species". During sampling, special attention was given to fragile gastropod specimens and, in particular, to shells with well preserved protoconchs, because this part of the shell contains diagnostic characters. Identification of almost all molluscs was done or checked by the author.

The terms "outcrops" or "sites" are used for sections a few metres in extent. For example, the famous outcrop of Saucats, "Le Peloua" (Burdigalian of Aquitaine; National Geological Reserve of Saucats-La Brède), is the outcrop of a single layer about 40 cm thick. Generally, sampling was conducted in just one homogeneous layer (the richest), which rarely exceeds 2 m in thickness (1 m is the mean value). The lateral extent of outcrops is also generally limited, in the order of a few metres. Conversely, in the Aquitanian of Meilhan, the huge quarry of "Vives" has been extended considerably since 1990 (LOZOUET et al., 2001b), allowing three separate samples to be taken. The extreme opposite facies consists of very thin detrital layers (4 cm thick) isolated in marl deposits but considered as "outcrops" because they are the only displaced representatives of the shallow-water molluscan fauna at a given time. In summary, almost all outcrops are entities restricted to a limited area (generally less than 20 m wide and 5 m thick), in contrast to the "regional" gathering of most earlier biodiversity studies. A total of 112 outcrops were investigated of which 104 were used to estimate species richness (Table 1). The Oligocene and Lower Miocene outcrops are the best represented.

All the outcrops of the Paris Basin (Paleogene), the Cotentin (Paleogene), the Loire Basin (Miocene) and the northern part of the Aquitaine (Oligocene and Miocene) consist of very shallow-water deposits. Nearshore calcareous facies characterise the Lutetian of the Paris Basin and Cotentin and the Stampian of the

Aquitaine Basin. Rupelian (PLAZIAT & LOZOUET, 2012) and other Palaeogene and Eocene deposits of the Paris Basin are represented mostly by sandy facies. Marly facies occur in the southern part of the Aquitaine basin comprising the deeper deposits (circalittoral to upper bathyal for the Upper Oligocene; circalittoral for the Lower and Middle Miocene). True coral reefs are absent from all deposits but large coral colonies (metre-scale) of the zooxanthellate corals have been observed in the Oligocene (particularly Ru-pelian) and in the Lower Miocene Adour sub-basin.

In an attempt to examine more precisely the results for generic richness, the distances between the main faunas reliably recorded from the Lower Oligocene to the Upper Miocene have been analyzed using multivariate correspondence analysis (CA). The data were transformed into a presence-absence table (Appendix Table 3). Multivariate techniques permit an exploration of the structure of the dataset. In contrast to other multivariate techniques such as principal component analysis (PCA), CA allows simultaneous analysis of variables (columns: malacofaunas) and observations (rows: genera). This method can be employed for datasets that contain numerous zero values in the original matrix. The software package PAST [PAleontological STatistics (HAMMER, 2013)], developed for structural study of palaeontological data, was used. The rarefaction curve and estimates of species richness were made using the software, EstimatesS 8 (COLWELL, 2006).

Change in species richness in Atlantic basins during the Cenozoic (Palaeogene and Neogene)

It is a truism to say that early study of the French Cenozoic was central to the development of geology as a science. Among the 18th Century pioneers, Jean-Etienne GUETTARD (1715-1786) was the first to publish a geological monograph and to draw a map, which included the fossiliferous deposits of the Stampian (Rupelian), south of Paris. It is also at this time that the young A.L. LAVOISIER (1743-1794), destined to become famous in chemistry, prepared the first geological section in the modern style (ELLENBERGER, 1989; LOZOUET, 2012). However, it is on the molluscan faunas that the main contributions to early reconstruction of Earth history were founded.

During the 19th Century Jean-Baptiste Pierre Antoine de MONET, chevalier de LAMARCK (1744-1829) and Gérard-Paul DESHAYES (1796-1875) described the faunas collected from the Eocene and Oligocene deposits of the Paris Basin. During the same period Barthélémy de BASTEROT (1800-1887) and Jean-Pierre Sylvestre de GRATELOUP (1782-1861) described the molluscs of the Aquitaine Basin and Félix DUJARDIN (1801-

1860) those of the Loire Basin (Touraine). Jacques Raoul TOURNOUËR (1822-1882) and Gustave Frédéric DOLLFUS (1850-1931) later published monographs on the faunas of the Eocene, Oligocene and Miocene of smaller basins opening on the Atlantic Ocean. Crowning these contributions, Maurice COSSMANN (1850-1924) was the most prolific author in paleomalacology. He described and revised thousands of species and published some memorable monographs (e.g., COSSMANN & PISSARO, 1904-1913). Albert PEYROT (1860-1939) continued the work of COSSMANN concerning the Oligocene and Neogene of the Aquitaine Basin and described the Neogene fauna of the Loire Basin. Maxime GLIBERT (1905-1984) later reviewed the faunas of the Miocene basin of the Loire. More recently Louis GOUGEROT (1915-1985) and Jacques LE RENARD undertook the description of many small species of the Parisian Eocene disregarded until the mid 20th Century (exactly 924 species, according to LE RENARD, 1999!).

With such a long and rich history, one might expect that these faunas were fully inventoried. However, this is not the case, because complete stratigraphic sequences have not been studied in all cases (e.g., in the Priabonian and the Upper Oligocene of the Aquitaine Basin) and "micro-molluscs" are still relatively neglected. As we shall see, the unexpected richness of the fauna of the Upper Oligocene of the Adour Basin revealed by DOCKERY and LOZOUET (2006) is a good illustration of the likelihood of future discovery of many more species.

General result

The richness of the reliably described faunas of the Eocene, Oligocene and Miocene (Fig. 2) of the French Atlantic coast ranges from 197 species of gastropods (in the Rupelian of the Paris Basin) to 1800 species in the Lutetian of Paris Basin (PACAUD, 2008, indicated "only" 1550 referenced species).

The most diverse faunas are:

Lutetian of the Paris Basin	1800
Upper Oligocene of the Aquitaine Basin	1285
Bartonian of the Paris Basin	1000
Lutetian of the Cotentin	1000
Lutetian of the Loire Basin	850
Lower Burdigalian of Aquitaine	722
Aquitanian of Aquitaine	700
Ypresian of the Paris Basin	600
Upper Burdigalian of Aquitaine	534

Palaeocene and Eocene data

Major sources for the Paleocene and Eocene molluscan record include Cossmann (1886-1913), fully illustrated in Cossmann and Pissarro (1904-1913). The work of Cossmann & Pissarro summarized a large volume of literature on 2,500 species of gastropods (updated by Le Renard and Pacaud, 1995; Pacaud, 2008). The most important additional reports are those of Gougerot (1969, 1970) and Gougerot and Le Renard (1980, 1981), with revisions of 924 gastropod species (including numerous new species, Le Renard, 1999). Other new Eocene data have been provided by J. Le Renard following intensive collecting and critical reappraisal from the Eocene of the Paris Basin (Le Renard, 2013) and the Cotentin deposits (Le Renard & Gain, 2012). The previous compilation by Dockery (1986) is also very useful.

▶ **Figure 2:** Gastropod richness of discrete faunas from the French Atlantic coast. Time scale is from Odin (1994), with Quaternary boundary modified. Modified from Lozouet (2012).
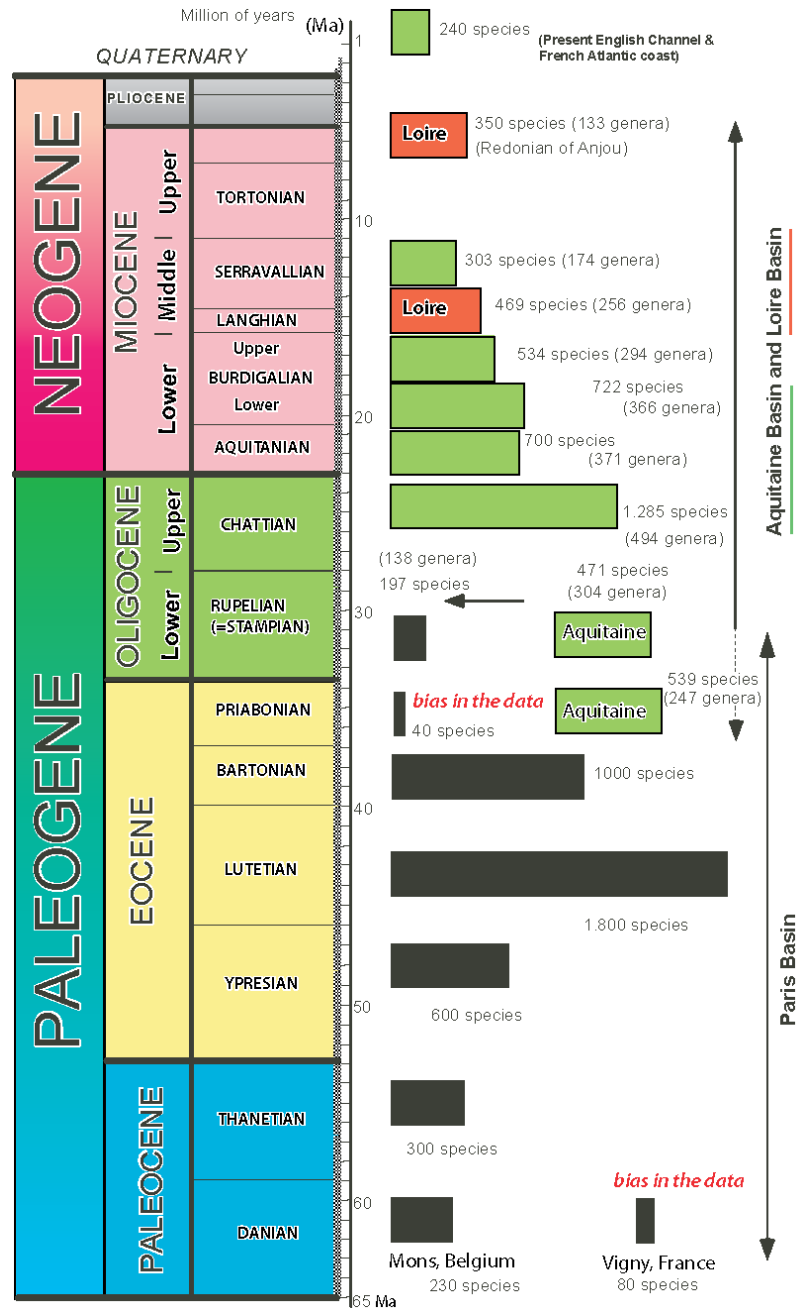
It is especially important to point out the low number of species recorded in the Priabonian (Ludian) and the Danian of the Paris Basin and other Atlantic outcrops, which deserves ecological explanation. The Danian sea includes the Paris area and the adjacent Mons Basin in Belgium (see Plaziat, 1981, Fig. 21). The Danian fauna of the Paris Basin (Pacaud et al., 2000) is mainly known from identifications based on limestone moulds in a subreefal facies from a single outcrop ("Montian" of Vigny, France) and from a core sampling near Mons (type of the abandoned Montian stage), Belgium, 200 kilometres north of Vigny. Only 240 species of gastropods have been recorded (Glibert, 1973).

In the case of the late Eocene (Priabonian stage), the "Ludian" facies of the Paris Basin is also poor in molluscs. Marine sand and mud deposits with a well preserved fauna are restricted to a single somewhat brackish environment outcropping only in the Vexin. The index fossil is a potamidid, *Potamidopsis vouastensis* (Boussac, 1905). Similar *Potamidopsis* communities were also developed in the Middle Eocene (Lutetian, Bartonian) and Oligocene of the Paris Basin. In the Bartonian *Potamidopsis crispiacensis* (Boussac, 1906) community (Mortefontaine Sands, Loisy) as well as in the Priabonian *Potamidopsis* community (Chavençon outcrop, Oise), I recorded a very similar biodiversity (20 and 22 gastropod species, respectively) compared with the 60 species recorded by Cavelier (1979) for the whole Priabonian fauna of the Paris Basin. The dramatically reduced species biodiversity in the Paris Basin near the end of the Eocene therefore appears to be an ecological and sampling bias (Cavelier, 1979) and should not be ascribed to global

climatic or other factors. This has been clearly demonstrated by the presence of a rich fauna of molluscs in Priabonian sections of Northern Europe: CAVELIER (1979) estimated that there are at least 732 species of molluscs at Latdorf.

In the Aquitaine Basin, Priabonian outcrops have recently become accessible in the southern Adour sub-basin. Thin detrital layers intercalated in bathyal marls harbour a rich fauna of Priabonian age (NP19/20; NOLF et al., 2002). Samples from just one outcrop have yielded at least 480 gastropod species. By comparison, one of the richest outcrops of the Middle Eocene of the Paris Basin (the Bartonian Baron quarry; DOLIN et al., 1980) has produced 500 species of gastropods following intensive sampling.

The evidently very incomplete malacofaunal record of the Danian and Priabonian suggests that it should not be incorporated into a study of the rate of regional change in the Atlantic European basins. In North America where the two most diverse Eocene molluscan faunas of the Gulf Coast are Early and Middle Bartonian in age (respectively 495 and 580 species, LOZOUET & DOCKERY, 2001), rather than Lutetian, the Priabonian faunas of the Jackson Group are also relatively rich (426 species according to DOCKERY & LOZOUET, 2006). It is therefore not appropriate to accept the Paris Basin Danian and the Priabonian malacofaunas as a reliable basis for a study of the evolution of biodiversity.

Oligocene and Miocene malacofaunas

The number of confirmed species, 3845, for the Oligocene and Miocene deposits of France is founded principally on my own data. For the Neogene of Aquitaine I identify 1500 species whereas COSSMANN and PEYROT (1909-1924) and PEYROT (1925-1935) documented 1337 species (from a total of 1459, erroneously including 122 Chattian species). We conclude that the Neogene faunas of Aquitaine have been relatively well known for a long time. This is not the case for the Oligocene faunas, with the exception of the Stampian (Rupelian) of the Paris Basin, for which we have added only 21 species (LOZOUET & MAESTRATI, 2012) to the 176 species documented by COSSMANN (1892, 1893). In the Stampian of the Aquitaine Basin, VERGNEAU (1967a, 1967b, 1968) recorded only 180-190 species, whereas my dataset contains 471 species.

I have identified 1285 species of gastropods in the Upper Oligocene of the southern Aquitaine Basin in stark contrast to the 142 species reported by COSSMANN and PEYROT (1909-1924) and PEYROT (1925-1935) for this interval and a dozen species described or reported by MAGNE and VERGNEAU-SAUBADE (1971, 1974), MAGNE and SAUBADE (1970, 1975), SAUBADE (1969) and SAUBADE and CAHUZAC (1978). By comparison, the modern Mediterranean Sea, considered a biodiversity hotspot of exceptional planetary value

(COLL et al., 2010), has only 1221 species (SABELLI & TAVIANI, 2014). Rich bivalve material has also been collected in the Chattian of the Adour outcrops but has been only very partially studied. A review of Glycymerididae (MAESTRATI & LOZOUET, 1996) revealed the presence of at least seven species, whereas only two were recorded by COSSMANN and PEYROT (1909-1924). In a preliminary, unpublished inventory, P. MAESTRATI recorded 330 species of Bivalvia. Given the number of small species studied only briefly until now, it is possible to estimate the actual richness of the bivalves as between 350 and 450 species. Altogether, the entire Upper Oligocene malacofauna of the Adour Basin probably contains between 1700 and 1800 or more molluscan species. This high number of species contrasts with the much lower number indicated in the Oligocene of the Mediterranean-Iranian Province by HARZHAUSER (2007, Fig. 5: > 300 species) and deserves explanation.

This discrepancy is the result of a strong bias in the fossil record due to poor preservation of molluscs throughout the entire Mediterranean region in the Oligocene. One of the effects is, for example, the poor representation or lack of micro-molluscs in the dataset. Poor representation due to small size is a classic problem in palaeontology (COOPER et al., 2006). Studies of modern faunas show that molluscs smaller than 10 mm constitute more than 50% of the species. By contrast, macromolluscs larger than 41 mm account only for 8% of the total (BOUCHET et al., 2002).

This unexpected richness greatly modifies our perception of trends in the evolution of biodiversity in the malacofaunas in the European Cenozoic. The biogeographical consequences are far from being fully identified. However, DOLIN and LOZOUET (2004) have already noted that many phyletic innovations described as characteristic of the Miocene (within Cypraeoidea in KAY, 1996; Nassariidae in CERNOHORSKY, 1984; Coninae in KOHN, 1990) appeared during the Late Oligocene. In the same way, some molecular phylogenic studies reveal an increase in the rate of cladogenesis of some unrelated tropical marine gastropod genera in the Indo-West Pacific (IWP) in Late Oligocene or Early Miocene times (WILLIAMS & DUDA, 2008).

Moreover, the recent recognition of the richness of the Upper Oligocene fauna of the Adour Basin is an excellent illustration that serious misinterpretations result from incomplete knowledge of the taxonomic composition of certain deposits. The negative implications are magnified where this gap in reliable data pertains to the stratigraphic record of France a cradle of historical geology, and a country where the fossil record has been regarded as well-known. This is reminiscent of the relative neglect of the Cenozoic molluscs of Westland (New Zealand) as pointed out by MAXWELL (1988).

Table 1: Stratigraphic distribution and numerical age (from the GeoWhen Database) of 104 outcrops sampled for estimation of species richness (see Fig. 3):

Stage and numerical age	Paris Basin Number of outcrops	Aquitaine Basin Number of outcrops	Loire Basin Number of outcrops
Lower Oligocene (Rupelian): 33.9 +/- 0.1 to 28.4 (+/- 0.1 Ma)	23	5	1
Upper Oligocene (Chattian): 28.4 +/- 0.1 to 23.03 +/- 0.05 Ma		26	
Lowe Miocene (Aquitanian): 23.03 to 20.43 +/- 0.05 Ma		9	
Lower Miocene (Burdigalian): 20.43 to 15.97 +/- 0.05 Ma		23	
Middle Miocene (Langhian): 15.97 to 13.65 +/- 0.05 Ma		6	6
Middle Miocene (Serravallian): 13.65 +/- 0.05 to 11.608 +/- 0.005 Ma		3	
Upper Miocene (Messinian): 7.246 To 5.332 +/- 0.005 Ma			2

How many species really were there in the Oligocene and Miocene basins of the French Atlantic Coast?

We propose a more precise estimation of the species richness from the data recorded in 104 outcrops that range from the Oligocene to the Upper Miocene of the French Atlantic coast (Table 1). Poorly sampled outcrops (with fewer than 500 specimens) are excluded. We retain 29 Lower Oligocene outcrops, 26 Upper Oligocene, 32 Lower Miocene, 15 Middle Miocene and only 2 Upper Miocene. A total of 275,000 specimens representing 3472 species have been examined.

A cumulative species curve was constructed using EstimatesS 8 (COLWELL, 2006) with 50 randomisations (Fig. 3). We also used the estimators "jacknife-1" and "jacknife-2", calculated with EstimatesS, in order to evaluate the potential species richness. The cumulative curve is far from saturated and estimator curves indicate a possible numbers of at least 4748 species (Jacknife-1) and up to 5330 species with Jacknife-2. It is interesting to compare these numbers with the 2187 species of gastropods in the modern tropical fauna of New Caledonia collected in a single peri-reefal locality (BOUCHET *et al.*, 2002), and with the estimate proposed for a more diverse region of 15,000 hectares at Panglao in the central Philippines (BOUCHET, 2009) of between 4000 and 14,000 species (note the magnitude of uncertainty!).
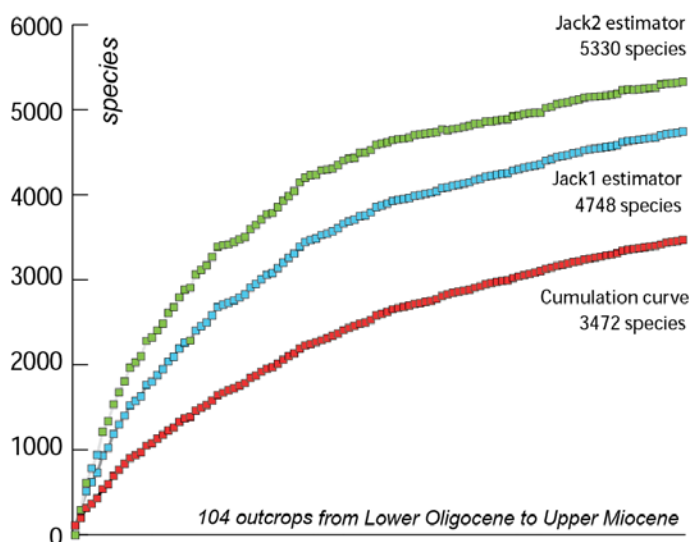
Figure 3: Cumulative species curves based on EstimatesS 8 (COLWELL, 2006) and Jacknife 1 (Jack1) and Jacknife 2 (Jack2) richness estimators. One hundred and four selected sites yielding 3472 species from Lower Oligocene to Upper Miocene have been included. The dataset comprises 3845 species for this interval.

Thus the total of 5330 gastropod species (high-end prediction) estimated for French Atlantic coastal deposits of the Oligocene to Miocene, representing an interval of about 25 million years, seems realistic.

Global estimation

From the data presented here, I suggest that the Palaeogene and Neogene basins of the French Atlantic coast contain at least 10 000 species of gastropods (about 4000-5000 or more for the Eocene; 5000 for the Oligocene and Miocene). In comparison, 4500 species of molluscs (Bivalvia plus Gastropoda) were reported by BEU and MAXWELL (1990) and BEU (1990) in the Cenozoic of New Zealand. However, BEU (2006) considered that

"in the best-preserved New-Zealand Cenozoic molluscan faunas, only 43% of the total preservable fauna is retained" (based on Cooper *et al.*, 2006), a proportion probably similar for French localities. More recently, Maxwell (2009) presented an estimate of 6000 species in New Zealand extrapolated from 3396 described species and only 2437 gastropod species. Also for New Zealand, A. Beu reappraisal (pers. comm., 2011) estimates an "eventual" total of 7000 species for the entire Cenozoic (including about 5000 gastropods). Darragh (1985) indicated that 1600 species of molluscs had been described from the Tertiary of Australia, but several hundred more are yet to be described. Dockery (1984, 1986) and Dockery and Lozouet (2006) reported about 3000 species of molluscs (Gastropoda and Bivalvia) from the Palaeogene of the northern Gulf Coastal Plain (Alabama-Mississippi). Thus, even if we consider that these estimates of regional specific richness are highly underestimated, it may be suggested that no other region in the world has as rich a Palaeogene and Neogene fossil record as the French Atlantic coast.

Patterns of species richness according to families from the Oligocene and the Miocene. Comparison with Middle Eocene and modern faunas

Based on the above reappraisal of West European fossil gastropod richness I selected the five families with the highest number of species from the dataset. Then I did the same for the faunas from the following six stratigraphic units: (1) Lower Oligocene and (2) Upper Oligocene of the Aquitaine Basin; for the Lower Miocene of the Aquitaine Basin: (3) Aquitanian, (4) Lower Burdigalian, (5) Upper Burdigalian; and the Langhian of the Loire Basin represents the Middle Miocene (6). In these faunas, the eight richest families (in decreasing order) are Turridae (*sensu lato*), Pyramidellidae, Nassariidae, Cerithiidae, Rissoidae, Muricidae, Cypraeidae and Eulimidae. Figure 4 shows the change over time of species numbers in these families.
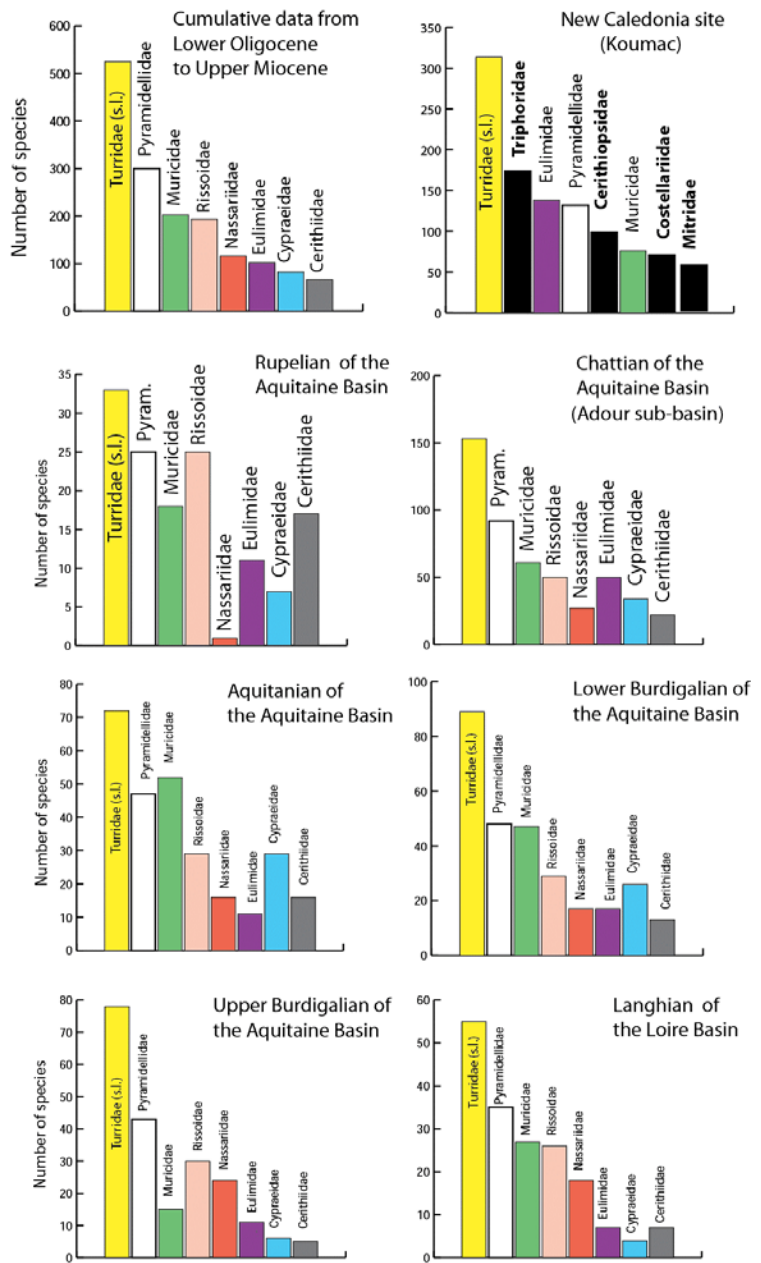
Figure 4: Species richness of the eight most diverse families of Gastropoda in seven selected intervals compared with one modern example. For each fauna, the number of species is given according to the new dataset. Turridae (*sensu lato*) and Pyramidellidae are generally best represented, followed by Muricidae and Rissoidae. Among the eight most diverse families represented for the modern site of New Caledonia (Koumac), four (in black) are under-represented in the fossil faunas.

In all faunas, the Turridae and Pyramidellidae occupied the first and second places; the Rissoidae and Muricidae generally shared the third and fourth places. Cerithiidae are better represented in the Lower Oligocene, while the Eulimidae are most numerous during the Upper Oligocene and the Cypraeidae in the Lower Miocene. In the Upper Burdigalian and in the Middle Miocene, Nassariidae are especially diverse. The Turridae (*sensu lato*), including the families (or subfamilies according to different authors) Conidae, Turridae and Drilliidae, are unquestionably the most diverse group of marine molluscs (Bouchet *et al.*, 2009). However, the number of species in the parasitic family Pyramidellidae is generally underestimated, probably because hosts have a patchy distribution and the shells of

the Pyramidellidae are small and are not identified adequately (Bouchet, 2009). The high number of species of Muricidae recorded in these Cenozoic deposits is surprising because this family is generally considered to have a relatively low species richness. This may be a bias due to the attractiveness of the Muricidae because of their larger size and varied morphology, permitting easy identification.

When we compare this distribution of fossil malacofaunas with that of the sub-reefal modern fauna of Koumac (New Caledonia), we find that the most species-rich family is also the Turridae (*sensu lato*), Triphoridae second, Eulimidae third, Pyramidellidae fourth, Cerithiopsidae fifth and Muricidae sixth (Bouchet *et al.*, 2002). The main difference between European mid-Cenozoic faunas and modern warm-water faunas is the modern diversification of highly specialized families such as the Triphoridae and Cerithiopsidae, perhaps a peculiarity of coral-reef environments of the Indo-West Pacific.

In the intensively studies Lutetian of the Paris Basin (Pacaud, 2008), the number of species of Triphoridae and Cerithiopsidae is low, about 20 (Gougerot & Le Renard, 1980, 1981). The most diverse family is the Turridae (*sensu lato*) with some 200 species. The other highly diverse families are Marginellidae (46 species), Cerithiidae (44 species), Volutidae (41 species), Pyramidellidae (39 species), Epitoniidae (36 species), Turritellidae (35 species) and Buccinidae (34 species). We may therefore question the extreme diversity of the Turridae (*sensu lato*), the low number of Pyramidellidae and the expanded numbers of the "top eight" families (Marginellidae, Cerithiidae, Volutidae, Turritellidae, Buccinidae). Are they features specific to the Paris Basin during the Lutetian, or is it a global Eocene pattern? The low number of Pyramidellidae is probably an artefact resulting from an underestimate of their species number (Le Renard, pers. comm., 2011; Gougerot, 1969, 1970; Le Renard & Pacaud, 1995). By comparison, in the quarry at Baron (Bartonian, Paris Basin), Dolin *et al.* (1980) documented more than 500 species of gastropods (half of the recorded gastropods of this sub-stage). The Turridae (*sensu lato*) comprise only 47 species, while the second group is the Pyramidellidae and the Volutidae, with 21 species each; Cerithiidae and Buccinidae follow, with 16 species. In this locality, there are only three species of Triphoridae and seven species of Cerithiopsidae. Additional data are necessary before we can state with confidence that the hegemony of Neogastropoda (Turridae *sensu lato*, Volutoidea, Buccinidae), highlighted by the Lutetian and Bartonian record of the Paris Basin, is a general (global) characteristic of the Eocene.

Finally, Oligocene faunas are more similar, in their general composition, to those of the Miocene than those of the Eocene. If we compare the Oligocene and Miocene faunas with a well studied rich European modern malacofauna from the Mediterranean Sea (Spain, Andalusia, Gofas *et al.*, 2011), we note that the richest families (in decreasing order) are the same: Pyramidellidae, Rissoidae, Turridae (*sensu lato*), followed by the Trochidae, Eulimidae, Nassariidae and Muricidae. Such close family biodiversity similarity suggests that the modern Atlantic-Mediterranean biogeographical province has a history reaching back to the Oligocene. However the usefulness of this parameter, intrafamilial species richness, as a proxy for global comparison seems limited, and it reveals only the main trend of the various basins.

Oligocene to Upper Miocene palaeobiogeographical reconstructions based on analyses of generic distributions

The genus is the standard category for this type of biogeographical analysis because fossils are not always well enough preserved for identification. The modern molluscan provinces were initially based on generic distribution (Woodward, 1866; Fischer, 1880-1887). However since Briggs (1974) a criterion of at least 10% endemic species is generally employed in the recognition of modern provinces (Briggs & Bowen, 2012). These authors divided the continental shelf into a series of large biogeographic regions that, in turn, contain smaller provinces. As a consequence, some very tiny islands may be recognized as a distinct province (*e.g.*, the Eastern Atlantic Region, consisting only of St Helena Island). Otherwise the identification of the warm-temperate provinces is questionable and they are now included with tropical provinces in larger warm regions (Briggs & Bowen, 2012). The endemism rate in the fossil deposits is generally poorly known and particularly difficult to determine at a specific level. In fact, such estimations depend so much on the preservation of the fossils that they must be used cautiously. Consequently, I focus here on significant trends in the evolution of the biogeographical regions (using analysis at generic level), rather than distinguish and describe the various provinces.

Generic richness

The gastropod basinal faunas may be compared in terms of richness. Generic richness varies from 32 (Rupelian of Brittany) to 494 (Chattian of the Adour Basin) with a mean of 220 and a median of 198. Brittany's (Rennes Basin, France) low diversity reflects poor sampling (only three ancient collections are available) but also the uniqueness of this semi-enclosed little basin. New, perfectly preserved material obtained from a drill-hole shows a depositional environment close to anoxic.

However, the low number of genera in the

Rupelian of Belgium (59) compared to 139 in the Mainz Basin, 138 in the Paris Basin and 304 in the Aquitaine Basin mainly reflects a latitudinal gradient in species richness, which is particularly clear during the Lower Oligocene.

The richest fauna is in the Chattian of the Aquitaine Basin (open to the tropical Atlantic domain which is connected to the Tethys Realm). It includes 494 genera whereas, in the Upper Oligocene of the Nordic Basin, only 198 genera have been recognized giving a ratio of 2.5 (494/198). In the Lower Oligocene the ratio is higher (5.2, with 304 genera in the Aquitaine Basin, and 59 genera in the North Sea Basin). On the other hand, in the Middle Miocene faunas, the ratio between the Loire Basin (256 genera) and the Nordic faunas (173) decreases to 1.5. It is only 1.2 between the more ecologically diverse Langhian of the Aquitaine Basin and the North Sea Basin (Fig. 5). The Upper Oligocene (Chattian) peak in southern Aquitaine gastropods is consistent with the generic richness of the zooxanthellate corals (z-corals) observed in the Aquitaine Basin (CAHUZAC & CHAIX, 1996). However BOSELLINI and PERRIN (2008) pointed out that this highest generic diversity of Chattian z-corals is exceptional compared to the Paleogene and Neogene coral faunas listed in the Mediterranean Region (including the Aquitaine Basin).
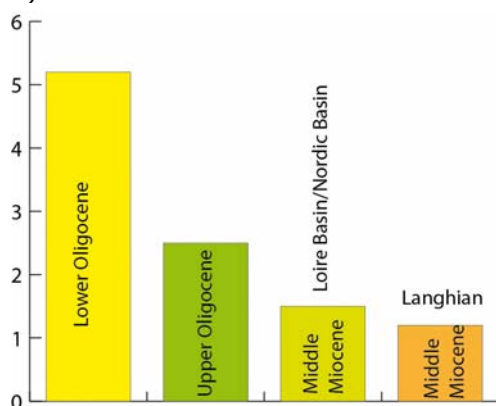
Figure 5: The ratios between number of genera in the Aquitaine basin or the Loire Basin and the North Sea Basin express a strong latitudinal gradient of diversity in the Oligocene, and its progressive reduction.

Changing latitudinal gradient of biodiversity in Oligocene to Upper Miocene: Global pattern from correspondence analysis of gastropod genera (Figs. 6-7)

The CA analysis involved 16 malacofaunas from which 4000 species were distinguished resulting in the identification of 761 genera (Appendix Table 3). The data were transformed into a presence-absence table, where each cell is quoted 0 if the genus is absent and 1 if the genus is present (Appendix Table 3). The two axes (first plane) represent 36.7% of the total variability (information) of the global samples.

The first axis distinguishes, on the positive side, the malacofaunas from Oligocene basins and, on the negative side, malacofaunas from Miocene basins. Axis 2 partly discriminates the North Sea Basin faunas (positive side) from the Aquitaine Basin faunas. The grouping of the 16 main discrete malacofaunas in homogeneous time-period clouds (Figs. 6-7) reveals the long-term changes recorded in the malacofaunas of the European Atlantic coasts, from the Oligocene to the Late Miocene.

The Rupelian cluster is the widest while the Chattian cloud is reduced. During the Miocene, the size of the clouds was more or less restricted. These results may be expressed alongside the ratios of richness in genera, demonstrating a stronger latitudinal gradient of diversity within the Lower Oligocene (Tethyan Region opposed to the Nordic Region) and its progressive reduction during and after the Upper Oligocene. Although some genera and families, such as the Strombidae, did not reach the Nordic Sea Basin or are poorly represented (Cypraeidae) in Miocene deposits, it appears unequivocal that the Miocene faunas of northern Europe and southern Europe are closer than their Oligocene counterparts.

The Oligocene transition and pre-Miocene extinction

The genera listed in Table 3 reveal that some classic Tethyan groups of genera, common in the Lower Oligocene of the Paris Basin, such as Ampullinidae (*Ampullinopsis*, *Deshayesia*), Potamididae (*Potamidopsis*), Pseudomelaniidae (*Bayania*) and Brachytrematidae (*Benoistia*), are unknown from the Belgian Basin. But most of these genera are common in the Mainz Basin. Conversely, tropical groups of genera comprising the Trochidae (*Lesperonia*), Turbinidae (several species of *Turbo*), Angariidae (*Angaria*), Seraphsidae (*Seraphs*), Strombidae (*Oostrombus*, *Strombus*), Cassidae (*Cassis*), Pickworthiidae (*Mareleptopoma*), Cerithiidae (*Gourmya*), Potamididae (*Serratocerithium*), Vasidae (*Vasum*) and Harpidae (*Morum*, *Eocithara*), are unknown in the Paris Basin but common in the Aquitaine Basin and most also occur in Italy. The development of coral patches several metres across in the Aquitaine Basin contrasts strongly with the total lack of hermatypic corals in the Stampian of the Paris Basin (CHAIX, 2012). During the Late Oligocene, some Tethyan groups reached the North Sea Basin, such as the Campanilidae (*Campanile*), the Harpidae (*Morum*), and the Olividae (*Oliva*), while some groups previously common in the Nordic Region also reached the Tethys Region (Nassariidae: *Keepingia*; Cassidae: *Galeodea*, *etc.*). In both domains, some modern genera of Nassariidae (*Nassarius*) and Turridae (*sensu lato*) (*Perrona*) appeared, whereas emblematic genera of the Palaeogene disappeared.
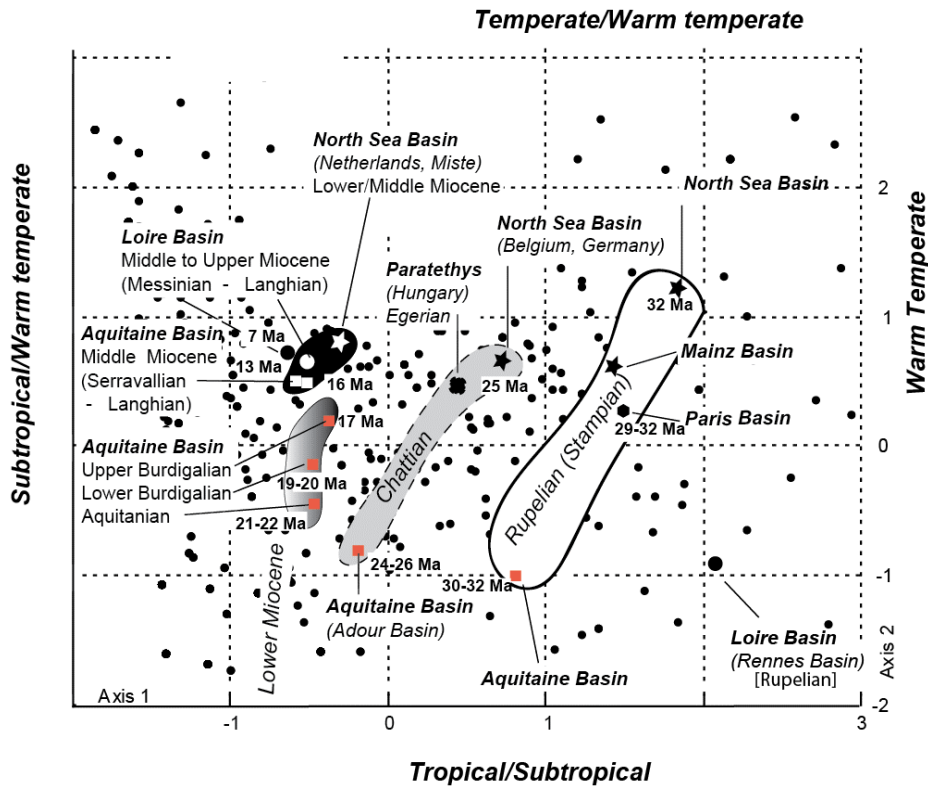
Figure 6: Diagram showing the relationships of Rupelian to Messinian faunas on the French Atlantic coast basins and those of the North Sea basins (Boreal Province) based on multivariate analysis (correspondence analysis) at the generic level.

The first factorial plane (F1 and F2) is used, representing 36.7% of the total variability (information) of the global sample. The dataset contains 761 genera recorded from the Oligocene to the uppermost Miocene. The four clusters show a clear evolution, especially in the relationship between the Nordic Basin and the Aquitaine Basin. Compare the greater extension of the Rupelian cluster (white) on axis 2, in contrast to the focusing of the Middle Miocene (black). Black dots represent the position of molluscan genera.
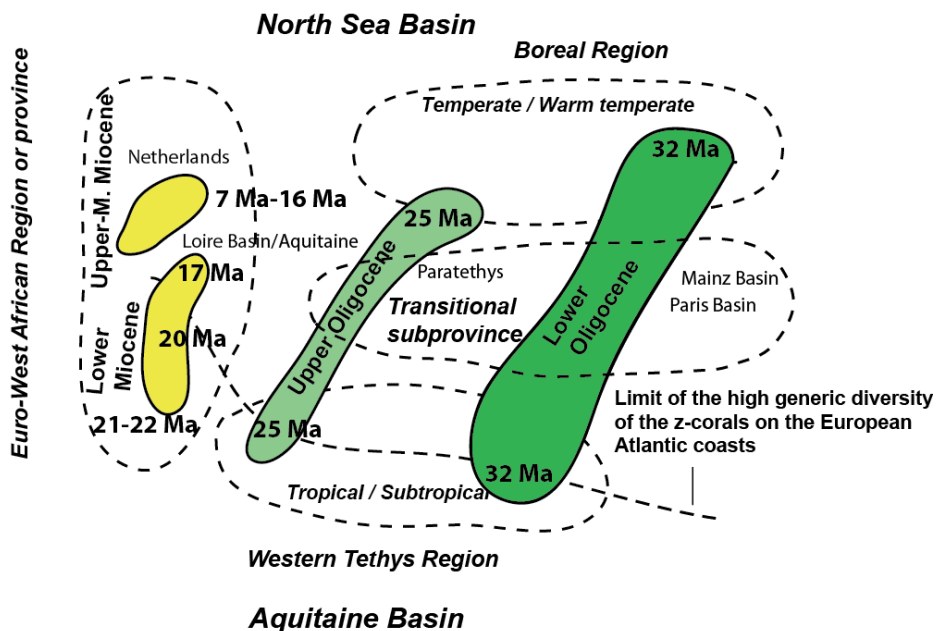
Figure 7: Interpretative diagram based on Figure 6, showing the spatio-temporal distribution of Lower Oligocene to Upper Miocene faunas (based on the distribution of 761 genera). For the area considered, three main biogeographical domains can be clearly identified. For the Lower Oligocene we recognized a Boreal Region comprising the North Sea basin, the Western Tethys Region comprising the Aquitaine Basin and a Transitional subunit (Mainz basin, Rennes basin and Paris Basin). Compare the distance between North Sea Basin and Aquitaine Basin during the Lower Oligocene (32 Ma), during the Upper Oligocene (25 Ma) and during the Miocene; the smallest cluster matches the interval 7 to 16 Ma. The North Sea basins and the Aquitaine Basin became a single biogeographical unit, the Euro-West African Region, during the Miocene.
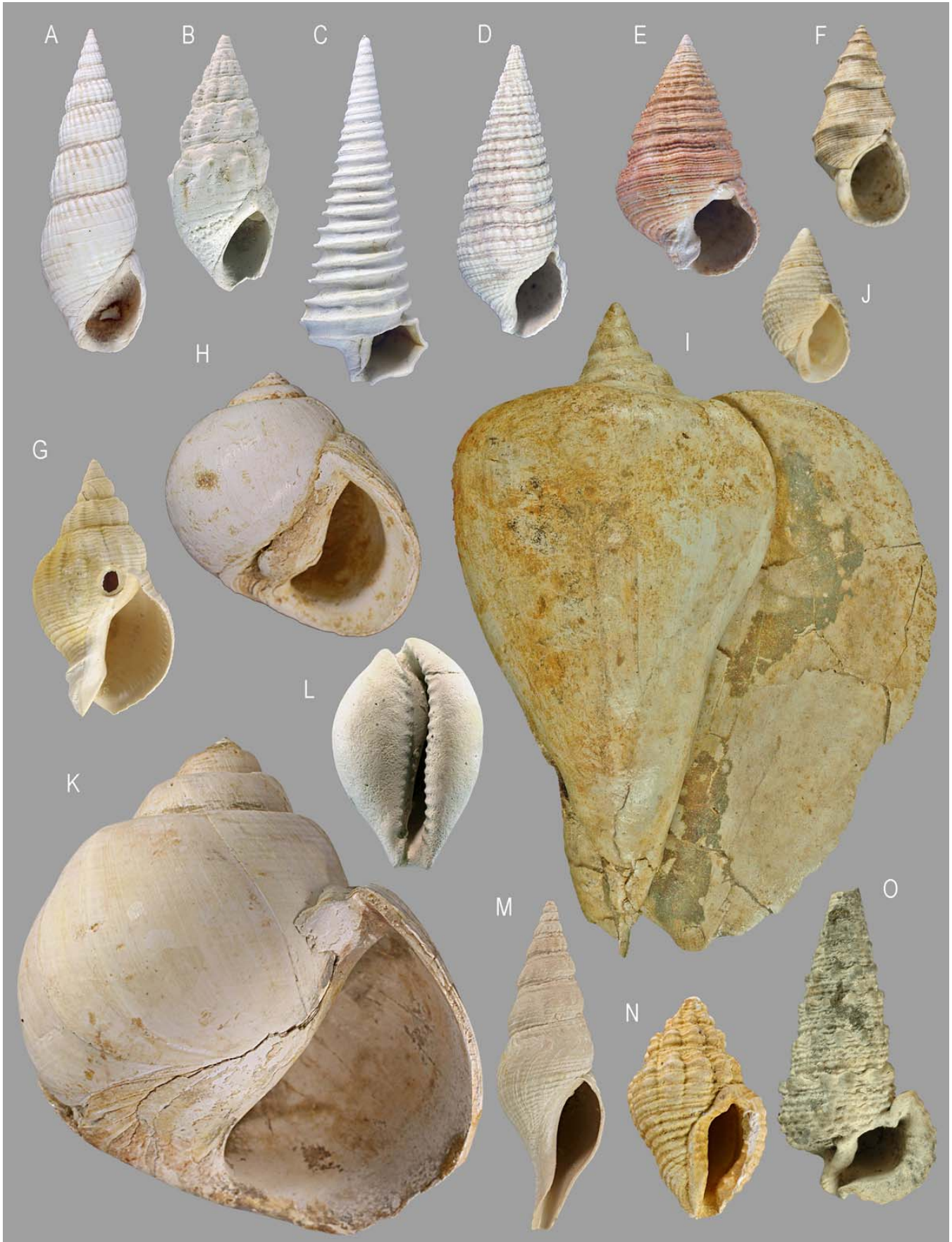
◀ **Figure 8**: The Rupelian "losers". All species are from the Paris Basin (except F, I and O, from the Aquitaine Basin, Landes). These species belong to genera coming to extinction during the Oligocene epoch but particularly common in the Paris Basin Stampian (30-40% of the gastropod fauna from the data of GITTON *et al.*, 1986) in the Lower Oligocene. The genera *Ampullinopsis* (I) and *Oostrombus* (J) contain giant Tethyan species reaching respectively 20 and 25 cm.

    A-B, *Bayania corrugata* (LAMARCK, 1804). (A) from Auvers-Saint-Georges, 27 mm, (B) Pierrefitte, Saint-Hilaire, 20 mm.
    C, *Potamidopsis trochleare* (typical morphotype) from Morigny Sands, "Trou à coquilles", Morigny-Champigny 28 mm.
    D, *Globulocerithium intratentatum* (DESHAYES, 1864). 1-2: Auvers-Saint-Georges, 26.5 mm.
    E, *Benoistia boblayi* (DESHAYES, 1824). Auvers-Saint-Georges, 18 mm.
    F, *Lesperonia trochoides* (FUCHS, 1870). "Lesperon", Dax, 10 mm.
    G, *Keepingia gossardii* (NYST, 1836). "Trou à coquilles", Morigny-Champigny, 31 mm.
    H, *Deshayesia cochlearia* (BRONGNIART, 1823). "Brunehaut", Morigny-Champigny, 29 mm.
    I, *Oostrombus auricularius* (GRATELOUP, 1834). "Espibos", Gaas, 140 mm.
    J, *Raulinia alligata* (DESHAYES, 1824). Auvers-Saint-Georges, 8.3 mm.
    K, *Ampullinopsis crassatina* (LAMARCK, 1804). "Brunehaut", Morigny-Champigny, 70 mm.
    L, *Praerosaria stampinensis* (SACCO, 1894). "Pierrefitte", Saint-Hilaire, 18 mm.
    M, *Glibertturricula vervoeneni* CADÉÉ & JANSSEN, 1985. Core of the "Station de Pompage", Ormoy-La-Rivière, 20 mm.
    N, *Editharus heberti* (MAYER, 1864). "Pont Royal", Étréchy, 17.5 mm.
    O, *Serratocerithium stroppus* (BRONGNIART, 1823). "Espibos", Gaas, 42 mm.

Finally, the pre-Neogene extinction of groups that were particularly common in the Early Oligocene or Late Oligocene deserves to be noted (Fig. 8). In the Rupelian (Lower Stampian sands of Jeurre and Morigny) of the Paris Basin, 11 samples analysed (size fraction > 4 mm) yielded a total of 6358 specimens (GITTON *et al.*, 1986). Thirty-three percent of the shells belong to the genera *Bayania, Benoistia* and *Potamidopsis* which become extinct at the end of the Oligocene (Fig. 8). Thus, this was subject to extinctions that greatly changed the composition of the European mollusc communities. At least 64 genera disappeared at the mid-latitude of Europe and from the Mediterranean realm before the Lower Miocene (Table 2). This result may be compared with the disappearance of 94 taxa from southern Europe (including the Mediterranean realm) during the Late Oligocene to Early Pliocene (VERMEIJ, 2011).

The Tethys Region and emergence of a Euro-West African Region

All the authors consider that the Aquitaine Basin was part of the Western Tethys Region during the Early and Late Oligocene. However HARZHAUSER *et al.* (2002, 2007) distinguished an Eastern Atlantic Province for the Oligocene of the Aquitaine and Iberia basins and a Mediterranean/Iranian Province for the Mediterranean to Iran basins, these palaeobiogeographic provinces being subunits of the Western Tethys Region. This opinion is not founded on a critical analysis of the whole fauna but on selected species. In fact, apart from the exceptional preservation of the molluscan faunas in the Oligocene of the Aquitaine Basin, there is no reason to separate them, for example, from their Italian counterparts. All the species cited by HARZHAUSER *et al.* (2002) as characteristic gastropods of the Mediterranean/Iranian Province also occur in the Aquitaine Basin. I therefore suggest that this separation is not justified on grounds of endemism.

Although the opinion of CAVELIER (1979) that the same Mesogean/Tethyan tropical region extended from the Aquitaine basin to Iran needs to be reassessed in the light of new faunal discoveries, this remains the best hypothesis. My recent collecting in the classic Italian outcrops (Rupelian of Castelgomberto Hills, Vicentin) confirms the views of the classical authors (*e.g.*, FUCHS, 1870), who recognized the same faunas in Italian and Aquitanian deposits. In Iran, HARZHAUSER (2004) identified 42 genera of gastropods from the Abadeh deposits (Lower to Upper Rupelian). For the time being only two (*Pseudophasianus* and *Rimella*) are not known from the Lower Oligocene of the Aquitaine basin. However, *Pseudophasianus* occurs in Italy, while other genera, although shared between the Aquitaine Basin and Iran [*Strombus* (*Tricornis*), *Peasiella, Astralium*], are absent.

The Paris and Mainz basins, being at the same latitudinal position but apparently without direct inter-communication, are situated in a transitional province, intermediate between warmer subtropical and temperate waters, as expressed by their position in the factorial diagrams (Figs. 6-7). The absence in these basins of "megathermic" mollusc groups as Strombidae, Vasidae and *Cassis* and the rarity of z-corals suggest that this subtropical to warm-temperate malacofauna should be included in the large Western Tethys Region as a transitional subunit. In the Paris Basin the endemism (at the specific level) was estimated by LOZOUET and MAESTRATI (2012) at about 6%. If we follow BRIGGS and BOWEN (2012), this rate is too low to consider this area as a separate province. For the Early Oligocene (Rupelian) northern Europe is generally placed in another biogeographical domain (CAVELIER, 1979), generally named the Nordic or Boreal Province or Region (Fig. 9). From my dataset of the Belgian Rupelian the gastropods share only 45% of species with the Paris Basin and 52% with the Mainz Basin, which also opened onto the palaeo-North Sea.

Last Oligocene European & Mediterranean appearance	Extinct during the Oligocene	IP occurrence	AW occurrence
Aiziella	*		
Ampullinopsis	*		
Aneurychilus	*		
Angaria		*	
Angistoma	*		
Aporrhais (Triaconthium)	*		
Arene			*
Bartonia	*		
Bayania	*		
Benoistia	*		
Boettgeriola	*		
Boreosiphopsis	*		
Bourdieria	*		
Charitodoron (s.l.)	*		
Cittarium			*
Conomitra	*		
Crommium	*		
Cryptoconus	*		
Deshayesia	*		
Diastoma		*	
Editharus	*		
Egerea	*		
Ellobium		*	
Eocithara	*		
Fastigiella			*
Gabrielona		*	*
Glibertturricula	*		
Globulocerithium	*		
Goergesia	*		
Hameconia	*		
Hortia		*	
Iravadia		*	
Keepingia	*		
Keilostoma	*		
Larocheopsis		*	
Lesperonia	*		
Littorinolacuna	*		
Neodesmeria	*		
Nucleolaria		*	
Nystia	*		
Pagodatrochus		*	
Oostrombus	*		
Potamidopsis	*		
Praehyalocylis	*		
Praerosaria	*		
Pseudomalaxis	*		
Raulinia	*		
Sandbergeria	*		
Seraphs	*		
Serratocerithium	*		
Sigatica	*		
Spinobrookula	*		
Sphaerocypraea		*	
Spoelia	*		
Stephopoma		*	*
Subepona	*		
Strebloceras		*	
Streptodictyon (Fredenia)	*		
Taphrostomia	*		
Thereitis	*		
Turbo (Amphiboliturbo)	*		
Turbo (Sabronia)	*		
Vicinocerithium	*		
Volvaria	*		
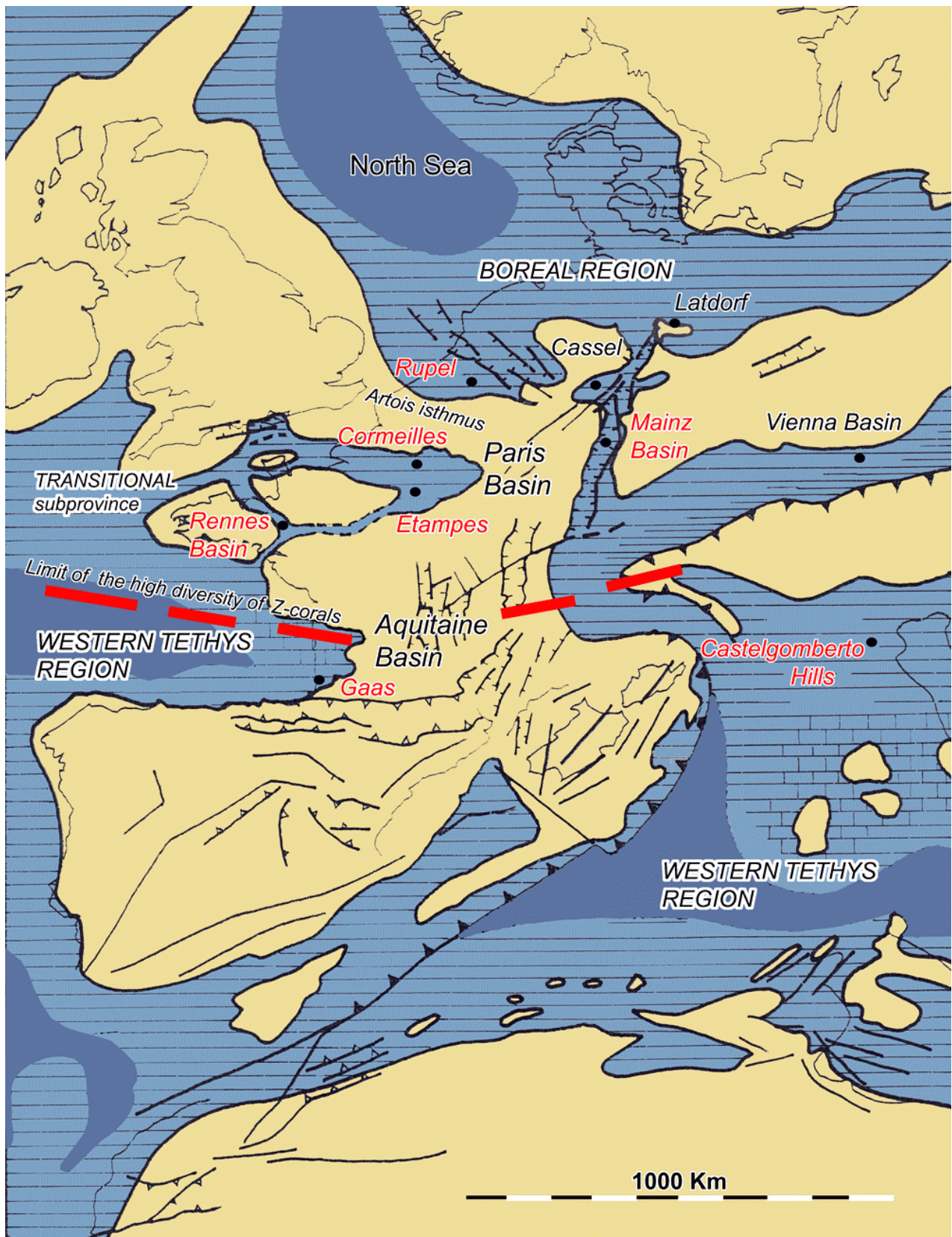
Figure 9: Reconstruction of European seas during the Early Oligocene (Late Rupelian, 32 - 29 Ma) with location of the main biogeographical areas. The main Rupelian localities are in red. Z-corals= zooxanthellate corals (LOZOUET, ed., 2012, modified after MEULENKAMP *et al.*, 2000).

◄ **Table 2**: Genera with last European/Mediterranean occurrence in the Oligocene: extinct in the Oligocene; Recent occurrence in the Indo-West Pacific (IP); Recent occurrence in the Western Atlantic (AW).
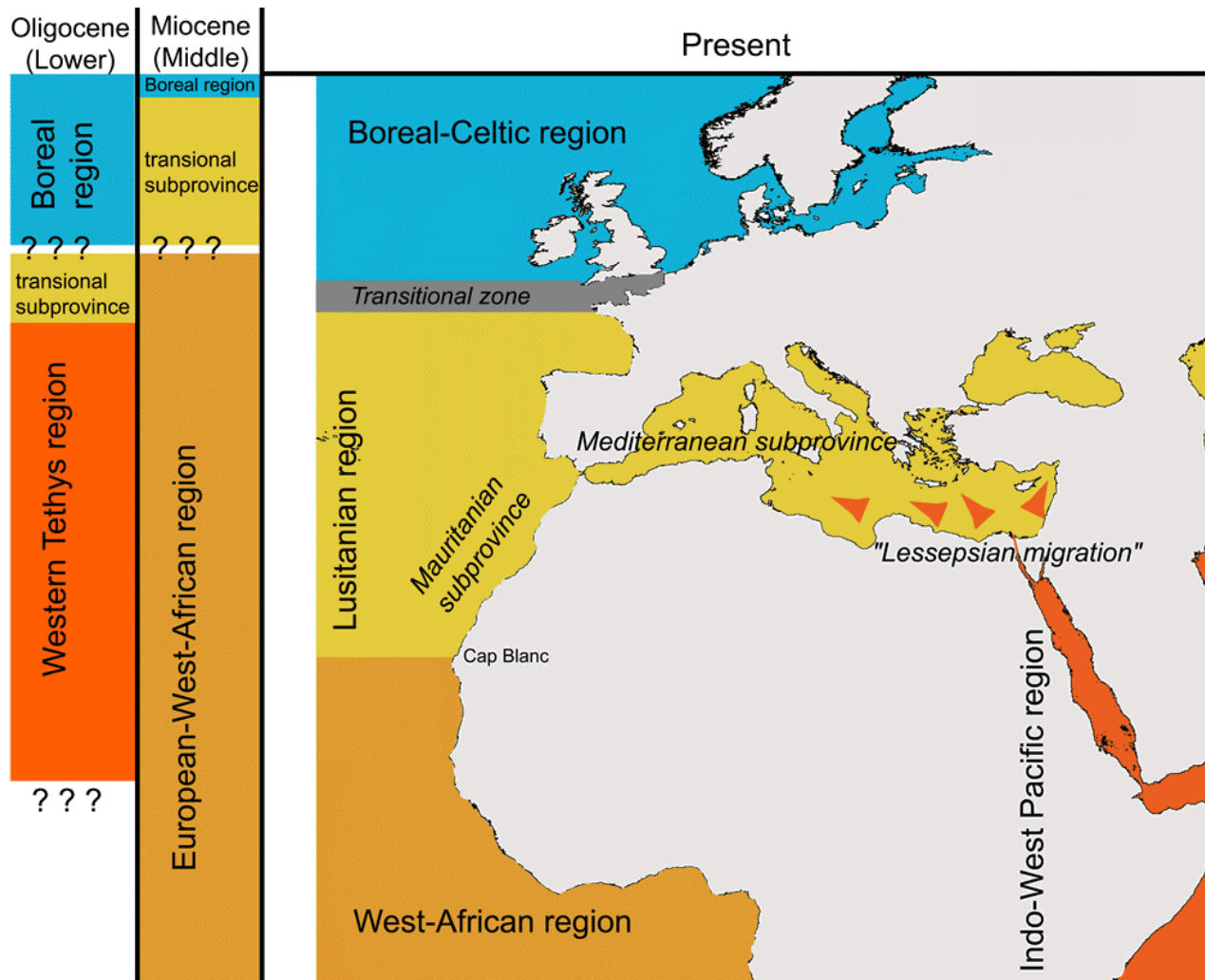
Figure 10: Global evolution of molluscan biogeographic regions in the north-eastern Atlantic during the Oligocene and the Miocene. Modern bioprovinces after GOFAS *et al.* (2011) and EKMAN (1953). The "Lessepsian migration" (POR, 1978; ZENETOS *et al.*, 2003), modern tropicalization of the Mediterranean biota which restores a biogeographical link between the Mediterranean and IWP, is also illustrated. Figure adapted from SILVA and LANDAU (2007).

We have shown that homogenization in the biogeographical distribution of gastropod genera began on the European Atlantic coasts during the Late Oligocene. This trend was amplified during the Miocene, possibly as a consequence of the tectonic connection between African and Eurasian littoral biotopes at the Oligocene/Miocene transition. This confirms the early intuitive conclusions of BRÉBION (1974, 1988) who claimed that, at that time, a large but somewhat homogeneous tropical to subtropical Eastern Atlantic faunal province succeeded the Palaeogene (pan-tropical) Tethys Province. This Eastern Atlantic Province probably extended from the Netherlands to Angola in the south (LOZOUET & GOURGUES, 1995). These authors coined the term Euro-West African Province in order to designate this new European/African marine biogeographic area because it has consisted in part of modern West African genera since the Early Miocene.

The close relationship between the modern West African biogeographical province (*Tropical Eastern Atlantic province* [TEA] of BRIGGS,

1974) and our Neogene *Euro-West African paleoprovince* is confirmed by generic affinities (LE LOEUFF & COSEL, 1998). BRÉBION (1974, 1988) preferred the term Mediterranean Province (or *Senegal Province*, *Guinean Province*), and HARZ-HAUSER *et al.* (2007) coined *Proto-Mediterranean Atlantic Region* for the same concept.

In the same way, KOWALEWSKI *et al.* (2002) used multivariate analyses at the species level in a study of the relationships between Parate-thys and Boreal malacofaunas for the Middle Miocene. The Aquitaine Basin was separated by KOWALEWSKI *et al.* (2002) and placed in a distinct SE North Atlantic Province, but they admitted, following F. STRAUCH (pers. comm. cited by KOWALEWSKI *et al.*, 2002), that a direct connection between Boreal Sea and southeastern North Atlantic is strongly supported by a very close correspondence of the concurrent Miocene faunas from the Aquitaine basin and the North Sea basin. In their demonstration they used a sample from Miste (the Netherlands) as a landmark of species distribution in the Late Burdigalian/Middle Miocene of the North Sea domain. In my analysis, using the same data

from Miste (but at the generic level), the multivariate distance between this extremely rich Nordic outcrop (more than 350 species of gastropods, JANSSEN, 1984a) and the Middle Miocene faunas of the Loire and Aquitaine basins is very short, implying that they belonged to the same or very close biogeographical domains. The absence of "megathermic" taxa such as *Strombus* in the North Sea basin seems to justify the distinction of this region as a sub-province. *Strombus* disappeared from the French Atlantic Coast during the Middle/Late Miocene and from the Iberian Atlantic Coast during the Pliocene (LANDAU *et al.*, 2011). However the recent discovery in the North Sea basin (Germany) of new thermophilous taxa such as *Melongena* and *Cabania* (MOTHS *et al.*, 2010) suggests that the greatest care must be taken in making a final conclusion.

SILVA and LANDAU (2007) and LANDAU *et al.* (2011) proposed a reconstruction of the evolution of the Euro-West African region (or Province) from the Pliocene to the present. In the Pliocene the European Atlantic Coast (excluding the Nordic Basin) belonged to a French-Iberian Province, whereas the Mediterranean Sea and the West African Coast were part of a Mediterranean-West African Province. For the modern biogeography GOFAS *et al.* (2011) distinguish the Lusitanian region for the area extending from the English Channel to Mauritania (with two sub-provinces, the Mediterranean and the Mauritanian), with the West African region south of Cap Blanc and the Boreal-Celtic region north of Brittany (Fig. 10).

Conclusions

In order to understand the marine faunal history of a region, it is necessary to discriminate between biodiversity changes that may result simply from variations in the quality of the fossil record and genuine evolution linked to climatic or other changes. The diversity estimates are greatly affected by several factors: the number of faunas that have been studied, how well studied the faunas are, diversity of sampled biotopes (over-represented or absent), taxonomic uncertainty, and the tyranny of a high number of specimens (including demonstration of the species identity of taxa and the difficulty of comparison among such large faunas). Thus, we can say that the present report is an aspirational outline. However, with estimates of the number of gastropod species greatly exceeding 10,000 in the Eocene to Miocene deposits of the French Atlantic region (4000-6000 for the Eocene; more than 5300 estimated species for the Oligocene and Miocene) this first comprehensive synthesis characterizes the exceptional diversity of this region with greater accuracy than before, while highlighting the requirement for further studies of these faunas.

Despite the unquestionably high species richness, some faunas remain only superficially known or unstudied (especially the Upper Eocene and Upper Oligocene molluscs). It is also clear that a continuous record of Oligocene and Miocene marine faunas is not preserved in all parts of Western Europe. On the other hand, when the local species richness of fossil molluscs is compared with the number of species now living along the modern French Atlantic coast, the drastic change must be underlined. About 240 species of shelled Gastropoda are recorded in the living fauna (S. GOFAS, pers. comm., 2010; see Fig. 2), differing markedly from the 1300 species recorded in the Upper Oligocene deposits of the Adour sub-basin or the 350 species listed in the Upper Miocene (Redonian) of the Loire Basin. However, even if the peak of diversity in the Upper Oligocene is overstated (due to a large bathymetric range), we cannot consider that the Miocene was a period of higher biodiversity than the Oligocene. Figure 2 indicates, rather, a gradual tendency towards impoverishment of the North Atlantic faunas during Miocene time. In fact, there is no clear peak in biodiversity.

Changes in the distribution of genera during the Oligocene to Late Miocene reveal a stronger latitudinal gradient in biodiversity within the Early Oligocene Atlantic domain (from the Tethyan region to the North Sea region). During the Early Oligocene (Rupelian) a transitional subtropical area (included to the vast Western Tethys region) is suggested around the latitudes of the Loire, Paris and Mainz basins. At this time, the North Sea Basin clearly belonged to another warm temperate region generally known as the Boreal region. The reduction of the latitudinal gradient during the Late Oligocene and the Miocene led to the development of an enlarged Euro-West African Province (Fig. 10). The closure of the Tethys seaway at the end of the Badenian (early Middle Miocene) favoured this process with the development of longitudinal exchanges instead of latitudinal exchanges. Indeed the segmented Tethys Ocean parallel to the equator gave birth to a Mediterranean Sea open to the Atlantic Ocean. This Tethys successor was a melting pot and a source of novelty, but cannot be compared with the enormous faunal reservoir preserved in the Eastern Tethys which became the Indo-West Pacific region in the Middle Miocene; its exceptional richness resulting from very long stability. Some sporadic links have been pointed out between European faunas and the new Indo-West Pacific region during the early Middle Miocene optimum (Badenian stage) through the Paratethys realm. This is indicated by the development of a particularly rich fauna and well expressed by the gastropod family Pickworthiidae (JANSSEN, 2004) and the echinoderm fauna (KROH, 2007). This underlines the long-lasting importance of the Tethys (or its Indo-West Pacific heir) as a reservoir of malacological biodiversity. The depressed

Miocene diversity in the Atlantic realm is reinforced during late Neogene times by other climatic events linked with global step-by-step cooling leading to the late Pleistocene "ice-house" period.

Last we note the extinction of groups that were particularly common in the Early Oligocene (Rupelian) or in the Late Oligocene. Thus the Oligocene suffered from extinctions that have greatly changed the composition of molluscan communities.

Acknowledgements

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Appendix

Source of data and main literature compiled

The major part of the datasets analyzed in this study were assembled through field work by the author and collaborators. The overall sampling effort may be gauged from the 113 person-days allocated to fieldwork in an Aquitaine quarry at Meilhan (Lozouet *et al.*, 2001b). The samples were sieved systematically, generally in fresh water. Items larger than 3-4 mm were sorted in the field while the finer fractions (3-0.5 mm) were sorted in the laboratory with the aid of a dissecting microscope. Considerable time was spent in sorting the finer fractions. For basins for which limited data have been collected by the author, the data are augmented from a critical compilation from the literature. "Personal collecting data" denotes exclusive use of personal data, "From literature and personal data" indicates both sources are used, "From literature" denotes exclusive use of bibliographic datasets. "Literature" contains the main publications for the faunas indicated.

Lower Oligocene:

Personal collecting data: Aquitaine Basin (France), Paris Basin (France).

Literature: Cossmann (1892, 1893), Vergneau (1967a, 1987b, 1968), Gitton *et al.* (1986), Lozouet (1985, 2011), Lozouet & Maestrati (1982).

From literature and personal data: Belgian, Mainz Basin (Germany) [Glibert & Heinzelin de Braucourt, 1954; Kuster-Wendenburg, 1973; Gürs, 1995; Gürs & Moths, 2002; Marquet *et al.*, 2008].

Upper Oligocene:

Personal collecting data: Aquitaine Basin (Adour Basin).

Literature: Magne & Vergneau-Saubade (1974), Saubade (1969), Saubade & Cahuzac (1978), Lozouet (1998, 1999, 2004).

From literature and personal data: Chattian of Germany and Denmark; Egerian (Hungary)

[Glibert, 1957; Janssen, 1978a, 1978b, 1979; Schnelter, 1985; Schnelter & Beyer, 1987, 1990; Báldi, 1973; Janssen, 1984b]

Lower Miocene:

Personal collecting data: Aquitanian (Aquitaine Basin), Lower Burdigalian (Aquitaine Basin), Upper Burdigalian (Aquitaine Basin).

From literature: Cossmann & Peyrot (1909-1924), Peyrot (1925-1932), Lozouet *et al.* (2001a, 2001b), Lozouet (2011).

Middle Miocene:

Personal collecting data: Langhian (Aquitaine Basin); Langhian (Loire Basin); Serravallian (Aquitaine Basin).

From literature: Langhian (Loire Basin) [Peyrot, 1938; Ivolas & Peyrot, 1900; Glibert, 1952, 1954]; North Sea Basin, Hemmoorian (Lower/Middle Miocene: Miste, Netherlands; Werder, Germany) [Janssen, 1984a; Moths *et al.*, 2010]

Upper Miocene:

Personal collecting data: Redonian (Loire Basin, France).

From literature: Brébion (1964).

Table 3: Datamatrix of genera used for multivariate analysis (correspondence analysis). Data transformed into a presence-absence table, where each cell has a 0 if the genus is absent and a 1 if the genus is present:

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Acamptogenotia	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	0
Acanthotrophon	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Acirsella	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0
Aclis	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1
Acmaea	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0
Acrilloscala	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Acteocina	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Acteon	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Adeuomphalus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Admetula	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Agaronia	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0
Agathodonta	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Agathotoma	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Aiziella	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Akera	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Alexia (*Tralia*)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Alvania	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1
Amaea	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0
Amalda	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0
Amathina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amaurellina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ammonicera	1	1	0	1	0	1	1	0	1	0	1	1	0	0	0	1
Amphithalamus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ampullinopsis	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Anachis	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Anacithara	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0
Anatoma	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0
Anazola	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1
Ancillarina	0	1	0	0	0	1	0	1	1	1	1	1	1	0	1	0
Ancillina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ancillus	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0
Andonia	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0
Aneurychilus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Angaria	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Angistoma	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Aphanitoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Aphera	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Apiocypraea	0	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0
Aporrhais	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	0
Aporrhais (*Triaconthium*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Architectonica	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0
Arene	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Aspa	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0
Aspella	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Asperdaphne	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Assiminea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Asteracmea	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Asthenotoma	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1
Astralium	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Astrosansonia	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Ataxocerithium	1	1	0	1	0	1	1	0	1	1	1	1	0	0	0	1
Athleta	1	0	1	1	0	1	0	1	1	1	1	1	0	1	1	0
Atlanta	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Attiliosa	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	1

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Atys	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0
Auricula	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Auricula (Pythiopsis)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Auricula?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Babella	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0
Babylonella	1	0	0	1	0	1	1	1	0	0	1	0	1	0	1	0
Babylonia	1	1	0	0	0	1	0	1	0	1	0	0	0	1	1	0
Balcis	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1
Barleeia?	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0
Bartonia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Bathytoma	1	1	1	1	0	1	1	1	0	1	1	0	1	0	1	0
Batillaria	0	1	0	0	0	1	0	0	1	1	0	1	1	0	0	0
Bayania	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0
Bela	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Bela (s.s.)	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1
Belomitra	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Benoistia	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Benthomangelia	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0
Benthonella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Benthonellania	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Benthovoluta?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Berthelinia	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0
Berthella	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0
Bicatillus	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0
Bistolida	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Bittium	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Boettgeriola	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Boettgeriola?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bolinus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Bolma	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1
Bonellitia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Boreosiphopsis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Borsonia	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Bourdieria	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Brachystomia	1	1	0	1	0	1	0	0	1	1	1	1	1	1	1	0
Brocchia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Brocchinia	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1
Brotia	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0
Bullichna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Bullina	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1
Bursa	0	1	0	0	0	1	0	0	1	1	1	0	1	0	1	0
Cabania	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Caecum	1	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1
Calcarata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Calliostoma	0	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1
Calliostoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
(*Eucasta*)																
Calliotropis	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0
Calyptraea	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Campanile	1	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0
Camporellina	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cancellaria	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0
Cancilla	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0
Candinia	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Cantharus	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1
Caperella	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capulus	0	0	0	1	0	1	1	0	0	0	1	1	0	1	1	0
Carinorbis	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1
Cassidula	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cassis	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Cavolinia	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Cavostella	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Ceratia	0	1	0	0	0	1	1	0	1	1	0	1	1	0	1	0
Cerithidium	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	1
Cerithiella	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0
Cerithioderma	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cerithiopsidella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cerithiopsidella (*Krachia*)	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0
Cerithiopsis	1	1	0	1	0	0	1	0	1	1	0	1	1	0	0	0
Cerithiopsis (*s.l.*)	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Cerithiscala	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cerithium	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Ceritoturris	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Charitodoron (*s.l.*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Charonia	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0
Cheila	0	1	0	1	0	1	1	0	1	1	0	0	0	0	0	0
Chevallieria	0	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0
Chicoreus	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1
Chileutomia	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Chrysallida	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Cima	0	1	0	0	0	1	1	0	1	0	1	0	1	0	1	0
Cingula	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Cingulina	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Circulus	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Cirsonella	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Cirsope	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cirsotrema	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	1
Cittarium	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Clanculus (*Clanculopsis*)	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	1
Clathrofenella	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Clathromangelia	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1
Clatrosansonia	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Clavatula	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Clavatula (s.l.)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Clavus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Clelandella	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clinura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Clio	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	0
Closia?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cocculina	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0
Cocculina (s.l.)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cochlespira	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0
Cochliolepis	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Colliculus	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1
Collonia	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0
Colpodaspis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Colpostomia	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Colubraria	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Columbella	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0
Comarmondia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Comitas	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Conomitra	1	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0
Conorbis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conus	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Copostoma	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Coralliophila	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0
Coriandra	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cornirostra	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Coronia	0	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0
Costellaria	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1
Costoanachis	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1
Crassispira	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1
Crassitoniella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Crassopleura	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1
Crenilabium	1	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0
Crepidula	0	0	0	1	0	0	1	0	1	1	1	1	1	1	1	0
Creseis	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0
Crisilla	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Crommium	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cryptoconus	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cyclodostomia	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Cylichna	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1
Cylichnella	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0
Cyllene	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Cymatiella	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Cymatium	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Cymatosyrinx	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	0
Cymia	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
Cypraea	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Cypraeacassis	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0
Cypraeopsis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cypraeorbis	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Dalliella	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Danilia	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Daphnella	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Daphnellopsis	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Decoriatrivia	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Dentimargo	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dermomurex	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	1
Dermomurex (Takia)	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Deshayesia	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Demoulia	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Diala	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Diaphana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Diastoma	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0
Dikoleps	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Diodora	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Discaclis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Discohelix	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Discotectonica?	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0
Distorsio	0	1	0	0	0	1	0	0	1	1	1	0	1	0	1	0
Dizoniopsis	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1
Dolabella?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dorsanum	0	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Dorsanum (Cyllenina)	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0
Drilliola	0	1	0	1	0	1	1	1	0	0	1	0	0	0	1	0
Ebala	1	1	0	1	0	1	1	0	1	1	1	1	1	0	1	0
Echinophoria	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0
Ecphora	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0
Edithais	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Editharus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Egerea	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Elachisina	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Ellobium (s.l.)	1	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0
Ellobium (s.s.)	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Emarginula	1	1	1	1	0	1	1	0	1	1	1	1	0	0	0	1
Eocithara	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epitonium	0	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Erato	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1
Eratopsis	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1
Eratotrivia	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Ergalatax	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Erosaria (Erosaria?)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ersilia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eudaronia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eudolium	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0
Eudolium (Galeodolium)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eulima	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1
Eulima (s.l.)	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0
Eulimella	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Eulimostraca	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eumetula	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Eunaticina	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0
Euspirocrommium	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euthria	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Euthriofusus	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0
Fastigiella	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Favartia	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1
Favartia (Caribiella)	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Favartia?	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Favriella	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Ficopsis	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Ficus	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Finella	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0
Fissilabia	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Fissurella?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Floribella	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Fossacypraea	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Fossarus	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Fusinus	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1
Fusinus (Gracilipurpura)	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Fusiturris	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Fusiturris?	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0
Gabrielona	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Gadinia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Galeatrivia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Galeodea	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0
Galeropsis	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Gania	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Gemmula	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Genota	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Genus incertae sedis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Gibberula	1	1	0	0	1	1	0	0	1	1	1	1	1	1	0	1
Gibborissoa	1	1	0	0	0	1	0	0	1	1	0	1	0	1	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Gibbula	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
Glibertiella	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Glibertturricula	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Globularia	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Globulocerithium	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Goergesia	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Gourmya	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Granosolarium	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Granulina	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
Granulolabium	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Granulolabium (*Tiaracerithium*)	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Graphis	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1
Gyrineum	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Gyrostoma	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Habromorula	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Haedropleura	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Haliotis (*Sulculus*)	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1
Haloceras	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Haminoea	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Harpa	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hastula	0	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0
Hebeseila	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hebeulima?	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Heliacus	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Hemiconus	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0
Hemiliostraca	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Hemitoma	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Hespererato	0	1	0	0	0	1	1	0	1	1	1	1	0	0	1	0
Hexaplex	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hilda	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Hinea	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Hipponyx	1	1	0	1	0	1	0	0	1	1	1	0	1	1	0	0
Homalocantha	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Homalopoma	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0
Hoploteropsis	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Hordeulima	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Hortia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hyala	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0
Hydrobia	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0
Inella	0	1	0	0	0	1	1	0	1	1	1	1	0	0	1	0
Iphitus (*s.l.*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Iravadia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ireneia	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0
Jaton	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	0
Jenneria	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Joculator	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Johnjagtia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Jousseaumea	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Jujubinus	1	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1
Julia	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Keepingia	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0
Keilostoma	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kestocenebra	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Kleinella	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Knefastia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laecochlis?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Laemodonta	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Laeviphitus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Lamellaria	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
Lamellitrochus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Larocheopsis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latirulus	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Latirus	0	1	0	1	0	1	0	0	0	1	1	0	1	1	0	0
Lepetella	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Leptoconchus	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Lesperonia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucodiscus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Leucorynchia	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0	1
Lienardia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limondinia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Linatella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lindapterys	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Liomesus	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Liostomia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Lissospira	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lissotesta	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0
Litiopa?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Littorina (s.l.)	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Littoriniscala	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Littorinolacuna	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Littorinopsis	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Lodderena	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lodderia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lophocochlias	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Loxotaphrus	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lucapinella	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Lusitanops (s.l.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lusitanops?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Lyncina	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Lyria	1	1	0	1	0	1	1	0	1	1	1	0	1	0	0	0
Lyrotyphis	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Macromphalus	0	1	0	0	0	1	0	0	1	0	0	1	0	1	1	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Malea	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Mandolina	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Mangelia	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1
Manzonia	1	0	1	1	0	1	1	0	1	1	1	1	1	1	0	1
Mareleptopoma	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0	0
Margarites	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0
Marginella (s.l.)	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Mathilda	0	1	0	0	0	1	1	1	1	1	1	0	0	0	1	0
Mauritia	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Medoriopsis	1	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0
Megalomphalus	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1
Melampus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Melanella	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1
Melanoides	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Melanopsis	0	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Melarhaphe	1	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0
Melongena	0	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0
Mercuria	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0
Merica	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1
Metaxia	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0	1
Metula	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0
Metuonella	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Metzgeria	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
Microglyphis	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0
Microliotia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Microstelma	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Microstilifer	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Mikro	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Miowateria	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Miralda	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Misteia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Mitra	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Mitrella	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1
Mitrolumna	0	1	0	0	0	1	1	1	1	1	0	1	0	0	0	1
Mitromorpha	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Modulus	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0
Modulus?	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Moelleriopsis	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Monodonta	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Monodontella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Monotigma	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0
Morula (s.l.)	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Morum (Oniscidia)	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0
Murchisonella	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0
Murex	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Murex (Haustellum)	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Murexsul	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0
Muricopsis	0	1	0	0	0	1	0	0	1	1	0	1	1	0	0	1
Muricopsis (s.l.)	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0
Naquetia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Naquetia?	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Narona (s.l.)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nassaria?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nassarina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nassarius	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Nassarius (Arcularia)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Natica	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Neodesmieria	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Neosimnia	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0
Nepotilla	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nerita	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0
Neritilia	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Neritopsis	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Neverita	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0
Nihonia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Nipteraxis	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0
Niso	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0
Nitidiclavus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Niveria	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nodilittorina	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
Nodiscala	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0
Nodulus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Norrisella	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Nozeba	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Nystia	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Nystiella	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Obtusella	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
Oceanida?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ocenebra	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Ocenebra (s.l.)	1	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0
Odostomella	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Odostomia	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Odostomia (?)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oliva (Strephona)	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1
Olivella	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Omalogyra	1	1	0	1	0	1	0	0	1	1	0	1	0	0	0	1
Omalogyra?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ondina	1	1	0	1	0	1	1	0	1	1	1	0	1	0	1	0
Onoba	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1
Oocorys	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Oostrombus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opalia	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Opaliopsis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ophieulima (s.l.)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Orania	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0
Orbitestella	1	1	0	1	0	1	1	0	1	1	1	0	0	0	0	0
Orinella	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Orthosurcula	1	0	1	1	0	1	1	1	0	1	1	0	1	0	1	0
Oscilla	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Otopleura	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Ovatella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Oxynoe	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pachycrommium	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Pagodatrochus	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Palisadia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Papuliscala	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Paradrillia	1	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0
Parastrophia	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1
Pareuchelus	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	1
Paroxystele	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1
Parviturbo	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Patella	1	1	0	1	0	1	1	1	0	1	0	1	0	1	0	0
Patelloida	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Paziella	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Paziella (s.l.)	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Peasiella	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Pedipes	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pelycidion	0	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0
Pereiraea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Perotrochus	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0
Perplicaria	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Perrona	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	1
Persicula	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Petrafixia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phenacovolva	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Philbertia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Philine	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	0
Phos	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0
Phyllocoma	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Phyllonotus	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1
Pisania	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Pisanianura	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Pisinna	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pisulinella	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Plecotrema (Plecotremopsis)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Plesiothyreus	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0
Plesiothyreus (s.l.)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Plesiotriton	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plesiotrochus	1	1	0	1	1	1	1	0	1	1	1	0	0	0	0	0
Pleurofusia	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0
Pleuroploca	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Pleurotomella	1	1	0	1	0	1	1	0	0	0	1	0	0	0	1	0
Pleurotomella (s.l.)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurotomoides	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1
Poirieria	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polinices	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Polygona	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Ponderia	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Ponderinella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Potamides	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0
Potamidopsis	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Praehyalocylis	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Praerosaria	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Praescissurella	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0
Proadusta	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Proplecotrema	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0
Propustularia	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0
Proscutum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Protoma	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Prozonarina	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Pseudamnicola	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocirsope	1	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1
Pseudococculina	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pseudofulgur	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Pseudomalaxis	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Pseudoneptunea	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pseudonoba	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Pseudorbis	0	1	0	0	0	1	0	0	1	0	1	1	1	1	0	0
Pseudorissoina	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pseudoscilla	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Pseudoscilla?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pseudotalopia?	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Pseudotaphrus	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Pseudotorinia	0	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0
Pterochelus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pterotyphis	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Pterymarchia	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Pterymarchia?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pterynopsis	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1
Pterynotus	0	1	0	1	0	1	1	0	1	1	1	1	1	0	0	0
Ptychocerithium	0	1	0	0	0	1	0	0	1	1	0	1	1	0	0	1
Pugilina	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Pupa	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Purpura	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Purpurellus	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1
Pusillina	1	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0
Pusionella	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
Pygmaepterys	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Pyramidella	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Pyrazisinus	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pythia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radocochlis	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Ranella	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Raphitoma	0	1	0	0	0	1	1	0	1	1	1	1	0	1	1	1
Raulinia	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0
Retizafra	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Retusa	1	0	0	1	0	1	1	0	0	1	1	1	1	1	0	0
Rhinoclavis	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Rhinoclavis (*Striovertagus*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Rimula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ringicula	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	0
Ringicula (*Ringiculocosta*)	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
Ringicula (*Ringiculospongia*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Rissoa	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1
Rissoella	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0
Rissoina	0	1	0	0	0	1	0	0	1	1	1	1	1	1	0	1
Rissoina (*Ailinzebina*)	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Rissoina (*Morchiella*)	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Rissoina (*Pachyrissoina*)	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Rissoina (*Phosinella?*)	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Rissoina (*Rissolina?*)	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1
Rissoina (*Zebinella*)	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1
Rotellorbis	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
Rotostoma	0	1	0	1	0	1	1	0	1	1	1	0	0	0	0	0
Roxania	0	1	0	1	0	1	1	0	1	1	1	0	0	0	1	0
Sabia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Sabinella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Saccoina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sandbergeria	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sansonia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sassia	1	1	1	1	0	1	1	1	0	1	0	0	0	1	1	0
Scabricola	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scalaspira	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Scalaspira (*Vagantospira*)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Scaliola	1	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0
Scaphander	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0
Scaphella	0	0	1	0	0	1	1	0	0	1	1	1	0	1	1	1
Schilderia	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1
Schuettemmericia	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0
Scissurella	0	1	0	0	0	1	0	0	1	1	1	1	0	1	0	1
Sconsia	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Scutus	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Searlesia	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Seguenzia	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Seila	1	1	0	0	0	1	1	0	1	1	1	1	1	0	0	1
Semicassis	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0
Seraphs	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Serratocerithium	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Setia	0	1	0	0	0	1	0	0	1	1	0	1	1	0	0	1
Sigatica	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Simnialena	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Sinezona	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Sinum	0	1	0	0	0	1	1	0	1	1	1	1	0	1	1	0
Siphocypraea	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Siphonalia (*s.l.*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Siphonaria	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0
Siphonochelus	1	0	1	1	0	1	1	0	0	1	1	0	1	0	1	0
Skenea	1	1	0	1	0	1	1	0	1	1	0	1	1	1	0	0
Skenea?	0	1	0	0	0	1	0	1	1	1	1	0	1	1	1	0
Skeneoides	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Skeneopsis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smaragdia	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
Solariella	0	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0
Solariorbis	1	1	1	1	0	1	0	1	1	1	1	1	0	1	1	0
Sphaerocina	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Sphaerocypraea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Spinobrookula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spinucella	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Spiratella	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0
Spiricella	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0
Spirolaxis	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0
Splendrillia	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0
Spoelia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Squamulinia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Stalioia	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Stazzania	1	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0
Stenothyrella	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenothyroides	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0
Stephopoma	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Stilifer (s.l.)	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Stolidoma	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Stolidomopsis	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Stosicia	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Stosicia (Isseliella)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Strebloceras	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Streptodictyon	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1
Streptodictyon (Fredenia)	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Streptodictyon (s.l.)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Streptolathyrus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strioterebrum	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0
Strombus	0	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0
Strombus (Tricornis)	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Styliferina	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Subterynotus	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Subula	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0
Sukashitrochus	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Sulcocypraea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Sveltella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Sveltia	0	1	0	0	0	1	1	0	0	1	0	0	1	1	1	0
Talassia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Talparia	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Taphrostomia	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Tarebia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Taurasia	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Tectarius	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Tectura	0	1	0	1	0	1	1	0	1	1	1	0	0	0	0	1
Tectus	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Teinostoma	0	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Telescopium	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tenagodus	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	1
Tenagodus (Agathirses)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Tenuicerithium?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tenuiscala	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Terebra	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Terebralia	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Teretia	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1
Thais	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Thala	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1
Thalotia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Thelecythara	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Theodoxus	0	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Thereitis	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Tibia	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	0
Tibia (*Sulcogladius*)	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Tjaernoeia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Tomopleura	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Tomura	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0
Tornatellaea	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Tornatina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tornus	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1
Trachypollia	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0
Tricolia	0	1	0	0	1	1	0	0	1	1	1	1	1	1	0	1
Trigonostoma	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Trigonostoma (*s.l.*)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Triphora (*s.l.*)	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Tripia	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Tritonoharpa	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Trituba	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0
Trivia	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Trochita	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Trogloconcha	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Trona	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Trophon	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Trophon?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trophonopsis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Trubatsa	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Truncatella	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0
Tuba	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Tubbreva	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
Tudicla	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0
Turbinella?	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Turbo	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turbo (*Amphiboliturbo*)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turbo (*Heteroninella*)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Turbo (*Marmarostoma*)	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Turbo (*Sabronia*)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turbonilla	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Turcica	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Turehua	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Turris	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Turriscala	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0
Turritella	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Turritella (Haustator)	1	1	0	0	1	1	0	0	1	1	1	0	0	0	0	0
Turritella (s.l.)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tylodina	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Tympanotonos?	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Typhina	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Typhinellus	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1
Typhis	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	0
Typhis (s.l.)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Umbilibalcis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Umbraculum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Unitas	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0
Vaginella	0	1	0	0	0	1	1	0	1	1	1	0	0	0	1	0
Vanikoro	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Varicospira	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Vasum	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Vatopsis	1	1	0	1	0	1	1	0	1	0	0	1	0	0	1	0
Ventrilia	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Vermetus	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Vermicularia	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1
Vermicularia?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicinocerithium	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vitreolina?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Vitta	1	1	1	1	0	1	1	1	1	1	1	0	1	1	0	0
Vitularia	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0
Volema	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Volutocorbis	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Volvaria	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Volvarina	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0
Volvatella	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Volvulella	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	0
Waikura	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Wanganella	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Williamia	1	1	0	1	0	1	1	0	1	1	1	0	0	0	0	0
Xanthodaphne	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Xenophora	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1

	LOWER OLIGOCENE					UPPER OLIGOCENE			LOWER MIOCENE			MIDDLE MIOCENE				UPPER MIOCENE
	LOBP	LOAQ	LONE	LOMA	LOR	UOA	UPN	UPPA	LMAA	LMLB	LMUB	MMLT	MMLA	MMSA	MMMT	MLB
Xenoskenea	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Zebina	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Zeidora	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Zonaria	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Zonarina	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0

Lower Oligocene: [LOBP] Basin of Paris, [LOAQ] Aquitaine Basin, [LONE] North Sea basin, [LOMA] Mainz Basin, [Rennes Basin]. Upper Oligocene: [UOA] Aquitaine (Adour) Basin, [UPN] North Sea basin, [UPPA] Paratethys; Lower Miocene: [LMAA] Aquitanian of Aquitaine Basin, [LMLB] Lower Burdigalian of Aquitaine Basin, Upper Burdigalian of Aquitaine basin [LMUB]; Middle Miocene: [MMLT]: Loire Basin, [MMLA] Langhian of Aquitaine basin, [MMSA] Serravalian of Aquitaine Basin, [MMSA] Middle Miocene of North Sea basin (Miste); Upper Miocene [MLB] (Messinian) of Loire Basin.