

A review of the fossil record of the Labridae

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(with 3 figures)

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Summary

The published fossil record of the Labridae is critically evaluated. In total, fossils from 14 genera are provisionally placed within the family (the Scaridae is recognized as a tribe Scarini within the Labridae). Numerous specimens, previously recorded as Labridae, are now placed within other families, most notably the Phylloodontidae (Elopiformes). The labrid tribe Hypsigeniyini is characterized by the possession of an unusual, derived, phylloodont dentition in the pharyngeal bones. Fossils of this clade are particularly abundant, especially specimens in the genus *Labrodon*. This material permitted a reconstruction of the biogeography of the Hypsigeniyini from its earliest record in the Eocene of Monte Bolca in Italy (*Phyllopharyngodon*), before extending across the central Tethys in the late Eocene (*Labrodon*), and from the New World to Europe, Sri Lanka, and New Zealand in the Miocene (*Labrodon*). The biogeographic expansion of the Hypsigeniyini in the fossil record strongly supports inferences from recent molecular phylogenetic evidence.

Keywords: fish fossils, evolution, biogeography, paleontology, wrasses, parrotfishes.

Contents

Introduction	126
Methods and systematic notes	127
The Fossil Record of the Labridae	130
Tribe Hypsigeniyini	130

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Tribe Scarini	148
Tribe indet.	151
Non-Labridae (previously placed in Labridae)	158
Concluding Discussion	177
Acknowledgements	179
References	179

Introduction

The Labridae is one of the most conspicuous groups of fishes in marine waters. Present on hard substrata from the shores of Norway in the north to New Zealand in the south, they are represented in fish assemblages from every rocky marine habitat on the globe (PARENTI & RANDALL 2011). The family has over 630 species in 88 genera (NELSON *et al.* 2016). They reach their zenith on coral reefs where there are approximately 510 species (COWMAN 2014). In recent years great progress has been made in resolving the relationships among lineages within the family. It is now recognized that the Odacidae and Scaridae are both minor clades within a much larger monophyletic Labridae. The Labridae *s.l.* range in size from the diminutive *Wetmorella* at 5.5 cm to the 229 cm *Cheilinus undulatus*. The wrasses and parrotfishes are critically important in many coral reef ecosystem processes from the invertebrate-feeding wrasses, including the cleaner wrasses, to herbivorous and detritivorous parrotfishes (WAINWRIGHT *et al.* 2004; BELLWOOD *et al.* 2012; KRAMER *et al.* 2015). Furthermore, the Labridae consistently rank as one of the top five families on coral reefs in terms of both species richness and abundance (BELLWOOD 1996; ACKERMAN & BELLWOOD 2000; BELLWOOD *et al.* 2002).

Despite the wealth of knowledge on the ecology, biology, and phylogenetic systematics of the group, our understanding of the fossil record of the Labridae has been limited, in spite of numerous fossils being placed within the family. This difficulty in examining the fossil record of the family has been in part due to the large number of descriptions, but also because of the fragmentary nature of many of the fossils (most being isolated teeth or pharyngeal bones). This latter feature makes it particularly difficult to place fossils within existing taxonomic categories with any degree of confidence. This problem is exacerbated by the lack of a morphology-based cladogram of the family; few fossil specimens can be placed within extant lineages based on morphology-based synapomorphies.

Such placement may be possible in small groups where morphological descriptions offer a clear morphology-based cladistics framework, as in *Pseudolabrus* (RUSSELL 1988), *Bodianus* (GOMON 1997), and parrotfishes (BELLWOOD 1994). Indeed, these cladistic analyses have been useful in evaluating the fossil record of the parrotfishes (BELLWOOD & SCHULTZ 1991). However, recent phylogenetic analyses have questioned the validity of many extant nominal genera (*e. g.*, *Coris*, *Halichoeres*, *Gomphosus*) (BERNARDI *et al.*

2004; BARBER & BELLWOOD 2005) and care is therefore needed when considering placing fossils in extant genera.

Nevertheless, the fossil record still provides an invaluable resource for inferring biogeographic distributions and the evolution of major lineages. The goal of this review, therefore, is to bring together the information on the published fossil record of the Labridae as a basis for further evaluations of the group.

Methods and systematic notes

Phylogenetic perspectives on the status of the Labroidei, Labridae and Scaridae

This review will specifically include taxa that have been placed in the Labridae. It will not include the potentially closely related labroid or pharyngognath forms such as the Tortonesidae (SORBINI 1983), *Sorbinia* (BELLWOOD 1995), and *Quasicichla* (BANNIKOV 2004). These taxa have a complex mosaic of derived and plesiomorphic morphological characters. Unfortunately, the morphological characters that have been used to define the Labroidei are not restricted to the Labroidei *s.s.* and therefore these early taxa with affinities to the Labridae, Pomacentridae and/or Cichlidae must remain *incertae sedis* (please see notes below). This review, therefore, only considers material that may be (or has been) placed within the Labridae. For fully articulated material the only synapomorphies that remain in fossils and can be used to place them in the Labridae are: a single supraneural, oligomerization of the caudal skeleton and pharyngognathy (STIASSNY & JENSEN 1987). As the latter two are relatively widespread features their utility is limited, the former however is most useful. Within this review, specimens are tentatively placed within the Labridae if they resemble extant labrids, however, it must be noted that in terms of fragmentary remains this is a particularly tentative placement and that isolated tooth plates cannot be placed within specific taxa unless they bear synapomorphies that are restricted to these anatomical structures. Examples where this is possible includes placement in the Hypsi-genyini (based on stacked phyllodont tooth rows; (BELLWOOD 1990) (Fig. 1), among the pseudodacines (based on the structure of the pharyngeal and oral jaws (BELLWOOD 1994) and in various genera within the parrotfishes (formerly Scaridae, based on tooth, jaw and pharyngeal structures) (BELLWOOD & SCHULTZ 1991; BELLWOOD 1994).

The family Labridae and the closely related families the Odacidae and Scaridae have traditionally been placed within the suborder Labroidei. The composition of Labroidei has changed over the years with the largest grouping including the Labridae (and Scaridae and Odacidae), Embiotocidae, Cichlidae and Pomacentridae (STIASSNY & JENSEN 1987). The characters uniting these families all revolved around the presence of pharyngeal jaws (including fused tooth-bearing 5th ceratobranchials and an articulation between the paired upper pharyngeals and the neurocranium). Molecular evidence, however, has demonstrated that this Labroidei *s.l.* is non monophyletic (MABUCHI *et al.* 2007; WAINWRIGHT *et al.* 2012; NEAR *et al.* 2013) and that the pharyngognath condition arose independently

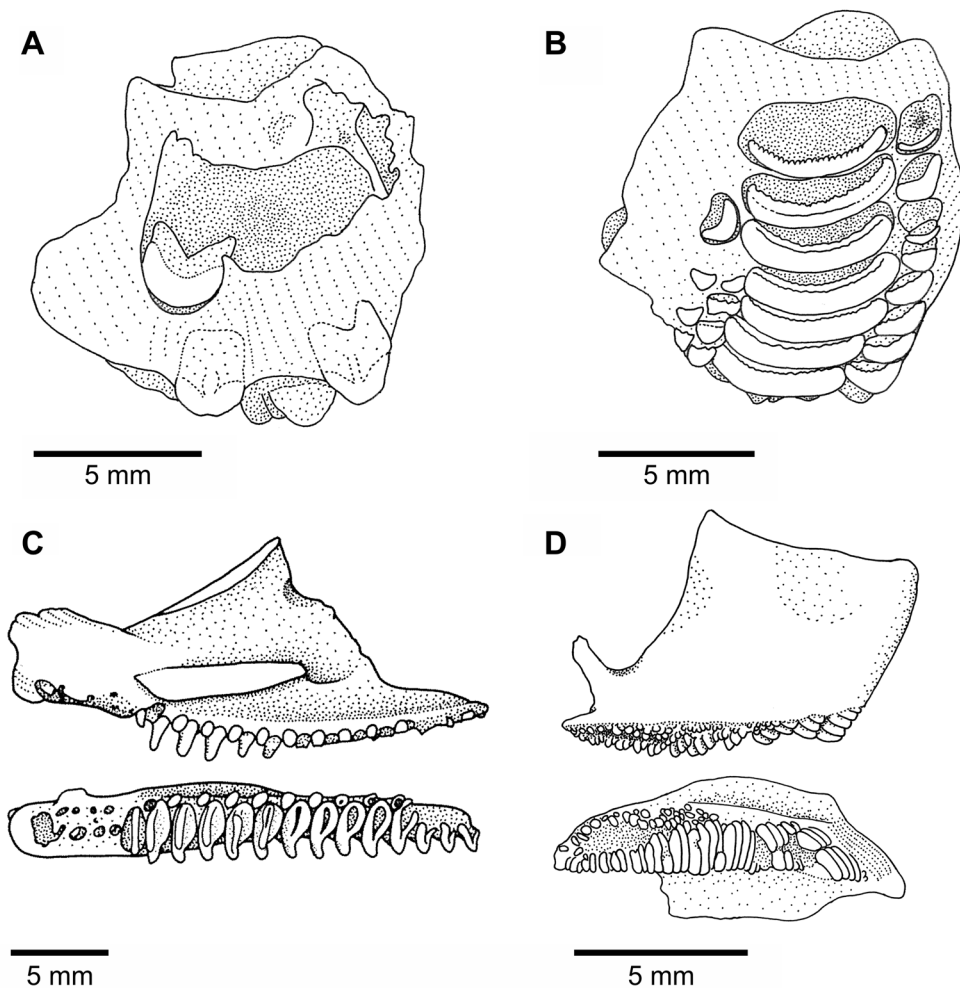


Fig. 1. Variation in pharyngeal tooth replacement patterns in the Labridae (upper pharyngeal bones shown (a and b in section, c and d lateral views). a) The plesiomorphic tooth replacement pattern in the Labridae with teeth developing in the alveolar cavity before erupting singularly on the surface (e.g., *Cheilinus*); b) The derived phyllodont condition in the Hypsigenyini, where teeth develop in distinct stacks with only the uppermost tooth (or teeth) emerging (e.g., *Bodianus*), a pattern also seen in the fossil hypsigenyine *Labrodon*; c) A modification of the plesiomorphic condition to produce tooth rows with teeth emerging from the alveolar region and moving posteriorly (left to right) (e.g., *Scarus*); d) The highly modified hypsigenyine *Pseudodax* with multiple oblique rows of stacked, phyllodont, teeth, a pattern found also in the fossil *Trigonodon*. Figures modified following BELLWOOD (1990) and (1994).

in the two clades (WAINWRIGHT *et al.* 2012) (and in several other groups [WAINWRIGHT & LONGO 2017]). The Labroidei *s.l.* are now split into two distinct clades: the Embiotocidae, Pomacentridae and Cichlidae and the older Labroidei containing just one family, the Labridae (MABUCHI *et al.* 2007; WAINWRIGHT *et al.* 2012; NEAR *et al.* 2013).

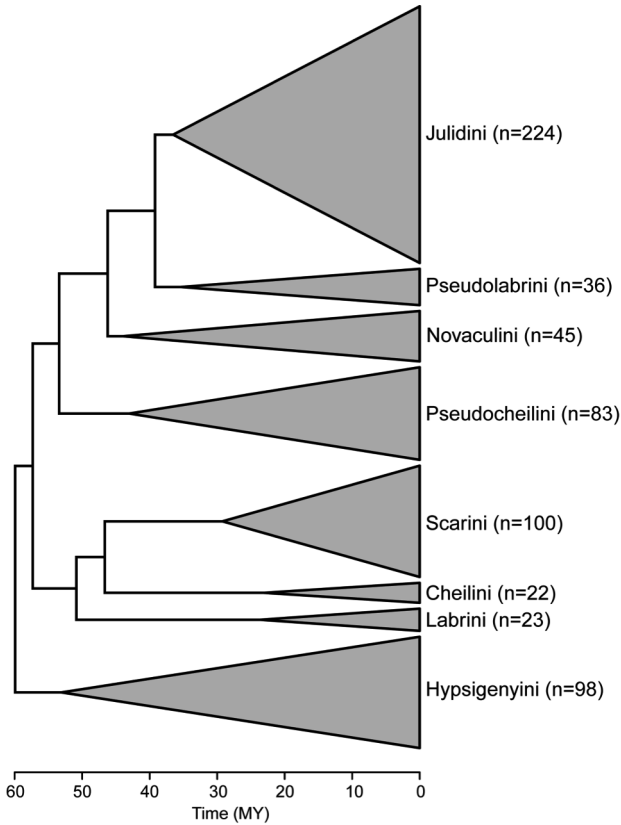


Fig. 2. Major clades within the Labridae including the Scarini (parrotfishes) as sister to the Cheilini (phylogeny following COWMAN & BELLWOOD [2011]). Number in parentheses are the approximate number of species in each tribe, the horizontal axis ages in millions of years.

The status of the three closely-related families the Labridae, Scaridae and Odacidae continues to cause confusion. While some authors retain the traditional separation, especially of the Labridae and Scaridae (*e.g.*, ALLEN & ERDMAN 2012; RANDALL & PARENTI 2014), the molecular evidence is unequivocal. The Labridae is a monophyletic family containing the Odacidae and Scaridae as separate clades within the broader labrid phylogeny. The Odacidae are just a minor group of wrasses within the Hypsigenyini. Given the need to recognize the parrotfishes as a distinct group (it is monophyletic with a broad suite of morphological synapomorphies and a distinct ecology [BELLWOOD 1994; BONALDO *et al.* 2014]) we recognize the parrotfishes as a separate tribe, the Scarini (scarines), that lies as the sister clade to the Cheilini (following GOMON & RUSSELL [in (BELLWOOD 1994)] and GOMON 1997). The term Scarini was first applied to parrotfishes by BONAPARTE, 1831. Together, the Scarini and Cheilini are sister to the Atlantic wrasses in the clade Labrini (Fig. 2). There is also distinct phylogenetic structure within the parrotfishes that reflects ecological and biogeographic trends (COWMAN *et al.* 2009; BONALDO *et al.* 2014). The tribe Scarini is, therefore, further divided into two subtribes, the Sparisomatina (previously recognized as the subfamily Sparisomatinae) and the Scarina (previously the subfamily Scarinae).

Nomenclatural details and abbreviations

Critical symbols introduced by RICHTER (1948: p. 54) and extended:

- * establishment of the species name.
- . the author(s) are sure that the quotation in the list is correct.
[no symbol] the author(s) do not have a motive for distinct inclusion but also no motive for a doubt.
- ? the quotation is doubtful.
- v. the author(s) have seen the original specimens and are sure that inclusion is correct.
- v the author(s) have seen the original specimens, but are not sure that the inclusion is correct.
- v? the author(s) have seen the original specimens but the condition or the circumstances do not allow a determination without doubt.
- non the quotation in this list is false.
- p the quotation in this list is correct only in part.
- / or

Abbreviations

- Jt Jaw-tooth.
- L Lower pharyngeal tooth plate.
- U Upper pharyngeal tooth plate.

The Fossil Record of the Labridae

Notice: The part of the fish preserved is noted in () by the authors. Only indications in “ ”

Tribe Hypsigenyini

Genus *Labrodon* Gervais, 1857

- . 1857 *Labrodon* – GERVAIS: 513–515, pl. 5, fig. 6, 6a, 6b (*Labrodon pavimentatum* GERVAIS, 1857).
- . 1858 *Nummopalatus* genre nouveau – ROUAULT: 101–102 (*N. Edwardsius*, sp. nov.).
- . 1863 *Plinthodus* nob. – COSTA: 37–39 (*Plinthodus Pisani*, nobis).
- p 1864 *Pharyngodopilus* – COCCHI: 59–61.
- . 1875a *Nummopalatus*, Marie ROUAULT, 1858 – SAUVAGE: 616.
- . 1876 *Nummopalatus Marie* ROUAULT. Bonan. – LAWLEY: 72–73.
- p 1880 *Labrodon* – SAUVAGE: 30–40.
- . 1909 *Labrodon* P. GERVAIS – STEFANO: 628–630.

Type species: *Labrodon pavimentatum* GERVAIS, 1857.

***Labrodon pavimentatum* GERVAIS, 1857**

- * 1857 *Labrodon pavimentatum* – GERVAIS: 513–515, pl. 5, fig. 6, 6a, 6b (Lower pharyngeal bone); sables marins de Montpellier [South France; Miocene].
- 1859 *Labrodon pavimentatum* – GERVAIS: 512, figs 44–46 (Lower pharyngeal bone); Montpellier [South France; Miocene. – same figures as in GERVAIS 1857].
- 1863 *Plinthodus Pisani*, nob. – COSTA: 39–40, 44–45, pl. 2b, figs 2A–D, 3A–C (Lower pharyngeal bone); Isola Pianosa presso quella dell’Elba [Italy; Pliocene].
- 1867–69 *Labrodon pavimentatum*, P. GERV. – GERVAIS: 235; Montpellier [France]; Pliocène.
- 1875a+b *Nummopalatus pavimentatus* P. GERVAIS sp. – SAUVAGE: 617–618, 642, pl. 23, fig. 3, 3a (Lower pharyngeal bone); Calcaire moellon de l’Herault, France; terrains tertiaires [Miocene]; [SAUVAGE 1875a+b puts *Nummopalatus alsinensis* COCCHI into the synonymy of *L. pavimentatus*, see also there].
- 1880 *Labrodon pavimentatum* – SAUVAGE: 33–34, pl. 2, fig. 5 (Lower pharyngeal bone); Saint Grégoire, terrains miocènes de Bretagne et de l’Herault, [and] le type figur, par GERVAIS provient des sables marins pliocènes des environs de Montpellier [France; Miocene].
- 1889 *Nummopalatus pavimentatum* P. GERVAIS, sp. – SIMONELLI: 212 (Lower and upper pharyngeal bones); Isola di Pianosa nel Mar Tirreno; Calcari pliocenici; 212 (“varie placche dentarie”); Montalcino, di Laiatico e di Orciano [Italy]; Pliocene.
- 1906a *Labrodon pavimentatum*, GERVAIS, 1857 – LERICHE: 314–318 (“Pharyngiens inférieurs” and “Pharyngiens supérieurs”); Cotes-du Nord: Le Quiou, Saint Juvat, Tréfumel. – Ille-et-Vilaine: Chartres-la-Poterie (gisement de la Chaussérie), Gahard, Saint-Grégoire. – Loire-Inférieur: Aigrefeuille, Le Landreau (gisement du Pigeon-Blanc), Noyal. – Maine-et-Loire: Charcé, Genneteil, Noyant-la-Gravoyère, Noyant-Méon, Saint-Saturnin (gisement du Haguineau), [Bretagne, Anjou, and Touraine, NW France]; Néogènes.
- 1909 *Labrodon pavimentatum* P. GERVAIS – STEFANO: 553, 557, 630–632, pl. 20, figs 3, 14, 15 (Lower pharyngeal bones); Orciano e San Quirico, [Tuscany, Italy]; Pliocene.
- 1912 *Labrodon pavimentatum* GERVAIS – STEFANO: 68, 72 (“diverse placche faringee superiore e inferiori”); dell’Emilia, [Italy]; Miocene, see MENESINI 1969: 45].
- 1912 *Labrodon pavimentatum* ? P. GERVAIS – PRIEM: 230 (“pharyngiens supérieurs”); Boutonnet, Hérault, S France; Burdigalien [Lower Miocene].
- 1916 *Labrodon pavimentatum* GERV., var. *ligustica* SACC. – SACCO: 175–176, pl. 1, fig. 2a–2b (“faringeo inferiore”); Zinola presso Savona [Italy]; nella marn grigia, Pliocene.
- 1916 *Labrodon multdens*, var. *Pisani* (COSTA) – SACCO: 176, pl. 1, figs 3a, 3b (“faringea inferiore”); Isola di Pianosa [Italy]; nel calcare un po’ travertinoide, Pliocene (sup.?).
- 1923 *Labrodon pavimentatum* GERVAIS – SANTUCCI: 208–209, 213, pl. 3, figs 1, 1a (Lower pharyngeal bone), 8, 8a (Upper pharyngeal bone); Via Roma, Genova [resp.] Zinola (Savona), Liguria, [Italy]; Pliocene.
- 1950 *Labrodon pavimentatum* GERVAIS – ZBYSZEWSKI & MOITINHO D’ALMEIDA: 375, 411, pl. 13, figs 239–240 (“Fragmento de placa dentária”), and 241 (“Placa faringiana superior”); Santa Maria, Acores; Vindoboniano [Miocene]; 384 [and] 387 [and] 390–391: Ilha Santa Maria, Acores; Vindoboniano [Miocene].
- 1954 *Labrodon pavimentatum* GERVAIS – SERRALHEIRO: 88, 100, 107, tab. 1, 118, pl. 4, fig. 118, (Pharyngeal bone); Aeroporto da Portela, Portugal; Helveciano Vc, Vindoboniano [Lower Miocene].
- 1954 *Labrodon pavimentatum* GERVAIS – SERRALHEIRO: 88; Ilha de Sta. Maria – Acores; Vindoboniano [Lower Miocene].
- 1957 *Labrodon pavimentatum* GERVAIS – LERICHE: 48–49, pl. 4, figs 15–16 (Upper pharyngeal bones), and 17–18 (Lower pharyngeal bone); Cotes-du-Nord: Le Quiou, Saint-Juval, Tréfumel. – Ille-et-Vilaine: Chartres-la-Poterie (La Chaussérie), Gahard, Saint-Grégoire. – Indre-et-Loire: Louans, Paulmy. – Loire-Inférieur: Aigrefeuille, le Landreau (le Pigeon Blanc), Noyal-sur-Brutz. – Maine-et-Loire: Chaz,-Henry, Genneteil, Noyant-la-Gravoyère, Noyant-Méon, Saint-Saturnin (le Haguineau) [NW France]; Savignéen [resp.] Pontilévien – Savignéen, [Miocene].

- 1960 *Labrodon pavimentatum* GERVAIS, 1857 – PAWLOWSKA: 425, 427, 432, pl. 3, fig. 17 (Upper pharyngeal bone); Pinczow, [Poland; Badenien] Middle Miocene.
- 1968 *Labrodon pavimentatum* GERVAIS, 1857 – JONET: 212–213, 220, pl. 1, fig. 1 a–c (Lower pharyngeal bone); Portela de Sacavém, Portugal; Helvetien Vc, Miocene).
- 1969 *Labrodon pavimentatus* GERVAIS 1859 – MENESINI: 44–45, 57, pl. 6, fig. 17 (Pharyngeal bone, fragment); Livello ad Aturia, [near Otranto, Italy]; Miocene.
- 1969 *Labrodon pavimentatus* – MENESINI: 57; Miocene in genere [and] Elveziano + Tortoniano [and] Pliocene.
- 1969 *Labrodon pavimentatum* GERVAIS, 1857 – CAPPETTA: 233–234, pl. 21, fig. 5 (? Upper pharyngeal bone, fragment); Loupian [SW Montpellier, South France; Miocene].
- 1969 *Labrodon pavimentatum* – CAPPETTA: Tab. IV + V; Herault [and] Bassin du Rhone [and] Bassin d'Aquitaine [and] Ouest de la France [France, and] Italie [and] Portugal [and] Allemagne [FRG]; Miocene moyen + sup.
- ? 1970 *Labrodon* GERVAIS – BALUK: 113 [and] 151 (“single pharyngeal teeth of teleosts and probably belong to the genus *Labrodon* GERVAIS”); Niskowa, near Nowy Sacz [Poland]; Lower Tortonian [Lower Badenien, Middle Miocene].
- 1973 *Labrodon pavimentatus* P. GERVAIS 1859 – BAUZÁ & PLANS: 108–109, 128, pl. 7, fig. 48 (? Lower pharyngeal bone); Ca'n Mayol (Olérdola), Balear [Spain]; Vindoboniense [Miocene].
- 1977 *Labrodon pavimentatus* GERVAIS 1857 – LANDINI: 234–241, pl. 1, figs 1–6 (Lower pharyngeal bones), fig. 7a–b (Upper pharyngeal bone); Piemonte, Toscana, Puglia, Sicilia [Italy]; Miocene; Liguria, Emilia, Toscana [Italy]; Pliocene.
- 2007 *Labrodon* GERVAIS 1857 – MARSILI *et al.*: pl. 2, fig. 7 (Montagna della Maiella, Italy; Early Miocene).

Type locality: Montpellier, France.

Age of type species: Miocene.

Type material: 1 lower pharyngeal bone.

Distribution of the type species:

Miocene: Elveziano: France; Balearic Islands. – Badenien: Poland. – Tortoniano: Balearic Islands.

Miocene, general: Emilia and Tuscany, Italy; Portugal.

Pliocene: Liguria, Emilia, Tuscany, Italy; France.

Remarks: Already SIMONELLI (1889) was of the opinion that *Plinthodus pisani* COSTA, 1863 and *Pharyngodopilus alsinensis* COCCHI, 1864 should be placed in synonymy with *Labrodon pavimentatum*.

Subsequently LERICHE (1906a: pp. 315–318) also STEFANO (1909: pp. 630), MENESINI (1969: p. 44) and LANDINI (1977: pp. 234–236) all placed the following species into synonymy with *L. pavimentatum*, the type species of *Labrodon*:

Abbas, *africanus* in SAUVAGE [non: *Pharyngodopilus africanus* COCCHI], *alsinensis*, *bazini*, *bourgeoisii* resp. *bourgeoisii*, *chantrei*, *cocchii*, *crassus*, *dilatatus*, *edwardsius*, *Gaudryi* (p.p.), *haueri* in COCCHI 1864, SAUVAGE, *etc.* [non: *Phyllodus haueri* MÜNSTER, *multidens* in SAUVAGE, *etc.* [non: *Phyllodus multidens* MÜNSTER], *poliodon* resp.

polyodon, *quenstedti*, *rhodonum*, *sacheri*, *soldanii*, *superbus* of the genera *Labrodon*, *Nummopalatus* resp. *Nummapalatus*, *Pharyngodopilus*, and *Sphaerodus*.

But according to the rules of nomenclature the valid species is probably *Sphaerodus poliodon* *i. e.*, *polyodon* SISMONDA, 1846. We have not changed this herein but further consideration is warranted.

Additional species:

? ***Pharyngodopilus Abbas*** – COCCHI 1864: 72, pl. 4, fig. 4, 4a (Tooth plate, fragment); Touraine [NW France]; Miocene.—*Pharyngodopilus abbas*, COCCHI – GERVAIS 1867–69: 235; faluns dans la Touraine [NW France; Miocene].—*Nummopalatus abbas*, COCCHI sp. – SAUVAGE 1875a: 627; Faluns de Touraine [NW France; Miocene]. Remarks: Already placed by LERICHE (1906a: p. 316) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Pharyngodopilus Africanus – COCCHI 1864: 68–70, pl. 4, fig. 7, 7a (Upper pharyngeal bone), pl. 4, fig. 8, 8a (Lower pharyngeal bone); dalla Costa occidentale d’Affrica [sic; resp.] Isole Canarie.—*Nummopalatus Africanus*, COCCHI sp. – SAUVAGE 1875a+b: 627–628, 642, pl. 22, fig. 15, 15a (Lower pharyngeal bone), fig. 14 (Pharyngeal bone, fragment); Faluns de St-Grégoire [NW France; Miocene].—*Labrodon africanus* – SAUVAGE 1880: 38–39; Faluns de Bretagne, [NW France; Miocene].—*Nummopalatus africanus* (COCCHI) – ROTHPLETZ & SIMONELLI 1890: 726 (“Dentalplatte”); La Vista, Gran Canaria; [Neogene].—*Labrodon africanus* (COCCHI), 1864 – JONET 1968: 216–218, 220, pl. 1, figs 5 a–c, 6 a–c (Right upper pharyngeal bone); Portela de Sacavém, Portugal; Helvétien Vc, Miocene.

Remarks: Already placed by LERICHE (1906a: p. 315) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Pharyngodopilus Alsinensis – COCCHI 1864: 74–77, pl. 4, fig. 15, 15a (Lower pharyngeal bone), pl. 5, fig. 3 (Upper pharyngeal bone), figs 4, 4a, 9, 9a, 10 (Lower pharyngeal bone); Pliocene d’Orciano (fig. 9), Miocene dell’isola di Pianosa (fig. 10), Pliocene di Montalcino, [and] Pliocene di Laiatico [Italy; Miocene and Pliocene].—*Nummopalatus Alsinensis*. COCCHI – LAWLEY 1876: 73 (diverse placche dentarie); Orciano, [Tuscany, Italy; Pliocene].—*Labrodon alsinensis* – SAUVAGE 1880: 34–36, 44, pl. 2, figs 2, 3, 3a, 4 (Lower pharyngeal bone); La Chausserie, Bretagne, [NW France; Miocene].—*Pharyngodopilus alsinensis* COCCHI – SIMONELLI 1880: 211; San Quirico d’Orcia [Tuscany, Italy; Pliocene].—*Pharyngodopilus alsinensis* COCCHI – VINASSA DE REGNY 1899: 84 (Lower pharyngeal bone, fragment); Sabbie gialle di Pieve del Pino; Argille di Monte San Giorgio, Bolognese, [Italy]; Pliocene.—*Nummopalatus alsinensis* COC. – BASSOLI 1907: 41 (“Pezzo inferiore e uno dei superiori”); Montese, Montegibbio, S. Giorgio, Pieve del Pino, regione Emiliana, [Italy; Neogene].

Remarks: Already given by SIMONELLI (1889: p. 212) and LERICHE (1906a: pp. 315, 317) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Nummopalatus Bazini, SAUVAGE – SAUVAGE 1875a+b: 625, 642, pl. 22, fig. 16 (Pharyngeal bone); Faluns du Quiou, près Rennes, [NW France; Miocene].—*Labrodon Bazini* – SAUVAGE 1880: 39; Faluns de Bretagne [NW France; Miocene].

Remarks: Already placed by LERICHE (1906a: p. 317) in synonymy with *Labrodon pavementatum*.

? ***Nummopalatus belgicus*** DAIMERIESM – DAIMERIESM 1892: XV; Saint-Gilles [Belgium]; Système laekenien [Middle Eocene].

? ***Pharyngodopilus Bourgeoisii*** – COCCHI 1864: 71–72, pl. 4, fig. 5, 5a (Tooth plate, fragment); Touraine [NW France]; Miocene (Fahluns [sic]).

Pharyngodopilus Bourgeoisii – COCCHI 1864: see also above.—*Pharyngodopilus Bourgeoisii*, COCCHI – GERVAIS 1867–69: 235; faluns dans la Touraine [NW France; Miocene].—*Nummopalatus Bourgeoisii*, COCCHI sp. – SAUVAGE 1875a+b: 626–627, 642, pl. 22, fig. 18 (Pharyngeal bone), Faluns de Quiou, près de Rennes, France [Miocene]; pl. 23, fig. 6 (Upper pharyngeal bone); de Geneteil, France [Miocene].—*Nummopalatus Bourgeoisii*. COCCHI – LAWLEY 1876: 73 (“Due placche furono”); Orciano, [Tuscany, Italy; Pliocene].—*Labrodon Bourgeoisii* – SAUVAGE 1880: 40–41; Faluns de Touraine, faluns de Quiou, près de Rennes, de Geneteil et de Charcé (Maine-et-Loire) [NW France; Miocene].

Remarks: SAUVAGE (1880) was of the opinion that *Ph.* resp. *N. abbas* should be placed in synonymy with *L. bourgeoisii*. – Already placed by LERICHE (1906a: pp. 316, 317, 318) in synonymy with *Labrodon pavementatum* GERVAIS, 1857.

Nummopalatus britannus, SAUVAGE – SAUVAGE 1875a+b: 627, 642, pl. 23, fig. 11, 11a (Lower pharyngeal bone); Faluns de Bretagne [NW France; Miocene].—*Labrodon britannus* – SAUVAGE 1880: 36 (“plaque pharyngienne inférieur”); Faluns de Bretagne [NW-France; Miocene].

Pharyngodopilus Canariensis – COCCHI 1864: 70–71, pl. 4, fig. 6, 6a (Upper pharyngeal bone); Isole Canarie; Miocene.

Odax carolinensis – LEIDY 1856: 396 (“portions of jaws and pharyngeal bones, with teeth”); Ashley River, South Carolina [USA].—*Pharyngodopilus carolinensis* – LEIDY 1877: 256–257, 261, pl. 34, fig. 19 (Lower pharyngeal bone), fig. 21 (Upper pharyngeal bone), ? : fig. 22 (“A mutilated upper maxillary with part of the dental armature”); ? : fig. 23–24 (“Dentale armature of two mandibles”); South Carolina [USA]; Phosphate Beds [Miocene].—*Labrodon carolinensis* LEIDY – LERICHE 1942: 93–94 (see LEIDY 1877); Caroline du Sud [USA]; “Ashley River Sands” et “Ashley phosphate beds”, Miocène; 98: Caroline du Sud; Miocène.

Remarks: For pl. 34, fig. 20: LEIDY (1877) stated “if not another species”. We are of the opinion that pl. 34, fig. 20 of LEIDY (1877) should not be identified as *Ph. carolinensis* and therefore we put this specimen separately in the list below as *Ph.* sp. LERICHE (1942: pp. 93–94) was of the opinion that *Labrodon carolinensis* should probably be placed in synonymy with *Labrodon pavementatum*, but we do not agree with LERICHE

(1942) because fig. 19 given by LEIDY (1877) shows a lower pharyngeal bone with irregularly distributed teeth; the teeth in the middle are not longitudinally elongated like in *L. pavimentatum*; perhaps fig. 20 in LEIDY (1877) only should be placed in synonymy with *Labrodon pavimentatum*.

Nummopalatus Chantrei, SAUVAGE – SAUVAGE 1875a+b: 618–619, 642, pl. 23, fig. 10 (Lower pharyngeal bone); Faluns de Bordeaux [W France; Lower Miocene].—*Labrodon Chantrei* – SAUVAGE 1880: 32–33, 44, pl. 2, fig. 6, 6a (Lower pharyngeal bone); faluns de Bordeaux [and] a Saint-Grégoire, Bretagne [NW France; Miocene].

Remarks: Already placed by LERICHE (1906a: p. 315) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Nummopalatus Cocchii, SAUVAGE – SAUVAGE 1875a+b: 623–624, 642, pl. 22, fig. 10 (Pharyngeal bone); Faluns de La Chaussairie, près Rennes [NW France; Miocene].—*Labrodon Cocchi* – SAUVAGE 1880: 39 (“piles dentaires et par le présence de cinq grandes dents a face masticante”; resp. “plaque pharyngienne”); Chausserie, Bretagne [NW France; Miocene].

Remarks: Already placed by LERICHE (1906a: p. 317) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

? ***Platylaemus Colei***, new [resp. only] *Platylaemus* – DIXON 1850: 205, 112, V, VI, Pl 10, fig. 23 (? Upper pharyngeal bone, fragment), pl. 12, fig. 11 (“Dental plate”), figs 12–13 (“Dental plates”; 2 fragments of the Lower pharyngeal bone); Bracklesham, Sussex [England; Middle to Upper Eocene].—*Platylaemus colei*, DIXON – WOODWARD 1901: 551 (Lower and upper pharyngeal bone); Sussex [England]; Middle Eocene.

Pharyngodopilus crassus – COCCHI 1864: 79–80, pl. 4, fig. 14, 14a (Lower pharyngeal bone), pl. 5, fig. 5; pl. 6, fig. 5, 5a (Upper pharyngeal bones); Orciano [and] non conosco la provenienza [Italy; Pliocene].—*Nummopalatus crassus*. COCCHI – LAWLEY 1876: 73 (“Due placche dentarie inferiore e altre due superiori”); argille di Orciano, [Tuscany, Italy; Pliocene].

Labrodon confertidens, sp. nov. – CHAPMAN & PRITCHARD 1907: 65–66, 72, pl. 5, fig. 7 (Lower pharyngeal bone); Grange Burn near Hamilton, Western Victoria, Australia; Base of the Kalimnan [Lower Pliocene, see CHAPMAN 1918: 27].—*Trygon* [resp.] *Trigon ensifer*, DAVIS – DAVIS 1888: 37–38, 48, Tab. [in part]; Wekpass [and] Broken River, New Zealand; [Miocene].—*Labrodon confertidens* CHAPMAN and PRITCHARD – CHAPMAN 1918: 27, 30, 32, pl. 9, fig. 14 (pharyngeal bone); Weka Pass; Broken River [Trelis-sick Basin, New Zealand]; Tertiary (Miocene).—*Labrodon confertidens*, CHAPMAN and PRITCHARD – CHAPMAN & CUDMORE 1924: 143; Beach at Portland; Victoria, [Australia], ? Janjukian, [? Oligocene]; 154 Portland Beach (? Janj) [? Oligocene]; Grange Burn, Victoria, [Australia]; Kal. (&? Janj.) [Pliocene, &? Oligocene]; 155–156, Victoria [Australia]; Janjukian to the Kalimnan [Oligocene to Pliocene].

Labrodon depressus, sp. nov. – CHAPMAN & PRITCHARD 1907: 66, 72, pl. 5, figs 8–9 (Lower pharyngeal bone); Beaumaris, Port Phillip, Australia; Kalimnan (base) [Lower

Pliocene, see CHAPMAN 1918: 27].—*Trygon* [resp.] *Trigon ensifer*, DAVIS – DAVIS 1888: 37–38, 48, tab. [in part], pl. 6, fig. 13, 13a–b (pavement teeth); Colebridge Gully [Trelissick Basin, New Zealand; Miocene, see CHAPMAN 1918: 27].—*Labrodon depressus* CHAPMAN and PRITCHARD – CHAPMAN 1918: 27, 30, pl. 6, fig. 13, 13a–b (Pavement teeth); Coleridge Gully, Trelissick Basin, New Zealand; Tertiary (Miocene).—*Nummopalatus depressus*, CHAPMAN and PRITCHARD sp. – CHAPMAN & CUDMORE 1924: 143–144, 154, 156, 162, pl. 11, fig. 43 (Lower pharyngeal bone); Grange Burn, near Hamilton, Victoria [and] Beaumaris, [Australia]; Kalimnan [Pliocene]; also from Coleridge Gully, Trelissick Basin, New Zealand; Miocene.

Pharyngodopilus dilatatus – COCCHI 1864: 77–79, pl. 5, figs 1, 2, 2a, 8; pl. 6, fig. 4 (Lower pharyngeal bones); Pliocene: Bagnaia presso San Quirico, Sassuolo nell'Emilia, [and] Laiatico; Miocene: San Frediano o di Casciana [Italy; Miocene and Pliocene].—*Nummopalatus dilatatus* COC. – BASSOLI 1907: 41; Montegibbio, regione Emiliana, [Italy]; miocene.—?: *Labrodon* sp. [cfr. *L. dilatatus* COCCHI sp.] – STEFANO 1909: 557, 633–635 (“due placche faringee inferiori”); Orciano, [Tuscany, Italy]; Pliocene.
Remarks: Already placed by LERICHE (1906a: p. 315) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Nummopalatus Edwardsius sp. nov. – ROUAULT 1858: 102 (“petites plaques dentaires”); S.-Juvat, S.-Grégoire, près Rennes [NW-France; Savignéen; Miocene].
Remarks: The type species of *Nummopalatus*. Was already placed by LERICHE (1906a: p. 315) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Trygon [resp.] ***Trigon ensifer***, DAVIS: see above under *Labrodon depressus*.

Labrodon [...] ***ex Pisanii***: see below in *Labrodon superbus*.

Nummopalatus Gaudryi, SAUVAGE – SAUVAGE 1875a+b: 619–621, 642, pl. 22, figs 5, 5a, (Lower pharyngeal bone), 5b (Pharyngeal bone), 5c, 6 (Upper pharyngeal bone); Faluns de Dax [SW France; Lower Miocene].—*Nummopalatus Gaudryi*. SAUVAGE – LAWLEY 1876: 74–75 (“Una placcha inferiore ed altre due delle superiori”); Orciano, [Tuscany, Italy; Pliocene].—*Labrodon Gaudryi* SAUVAGE – PRIEM 1912: 241 (“Pharyngiens inférieurs”); Dax, [SW France]; Burdigalien [Lower Miocene].
Remarks: Already placed by LERICHE (1906a: p. 317) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Phyllodus Haueri. – MÜNSTER 1846: 6–7, 28, 66, pl. 1, fig. 1a–c (Upper pharyngeal bone), 1d (isolated teeth from ? the pharyngeals or oral teeth, eventually also of Sparidae); Neudörfl [Devinska Nova Ves (= Neudorf an der March), [Slovakia]; Middle-Upper Badenien, Middle Miocene].—p.p. *Labrus* – MEYER 1846: 471; Wiener Becken [Slovakia; Badenien, Middle Miocene].—*Phyllodus Haueri* MÜNSTER – HÖRNES 1848: 14, Nr. 44; Neudorf [a.d. March = Devinska Nova Ves, [Slovakia]; Badenien, Middle Miocene].—*Pharyngodopilus Haueri* MÜNST. – COCCHI 1864: 67–68, pl. 4, fig. 13 (Upper pharyngeal bone); dal bacino di Vienne [Austria; Middle Miocene].—*Nummopalatus Haueri*, DE MÜNSTER sp. – SAUVAGE 1875a+b: 621–623, 642, pl. 22, fig. 19 (Upper pharyngeal bone); au Quiou, près de Rennes, France; pl. 23, fig. 4 (Upper pharyngeal

bone); Molasse de Magnard, [France]; fig. 5 (Lower pharyngeal bone); St-Grégoire près de Rennes [NW France; Miocene].—*Nummopalatus Haueri*. MÜNSTER – LAWLEY 1876: 73; argille del Volterrano e dai cercatori in Orciano; [Tuscany, Italy; Pliocene].—*Labrodon Haueri* – SAUVAGE 1880: 30–32, 44, pl. 2, fig. 7 (Lower pharyngeal bone), fig. 8 (Pharyngeal bone); Quiou, Saint-Grégoire [and] La Chausserie, environs de Rennes, Bretagne; Faluns [NW France; Miocene].—*Labrodon Haueri* v. MÜNSTER sp. – SEGUENZA 1900: 464, 469, 512, pl. 6, fig. 9 (“placca superiore destra”); Nizza, Provincia di Messina, [Sicily, Italy]; Miocene medio (Elveziano) [Middle Miocene].—*Labrodon (Phyllodon) Haueri* MÜNST. – SCHUBERT 1906: 695; Wiener Becken [Slovakia; Badenien, Middle Miocene].—?: *Labrodon* aff. *haueri* (DE MÜNSTER), 1846 – JONET 1968: 213–214, 220, pl. 1, fig. 2 a–b (Right upper pharyngeal bone); Portela de Sacavém, Portugal; Helvétien Vc, Miocene.—*Labrodon haueri* (MÜNSTER.) – SCHULTZ in BRZOBHATÝ & SCHULTZ 1978: 445 (the quotation of MÜNSTER 1846 only).—*Labrodon haueri* (MÜNSTER, 1846) – SCHULTZ 2013: 338–339 (Devinska Nova Ves, [Slovakia]: Badenium, [Middle-Miocene]).

Remarks: The citations to this material in SAUVAGE (1875a+b and 1880) were placed by LERICHE (1906a: p. 317) as *Nummopalatus Haueri* (non *Phyllodus Haueri*, MÜNSTER) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Nummopalatus heterodon, SAUVAGE – SAUVAGE 1875 a+b: 629–630, 642, pl. 22, figs 11–13; pl. 23, figs 7, 8, 8a (Pharyngeal bone); Faluns de Bretagne [NW France; Miocene]; fig. 8, 8a (Pharyngeal bone); Faluns de Mimbaste, près de Dax [W France; Lower Miocene].—*Labrodon heterodon* – SAUVAGE 1880: 37; faluns de Mimbaste, près de Dax [SW France; Lower Miocene].—*Labrodon heterodon* (SAUVAGE, 1875) – SCHULTZ 2013: 339 (Atlantic Province: Miocene).

Labrus Ibbetsoni – AGASSIZ 1833–1843, 5/1: 116 (“pharyngien inférieur”); Chaux-de-Fonds, Molasse suisse [? Ottnangien; Lower Miocene].—*Labrus Ibbertsoni* AG. – GIEBEL 1848: 103; Schweizer Molasse [non: Wiener Becken. – Switzerland; Lower Miocene].—*Labrus Ibbetsoni*, AGASS. – GERVAIS 1857: 513; molasse de la Suisse [Switzerland; Lower Miocene].—*Labrus Ibbetsoni* L. AGASSIZ – LERICHE 1927a: 100; Molasse Suisse [Switzerland]; Miocene [Lower Miocene].

Remarks: nomen nudum – already WOODWARD (1901: p. 540) noted it as “undescribed”, and LERICHE (1927a: p. 100) stated that this name should be cancelled in the fish list of the Molasse of Switzerland].

Pharyngodopilus Lepsii. n.sp. – WITTICH 1898: 42–44, pl. 1, fig. 5 (Upper and lower pharyngeal bone); in der nächsten Nähe von Alzey, theils an der Wirtsmühle, theils bei Weinheim, Mainzer Becken, [FRG]; aus dem mitteloligocänen Meeressand [Middle Oligocene].—*Labrodon lepsii*, WITTICH – WEILER 1922: 107, 127 (“schlecht erhaltener” ... “Schlundknochen”); Weinheim [resp.] Meeressand von Alzey, Mainzer Becken [FRG; Middle Oligocene].

Phyllodus multidentis – MÜNSTER 1846: 7–9, 28, 66, pl. 1, fig. 5a–c (Lower Pharyngeal bone); Neudörfl [Devinska Nova Ves (= Neudorf an der March), [Slovakia]; Middle-Upper

Badenien, Middle Miocene].—p.p. *Labrus* – MEYER 1846: 471; Wiener Becken [Slovakia; Badenien, Middle Miocene].—*Phyllodus multidentis* MÜNSTER – HÖRNES 1848: 14, Nr. 45; Neudorf [an der March = Devinska Nova Ves, [Slovakia]; Badenien, Middle Miocene].—*Pharyngodopilus multidentis* MÜNST. – COCCHI 1864: 63–67, pl. 4, fig. 9 (Lower pharyngeal bone), figs 10–12 (Upper pharyngeal bone); Vienna [Austria; Middle Miocene].—*Nummopalatus multidentis*, DE MÜNSTER – SAUVAGE 1875a+b: 629, 642, pl. 23, fig. 9 (Lower pharyngeal bone); Faluns de la Bretagne [NW France; Miocene].—*Labrodon multidentis* – SAUVAGE 1880: 38 (“plaque inférieure”); Bretagne, [NW France; Miocene].—*Labrodon multidentis* v. MÜNSTER sp. – SEGUENZA 1900: 464, 469, 513–514, pl. 6, fig. 8 (?: “placca superiore”); Nizza, Provincia di Messina, [Sicily, Italy]; Miocene medio (Elveziano) [Middle Miocene].—*Labrodon (Phyllodon) multidentis* MÜNST. – SCHUBERT 1906: 695; Wiener Becken [Slovakia; Badenien, Middle Miocene].—*Labrodon multidentis* MÜNSTER sp. – PRIEM 1912: 230; Loupian, [Hérault, S France]; Helvétien, [Miocene].—*Nummopalatus multidentis* MÜNST. sp. – SCHLOSSER 1923: 142–143, fig. 245 a (Lower pharyngeal bone), b (Upper pharyngeal bone); Neudörfel [= Neudorf an der March = Devinska Nova Ves, Slovakia]; Miocän [Badenien, Middle Miocene].—*Nummopalatus multidentis*, de Münster – ROCABERT 1934: 100–101, 105, pl. 5, figs 7–8 (Lower pharyngeal bone, fragment); Olèrdola [Catalonia, E-Spain]; tortonia [Upper Miocene].—*Labrodon multidentis*, MÜNSTER – BAUZÁ RULLÁN *et al.* 1963: 235–236, pl. 13, fig. 1 (Upper pharyngeal bone); Santa Margarita, [Mallorca, Spain]; Vindoboniense, [Miocene].—*Labrodon multidentis* DE MÜNSTER 1846 – BAUZÁ & PLANS 1973: 109–110, 128, pl. 7, figs 49, 50, 53 (Upper pharyngeal bones), 51–52 (Lower pharyngeal bones); Can Mayol (Olérola) [and] Mas Granell (Vilafranca), Neogeno Catalano balear [Spain]; Mioceno.—*Labrodon multidentis* (DE MÜNSTER), 1846 – JONET 1968: 215–216, 220, pl. 1, figs 3a–c, 4a–c (Lower pharyngeal bone); Portela de Sacaém, Portugal; Helvétien Vc, Miocene.—*Labrodon multidentis* (MÜNST.) – SCHULTZ in BRZOBOHATÝ & SCHULTZ 1978: 445 (the quotation of MÜNSTER 1846 only).—Labridae indet. – SCHULTZ, BRZOBOHATÝ & KROUPA 2010: 495, pl. 3, fig. 12a, b (Kienberg bei Mikulov, CFR, Middle Badenian [Middle Miocene].—p.p. Labridae div. indet. gen. et spec. – SCHULTZ 2013: 336–337 (Kienberg bei Mikulov, CFR, Middle Badenian [Middle Miocene].—*Labrodon multidentis* (MÜNSTER, 1846.) – SCHULTZ 2013: 339–340 (Kaisersteinbruch [Austria] + Devinska Nova Ves, [Slovakia]; Badenium [Middle Miocene], pl. 69, fig. 2a, b (Retznei, Steiermark: Badenium [Middle Miocene].

Remarks: SAUVAGE (1875a+b) and (1880) put *Phyllodus subdepressus* MÜNSTER into the synonymy of *N. multidentis*. – LERICHE (1906a: p. 315) put the citations of *Ph. multidentis* given by SAUVAGE (1875a+b) and (1880) into the synonymy of *Labrodon pavimentatum* GERVAIS, 1857.

Labrodon multidentis*, var. *Pisanii (COSTA): see above in *Labrodon pavimentatum*

Remarks: Already SIMONELLI (1889) was of the opinion that *Pisani* (COSTA) should be placed in synonymy with *Labrodon pavimentatum*.

Nummopalatus cf. multidentis MÜNSTER – SURARU, STRUSIEVICI & LASZLO 1980: 178–179, pl. 1, figs 2–3 (Lower pharyngeal bone); “an der Wehre”, Cluj-Napoca [Transylvanian

Basin, Romania]; Eozän.—*Lachnolaimus multidentis* (MUNSTER) – DICA 2002: 42, pl. I, figs 3, 4 (Somes Dam, (Cluj Napoca area) [Romania]: Cluj Limestone [Late Eocene]. – Turnu Rosu (Sibiu district) [Romania]: Nisului Valley Formation [Late Eocene].

? *Platylaemus nigeriensis* E.I.WH. – CASIER in DARTEVELLE & CASIER 1959: 398 (no indication); Nigeria; Eocene.

Labrodon [...] *Pisanii*: see above in *Labrodon multidentis*, var. *Pisanii*, or below in *Labrodon superbus*.

Sphaerodus poliodon E.SISMD. – E. SISMONDA 1846: 19–21, 85, 87, pl. 1, figs 5–7 (Tooth plate, fragment); nell'arenaria miocenica del colle di Torino [Italy; Middle Miocene].—*Sphaerodus poliodon* E.SISM. – SISMONDA 1861: 22; Aren. serpent. mioc.med.; Torino [Italy; Middle Miocene].—*Pharyngodopilus polyodon* – COCCHI 1864: 61–62, pl. 4, fig. 3, 3a, 3b (Tooth plate, fragment); Miocene del colle di Torino [Italy; Middle Miocene].—*Nummopalatus polyodon*, E. SISMONDA sp. – SAUVAGE 1875a: 629 (“fragment de plaque inférieure”); Faluns de Bretagne [NW France; Miocene].—*Labrodon polyodon* – SAUVAGE 1880: 38; faluns de Bretagne [NW France; Miocene].

Pharyngodopilus Quenstedti – PROBST 1874: 277–279, 298, pl. 3, fig. 1 (nearly complete upper pharyngeal bone), fig. 2 (Lower pharyngeal bone); Molasse von Baltringen [Württemberg, FRG; Obere Meeresmolasse, Lower Miocene].—?: *Labrodon Quenstedti* PROBST – SCHUBERT 1906: 695; Wiener Becken [Slovakia and E-Austria; Badenien, Middle Miocene].—*Labrodon (Phyllodon) quenstedti* (PROBST, 1874.) – SCHULTZ 2013: 340 (Zogelsdorf [Austria] + Western Paratethys: Lower Ottnanium [Lower Miocene].

Nummopalatus Rhedonum, SAUVAGE – SAUVAGE 1875a+b: 624, 642, pl. 22, fig. 17 (? Upper pharyngeal bone); Faluns de Bretagne [NW France; Miocene].—*Nummopalatus Rhedonum*. SAUVAGE – LAWLEY 1876: 74 (“una placcha superiore”); Orciano, [Tuscany, Italy; Pliocene].—*Labrodon rhedonum* – SAUVAGE 1880: 39–40; Bretagne [NW France; Miocene].
Remarks: Already placed by LERICHE (1906a: p. 317) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Nummopalatus Sacheri, SAUVAGE – SAUVAGE 1875a+b: 624–625, 642, pl. 22, figs 7, 8, 9 (? Upper pharyngeal bones); Saint-Grégoire, près Rennes, [NW France; Miocene].—*Nummopalatus Sacheri*. SAUVAGE – LAWLEY 1876: 74 (“Tre placche superiori”); Orciano, [Tuscany, Italy; Pliocene].—*Labrodon Sacheri* – SAUVAGE 1880: 36–37; Saint-Grégoire [and] La Chausserie, Bretagne, [NW France; Miocene].
Remarks: Already placed by LERICHE (1906a: p. 317) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

Pharyngodopilus Sellae – COCCHI 1864: 81–82, pl. 5, fig. 11, 11a (Lower pharyngeal bone); Pianosa [Italy]; Miocene.—*Nummopalatus Sellae*. COCCHI – LAWLEY 1876: 74 (“una placca”); Orciano Pisano, [Tuscany, Italy; Pliocene].—*Nummopalatus Sellae* COCCHI sp. – SIMONELLI 1889: 213 (“placca inferiore” [and] “due placche faringee superiori”); Isola Pianosa [near Elba, Italy]; Calcari pliocenici.

Labrodon sinhaleyus sp. nov. – DERANIYAGALA 1937: 363–364, fig. 7 (Pharyngeal bone); Ceylon [Sri Lanka]; Miocene.

Pharyngodopilus Soldanii – COCCHI 1864: 82–86, pl. 5, fig. 6; pl. 6, fig. 6 (Upper pharyngeal bones); Toscana [and] Sicily [Italy].—Glos[sopetra] ad similitudinem lapidis qui ovarius, oolites, amites, vel etiam illius qui Pisolithus dicitur – SOLDANI 1780: 126, pl. 15, fig. 77 B, C, D; (Lower pharyngeal bone); Toscana [Italy; Pliocene].—*Pharyngodopilus Soldanii* COCCHI – SIMONELLI 1880: 211; San Quirico d’Orcia [Tuscany; Italy; Pliocene].
Remarks: Placed by LANDINI (1977: p. 242) in synonymy with *Labrodon superbus* COCCHI, 1864.

Labrodon – GERVAIS 1867–69: 237, 238, pl. 48, fig. 1 (Pharyngeal bone); Castries, Hérault [S France]; Miocene.

Labrodon ? – GERVAIS 1867–69: 240, pl. 46, figs 3, 4 (Pharyngeal bone); Martigues (Bouches-du-Rhone) [France]; terrains miocènes.—*Labrodon ?* sp. – PRIEM 1912: 220 (“*plaque pharyngienne supérieur figurée par P. GERVAIS 1867–69 (Zool. Pal. gén., p. 240, pl. XLVI, figs 3–4)*”); Mollasse des Martigues (Bouches-du-Rhone) [SE France]; Miocène.

Labrodon sp.: Pharyngodopilus carolinensis [...] if not another species – LEIDY 1877: 257, 261, pl. 34, fig. 20 (Lower pharyngeal bone); South Carolina [USA]; Phosphate Beds [Miocene].

Remarks: See also above for *Ph. carolinensis*.

Labrodon sp. (cfr. L. dilatatus COCCHI sp.) – STEFANO 1909: 557, 633–635, etc.: see above in *Labrodon dilatatus*.

Labrodon sp. – STEFANO 1909: 553, 557, 636 (“*frammenti di placche faringee superiori ed inferiori*”); Orciano e San Quirico, [Tuscany, Italy]; Pliocene.

Labrodon sp. – PRIEM 1912: 241 (“*Pharyngien inférieur*”); Rimbez, [SW France]; Burdigalien, [Lower Miocene].

Labrodon sp. – PRIEM 1914: 125, pl. 3, fig. 14 (“*pharyngien supérieur*”); Saint Médard-en-Jalle (Gironde) [SW France]; Burdigalien [Lower Miocene].

Labrodon sp. – LERICHE 1927a: 100 (“*fragment de pharyngien supérieur*” [not figured]); La Chau, près Sainte-Croix (canton de Vaud), [Switzerland]; Burdigalien [Lower Miocene].

Remarks: See also above for *Labrus ibbetsoni*.

Labrodon sp. – BRZOBOHATÝ & SCHULTZ 1971: 735–736, pl. 7, fig. 6 (Upper pharyngeal bone, fragment); Zogelsdorf [near Eggenburg, Lower Austria; Eggenburgien, Lower Miocene].—*Labrodon heterodon* SAUV. – DE ALESSANDRI & SCHAFFER 1925: 40, 41 (Zogelsdorf [near Eggenburg, Austria]; Eggenburgium [Lower Miocene].—*Labrodon* sp. (2) – SCHULTZ 2013: 341 (Zogelsdorf [near Eggenburg, Austria]; Eggenburgium [Lower Miocene]).

? **Labrodon sp.** – PRIEM 1908: 101; Sables de Cuise-la-Motte, Bassin Parisien [France]; Ypresien [Lower Eocene].

Remarks: Also PRIEM (1908) revised the specimen of figs 31, 31a of plate 68 published by GERVAIS (1848–52). – see also above the remarks for *Nummopalatus* sp.

? *Labrodon* sp. *indet.* – WHITE 1931: 98 (“the fragment of a small plate”); Dulwich, S London, Surrey [United Kingdom]; Woolwich Beds, Landenian [Upper Paleocene].

Remarks: WHITE (1931) wrote: “*It is typical of the genus*” [*Labrodon*] “*but quite indeterminate*”.

? *Nummopalatus* sp. – SAUVAGE 1875a: 617 (“un fragment de plaque pharyngienne inférieur”); France; un niveau inférieur au Miocène.

Remarks: SAUVAGE (1875a: p. 617) was of the opinion, that the specimen of figs 31, 31a on plate 68 of GERVAIS (1848–52), called *Phylloodus*, comes from “*un niveau inférieur au Miocene*” and should be called *Nummopalatus* sp.

? *Nummopalatus* sp. – BASSANI 1879: 53–54, 70, pl. 5, fig. 16 (Fragmentary pharyngeal bone); Gahard, Ille-e-Vilaine [France]; miocene medio.

Nummopalatus sp. – BRZOBHATÝ & SCHULTZ 1971: 736, pl. 7, fig. 5a–c (Lower pharyngeal bone); Kühnring [near Eggenburg, Lower Austria; Eggenburgien, Lower Miocene].—*Trochocopus* sp. – DE ALESSANDRI & SCHAFFER 1925: 40, ? 41 (Kühnring bei Eggenburg [Austria]: Eggenburgium [Lower Miocene]).—*Trochocopus* sp. – SCHULTZ in STEININGER 1971: 134 (Kühnring bei Eggenburg [Austria]: Eggenburgium [Lower Miocene]).—*Labrodon* sp. (1) – SCHULTZ 2013: 340–341 (Kühnring bei Eggenburg [Austria]: Eggenburgium [Lower Miocene]).

Phylloodus subdepressus – MÜNSTER 1846: 9–10, 28, 66, pl. 1, fig. 7a–d (Upper pharyngeal bone); Neudörfel [Devinska Nova Ves (= Neudorf an der March), [Slovakia]; Middle-Upper Badenien, Middle Miocene].—*Phylloodus subdepressus* MÜNSTER – HÖRNES 1848: 14, Nr. 46; Neudorf [a.d. March = Devinska Nova Ves, [Slovakia]; Badenien, Middle Miocene].—“*Labrodon*” *dubdepressus* (MÜNSTER, 1846) – SCHULTZ 2013: 340 (Devinska Nova Ves, [Slovakia]; Badenien, Middle Miocene).

Remarks: Placed by COCCHI (1864: p. 63) and SAUVAGE (1875a: p. 629) in synonymy with *Labrodon multidens* (MÜNSTER, 1846).

Pharyngodopilus superbus – COCCHI 1864: 72–73, pl. 4, figs 16, 16a–d (Lower pharyngeal bone), pl. 5, figs 6a, 6b; pl. 6, figs 7, 7a, 8 (Upper pharyngeal bone); Orciano [resp.] Toscana [Italy]; Pliocene.—?: *Pharyngodopilus superbus* ? – COCCHI 1864: pl. 5, figs 7, 7a (Upper pharyngeal bone).—*Nummopalatus Superbus*. COCCHI – LAWLEY 1876: 74 (“una placca”); Orciano, [Tuscany, Italy; Pliocene].—*Pharyngodopilus superbus* COCCHI – SIMONELLI 1880: 211; San Quirico d’Orcia [Tuscany, Italy; Pliocene].—*Nummopalatus superbus* COCCHI sp. – SIMONELLI 1889: 212–213 (“Placca faringea superiore sinistra”); Isola di Pianosa nel Mar Tirreno [Italy]; Calcari pliocenici.—*Nummopalatus superbus* COCCHI – BASSOLI 1907: 41; regione Emiliana; Pliocene.—*Labrodon superbus* COCCHI sp. – STEFANO 1909: 557, 632–633, pl. 20, figs 13, 16 (Lower pharyngeal bones); Orciano e San Quirico, [Tuscany, Italy]; Pliocene.—*Labrodon superbus* COCCHI sp. – STEFANO 1912: 68–70, 72 (“placche faringee inferiori”); dell’Emilia, [Italy; Neogene].—*Labrodon superbum*, var. ex *Pisanii* SACCO – SACCO 1916: 177, pl. 1, figs 4a, 4b (“placca

faringea superiore sinistra”); Isola di Pianosa [Italy]; Pliocene (sup.).—*Labrodon superbum* COCCHI sp. – SANTUCCI 1923: 210–211, 213, pl. 3, figs 9, 9a (Upper pharyngeal bone); Savona, Liguria, [Italy]; Pliocene.—*Labrodon superbus* COCCHI 1864 – LANDINI 1977: 241–244, pl. 2, fig. 1a–b (Lower pharyngeal bone), figs 2–5 (Upper pharyngeal bones); Liguria, Emilia, Toscana [Italy]; Pliocene.

Remarks: LANDINI (1977) placed *L. superbum*, var. ex *Pisanii* of SACCO (1916) into the synonymy of *Labrodon superbus*.

? ***Labrodon aff. superbus*** (COCCHI), 1864 – JONET 1968: 218–219, 220, pl. 1, fig. 7 (Left upper pharyngeal bone); Portela de Sacavém, Portugal; Helvétien Vc, Miocene.

Remarks: Already placed by LERICHE (1906a: p. 317) in synonymy with *Labrodon pavimentatum* GERVAIS, 1857.

[**indet.**] – COCCHI 1864: pl. 6, fig. 9 (? Lower pharyngeal bone).

Remarks: LERICHE (1906a: pp. 315–318), STEFANO (1909: p. 630), MENESINI (1969: p. 44) and LANDINI (1977: pp. 234–236) place all the following species in synonymy with *L. pavimentatum*, the type species of *Labrodon*: *Abbas*, *Africanus* in SAUVAGE [non: *Pharyngodopilus Africanus* COCCHI], *Alsinensis*, *Bazini*, *Bourgeoisii* resp. *Bourgeoisii*, *Chantrei*, *Cocchii*, *crassus*, *dilatatus*, *Edwardsius*, *Gaudryi* (p.p.), *Haueri* in COCCHI (1864), SAUVAGE, etc. [non: *Phyllodus Haueri* MÜNSTER, *multidens* in SAUVAGE, etc. [non: *Phyllodus multidens* MÜNSTER], *polyodon*, *Rhedonum*, *Quenstedti*, *Sacheri*, *Soldanii*, *superbus* of the genera *Labrodon*, *Nummopalatus* resp. *Nummapalatus*, *Pharyngodopilus*, and *Sphaerodus*.

Genus *Phyllopharyngodon* BELLWOOD, 1990

1990 *Phyllopharyngodon* nov. gen. – BELLWOOD: 149.

Type and only species: *Phyllopharyngodon longipinnis* BELLWOOD, 1990.

***Phyllopharyngodon longipinnis* BELLWOOD, 1990**

1990 *Phyllopharyngodon longipinnis* sp. nov. – BELLWOOD: 150 ff., figs 1–3 (Monte Bolca [Italy]: Eocene).

Remarks: Based on synapomorphies, this species and genus may be placed in the Labridae (possessing a single supraneural) and the Hypsigenyini (phyllodont pharyngeal dentition).

Genus *Trigonodon* SISMONDA, 1847

non 1843 *Radamas* – MÜNSTER: 52.

L. 1846 *Radamas* n.g. – MÜNSTER: 11–12, 28, 66, pl. 1, fig. 6 a–c (*Radamas Jugleri* MÜNSTER, 1846).

Jt * 1847 *Trigonodon* – SISMONDA in MICHELOTTI: 352.

L. 1848 *Asima* – GIEBEL: 183–184 (*Radamas Jugleri* MÜNSTER, 1846).

Jt. 1849 *Trigonodon* – SISMONDA: 25.

Jt. 1858 *Sargus* – ROUAULT: 100.

- L . 1861 *Scarus* – MICHELOTTI: 355 (*Scarus miocenicus* MICHELOTTI, 1861).
 Jt . 1861 *Trigonodon* – SISMONDA: 22.
 L . 1864 *Taurinichthys*, nov. gen. – COCCHI: 87–88 (*Taurinichthys miocenicus* (MICHELOTTI, 1861)).
 Jt . 1864 *Scarus* ? – COSTA: 128–129.
 L . 1875b *Taurinichthys* COCCHI – SAUVAGE: 631 (*Taurinichthys miocaenicus*).
 Jt . 1875b *Sargus* – SAUVAGE: 632.
 Jt . 1879 *Sargus* – BASSANI: 48.
 Jt . 1880 *Sargus* – SAUVAGE: 27.
 U . 1880 *Stylodus* – SAUVAGE: 41–42 (*Stylodus lebescontei* SAUVAGE, 1880).
 L . 1880 *Taurinichthys* – SAUVAGE: 43 (*Scarus miocaenicus* MICHELOTTI, 1861)
 L . 1890 *Taurinichthys* – SACCO: 296, Nr. 4676.
 L . 1890 *Scarus* (*Trigonodon*) – SACCO: 296, Nr. 4684 [only the name in a list with distributions]
 Jt . 1890 *Scarus* (*Trigonodon*) – SACCO: 296, Nr. 4689 [only the name in a list with distributions]
 Jt . 1895 *Sargus* (*Trigonodon*) – BASSANI: 6–10.
 Jt . 1901 *Trigonodon*, SISMONDA – WOODWARD: 531.
 L . 1901 *Asima* – WOODWARD: 536–537. (*Asima jugleri*; referred to Sparidae).
 U . 1901 *Stylodus* – WOODWARD: 553.
 L . 1901 *Taurinichthys* – WOODWARD: 553.
 Jt . 1906a *Trigonodon* – LERICHE: 311.
 LU . 1906a *Taurinichthys* – LERICHE: 318.
 L . 1906 *Asima* – SCHUBERT: 692.
 Jt . 1910 *Trigonodon* E.SISMONDA – DE STEFANO: 196.
 Jt . 1923 *Trigonodon* SISMONDA – BROILI & SCHLOSSER: 139.
 Jt . 1927 *Trigonodon* SISMONDA, 1849 – ARAMBOURG: 219.
 L . 1948 *Taurinichthys* – BAUZÁ RULLÀN: 231.
 L . 1957 *Taurinichthys* COCCHI – LERICHE: 49 (*Taurinichthys miocenicus* MICHELOTTI, 1861).
 U . 1957 *Stylodus* SAUVAGE – LERICHE: 49 (*Stylodus lebescontei* SAUVAGE).
 Jt . 1957 *Trigonodon* SISMONDA – LERICHE: 50.
 LU . 1957 *Scarus* – SIGNEUX in LERICHE: 50, footnote 1 (*Scarus miocenicus* MICHELOTTI, 1861).
 L . 1963 *Taurinichthys* – BAUZÁ RULLÀN *et al.*: 234, pl. 12.
 Jt . 1963 *Trigonodon* – BAUZÁ RULLÀN *et al.*: 243, pl. 14/3.
 L . 1964 *Taurinichthys* – OBRUTSCHEW: 458.
 U . 1964 *Stylodus* – OBRUTSCHEW: 458.
 U . 1969 *Scarus* FORSKAL, 1775 – CAPPETTA: 234–236, pl. 21, fig. 4 (*Scarus miocenicus* MICHELOTTI, 1861).
 non . 1969 *Scarus* FORSKAL, 1775 – CAPPETTA: 234–236, pl. 21, fig. 6.
 Jt . 1971 *Trigonodon* – BAUZÁ RULLÀN: 368, pl. 27, figs 9, 10; 369, pl. 28, figs 1–2; 383.
 L . 1971 *Taurinichthys* – BAUZÁ RULLÀN: 370, pl. 29, figs 1–5; 394
 L . 1975 *Scarus* – JONET *et al.*: 214.
 U . 1975 Labridé inc. sed. / Labridé indéterminé – JONET *et al.*: 215, pl. 1, fig. 16.
 L . 1978 *Asima* GIEBEL, 1848 – SCHULTZ: 207 (*Asima jugleri* (MÜNSTER, 1846)).
 L . 1978 *Asima* – SCHULTZ in BRZOBOHATÝ & SCHULTZ: 445, pl. 2, figs 20 a, b, 21 a, b.
 L . 1984 *Taurinichthys* – MORNAND: 12.
 U . 1984 *Stylodus* – MORNAND: 12.
 J . 1984 *Trigonodon* – MORNAND: 14.
 LU . 1998 *Asima* – SCHULTZ: 126, pl. 57, figs 6–8.
 J . 1998 *Trigonodon* – SCHULTZ: 126, pl. 57, fig. 10.
 Up . 2002 *Asima* – HIDEN: 4.
 J . 2002 *Trigonodon* – HIDEN: 4.
 LUJt . 2004 *Trigonodon* SISMONDA, 1847 – SCHULTZ & BELLWOOD: 288–290.
 UJt . 2007 *Trigonodon* SISMONDA, 1847 – MARSILI *et al.*: pl. 2, figs 12–14.
 LUJt . 2013 *Trigonodon* SISMONDA in MICHELOTTI, 1847 – SCHULTZ: 341.

Type and only species: *Trigonodon oweni* SISMONDA in MICHELOTTI, 1847: p. 352. Note that *Trigonodon oweni* is a synonym of *Trigonodon jugleri* (MÜNSTER, 1846), see below.

Type locality: terrains miocènes de Italie septentrionale.

Type species of synonyms: *Radamas jugleri* MÜNSTER, 1846. – Synonyms: *Trigonodon oweni* SISMONDA, 1847.—*Scarus miocenicus* MICHELOTTI, 1861.—*Taurinichthys sacheri* SAUVAGE, 1875b.—*Stylodus lebescontei* SAUVAGE, 1880.—*Taurinichthys villaltai* BAUZÁ RULLÁN, 1948).—Complete list of synonymies see below.

Type material: Lower pharyngeal bone, fragment.

Diagnosis: Oral jaw elements with 1–2 enlarged incisiform teeth, upper pharyngeal bones with multiple oblique tooth rows, lower pharyngeal bone (fused 5th ceratobranchials) with raised toothed margin, rounded posteriorly, angular anteriorly, enclosing a granulated toothed area.

Remarks: Because the genus name *Radamas* MÜNSTER is preoccupied by MÜNSTER himself (MÜNSTER 1843: p. 52, pl. 14, fig. 1) for a palaeocoic holocephalan (Radamantidae), *Radamas macrocephalus*, therefore GIEBEL (1848) introduced the new genus name *Asima*. It is remarkable that WOODWARD (1901: p. 536) and later JORDAN (1963: p. 698) arranged *Asima* within the Sparidae. This is contrary to MICHELOTTI (1861) who placed his species *miocenicus* within *Scarus*. COCCHI (1864) put *Taurinichthys* as an “Appendice” in the Pharyngodopilidae and in the Labroidi. Notably, SAUVAGE (1880) already compared the upper pharyngeal bones of his new genus, *Stylodus*, with those of *Pseudodax molluccanus*, BLK. We cannot understand why SAUVAGE (1880) did not unite the lower pharyngeal bone, called *Taurinichthys Sacheri*, with his *Stylodus*. Later LERICHE (1906a: p. 318) noticed that in older literature *Taurinichthys Sacheri* was used for the lower pharyngeal bones, and *Stylodus Lebescontei* for the upper ones. JORDAN (1963: pp. 722–723) put *Stylodus* in the Labridae, and *Taurinichthys* in the Sparisomidae [= Sparisomatinae?].

The genus *Trigonodon* also makes an Odyssey through different families. SISMONDA (1847) placed it in the Gymnodontes, then in SISMONDA (1849) in the Tetraodonti. WOODWARD (1901) and LERICHE (1906a), and later also SCHLOSSER (1923), were of the opinion that *Trigonodon* is a genus in the family Sparidae. Finally, the complete dentary from the ZAPFE collection (NHMWien 1997z0178/1970) made it possible to find the correct place for these taxa: the material is nearly identical to *Pseudodax moluccanus*: so the fossil teeth of *Trigonodon* are from the Labridae, tribe Hypsigenyini (see SCHULTZ & BELLWOOD 2004: p. 288 ff.). Additionally, *Taurinichthys* and *Stylodus* are parts of the nomenclatural oldest genus (SCHULTZ & BELLWOOD 2004: p. 288 ff.): *Trigonodon* SISMONDA, 1847.

***Trigonodon jugleri* (MÜNSTER, 1846)**

- L * 1846 *Radamas Jugleri*, MÜNSTER – MÜNSTER: (11–12), 28, 66, pl. 1, fig. 6a–c (Lower pharyngeal bone, fragment); Neudörf [Devinska Nova Ves (=Neudorf an der March) [Slovakia]; Middle-Upper Badenien, Middle Miocene].
- Jt . 1847 *Trigonodon Oweni*. SISMONDA – SISMONDA in MICHELOTTI: 352 (terrains miocènes de Italie septentrionale).
- L . 1848 *Asima Jugleri* – GIEBEL: 184; aus dem Wiener Tertiärbecken [Devinska Nova Ves (= Neudorf an der March) [Slovakia]; Middle-Upper-Badenien, Middle Miocene].
- L . 1848 *Radamas Jugleri*, MÜNSTER – HÖRNES: 14, Nr. 49; Neudorf [an der March = Devinska Nova Ves [Slovakia]; Middle – Upper Badenien, Middle Miocene].
- Jt . 1849 *Trigonodon Oweni* E. SISMD. – SISMONDA: 25–26, 87, pl. 1, figs 14–16 (isolated tooth); del colle di Torino; [? Upper Oligocene]; 85: Torino, Piemont [Italy]; terziaria media [? Upper Oligocene].
- ? 1854 Dente indeterminato – COSTA, 2: 361, pl. 5, fig. 24 (isolated tooth); S-Italy.
- Jt . 1854 *Scarus?* – COSTA, 3: 128, pl. 12, fig. 11 (Oral tooth plate); Pizzini [Calabria, S-Italy: Elveziano, Middle Miocene].
- L . 1855 *Asima Jugleri* – GIEBEL: 106. [no indication of geographical or stratigraphical distribution but referring to MÜNSTER 1846].
- Jt . 1858 *Sargus Sioni*, sp. nov. – ROUAULT: 100 (isolated tooth or teeth); S.-Juvat [and] S.-Gregoire [near Rennes, NW-France; Savignéen, Miocene].
- L . 1861 *Scarus miocenicus*, MICHELOTTI – MICHELOTTI: 355, pl. 10, figs 3, 3a, 3b (Lower pharyngeal bone, fragment); Colline de Turin [Italy; Elveziano, Middle Miocene].
- L . 1864 *Taurinictyhs miocenicus* [resp.] *Miocenicus* MICHEL. – COCCHI: 88, 87, pl. 6, figs 10, 10a, 10b (Lower pharyngeal bone, fragment); Miocene della collina di Torino [Italy; Middle Miocene].
- L ? 1867–69 Plaque dentaire d'un poisson indéterminé – GERVAIS: 238, pl. 48, fig. 2 (? Lower pharyngeal bone); Castries, Hérault [S France]; Miocene.
- non 1874 *Scarus Baltringensis* n.sp. – PROBST: 282–283, pl. 3, fig. 7 (Molasse von Baltringen).
- ? 1874 *Scarus Baltringensis* n.sp. – PROBST: 282–283, pl. 3, figs 8–11 (Molasse von Baltringen).
- L . 1875b *Taurinictyhs Sacheri* – SAUVAGE: 631, 642, pl. 22, fig. 20 (fragment); Faluns de Bretagne [NW France; Miocene].
- Jt . 1875b *Sargus Sioni*, M. ROUAULT – SAUVAGE 1875b: 632, 642, pl. 22, figs 3, 3a (isolated tooth),
- ? 1875b *Sargus Sioni*, M. ROUAULT – SAUVAGE 1875b: 632, 642, pl. 22, figs 4, 4a; (? fragment of a pharyngeal); St-Juvat [and/or] St-Grégoire [near Rennes, NW-France; Savignéen, Miocene].
- Jt . 1879 *Sargus Sioni* M. ROUAULT – BASSANI: 49–50, 70, pl. 5, figs 13, 14 (isolated teeth); Gahard, Ille-e-Vilaine [France]; miocene medio.
- U . 1880 *Stylodus Lebescontei* – SAUVAGE: 41–42, 44, pl. 2, figs 12, 12a–c (Saint-Grégoire, Bretagne, [NW France; Miocene].
- L . 1880 *Taurinictyhs Sacheri* – SAUVAGE: 43, 44, pl. 2, figs 10–11 (La Chausserie, faluns de Bretagne, [NW France; Miocene].
- L . 1890 *Taurinictyhs miocenicus* MICHT. – SACCO: 296, Nr. 4676.
- L . 1890 *Scarus miocenicus* MICHT. – SACCO: 296, Nr. 4684.
- Jt . 1890 *Scarus Oweni* SISMD. (*Trigonodon Oweni* SISMD.) – SACCO: 296, Nr. 4689 [only the name in list with distributions]; Piemont [Italy]; Elveziano [?].
- Jt . 1895 *Sargus* [*Trigonodon*] *Oweni* E. SISMONDA – BASSANI: 6–10, figs A, A', A'', B, C, D, pl. 1, figs 3, 3a, 3b (isolated teeth); collina di Torino, Pizzo, Cerisano, Catanzaro, Soverato e Pizinni [Italy]; Elveziano [Middle Miocene].
- Jt . 1897 *Trigonodon Oweni* SIM. – DE ALESSANDRI: 25–26 (“un piccolo dente”); Vignale, Basso Monferrato [Italy]; (4) Elveziano [Middle Miocene]; 26: Monte Titano, Sardegna; Miocene; 26: Vienna; Miocene.
- Jt . 1901 *Trigonodon oweni*, SISMONDA – WOODWARD: 531 (isolated teeth); Tuscany [Italy]; Pliocene.

- L . 1901 [...] indeterminate teeth have also been referred to Sparidae [...] *Asima jugleri* [...] – WOODWARD: 536–537. [only in a list with synonyms].
- U . 1901 apparently Labroid [...] *Stylodus lebescontei*, H.E. SAUVAGE – WOODWARD: 553. [only a repetition of SAUVAGE's statement].
- L . 1901 apparently Labroid [...] *Taurinichthy miocenicus* – WOODWARD: 553. [only in a list with synonyms].
- L . 1901 apparently Labroid [...] *Taurinichthys sacheri*, H.E. SAUVAGE – WOODWARD: 553. [only repetition of SAUVAGE's statement].
- Jt . 1904 *Trigonodon Oweni* SISMONDA – PRIEM: 291.
- Jt . 1906a *Trigonodon Sioni*, ROUAULT, 1858 – LERICHE: 311–314.
- LU . 1906a *Taurinichthys Sacheri*, SAUVAGE, 1875 – LERICHE: 318–320: Ille-et-Vilaine: Chartres-la-Poterie (gisement de la Chaussérie), Saint-Grégoire, [NW France; Miocene].
- L . 1906 *Asima Jugleri* GIEB. – SCHUBERT: 692; Neudorf [an der March = Devinska Nova Ves, Slovakia]; Miocèn [Middle – Upper Badenien, Middle Miocene].
- L . 1906 *Asima Jugleri* GIEB. – SCHUBERT: 692 (Mittelmioçän).
- Jt . 1910 *Trigonodon Oweni* SISMONDA – DE STEFANO: 194–198, pl. 2, fig. 16 [? fig. 15]
- L ? 1912 Labrid, ou Sparidé indéterminé – PRIEM: 230 (= GERVAIS 1867–1869: 238, pl. 48, fig. 2); (? Lower pharyngeal bone, fragment); Castris, Hérault [S France]; Miocène.
- Jt . 1927 *Trigonodon oweni* SISMONDA – ARAMBOURG: 219–221, fig. 46 A, B, pl. 12, figs 4–9.
- Jt ? 1937 *Trigonodon oweni* SISM. – SARRA: 56, fig. 2 [not a typical tooth]
- non 1937 *Trigonodon oweni* SISM. – SARRA: 56, figs 3, 4 [fig. 4 in our opinion a tooth of *Diplodus jomnitanus* (VALENCIENNES)].
- L . 1948 *Taurinichthys Villaltai* n.sp. – BAUZÁ RULLÀN: 231–233, pls 12, 13 (Lower pharyngeal bones, fragments); Mallorca, [Spain]; Vindoboniense [Miocene].
- non 1949 *Trigonodon Oweni* SISMONDA, 1849 – BAUZÁ RULLÀN: 214, pl. 13, figs 1–6.
- U . 1950 *Taurinichthys villaltai* – BAUZÁ RULLÀN: 63–66, pl. 11, figs 1–3, pl. 12, figs 4–5 (Upper pharyngeal bones); Santa Margarita [Mallorca, Spain; Miocene].
- L . 1957 *Taurinichthys miocenicus* MICHELOTTI – LERICHE: 49, 50, pl. 4, figs 28–29 (Lower pharyngeal bones, fragments); Ille-et-Vilaine: La Chaussérie, Saint-Grégoire, [NW France]; Savignéen [Miocene].
- U . 1957 *Stylodus lebescontei* SAUVAGE – LERICHE: 49–50, pl. 4, figs 30–31: Ille-et-Vilaine: Saint-Grégoire, [NW France]; Savignéen [Miocene].
- Jt . 1957 *Trigonodon oweni* SISMONDA – LERICHE 1957: 50–51, pl. 4, figs 32–35 (isolated teeth); Chaz, Henry [resp.] Saint-Grégoire, Bretagne [NW France]; Savignéen [Miocene]; 51: Cotes-du-Nord: Le Quiou, Saint-Juvat, Tréfumel. – Ille-et-Vilaine: Chartres-la-Poterie (La Chaussérie), Gahard, Saint-Grégoire. – Indre-et-Loire: Louans, Paulmy. – Loire-Inférieure: Aigrefeuille, le Landreau (le Pigeon Blanc), Noyal-sur-Brutz. – Maine-et-Loire: Chaz,-Henry, Genneteil, Noyant-la-Gravoyère, Noyant-Méon, Saint-Saturnin (le Haguineau) [NW France]; Savignéen [and] Pontilevien [and] Redonien [Miocene].
- LU . 1957 *Scarus miocenicus* MICHELOTTI, 1861 – SIGNEUX in LERICHE: 50, footnote 1.
- L . 1963 *Taurinichthys villaltai*, BAUZÁ – BAUZÁ RULLÀN & al.: 234–235, pl. 12; Santa Margarita (Mallorca) [Spain]; Vindoboniense, [Miocene].
- Jt . 1963 *Trigonodon oweni*, SISMONDA, 1849 – BAUZÁ RULLÀN *et al.*: 243, pl. 14, fig. 3.
- Jt ? 1963 *Trigonodon oweni*, SISMONDA, 1849 – BAUZÁ RULLÀN *et al.*: 243, pl. 14, figs 4, 5.
- Jt . 1963 *Trigonodon sioni*, M. ROUAULT, 1858 – BAUZÁ RULLÀN *et al.*: 243–244, pl. 14, figs 6, 7.
- U . 1969 *Scarus miocenicus* MICHELOTTI, 1861 – CAPPETTA: 234–236, pl. 21, fig. 4 A, B (Upper pharyngeal bone, fragment); Loupian [SW Montpellier, South France; Miocene].
- p.p. 1969 *Scarus miocenicus* – CAPPETTA: Tab. IV; Hérault [and] Bassin du Rhone [France, and] Allemagne [FRG]; Miocene moyen.
- non 1969 *Scarus miocenicus* MICHELOTTI, 1861 – CAPPETTA: 234–236, pl. 21, fig. 6A, B (Oral dental plate ?, fragment); Loupian [SW Montpellier, South France; Miocene].
- Jt . 1971 *Trigonodon oweni* – BAUZÁ RULLÀN: 368, pl. 27, figs 9, 10; 369, pl. 28, fig. 2.

- Jt . 1971 *Trigonodon oweni* – BAUZÁ RULLÁN: 368, pl. 28, fig. 1; 383.
- Jt . 1971 *Taurinichthys villaltai* – BAUZÁ RULLÁN: 370, pl. 29, figs 1–5; 394.
- U . 1975 Labridé inc. sed. / Labridé indéterminé – JONET *et al.*: 215, pl. 1, fig. 16.
- Jt . 1975 *Trigonodon elongatus* nov. sp. – JONET *et al.*: 212–213, 227, pl. 2, figs 22a, b, 24 a, b.
- Jt . 1975 *Trigonodon oweni* SISMONDA – JONET *et al.*: 212, 227, pl. 2, fig. 25.
- L . 1975 *Scarus miocenicus* MICHELOTTI – JONET *et al.*: 214–215, 228, pl. 2, figs 33, 34.
- LU . 1978 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 207–213, pl. 1, fig. 7a–c (LP, fragment; it is the reprint of the figure published by MÜNSTER 1846), figs 8, 9, 10a, b (Up, fragments), fig. 11a, b (Lp, complete specimen), fig. 12a, b (Lp, fragment); Neudorf an der March [= Devinska Nova Ves, Slovakia; Middle – Upper Badenien, Middle Miocene].
- LU . 1978 *Asima jugleri* (MÜNSTER) – SCHULTZ in BRZOBHATÝ & SCHULTZ 1978: 445, pl. 2, fig. 20 a, b (Lp) and pl. 2, fig. 21 [ab] (Up, fragments).
- L . 1984 *Taurinichthys miocenicus* (MICH.) – MORNAND: 12, fig. “1”.
- U . 1984 *Stylodus lebescontei* SAUVAGE – MORNAND: 12, fig. “2”.
- Jt . 1984 *Trigonodon oweni* SISMONDA – MORNAND: 12, fig. “3a”.
- L . 1991 *Asima jugleri* (MÜNSTER, 1846) – BELLWOOD & SCHULTZ: 57 (Upper Badenian, Middle Miocene: Devinska Nova Ves (= Neudorf an der March) [Slovakia]).
- L . 1991 *Asima villaltai* (BAUZÁ, 1948) – BELLWOOD & SCHULTZ: 57 (Miocene, Vindobonian: Muro, Mallorca).
- L? . 1992 *Taurinichthys* sp. indet. – SOLT: 496 [not seen by us].
- L . 1998 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 126, pl. 57, figs 6, 7 (Devinská Nová Ves [= Neudorf an der March, Slovakia]: oberes Badenien [Middle Miocene]).
- U . 1998 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 126, pl. 57, fig. 8 (Devinská Nová Ves [= Neudorf an der March, Slovakia]: oberes Badenien [Middle Miocene]).
- Jt . 1998 *Trigonodon oweni* SISMONDA – SCHULTZ: 126, pl. 57, fig. 10 (Devinská Nová Ves [= Neudorf an der March, Slovakia]: oberes Badenien [Middle Miocene]).
- LUJ . 2004 *Trigonodon jugleri* (v. MÜNSTER, 1846) – SCHULTZ & BELLWOOD: 290–292, pl. 1, figs 1–9 (Devinská Nová Ves [= Neudorf an der March, Slovakia]: oberes Badenien [Middle-Miocene]).
- JtU . 2007 *Trigonodon jugleri* (v. MÜNSTER, 1846) – MARSILI *et al.*: pl. 2, figs 12–14 (Montagna della Maiella, Italy; Early Miocene).
- LUJ . 2013 *Trigonodon jugleri* (MÜNSTER, 1846) – SCHULTZ: 341–344 [different localities: Lower – Upper Miocene: Central Paratethys. – Miocene and Pliocene: Mediterranean and Atlantic province], pl. 69, figs 6a, b, 7a–c, 8a, b (Müllendorf, Kreidesteinbruch: Badenien + Devinská Nová Ves [= Neudorf an der March, Slovakia]: Badenium [Middle-Miocene]).

Type location: Neudörfel [= Devinska Nova Ves = Neudorf an der March, Slovakia].

Age: Tertiär-Formation [Middle – Upper Badenien, Middle Miocene].

Remarks: The genus *Trigonodon* was placed in the “Fam. Gimnodonti” by SISMONDA (1847), into Sparidae by BASSANI (1879), WOODWARD (1901) and also by SCHLOSSER (1923), into Plectognathes [= Tetrodontiformes] by LERICHE (1957) and by BERG (1958: p. 282). The latter mentioned that *Trigonodon* was also placed in the Scaridae; a placement followed by SACCO (1890). PRASAD & SAHNI (1987: p. 9) used the Trigonodontidae which they put into the Tetraodontiformes.

It is possible that the material in figs 4 and 4a of pl. 22 published by SAUVAGE (1875b) is a fragment of a pharyngeal of a Scaridae [now Scarini in the Labridae]; but a careful re-examination is needed.

SACCO (1890: p. 296) was – in a list of fossils, without explanation – of the opinion that *Trigonodon oweni* SISMD. is a *Scarus* (*Scarus oweni* SISMD.). BASSANI (1895: p. 9)

put *Scarus?* of COSTA (1854) into the synonymy of *Sargus* [*Trigonodon*] *oweni* E. SISMONDA.

As SISMONDA in MICHELOTTI (1847), WOODWARD (1901: p. 531) also LERICHE (1957) put *oweni* into the genus *Trigonodon*. Also, the genus *Sargus*, Sparidae, was used; see SAUVAGE (1880: p. 632), BASSANI (1895: p. 9), and WOODWARD (1901: p. 531). As noted above WOODWARD (1901: p. 531) thought that the material in figs 10 and 11 on plate 3 published by PROBST (1874) may be placed in *Trigonodon*; we think that PROBST (1874) could be right and that this material is *Scarus* – a detailed re-examination is clearly required.

Based on synapomorphies, this species and genus may be placed in the Hypsigenyini (phyllodont pharyngeal dentition).

Tribe Scarini

Remarks: According to JORDAN (1963: p. 19) the genus *Scarus* introduced by GRONOW (1763) has a type species which belongs in *Labrus* and therefore JORDAN (1963) nominated the genus *Callyodon* also introduced by GRONOW (1763) instead of *Scarus*. Because GRONOW (1763) does not use a binominal nomination it is best to forget GRONOW's descriptions and to use the binominal name published by FORSKAL (1775: p. 25): *Scarus*.

Genus *Bolbometopon* SMITH, 1956

* 1956 *Bolbometopon* – SMITH: 8.

Type species: *Scarus muricatus* VALENCIENNES in CUVIER & VALENCIENNES, 1839.

Type locality: Java, Indonesia.

Age of type species: recent.

Additional fossil species:

Teleostei sedis incertae – MARTIN 1883–87: 21–23, 298, pl. 1, figs 9, 9a, 10 (isolated teeth) [non 21–23, pl. 1, figs 8, 8a, 11]; Ngembak, Java [Indonesia] miocaene Formation [Miocene] (MARTIN 1883–87: 335 also 369.—*Pseudoscarus* or an allied genus – de BEAUFORT 1928: 5 (“fragments of very large teeth from the jaw” and material published by MARTIN 1883–87); Kleripan, Central Java *i. e.*, Ngembak, Java [Indonesia]; old-miocene [and the stratigraphical position given in MARTIN 1883–87: pp. 368–371 as “Miocaen”].

***Callyodon* sp.** – DERANIYAGALA 1937: 364, fig. 8 (left, upper tooth plate, fragment); Ceylon [Sri Lanka]; Miocene.

***Bolbometopon* sp.** – BELLWOOD & SCHULTZ 1991: 59–61, fig. 1, pl. 1, fig. 1a, b (East shore, Dutch Bay, Aruakollu (Muringè, Malé), NW Province, Sri Lanka: Mala beds, Upper Miocene).

Remarks: Based on synapomorphies BELLWOOD (1994), this material may be placed in the *Cetoscarus-Bolbometopon* clade (possessing reduced cement on the outer face of a fused beak-like jaw) and in *Bolbometopon* based on a single autapomorphy (nodules at the base of each tooth) BELLWOOD & SCHULTZ (1991).

Genus *Calotomus* GILBERT, 1890

* 1890 *Calotomus* – GILBERT: 70.

Type species: *Calotomus xenodon* GILBERT, 1890.

Type locality: Caroline Islands.

Age of type species: recent.

Additional fossil species:

Calotomus preisli n.sp. – BELLWOOD & SCHULTZ 1991: 61 ff., figs 2–5, pl. 2, figs 3–4, pl. 3, figs 5–6 (St. Margarethen, Burgenland [Austria]: NN6, Upper Badenian, Middle Miocene).—*Calotomus preisli* BELLWOOD & SCHULTZ, 1991 – SCHULTZ 2013: 344, pl. 63, fig. 3, pl. 65, fig. 1a, b, pl. 69, figs 10a, b, 11a, b (St. Margarethen, Burgenland, E Austria); NN6 Ober-Badenium, Mittelmiozän [Upper Badenian, Middle Miocene]. – Bad Deutsch-Altenburg: Badenium [Middle Miocene].

Remarks: Based on synapomorphies BELLWOOD (1994) and BELLWOOD & SCHULTZ (1991), this species may be placed in the Scarini (possessing an upper pharyngeal with 1–3 rows of teeth; lateral canines) and in *Calotomus* (autapomorphy: a conical tooth on the ventral surface of the premaxilla).

Non Scarini?

The following material is not placed within the Scarini. It either lacks features or synapomorphies to warrant inclusion or has been placed there in error.

Scarus Baltringensis n.sp. – PROBST 1874: 282–283, 298, pl. 3, fig. 7 (Dental plate, fragment); Molasse von Baltringen [Württemberg, FRG; Obere Meeresmolasse, Lower Miocene].—*Scarus baltringensis* PROBST – WITTICH 1898: 44, 46–47, pl. 1, fig. 6 (Dental plate, fragment); in der nächsten Nähe von Alzey, theils an der Wirtsmühle, theils bei Weinheim, Mainzer Becken, [FRG]; aus dem mittel-oligocänen Meeressand [Middle Oligocene].—*Scarus* aff. *baltringensis*, PROBST – WEILER 1922: 107–109, 127, 133, pl. 1, figs 30–32 (Dental plate); Weinheim, Mainzer Becken, [FRG]; Alzeier Meeressande [Middle Oligocene].—*Scarus baltringensis* PROBST – PEYER 1928: 413–417, fig. 1 (Dental plate); Benken am Kohlfirst, Kt. Zürich, [Switzerland]; Vindobon [Lower Miocene]. BELLWOOD & SCHULTZ 1991 suggest that *S. baltringensis* is an oral jaw toothplate fragment from the Oplegnathidae.

Otolithus (Pseudoscarus) crenulatus, sp. n. – FROST 1934: 431, pl. 15, fig. 17 (Otolith); Barton, Hampshire, Southern England; Upper Eocene.

Remarks: The identification of otoliths of the Labridae involves many uncertainties and few diagnostic features and therefore otoliths are difficult to place.

Scarid. (?) ind. – CASIER 1946: 142–143, 188–189, pl. 3, figs 10a–c (Dental plate), 11 (Pharyngeal bone, fragment); Forest-lez-Bruxelles, [Belgium]; Sables Nummulites planulatus, Ypresien [Lower Eocene]. BELLWOOD & SCHULTZ (1991) state not scarid [scarin].

Scarus priscus n.sp. – WITTICH 1898: 44–47, pl. 1, fig. 7a–c (Dental plate, fragment); in der nächsten Nähe von Alzey, theils an der Wirtsmühle, theils bei Weinheim, Mainzer Becken, [FRG]; aus dem mitteloligocänen Meeressand [Middle Oligocene].—*Scarus priscus*, WITTICH – WEILER 1922: 109, 127; Weinheim, Mainzer Becken, [FRG]; Meeressand von Alzey [Middle Oligocene].

Remarks: BELLWOOD & SCHULTZ (1991) place this material in the Oplegnathidae.

Scarus sp. – WEILER 1922: 109, 133, 135, pl. 1, fig. 22 and pl. 3, fig. 4a (premaxillary bone); Weinheim, Mainzer Becken, [FRG]; Alzeyer Meeressande [Middle Oligocene].

Scarus ? sp. – WEILER 1922: 109–110, 134, pl. 2, fig. 4a–b (Otolith); Weinheim, Mainzer Becken, [FRG]; Alzeyer Meeressande [Middle Oligocene].

Sparisoma sp. – NOLF 1988: 94, 113, 144, pl. 13, fig. 4 (Otolithe); Cauneille, Aquitaine, sud-ouest de la France; Eocene superieur, NP 20.

Scarus suevicus – PROBST, 1874: 281–282, 298, pl. 3, fig. 6a, 6b (Dental bone, fragment); Molasse von Baltringen [Württemberg, FRG; Obere Meeresmolasse, Lower Miocene].

Remarks: WOODWARD (1901: p. 553) was not against the identification of this material as *Scarus*.

Scarus – PROBST 1874: 283–285, 298, pl. 3, figs 8–9 (Isolated teeth of upper and lower pharyngeal bone), figs 10–11 (Isolated teeth); Molasse von Baltringen [Württemberg, FRG; Obere Meeresmolasse, Lower Miocene].

Remarks: SAUVAGE (1880: p. 27) and BASSANI (1895: p. 9) were of the opinion that the figs 10 and 11 of pl. 3 of PROBST (1874) are teeth of *Sargus sioni* and therefore of Sparidae, see above in ? Scaridae, *Sargus sioni*.

Remarks: WOODWARD (1901: p. 530) was of the opinion that the originals of the figs 8 and 9 on pl. 3 given by PROBST (1874) – erroneously assigned as *Scarus baltringensis* by SAUVAGE (1880), BASSANI (1895), and by WOODWARD (1901) – are teeth of *Sargus incisivus*, and the originals of figs 10 and 11 are teeth of *Trigonodon oweni*; see also there below in Tetraodontiformes. Because PROBST described also teeth of *Sargus* we think that PROBST could be right; a re-evaluation is necessary.

Scarus tetrodon POMEL – LERICHE 1906b: 349 (no indications); Cuise-Lamotte (Oise), Bassin parisien [France]; “Sables glauconieux moyens, Yprésien” [Lower Eocene].

Remarks: A nomen nudum; see also WOODWARD (1901: p. 553).

Family Labridae

Tribe indet.

Genus *Bellwoodilabrus* BANNIKOV & CARNEVALE, 20102010 *Bellwoodilabrus* n. gen. – BANNIKOV & CARNEVALE: 204.Type and only species: *Bellwoodilabrus landinii* BANNIKOV & CARNEVALE, 2010.***Bellwoodilabrus landinii* BANNIKOV & CARNEVALE, 2010**2010 *Bellwoodilabrus landinii* n. gen., n. sp. – BANNIKOV & CARNEVALE: 204 ff., figs 1–4 (Monte Bolca [Italy]: Eocene).

Remarks: Based on synapomorphies, this species and genus may be placed in the Labridae (single supraneural).

Genus *Coris* LACEPÈDE, 1801* 1801 *Coris* – LACEPÈDE: 96.Type species: *Coris aygula* LACEPÈDE, 1801.

Type locality: Mauritius.

Age of type species: recent.

Additional fossil species:

Coris sigismundi (KNER, 1862): *Julis Sigismundi*, m. – KNER 1862: 488–490, pl. 1, fig. 1 (imperfect fish); Margarethen [St. Margarethen, Austria. – Upper Badenien, Middle Miocene].—*Julis Sigismundi* KNER – BASSANI 1880: 103, Nr. 19.—*Julis Sigismundi* – WOODWARD 1901: 541.—*Julis Sigismundi* KNER – SCHUBERT 1906: 695; Margareten [St. Margarethen, Burgenland, E Austria]; Mittelmiocän [Upper Badenien, Middle Miocene].—*Julius sigismundi* KN. – SCHULTZ in BRZOBHATÝ & SCHULTZ 1978: 445 [the quotation of KNER only]; St. Margarethen, Bgld., Eastern Austria; [Upper Badenien, Middle Miocene].—*Julis sigismundi* KNER, 1862 – BELLWOOD & SCHULTZ 1991: 68 (St. Margarethen, Burgenland [Austria]: NN6, Ober-Badenium, Mittel-Miozän).—*Julis sigismundi* HECKEL – HOFMANN 2001: 221.—*Julis sigismundi* HECKEL/ *Julis sigismundi* – SCHULTZ 2001: 22 (2x).—*Coris sigismundi* (KNER, 1862) – SCHULTZ 2013: 337, pl. 59, fig. 3; pl. 60, fig. 2 (St. Margarethen, Burgenland [Austria]: NN6, Ober-Badenium, Mittel-Miozän).—*Coris sigismundi* (KNER, 1862) – CARNEVALE 2015: 124–130, figs 1–4, pls 1, 2 (St. Margarethen, Burgenland [Austria]: NN5b, Late Badenian, Middle Miocene).

Remarks: WOODWARD (1901: p. 541) agreed with KNER in placing this fish in *Julis*. CARNEVALE (2010) [pers. comm.] and CARNEVALE (2015) again placed it in *Coris*

(SCHULTZ 2013: p. 337). Based on synapomorphies, this material may be placed in the Labridae (single supraneural); there are currently no morphological synapomorphies identified for *Coris* and its phylogenetic status remains uncertain BARBER & BELLWOOD (2005).

Genus *Eocoris* BANNIKOV & SORBINI, 1990

1990 *Eocoris* nov. gen. – BANNIKOV & SORBINI: 134.

Type and only species: *Eocoris bloti* BANNIKOV & SORBINI, 1990.

***Eocoris bloti* BANNIKOV & SORBINI, 1990**

1990 *Eocoris bloti* sp. nov. – BANNIKOV & SORBINI: 134 ff., figs 1–4, pl. 1 and pl. 2, fig. 1 (Monte Bolca [Italy]: Eocene).

Remarks: Based on synapomorphies, this species and genus may be placed in the Labridae (single supraneural).

Genus *Labrobolcus* BANNIKOV & BELLWOOD, 2015

2015 *Labrobolcus* gen. nov. – BANNIKOV & BELLWOOD: 6.

Type and only species: *Labrobolcus giorgioi* BANNIKOV & BELLWOOD, 2015.

***Labrobolcus giorgioi* BANNIKOV & BELLWOOD, 2015**

2015 *Labrobolcus giorgioi* sp. nov. – BANNIKOV & BELLWOOD: 6 ff., figs 1–4 (Bolca locality, Pesciara cave site, northern Italy: Lower Eocene, late Ypresian – middle Cuisian).

Remarks: Based on synapomorphies, this species and genus may be placed in the Labridae (single supraneural).

Genus *Symphodus* RAFINESQUE, 1810

* 1810 *Symphodus* – RAFINESQUE: 41.

Type species: *Symphodus fulvescens* RAFINESQUE, 1810: p. 41

Type locality: Sizilia.

Age of type species: recent.

***Symphodus westneati* CARNEVALE, 2015**

- 2015 *Symphodus westneati* sp. nov. – CARNEVALE: 130–135, figs 5–7, pl. 3 (St. Margarethen, Burgenland [Austria]: NN5b, Late Badenian, Middle Miocene).
 2013 *Ctenolabrus agassizi* (MÜNSTER, 1846) – SCHULTZ: 337 [p.p.], pl. 60, fig. 1 (St. Margarethen, Burgenland [Austria]: NN6, Ober-Badenium, Mittel-Miozän).

Remarks: Based on synapomorphies, this material may be placed in the Labridae (single supraneural).

Genus *Wainwrightilabrus* CARNEVALE, 2015

- * 2015 *Wainwrightilabrus* gen. nov. – CARNEVALE: 135.

Type and only species: *Wainwrightilabrus agassizii* (MÜNSTER, 1846).

Type locality: Margarethen, Burgenland [Austria]: NN5b, Late Badenian, Middle Miocene.

***Wainwrightilabrus agassizi* (MÜNSTER 1846)**

- 1846 *Notaeus Agassizii*, MÜNSTER – MÜNSTER: 27–28, 31, 66, pl. 3, fig. 2 (imperfect fish); “Margarethen” [St. Margarethen, Burgenland, E Austria; Leithakalk, Upper Badenien, Middle Miocene].
 1847 *Labrus Agassizii* HECKEL – HECKEL: 329.
 1848 *N.[otaeus] Agassizii* MÜNSTER. / *Notaeus Agassizii* – GIEBEL: 129, 416.
 1848 *Labrus Agassizii* HECK. – HÖRNES: 14, Nr. 36; Margarethen in Ung. [St. Margarethen, Burgenland, E Austria; Upper Badenien, Middle Miocene].
 1849 *Labrus Agassizi* (*Notaeus*-Art bei MÜNSTER) – HECKEL: 500.
 1852a *Notaeus Agassizii* – HECKEL: 177 (Margarethen im Leithagebirge).
 1855 *Notaeus Agassizii* – HECKEL: 168.
 1856 *Labrus Agassizii* HECK. – HECKEL: 268–271, pl. 15, figs 2–4 (2 specimens of imperfect fish); Margarethen [St. Margarethen, Burgenland, E Austria]; Grobkalke des Leithagebirges [Upper Badenien, Middle Miocene].
 1862 *Julis Agassizii* oder vielleicht besser [...] *Julis Münsteri* – KNER: 486–487; Leithagebirge [E Austria; Badenien, Middle Miocene].
 1862 *Julis Münsteri* – KNER: 487: a new name for *Julis agassizi* only and not valid; see there above.
 1880 *Labrus agassizi* [HECK.] (*Notaeus agassizi* MÜNSTER.) – BASSANI: 103, Nr. 21.
 1887–90 *L.[abrus] (Notaeus) Agassizi* MSTR.) – ZITTEL: 289–290.
 1901 *Julis agassizi* or *Julis muesteri* – WOODWARD: 540.
 1906 *Labrus (Julis?) Agassizi* HECK. – SCHUBERT: 695; Margarethen [St. Margarethen, Burgenland, Eastern Austria]; Mittelmiozän [Upper Badenien, Middle Miocene].
 1978 *Labrus agassizi* (MÜNSTER.) – SCHULTZ in BRZOBOHATÝ & SCHULTZ: 445 ([only the quotation of HECKEL 1856] and [?] several isolated oral teeth); St. Margarethen, Burgenland, and Gainfarn, Vöslau, Lower Austria, all Eastern Austria, and Devinska Nova Ves (= Neudorf an der March [Slovakia]). Upper resp. Middle Badenian, Middle Miocene].
 1991 *Labrus agassizi* (MÜNSTER, 1846) – BELLWOOD & SCHULTZ: 68 (St. Margarethen, Burgenland [Austria]: NN6, Ober-Badenium, Mittel-Miozän).

- 2001 *Julis agassizi* (MÜNSTER) – HOFMANN: 221.
 2001 *Julis agassizi* HECKEL – SCHULTZ: 22 (St. Margarethen, Burgenland [Austria]: NN6, Ober-Badenium, Mittel-Miozän).
 2013 *Ctenolabrus agassizi* (MÜNSTER, 1846) – SCHULTZ: 337 [p.p.], pl. 59, figs 1–2 (St. Margarethen, Burgenland [Austria]: NN6, Ober-Badenium, Mittel-Miozän).
 Remarks: WOODWARD (1901: p. 540) noticed that the systematic position of this species in *Labrus* or *Crenilabrus* is correct. CARNEVALE (2010) [personal communication] transferred it into *Crenilabrus* (SCHULTZ 2013: p. 337). Later CARNEVALE (2015) created the new genus *Wainwrightilabrus* for *agassizi* MÜNSTER, 1846.
 2015 *Wainwrightilabrus agassizi* (MÜNSTER 1846) – CARNEVALE: 135–141, figs 8–11, pls 4, 5 (St. Margarethen, Burgenland [Austria]: NN5b, Late Badenian, Middle Miocene).

Remarks: The correct name is *agassizii* as it was introduced by MÜNSTER (1846).
 – Based on synapomorphies, this material may be placed in the Labridae (single supraneural).

Genus *Zorzinilabrus* BANNIKOV & BELLWOOD, 2017

2017 *Zorzinilabrus* gen. nov. – BANNIKOV & BELLWOOD: 6–7.

Type and only species: *Zorzinilabrus furcatus* BANNIKOV & BELLWOOD, 2017.

Zorzinilabrus furcatus BANNIKOV & BELLWOOD, 2017

2017 *Zorzinilabrus furcatus* sp. nov. – BANNIKOV & BELLWOOD: 7, figs 1–2 (Monte Bolca locality, Pesciara cave site; Early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone).

Remarks: Based on synapomorphies, this species and genus may be placed in the Labridae (single supraneural).

Labridae indet.

The following material lacks characters or synapomorphies to confidently place it within the Labridae:

Genus *Crenilabrus* CUVIER, 1815

* 1815 *Crenilabrus* – CUVIER: 357.

Type species: *Labrus lapina* FORSKAL = *Labrus pavo* LINNAEUS, 1758: p. 283, nr. 8. [= *Thalassoma pavo*].

Type locality (of *Labrus pavo*): “M. Mediterraneo ad Syriam”.

Age of type species: recent.

Additional fossil species:

? *Crenilabrus eocenicus* E.I. WHITE – CASIER in DARTEVELLE & CASIER 1959: 398 (no indication); Nigeria, Eocene.

Otolithus (Crenilabrus) simplicissimus sp. nov. – SCHUBERT 1906: see below: unknown family.

Labrodon Roveretoi n.sp. – SANTUCCI 1923: 210–211, 213, pl. 3, fig. 10, 10a (Lower pharyngeal bone); Borghetto Santo Spirito, Liguria [Italy]; Pliocene.

Remarks: fig. 10 of SANTUCCI shows a lower pharyngeal bone similar to that of *Crenilabrus pavo*; see KNER (1860: pl. 1, fig. 1).

? *Crenilabrus* sp. – STEFANO 1909: 553, 557, 636, pl. 20, figs 9–10 (Lower pharyngeal bones); Orciano, [Tuscany, Italy]; Pliocene.

Crenilabrus Szajnochae, DE ZIGNO, 1887: see below in non-Labridae, *Eolabroides szajnochae*.

? *Labrus (Crenilabrus) Woodwardi*, KRAMB. GORJ. – GORJANOVIC-KRAMBERGER, 1891: 63–64, 72, pl. 2, figs 4 (imperfect fish), 4a (preoperculum), 4b (dentary), 4c (pharyngeals teeth); Dolje [near Zagreb, Croatia, Jugoslavia]; sarmatico [Middle Miocene].—*Labrus (Crenilabrus) Woodwardi* G.-K. – SCHUBERT 1906: 695; Dolje [N Zagreb, Jugoslavia]; Obermiocän [Sarmatian, Middle Miocene].

Remarks: WOODWARD (1901: pp. 540–541) wrote “referred to this genus” [*Labrus*] “and to *Crenilabrus*, but the systematic position” ... “is very doubtful”.

Other Labridae indet

Genus *Xirichthys* CUVIER, 1814

* 1814 *Xirichthys* – CUVIER: 87.

Type species: *Coryphaena novacula* LINNAEUS, 1758.

Type locality: Mediterranean.

Age of type species: recent.

List of additional species (no synonymy):

Xirichthys sp. – NOLF & BRZOBHATÝ 2009: 332, 333, 350–351, pl. 6, fig. 6 (Winkeltoni and Kreuzschaller, Wetzelsdorf, Steiermark: Lower Badenian [Middle Miocene]).—*Xirichthys* sp. – SCHULTZ 2013: 341, 344, pl. 88, fig. 8a, b (Winkeltoni and Kreuzschaller, Wetzelsdorf, Steiermark: Lower Badenian [Middle Miocene]). Remark: The fossil record of this genus is based on otoliths; the placement of this material within the Labridae is therefore equivocal.

Labrodon batesfordiensis, sp. nov. – CHAPMAN & CUDMORE 1924: 143, 154, 155, 162, pl. 11, figs 41, 42 (“Lower pharyngeal bone”); Batesford, Victoria, [Australia]; Janjukian [Oligocene].

Tautoga (Protautoga) conidens – LEIDY 1873a: 15 (premaxillary with teeth and portion of another with the first tooth); Virginia, [USA]; Miocene.—*Tautoga (Protautoga) conidens* – LEIDY 1873b: 312 (a premaxillary with teeth, and portion of another with the first tooth), Virginia, [USA]; Miocene.—*Protautoga conidens* – LEIDY 1873c: 346–347, pl. 32, figs 56 (premaxillary bone, fragment), 57 (premaxillary bone with teeth); Richmond, Virginia [USA]; Miocene.—*Protautoga conidens* LEIDY – LERICHE 1942: 94 (“fragments de premaxillaires”); Richmond, Virginie [USA]; Formation de Calvert [Middle Miocene]; 98: Région du Chesapeake et Caroline du Nord [USA]; Formation de Calvert [Middle Miocene].

Labrus eocaenus nov. sp. – CASIER 1946: 141–142, pl. 3, fig. 18a–d (isolated oral and pharyngeal teeth); Forest-lez-Bruxelles, [Belgium]; Sables *Nummulites planulatus*, Yprésien [Lower Eocene]; 188–189 (“Dents orales et pharyngiennes isolées”); Forest (Bruxelles) [Belgium]; Yprésien [Lower Eocene].

? ***Anchenilabrus frontalis*** – AGASSIZ 1845a: 47; [England]; l’argile de Londres [Lower Eocene. – nomen nudum].—*Auchenilabrus frontalis* – AGASSIZ 1845b: 308 (no indication); Sheppey [England]; London Clay [Lower Eocene. – nomen nudum].—*Anchenilabrus frontalis* – AGASSIZ 1847: 128; [England]; London-Thon (Lower Eocene).—*Anchenilabrus frontalis* AG. – GIEBEL 1848: 104; Sheppy [England]; im Londonthone [Lower Eocene].—Anchénilabre – GERVAIS 1857: 513 [“n’a pas été décrit”: nomen nudum].—*Auchenilabrus frontalis* – WOODWARD 1901: 552.—‘*Auchenilabrus frontalis*’ AGASSIZ, 1845: 308 (nomen nudum) – CASIER 1966: 226.

? ***Protautoga longidens*** n.sp. – DE ALESSANDRI 1895: 729, 730, pl. 1, figs 11, 11a, 11b (isolated oral tooth); Paran, Republica Argentina; [no indications].

Labrus merula – VOLTA 1796: 155–156, pl. 37 (imperfect fish); [Monte Bolca, Italy; Lower Eocene].—*Labrus Valenciennesii* – AGASSIZ 1835: 293, 305; Monte Bolca [Italy; Lower Eocene].—*Labrus Valenciennesii* AGASS. – AGASSIZ 1833–44: 5/1: 116, pl. 39, fig. 2 (“Sous le nom *Labrus microdon* AGASS.”), (imperfect fish); Monte Bolca [Italy; Lower Eocene].—*Labrus Valenciennesii* AG. – GIEBEL 1848: 103; Monte Bolca [Italy; Lower Eocene].—*Labrus Valenciennesii* – GERVAIS 1857: 513; Monte Bolca [Italy; Lower Eocene].—*Labrus Valenciennesi*, L. AGASSIZ, 1835 – LERICHE 1906b: 386 (the name only in a list); Monte Bolca [Italy]; Eocène.—*Labrus (?) valenciennesi* AGASSIZ, 1833–1844 – BLOT 1980: 377 (imperfect fish); Mont Bolca, Province de Verona, [Italy; Lower Eocene].

Remarks: WOODWARD (1901: pp. 540–541) noticed that the systematic position is “very doubtful”.

Labrus microdon AGASS. – AGASSIZ 1833–44: Vol. 5, pl. 39, fig. 2 [see above: *Labrus merula* [resp.] *Labrus valenciennesii*].

? ***Platylaemus mokattamensis*** n.sp. – WEILER 1929: 14–15, pl. 5, figs 9–13, 15–16 (“Obere Kaupplatten”), pl. 3, fig. 5 [and] pl. 5, figs 1–3, 14, 17–19 (“Untere Kauplatte”); bei Kairo [Egypt]; Unterer Mokattam [Middle Eocene]; 48: Ägypten; Mitteleozän.

? *Nummopalatus paucidens* n.sp. – PRIEM 1901: 497–498, pl. 11, fig. 18 (“plaque pharyngienne supérieur”; tooth plate); environs de Reims [Paris Basin, France], Agéien, Eocène inférieur.—*Labrodon paucidens*, PRIEM, 1902 – LERICHE 1906b: 350 (no indication); environs d’Epernay, Bassin parisien [France]; Yprésien [Lower Eocene]; 351 [and] 376: Bassin de Paris [France]; Yprésien [Lower Eocene].—*Labrodon paucidens* PRIEM – PRIEM 1908: 101, 128 (“plaque pharyngienne supérieure”); Environs d’Epernay, Bassin Parisien, [France]; Yprésien [Lower Eocene].—*Labrodon paucidens* PRIEM – LERICHE 1923: 196 (no indication); Faluns de Pourcy, Sables a Unios et Térédines, Yprésien [Lower Eocene].

Labrus priscus. LAWLEY – LAWLEY 1876: 71–72 (“Una placca di denti faringei superiore sinistra”); Spedaletto verso Volterra, [Tuscany, Italy; Pliocene].

Remarks: WOODWARD (1901: p. 540) noticed that the systematic position is “very doubtful”.

Platylaemus. – see above in *Labrodon: Platylaemus colei*.

Labrodon sp. – PRIEM 1908: 101, 128 (“plaque pharyngienne inférieur”); Trou du Han, Bassin Parisien, [France]; Yprésien [Lower Eocene].

Labrodon (?) sp. – LERICHE 1942 *etc.*, see below in: Phylloodontidae, *Phylloodus elegans*.

Labroide – SAUVAGE 1883: 490–491, 503, pl. 12, fig. 15, 15a (Pharyngeal bone, fragment); Bretagne [NW-France]; Miocène.—unnamed pharyngeal – WOODWARD 1901: 553 [SAUVAGE’s indications only]; Brittany [NW France]; Miocene.

Choerops – DE BEAUFORT 1928: 5 (“a series of crowded round molariform teeth of different size, are almost certainly pharyngeal teeth of Labridae. One piece consists of the almost complete lower pharyngeal of a fish allied to *Choerops*, and another one is possibly one of the upper pharyngeals of the same species.”); Kleripan, Central Java [Indonesia]; old-miocene rocks.

? *Nummopalatus Vaillanti* n.sp. – PRIEM, 1901: 497, pl. 11, figs 16–17 (“plaque pharyngienne supérieur”, tooth plate); environs de Reims [Paris Basin, France]; Agéien, Eocène inférieur.—*Labrodon Vaillanti*, PRIEM, 1902 – LERICHE 1906b: 350 (no indication); environs d’Epernay (Marne), Bassin parisien [France]; Yprésien [Lower Eocene]; 351 [and] 376: Bassin de Paris [France]; Yprésien [Lower Eocene].—*Labrodon Vaillanti* PRIEM – PRIEM 1908: 101, 128 (“plaques pharyngiennes superieures”); Environs d’Epernay, Bassin Parisien, [France]; Ypresien [Lower Eocene].—*Labrodon Vaillanti* PRIEM – LERICHE 1923: 196 (no indication); Bassin de Paris [France]; Faluns de Pourcy, Sables a Unios et Térédines, Yprésien [Lower Eocene].

Labrus Valenciennesii AGASS. – see above: *Labrus merula* VOLTA, 1796.

? **Labroid(en)** – PROBST 1874: 279–280, 298, pl. 3, figs 3 (Isolated jaw tooth), 4 (jaw bone, fragment), 5 (fin spine); Molasse von Baltringen [Württemberg, Germany; Obere Meeresmolasse, Lower Miocene].

labroide indéterminé [resp.] **Labridé** – LERICHE 1900: 179, pl. 1, fig. 6 (Pharyngeal bone); environs d'Épernay (Marne) [Paris Basin, France]; sables à Unios et Térédines [Ypresien; Lower Eocene].

Labridae indéterminés [resp.] **Labridé indét.**, voisin de *Tautoga* – PRIEM 1901: 498–499, figs 5–6 (“Fragment de plaque pharyngienne”); environs de Reims [Paris Basin, France]; Agéien, Eocène inférieur; pl. 11, figs 19–20 (“fragment de plaques portant des dents triturantes”), Cernay, environs de Reims [Paris Basin, France]; Eocène inférieur; 504 (Plaque pharyngienne supérieure); Conglomerat de Cernay, environs de Reims [Paris Basin, France]; Eocène inférieur.

Labridés indéterminés – PRIEM 1908: 86, 87, 128; Bassin Parisien [France]; Thanétien [and] Ypresien supérieur [Upper Paleocene and Lower Eocene].

? **Labridé indéterminé** – CASIER 1958: 41, pl. 2, fig. 7 (“Quatre dents isolées”); Bissex Hill, Ile de Barbade [Barbados]; Formation de Bissex Hill, Aquitanien, Miocène inf. [modern stratigraphic position: NN 5, Lower Middle Miocene].—**Labridae** (vel **Sparidae**) ind. – CASIER 1958: 49: Ile de la Barbade [Barbados]; Formation de Bissex Hill [modern stratigraphic position: NN 5, Lower Middle Miocene Hill].

p.p. **Labridae div. indet. gen. et spec.** – SCHULTZ 2013: 336–337 (+: Korneuburger Becken: Karpatium [Lower Miocene]. – Mühlbach am Manhartsberg and Bad Vöslau [E-Austria]; Mittelmiozän [Upper Badenien, Middle Miocene], pl. 69, fig. 1a, b (Plesching, NE Linz [Austria]: unteres Otnagium [Lower Miocene]), fig. 3a, b (St. Margarethen, Burgenland [E-Austria]; Mittelmiozän [Upper Badenien, Middle Miocene]), fig. 4a, b (Müllendorf, Burgenland [E-Austria]; Mittelmiozän [Upper Badenien, Middle Miocene]).

Labridae indet. gen. et spec. (2) – SCHULTZ 2013: 337 (Hernals [Wien 17]: ? Sarmatium [Middle Miocene]).—Ueberreste eines fossilen Fisches aus der Familie der Lippfische (Labroiden) – HECKEL 1852a: 176 (Hernals).—Ueberreste von Fisches aus der Familie der Labroiden – HECKEL 1852b: 161 (Hernals).

Non-Labridae (previously placed in Labridae)

in Elopiformes, Phyllodontidae ?

Genus *Pseudoegertonia* CASIER in DARTEVELLE & CASIER, 1949

* 1949 *Pseudoegertonia* nov. – CASIER in DARTEVELLE & CASIER: 229.

1952 *Pseudoegertonia* DARTEVELLE et CASIER 1949 – ARAMBOURG: 254.

1959 *Pseudoegertonia* DARTEVELLE et CASIER, 1949 – CASIER in DARTEVELLE & CASIER: 360–361.

Type species: *Pseudoegertonia straeleni* CASIER in DARTEVELLE & CASIER, 1949.

***Pseudoegertonia straeleni* CASIER in DARTEVELLE & CASIER, 1949**

- 1943 *Pseudoegertonia straeleni* nov. gen., nov. sp. – CASIER in DARTEVELLE & CASIER: 91 (no indication); [Central Africa].
- * 1949 *Pseudoegertonia straeleni* nov. sp. – CASIER in DARTEVELLE & CASIER: 230, pl. 19, fig. 7 (Upper pharyngeal bone); Landana, Enclave de Cabinda [Central Africa]; couche 4 [Montien, Paleocene].
- 1959 *Pseudoegertonia straeleni* D. et C. – CASIER in DARTEVELLE & CASIER: 377 (no indication); Landana, Couches 15, Enclave de Cabinda [Central Africa]; 392: Landana, couche 4; Paléocènes et Eocènes; 410: Enclave de Cabinda; Montien, Paléocènes; 542, pl. 19, fig. 7 [caption only] (“Plaque dentaire pharyngienne supérieur”); Landana, couche 4, Enclave de Cabinda.

Type locality: Landana, Enclava de Cabinda, couche 4, Bas-Congo, Central Africa.

Age of type species: Montien, Paleocene.

Type material: “une plaque pharyngienne complète et parfaitement conservée, avec l’os pharyngien.” (DARTEVELLE & CASIER 1949: p. 230).

Remarks: CASIER in DARTEVELLE & CASIER (1949: p. 229) and (1959: p. 360) placed his new genus *Pseudoegertonia* within the Phyllodontidae resp. in “Pseudophyllodontinae?”. ARAMBOURG (1952) placed it within the Labridae.

Additional species:

Pseudoegertonia bebianoi nov. sp. – CASIER in DARTEVELLE & CASIER 1949: 230–231, pl. 19, figs 2, 5 [and] 6 (Fragments of dental plates), 3–4 (Isolated teeth), ? 8–9 (fragments of dental plates); Manzadi, Bas-Congo; couches paléocènes; [and] Landana, Enclave de Cabinda [Central Africa; no indication].—*Pseudoegertonia bebianoi* D. et C. – CASIER in DARTEVELLE & CASIER 1959: 374 (no indication); Manzadi pt. IV [and] VI; 377: Landana, Couches 1 ... 5, Landana, Enclave de Cabinda [Central Africa]; 388: Manzadi, Point IV, Base [and] Point VI; 392: Landana 3 [and] 5; Paléocènes et Eocènes; 410–411: Manzadi VI et ... la base du point IV; Bas-Congo; Montien, Paléocènes; 542, pl. 19, figs 2, 5 [and] 6 (“Groupes des dents”), figs 3, 4 (isolated teeth); Manzadi, point IV, Bas-Congo.—?: *Pseudoegertonia bebianoi* (?) D. et C. – CASIER in DARTEVELLE & CASIER 1959: 542, pl. 19, figs 8–9 (“Fragments de plaques dentaires pharyngiennes”); Landana, couches 3 et 5, Enclave de Cabinda.

Pseudoegertonia salvani nov. sp. – ARAMBOURG 1952: 254–256, fig. 55A, B (“Série des dents”); d’Oued Zem [Morocco]; Thanetien [Upper Paleocene].—*Pseudoegertonia salvani* ARAMB. – BOUJO 1976: 66 (no indication); Ouled Abdoun [and] Ganntour [and] Meskala, Maroc occidental; Montien [Paleocene]; 66 (no indication); Ouled Abdoun [and] Ganntour, Maroc occidental; Thanétien [Upper Paleocene].

***Pseudoegertonia* (?) sp.** – CASIER in CASIER & DARTEVELLE 1943: 91. [the name only].—*Pseudoegertonia* sp. – CASIER in DARTEVELLE & CASIER 1959: 410–411 (no indication); Bololo, Bas-Congo; Eoc[ene] + Mioc[ene] (remaniés).

in Elopiformes, Palaeolabridae ESTES, 1969c

Genus *Palaeolabrus* CASIER, 1967

- * 1967 *Palaeolabrus* n.g. – CASIER: 37.
 1976 *Palaeolabrus* – ESTES: 503.
 1989 *Palaeolabrus* – BRYANT: 30: Western Interior of North America; Lancian [and] Puercan [and] Torrejonian, Upper Maastrichtian [and] Danien [and] Thanetien [Upper Paleocene].

Type species: *Palaeolabrus dormaalensis* CASIER, 1967.

***Palaeolabrus dormaalensis* CASIER, 1967**

- * 1967 *Palaeolabrus dormaalensis* n.g., n.sp. – CASIER: 37–38, pl. 8, figs 6–8.
 1969c *Palaeolabrus dormaalensis* CASIER, 1967 – ESTES: 2, pl. 1, figs a–b (“right vomer”); Belgium; Paleogene.
 1987 *Palaeolabrus dormaalensis* CASIER, 1967 – PRASAD & SAHNI: 10–11, 15, pl. 3, fig. 29 (“dermopalatine tooth”); Asifabad, Central India; Late Cretaceous to Early Paleocene.

Type locality: Dormaal, Brabant [Belgium].

Age of type species: Landénien [Upper Paleocene].

Type material: “Pharyngien (inférieur ?)”.

Remarks: CASIER (1967) erected this genus within the Labridae, but ESTES (1969c) erected the new family Palaeolabridae and removed it to the ? Amiiiformes; later PATTERSON (1973) and ESTES (1976: p. 503) placed it as Teleostei incertae sedis; so did PRASAD & SAHNI (1987: p. 10). BRYANT (1989: pp. 25–26) again placed it within the Elopiformes.

Additional fossil species:

Palaeolabrus montanensis, n.sp. – ESTES 1969c: 2–7, pl. 1, figs c–f (“left [resp.] right vomer (?)”), g–h (“symphyisial coronoid”), i–j (“dermopalatine”), pl. 2, figs a–b (“fragments of left entopterygoid”), c (“premaxilla”), d–e (“right dentary”), pl. 3, figs a–b (“dentary”), fig. d (“teeth from type left vomer”); Bug Creek Anthills, McCone County, Montana [USA], Hell Creek Formation, late Cretaceous.—?: *Palaeolabrus* cf. *P. montanensis* ESTES, 1969 – ESTES 1976: 503 (“a fragmentary right dentary”); Carter County, Montana [USA]; Tongue River Formation, middle Paleocene.—*Palaeolabrus montanensis* ESTES 1969 – BRYANT 1989: 26 (“dentaries, vomers, vertebrae, and coronoid fragments”) Bug Creek Anthills localities, Montana [USA]; 26 (“vertebra”) Tullock Formation; 26 (“dentary fragment”) Wyoming; Lance Formation; 26 (“a vertebra”) Hell Creek Fm.; Lancian-Torrejonian, Upper Maastrichtian, Upper Cretaceous – Thanetien, Upper Paleocene; 28, fig. 9 (premaxilla); Bug Creek Anthills, Montana.

in Elopiformes, Phyllodontidae

Genus *Egertonia* COCCHI, 1864

- * 1864 *Egertonia* – COCCHI: 57–58.
 1966 *Egertonia* COCCHI, 1864 – CASIER: 226.
 1969b *Egertonia* COCCHI, 1864 – ESTES: 321.

Remarks: WHITE (1931: p. 95) introduced for *Phyllodus* a special subfamily, Phyllodontinae, within the Labridae. CASIER in DARTEVELLE & CASIER (1943: p. 91) established for *Phyllodus* and *Egertonia* the special family, Phyllodontidae, which he placed close to the Labridae. Finally ESTES (1969a) put the Phyllodontidae in the Albuloidei in the Elopiformes; following the suggestion of MYERS (1936). LERICHE (1951) and GURR (1962: p. 440) on the other hand placed *Phyllodus* again in the Labridae. See also CASIER (1946: pp. 138–140), CASIER (1958: p. 24) and BRYANT (1989: p. 26).

Type species: *Egertonia isodonta* COCCHI, 1864.

Egertonia isodonta COCCHI, 1864

- * 1864 *Egertonia isodonta* – COCCHI: 58–59, pl. 4, figs 1, 2 (Tooth plate, called *E. insignis* but corrected by COCCHI 1864: 89 in *E. isodonta*); dall'isola di Scheppy [England; Lower Eocene].
- 1901 *Egertonia isodonta* COCCHI – PRIEM: 496, pl. 11, fig. 15 (Tooth plate); environs de Reims [Paris Basin, France]; Agéien, Eocène inférieur.
- 1908 *Egertonia isodonta* COCCHI – PRIEM: 101, 128 (“fragments de plaques pharyngiennes”); Epernay [and] Pourcy (Marne), Bassin Parisien [France]; Agéien, Yprésien [Lower Eocene].
- 1923 *Egertonia isodonta* COCCHI – LERICHE: 187, 195 [and] 200 (“Pharyngien”); Monthelon (Marne), Bassin de Paris [France]; Sables à Unios et Térédines, Yprésien [Lower Eocene].
- 1936 albulid fish [*Albula* or *Dixonia*] – MYERS: 83, fig. 1A–C, 84–85 (“Crushing dentition”); Liverpool Point, Maryland [USA]; Aquia Eocene.
- 1938 *Egertonia isodonta* COCCHI – WHITE: 370 (“upper pharyngeal dentition”); Maryland [USA]; Eocene.
- 1967 *Egertonia isodonta* COCCHI – CASIER: 48–49, tab. 2: Bassin Belge; Yprésien [Lower Eocene, and] Lutétien [and] Lédien [Middle Eocene].

Remarks: PRIEM (1908: p. 101) was of the opinion that *Egertonia Gosseleti* is identical with *Egertonia isodonta*. MYERS (1936) compared it correctly with the Albulidae but he did not know that such tooth plates were already published as *Egertonia*. This was corrected by WHITE (1938) in the book review of MYERS (1936). See also CASIER (1958: p. 24) and (1966: p. 226 ff.) and ESTES (1969a: p. 321).

Additional species:

Egertonia gaultina, CORNUEL – CORNUEL 1877: 620, 626, pl. 11, figs 31–32 (“Plaque pharyngienne”); Moutier-en-Der, Haute-Marne [France]; Gault supérieur, néocomien [Lower Cretaceous].

Egertonia Gosseleti, nov.sp. – LERICHE 1900: 175–176, 194, fig. 1, pl. 1, fig. 1, 1a (Tooth plate); Cuis, environs d’Epernay (Marne) [Paris Basin, France; Lower Eocene].—*Egertonia gosseleti*, C.H. LERICHE – WOODWARD 1901: 551 [no new informations].—*Egertonia Gosseleti* – PRIEM 1908: 101; Cuis (Marne) [France]; Agéien [Lower Eocene].—*Egertonia Gosseleti*, LERICHE, 1900 – LERICHE 1906b: 347–348 (“plaques pharyngiennes”); Cuis (Marne), Bassin parisien [France]; Yprésien [Lower Eocene], 351 [and] 376: Bassin du Paris [France]; Yprésien [Lower Eocene].—*Egertonia Gosseleti* LERICHE – LERICHE 1923: 187 [and] 195 (“dents”); Monthelon (Marne) [France]; Sables à Unios et Térédines, Yprésien Lower Eocene].

Remarks: LERICHE (1906b) put the figured specimen of *Egertonia isodonta* published by PRIEM (1901) with ? into the synonymy of *Egertonia Gosseleti* but PRIEM (1908) did not agree with LERICHE; see below for *Egertonia isodonta*.

Egertonia insignis – COCCHI, 1864: pl. 4, figs 1–2 (Tooth plate).

Remarks: See *E. isodonta*, because it is a second name only used in the explanations for plate 4, corrected by COCCHI (1864: p. 89).

***Egertonia* sp. (cf. *isodonta* COCCHI)** – CASIER 1967: 38, pl. 8, figs 11a–b (isolated tooth), 12 (fragment of tooth plate); Dormaal, Brabant [Belgium]; Landénien [Upper Paleocene].

***Egertonia* sp.** – LERICHE 1923: 190 [and] 195 (“pharyngien”); Limay (Seine-et-Oise), Bassin de Paris [France]; Calcaire grossier, Lutétien [Middle Eocene].

***Egertonia* sp.** – CASIER in DARTEVELLE & CASIER 1943: 91 (no indication); [Central Africa].—*Egertonia* sp. – CASIER in DARTEVELLE & CASIER 1959: 377 (no indication); Landana, couche 6–12 [and] ? 30–31, Enclave de Cabinda; 392: Landana, couche 8; 398: Bas-congo et régions voisines; Eocène; 410: Landana, couches 0–26, Enclave de Cabinda; Montien, Paléocènes; 410: Landana, couche 30–32, Enclave de Cabinda; Lutétien, Eocène s.str.; 542, pl. 19, fig. 1 (“Fragment de plaque pharyngienne”); Landana, couche 8, Enclave de Cabinda; [Paleocene].

***Egertonia* sp.** – CASIER 1946: 140–141, 188–189, pl. 3, fig. 20a–b (“Une dent pharyngienne”); Saint-Josse-ten-Noode, Belgique; Yprésien [Lower Eocene].

Remarks: CASIER (1946: pp. 138–140) was the first who put *Egertonia* – and *Phyllodus* – in a separate family, Phyllodontidae; see also CASIER in DARTEVELLE & CASIER (1949: pp. 229–231).

***Egertonia* sp.** – GURR 1962: 440 (“isolated teeth”); Herne Bay, Kent, United Kingdom; Woolwich Bottom Bed, Sparnacien [Lower Eocene].

Remarks: Following LERICHE (1951), GURR (1962) placed *Egertonia* again in Labridae although CASIER (1946: pp. 138–140) established a new family, Phyllodontidae, for *Egertonia* and *Phyllodus*.

***Egertonia stromeri* sp. nov.** – WEILER, 1929: 16–17, pl. 3, fig. 8 (“Oberer Schlundknochen”); nördlich von Qasr Qerun, N. Fajum, 17–18, pl. 3, figs 6–7 (“Unterer Schlundknochen”); Qasr es Sagha [both Egypt]; Sagha-Stufe [resp.] Mittlere Sagha-Stufe [Upper Eocene]; 48: Ägypten: Obereozän.

in Elopiformes, Phyllodontidae

Genus *Phyllodus* AGASSIZ, 1843

* 1843 *Phyllodus* – AGASSIZ, 2/part 2: 238.
1864 *Phyllodus* AGASS. – COCCHI: 25.
1966 *Phyllodus* AGASSIZ, 1839, 2 – CASIER: 228.

Remarks: WHITE (1931: p. 95) introduced for *Phyllodus* a special subfamily, Phyllo-dontinae within the Labridae. CASIER in DARTEVELLE & CASIER (1943: p. 91) established for *Phyllodus* and *Egertonia* the special family, Phyllo-dontidae, which was thought to be closely related to the Labridae. Finally ESTES (1969a) placed the Phyllo-dontidae into the Albuloidei in the Elopiformes implementing the changes that MYERS (1936) had suggested. LERICHE (1951) and GURR (1962: p. 440) on the other hand placed *Phyllodus* again in Labridae. See also CASIER (1946: pp. 138–140), CASIER (1958: p. 24), BRYANT (1989: p. 26). GILDERSLEEVE (1933: p. 386) presented a list with 31 species of *Phyllo-dus* which are also discussed here; most are species of *Phyllodus*, but *haueri* MÜNSTER, *multidens* MÜNSTER, and *subdepressus* MÜNSTER are representatives of *Labrodon*, Labri-dae, while *depressus* MÜNSTER, and *umbonatus* MÜNSTER are Sparidae.

Type species: *Phyllodus toliapicus* AGASSIZ, 1843.

***Phyllodus toliapicus* AGASSIZ, 1843**

- * 1843 *Phyllodus toliapicus* AGASS. – AGASSIZ (1843, 2/part 2): 239, 2/Atlas: pl. 69a, figs 1–3 (Tooth plate); Sheppy [England; Lower Eocene].
- 1845a *Phyllodus toliapicus* – AGASSIZ: 47; [England]; de l’argile de Londres [Lower Eocene].
- 1847 *Phyllodus toliapicus* – AGASSIZ: 128; [England]; London-Thon [Lower Eocene].
- 1840 *Phyllodus* – OWEN 1840–45: 138.
- 1840–45 *Phyllodus* [resp.] *Phyllodus toliapicus* – OWEN 1840–45: 140, 13, pl. 44, fig. 2.
- 1864 *Phyllodus toliapicus* – COCCHI: 40–43, pl. 2, figs 8, 9 (Tooth plates); dall’argile di Londra [England; Lower Eocene].
- 1892 *Phyllodus toliapicus*, AG. – DAIMERIES: XIV; Schaerbeek [Belgium]; Système ypresien [Lower Eocene]; Calevoet, Scherbeek, Saint-Gilles [Belgium]; Système bruxellien; Saint-Gilles [Belgium]; Système laekenien [Middle Eocene].
- 1901 *Phyllodus elegans* – EASTMAN 1901: 112–113 (“unique dental plate(s)”; New Jersey [USA]; Eocene.
- 1905 *Phyllodus toliapicus* L. AGASSIZ, 1844 – LERICHE: 80 (“dents pharyngiennes group, es ou isolées”); Saint-Josse-ten-Noode, [and] Schaerbeek, Belgique; Yprésien [Lower Eocene]; 165–166 (“pharyngien”); Uccle (Calevoet) [and] Saint-Gilles, Belgique; Bruxellien, [Middle Eocene].
- 1906b *Phyllodus toliapicus*, L. AGASSIZ, 1844 – LERICHE: 169–170 (“dents pharyngiennes groupées ou isolées”); Saint-Josse-ten-Noode [and] Schaerbeek, Belgique; Yprésien [Lower Eocene]; 171, 172: Yprésien belge [Lower Eocene]; 260–261 (pharyngiens); Uccle-Calevoet [and] Saint-Gilles, Belgique; Bruxellien [Middle Eocene]; 270: Belgique; Lutétien [Middle Eocene]; 272 [and] 295 [and] 332: Lutétien [and] Yprésien.
- 1908 *Phyllodus toliapicus*, L. AGASSIZ – LERICHE: 255, pl. 6, fig. 2 (“Pharyngien”); Pourcy (Marne) [France]; Yprésien [Lower Eocene].
- 1923 *Phyllodus toliapicus* L. AGASSIZ – LERICHE: 195 (no indication); Faluns de Pourcy, Bassin de Paris [France]; Sables a Unios et Térédines, Yprésien [Lower Eocene].
- 1931 *Phyllodus toliapicus* AGASSIZ – WHITE: 95–98, figs 159–161 [and] pl.[1], fig. 6 [and] 6a (“Upper pharyngeal plate”); Abbey Wood, E London, Kent [United Kingdom]; Blackheath Beds, Ypresian [Lower Eocene]; fig. 162 (“Imperfect lower pharyngeal plate”); Isle of Sheppey, E London [United Kingdom; Lower Eocene]; pl. [1], fig. 7 [and] 7a (“Lower pharyngeal plate”); 97 (no indication); [additionally] (?) High Halstow, Kent; Oldhaven Beds; [and] Ayot Green [N London, United Kingdom]; [both] Ypresian [Lower Eocene]; 29 (no indications); England; Landenian (Upper Paleocene, and) Ypresian [and] Lutetian [Lower and Middle Eocene].

- 1933 *Phyllodus toliapicus* AGASSIZ – GILDERSLEEVE: 386–387, 382, figs 1–6 (Pharyngeal tooth plates); Virginia [USA]; Eocene.
- 1935 *Phyllodus toliapicus* AGASSIZ – ARAMBOURG: 433–434 [and] 437 (“piles dentaires isolées”); Ouled Abdoun, Maroc; Sparnacien-Yprésien (Lutétien ?) [Lower and ? Middle Eocene], 434: bassin Anglo-parisien et du bassin Belge; Yprésien-Lutétien [Lower and Middle Eocene].
- 1942 *Phyllodus toliapicus* L. AGASSIZ – LERICHE: 40 (“plaques pharyngiennes”); New-Jersey [USA]; Formation d’Aquia, [Lower/Middle Eocene]; Richmond, Virginie [USA]; Groupe de Pamunkey, [Lower/Middle Miocene]; Belvedere Beach, Virginie [USA]; Formation d’Aquia, [Lower/Middle Eocene], 43 [Virginia and New Jersey, USA]; groupe de Pamunkey [Lower and Middle Eocene].
- 1946 *Phyllodus toliapicus* L. AGASSIZ, 1844 – CASIER: 138–140, pl. 3, fig. 8a–c (“Plaque dentaire pharyngienne inférieure”); Forest-lez-Bruxelles, Belgique; Yprésien [Lower Eocene]; 139 [and] 188–189 (“Plaque pharyngienne [and] “Dents phar. isolées”); Quenast [and] Saint-Josse-ten-Noode [and] Maulde; Yprésien [Lower Eocene]; 140.
- ? 1946 *Phyllodus* sp. – CASIER: 188 (“Dents phar. isolées”); Quenast, Belgique; Yprésien [Lower Eocene].
- 1951 *Phyllodus toliapicus* L. AGASSIZ, 1844 – LERICHE: 513–514.
- 1952 *Phyllodus toliapicus* – ARAMBOURG: pl. 37, figs 36–42 (“Piles dentaires pharyngienne”); Ouled Abdoun, Maroc; Yprésien [Lower Eocene].
- 1959 *Phyllodus toliapicus* L. AGASSIZ – CASIER in DARTEVELLE & CASIER: 398 (no indication); Maghreb [Morocco]; Eocenes.
- ? 1967 *Phyllodus* sp. (? *toliapicus* L. AGASSIZ, 1844) – CASIER: 40–41 (“Une dent pharyngienne”); Dormaal, Brabant [Belgium]; Landénien [Upper Paleocene].
- 1967 *Phyllodus toliapicus* AGASSIZ – CASIER: 48–49, tab. 2: Bassin belge [Belgium]; Yprésien and Lutétien [Lower and Middle Eocene].
- 1976 *Phyllodus toliapicus* AG. – BOUJO: 66 (no indication); Ouled Abdoun, Maroc occidental; Thanétien [Upper Paleocene]; 66 (no indication); Ouled Abdoun [and] Atlas, Maroc occidental; Yprésien [Lower Eocene].

Type locality: Sheppey, England.

Age of type species: Lower Eocene.

Type material: Tooth plate.

Remarks: See also *Ph. elegans*, because EASTMAN (1901) put that species as “a young example” into the synonymy of *Ph. toliapicus*. The above given quotations for “*Phyllodus* (two species)” should be placed in the list provided above for *Phyllodus toliapicus*; see the remarks there.

WHITE (1931: p. 95) and LERICHE (1942: p. 40) put the following species into the synonymy of *Ph. toliapicus*: *Ph. planus* AGASSIZ, 1844; *Ph. polyodus* AGASSIZ, 1844; *Ph. marginalis* AGASSIZ, 1844; *Ph. irregularis* AGASSIZ, 1844; *Ph. medius* AGASSIZ, 1844; *Ph. petiolatus* OWEN, 1854; *Ph. colei* COCCHI, 1864; *Ph. hexagonalis* COCCHI, 1864; *Ph. speciosus* COCCHI, 1864; *Ph. bowerbanki* COCCHI, 1864; *Ph. secundarius* COCCHI, 1864; *Ph. submedius* COCCHI, 1864; additionally in WHITE (1931: p. 95): *Ph. gervaisi* COCCHI, 1864; *Ph. deborrei* WINKLER, 1876; and *Phyllodus gaudryi* PRIEM, 1902; additionally in LERICHE (1942: p. 40): *Ph. hipparionyx* EASTMAN, 1901. Also *Ph.*, published by LERICHE (1927b: p. 18) – see there above – should be placed in synonymy with *Ph. toliapicus*. CASIER (1946) was the first to put *Phyllodus* in a special family Phyllodontidae; see also CASIER (1966: p. 228 ff.) or ESTES (1969a: p. 319 ff.).

Additional species:

Phyllodus – GERVAIS 1848–1852, Poisson fossiles (1): 5, pl. 68, fig. 30, 30a (Tooth plate); sables Éocènes de Rethueil, dans le bassin de Paris [France; Eocene].—*Phyllodus* – GERVAIS 1859: 515, pl. 5, fig. 30, 30a (“Petite plaque pharyngienne”, tooth plate); Rethueil, bassin de Paris [France]; sables Éocènes.—*Labrodon* sp. – PRIEM 1908: 101. Remarks: COCCHI (1864: pp. 50–53, 56) put the material figured by GERVAIS (1848–1852) into the synonymy of *Phyllodus medius* AGASSIZ.

? ***Phyllodus*** – GERVAIS 1848–1852, Poissons fossiles (1): 5, fig. 31, 31a (Tooth plate); de Cuise-la-Motte (Oise) [France; Lower Eocene].—*Phyllodus* – GERVAIS 1859: 515, pl. 5, fig. 31, 31a (“Petite plaque pharyngienne”, tooth plate); Cuis-la-Motte (Oise) [France; Eocene].—*Labrodon* sp. – PRIEM 1908: 101.

Remarks: COCCHI (1864: p. 57) called this figured specimen “*almeno provvisorio, Ph. Gervaisi*”.

Phyllodus Bowerbanki – COCCHI 1864: 36–38, pl. 2, figs 2, 2a, 3, 4 (Tooth plates); dalle argille di Londra e furono rinvenuti nell’isola di Sheppy [England; Lower Eocene].

Remarks: Already placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) in synonymy with *Ph. toliapicus*, see below.

Phyllodus centralis n.sp. – CASIER 1967: 38–40, fig. 8a–b (“Dent pharyngienne de pile centrale”), 9a–c (“Pile dentaire pharyngienne centrale”), pl. 8, figs 13 (“Dent pharyngienne, vue par la face orale”), 14 (“Pile dentaire centrale accompagn, e de deux piles laterales, face orale”); France, Faluns de Pourcy [? Lower Eocene].

Phyllodus Colei – COCCHI 1864: 27–28, pl. 1, fig. 1, 1a, 1b (Tooth plate); argille dell’Isola Sheppy [England; Lower Eocene].

Remarks: Already placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) in synonymy with *Ph. toliapicus*, see below.

? ***Phyllodus cretaceus*** m. – REUSS 1844a: 161, 222, 257, Nr. 22 (“Zähne”); am südlichen Fusse des Borzen bei Liebschitz, Böhmen [CFR]; Conglomeratschichten, Kreide.—*Phyllodus cretaceus* REUSS – REUSS 1845: 11, pl. 4, figs 62, 63a, b, pl. 12, fig. 16a–c (isolated teeth); Borzen, Böhmen [Bohemia, CFR]; Cretaceous.—*Phyllodus cretaceus* – COCCHI 1864: 26–27.

Phyllodus curvidens – MARSH 1869: 229 (“dental plate”); Shiloh, Cumberland County, New Jersey [USA]; Miocene.—*Phyllodus curvidens*, MARSH – COPE 1876: 362 [only the name in a list]; Cumberland County, New Jersey [USA]; Miocene.—*Phyllodus curvidens* – EASTMAN 1901: 111 and 112–113 [“unique dental plate(s)”]; New Jersey [USA]; Miocene.—*Phyllodus curvidens* MARSH – EASTMAN 1904: 93 (nothing written); New Jersey [USA]; Miocene.

Phyllodus DeBorrei WINKLER – WINKLER 1878: 28–30, pl. 2, figs 14–15 (Tooth plates), fig. 16–18 (Isolated teeth); zone remaniée entre les sables ypresiens et les sables blancs bruxelliens [Belgium; Middle Eocene, and] St. Josse ten Noode près de Bruxelles [Belgium]; sables ypresiens [Lower Eocene].—*Phyllodus ? deBorrei*, WINKL. – DAIMERIES

1892: XIII-XIV; Saint-Josse-ten-Noode [Belgium]; Système ypresien [Lower Eocene]; Calevoet [Belgium]; Système bruxellien [Middle Eocene].

Remarks: LERICHE (1905: p. 166) and LERICHE (1906b: p. 261) placed *Ph. deborrei* in synonymy with *Phyllodus toliapicus* AGASSIZ, also WHITE (1931: p. 95).

Phyllodus duvali [POMEL, 1847] – WOODWARD 1901: 550 (“merely names for fossils from the Lower Eocene of Cuise-Lamotte, Oise”).—*Phyllodus Duvalii* POMEL – LERICHE 1906b: 349 (no indications); Cuise-Lamotte (Oise), Bassin parisien [France]; “Sables glauconieux moyens”, Yprésien [Lower Eocene].

Remarks: A nomen nudum.

Phyllodus elegans – MARSH 1869: 228–229 (“a pharyngeal, dental plate, with the teeth in an excellent state of preservation”); Farmingdale, New Jersey [USA]; Eocene.—*Labrodon* (?) sp. – LERICHE 1942: 41 and 43 (see above in MARSH 1869); New Jersey [USA]; groupe de Pamunkey [Lower and Middle Eocene].

Remarks: EASTMAN (1901) was of the opinion, that “it is probable from MARSH’s brief description, that *P. elegans* is a young example of *P. toliapicus*”. – see also there below. Considering GILDERSLEEVE (1933), LERICHE (1942) was of the opinion, that MARSH’s *Phyllodus elegans* could be a *Labrodon*. However, we think it is most likely to be a *Phyllodus* because no *Labrodon* is known from Eocene layers, and *Phyllodus* is common in the Eocene. However, the presence of *Phyllopharyngodon* in the Eocene of Italy suggests that Labridae with phyllodont dentition were present in the Eocene.

Phyllodus Gaudryi n.sp. – PRIEM 1901: 494–496, fig. 4, pl. 11, fig. 14 (“Plaque pharyngienne”, Tooth plate, fragment); environs de Reims [Paris Basin, France]; Agéien, Eocene inférieur.—*Phyllodus Gaudryi*, PRIEM, 1902 – LERICHE 1906b: 348 (no indication); environs d’Epernay (Marne), Bassin parisien [France]; Yprésien [Lower Eocene]; 351 [and] 376: Bassin de Paris; Yprésien [Lower Eocene].—*Phyllodus Gaudryi* PRIEM – PRIEM 1908: 101, 128: Environs d’Epernay (Agéien), Pourcy (Marne), Bassin Parisien [France]; Yprésien [Lower Eocene].—*Phyllodus Gaudryi* PRIEM – LERICHE 1923: 195 (no indication); Faluns de Pourcy, Bassin de Paris [France]; Sables a Unios et Térédines, Yprésien [Lower Eocene].

Remarks: Already placed by WHITE (1931: p. 95) in synonymy with *Phyllodus toliapicus*; see below.

Phyllodus Gervaisi – COCCHI 1864: 57 (Tooth plate); Cuis-la-Motte [Paris Basin, France]; Eocene.—*Phyllodus Gervaisi* – PRIEM 1908: 101, 128; Sables de Retheuil (Aisne), Bassin Parisien [France]; Yprésien [Lower Eocene].—*Phyllodus Gervaisi* COCCHI – LERICHE 1923: 195 (no indication); Sables de Cuise, Yprésien [Lower Eocene].

Remarks: COCCHI (1864: p. 57) established the new species for the specimen of fig. 31 and 31a in GERVAIS (1848–52), Poissons fossiles (1): 5, pl. 68, but COCCHI (1864: p. 57) used fig. 30 incorrectly – it should be written 31; the fig. 30 is referred by COCCHI (1864: p. 50) to *Phyllodus medius*; but see also WOODWARD (1901: p. 550). WHITE (1931: p. 95) placed it in synonymy with *Ph. toliapicus*; see below.

Phyllodus hexagonalis – COCCHI 1864: 28–30, pl. 1, fig. 2 (Tooth plate, anterior fragment), fig. 3, 3a (Tooth plate); nel Red Crag rimaneggiatovi dal London Clay (fig. 2), dall'isola di Sheppy (fig. 3, 3a) [England; Lower Eocene].

Remarks: Already placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) in synonymy with *Ph. toliapicus*, see below.

Phyllodus hipparionyx n.sp. – EASTMAN 1901: 113 (“detached dental plate”); Maryland [USA]; Eocene.

Remarks: EASTMAN (1901) took WYMAN's figure 9a, published in 1850 and identified as *Phyllodus*, and placed it in synonymy with *Ph. hipparionyx*, see below. LERICHE (1942: p. 40) had already placed it in synonymy with *Ph. toliapicus*, see below.

Phyllodus inconstans POMEL – LERICHE 1906b: 349 (no indications); Cuise-Lamotte (Oise), Bassin parisien [France]; “Sables glauconieux moyens, Yprésien [Lower Eocene].

Remarks: A nomen nudum.

Phyllodus irregularis – AGASSIZ 1843, 2/2: 241 [nomen nudum].—*Phyllodus irreglularis* – AGASSIZ 1845a: 47; [England]; de l'argile de Londres [Lower Eocene].—*Phyllodus irregularis* – AGASSIZ 1847: 128; [England]; London-Thon [Lower Eocene].—*Phyllodus irregularis* – COCCHI 1864: 48–50, pl. 3, fig. 7, 7a (Tooth plate); provengono dal solito terreno del London Clay [England; Lower Eocene].

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) in synonymy with *Ph. toliapicus*, see below.

Phyllodus latidens POMEL – LERICHE 1906b: 349 (no indications); Cuise-Lamotte (Oise), Bassin parisien [France]; “Sables glauconieux moyens, Yprésien [Lower Eocene].

Remarks: A nomen nudum.

Phyllodus levesquei [POMEL, 1847] – WOODWARD 1901: 550 (“are merely names for fossils from the Lower Eocene of Cuise-Lamotte, Oise”).—*Phyllodus Levesquei* POMEL – LERICHE 1906b: 349 (no indications); Cuise-Lamotte (Oise), Bassin parisien [France]; “Sables glauconieux moyens”, Yprésien [Lower Eocene].

Remarks: A nomen nudum.

Phyllodus marginalis AGASS. – AGASSIZ, 1843, 2/2: 240–241, 2/Atlas: pl. 69a, figs 8–9 (Tooth plate); Sheppy [England]; de l'argile de Londres [Lower Eocene].—*Phyllodus marginalis* – AGASSIZ 1845a: 47; [England]; de l'argile de Londres [Lower Eocene].—*Phyllodus marginalis* – AGASSIZ: 128; [England]; London-Thon [Lower Eocene].—*Phyllodus marginalis* ? – GERVAIS 1848–52, Explication des planches 67 a 70, Poissons (1): 2, pl. 67, figs 5, 5a (Tooth plate), 6, 6a, 6b (Isolated tooth); Cuise-la-Motte [Paris Basin, France; Lower Eocene].—*Phyllodus marginalis* – COCCHI 1864: 34–35, pl. 2, fig. 1, 1a (Tooth plate); È delle argille di Londra e fu raccolto a Sheppy [England; Lower Eocene].—*Phyllodus marginalis*, AG. – DAIMERIES 1892: XIV; Hougaerde, Calevoet [and] Schaerbeek [Belgium]; Système bruxellien [Middle Eocene].—*Phyllodus marginalis* ? AG. – PRIEM 1908: 101, 128; Cuise-la-Motte, Bassin Parisien [France]; Ypresien [Lower Eocene].—*Phyllodus marginalis* AGASSIZ – GILDERSLEEVE 1933: 387, 382, figs 11–14 (Pharyngeal tooth plate); Virginia [USA]; Eocene.

Remarks: WHITE (1931: p. 95) and LERICHE (1942: p. 40) placed it in synonymy with *Ph. toliapicus*, see below. LERICHE (1906b: p. 348) put GERVAIS's (1852) *Phyllodus marginalis* ? as a separate species but without a species name.

Phyllodus medius – AGASSIZ, 1843: 241 [nomen nudum].—*Phyllodus medius* – AGASSIZ 1845a: 47; [England]; de l'argile de Londres [Lower Eocene].—*Phyllodus medius* – AGASSIZ 1847: 128; [England]; London-Thon [Lower Eocene].—*Phyllodus medius* – COCCHI 1864: 50–53, 56, pl. 2, figs 10–12, 14 (Tooth plates); dalle argille eoceniche di Sheppy [England; Lower Eocene].—*Phyllodus medius* AG. – SCHLOSSER 1923: 142, fig. 244 (Tooth plate); Sheppey [England]; Londonton [Lower Eocene].—*Phyllodus medius*? AGASSIZ – GILDERSLEEVE 1933: 388, 382, figs 15–18 (Pharyngeal tooth plate); Virginia [USA]; Eocene.

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus petiolatus OWEN.—*Phyllodus* – OWEN 1840–45: 138–140; 13, pl. 44, fig 2, pl. 47, figs 1–2 (Tooth plate).—*Phyllodus petiolatus* – COCCHI 1864: 45–48, pl. 3, figs 1–6 (Tooth plate); dall'argilla di Sheppy [England; Lower Eocene].—*Phyllodus polyodus* – GIEBEL 1855: 106, pl. 44, fig. 2 (Tooth plate).

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus planus AGASS. – AGASSIZ 1843, 2/2: 239–240, 2/Atlas: pl. 69a, figs 4–5 (Tooth plate); Sheppy [England]; l'argile de Londres [Lower Eocene].—*Phyllodus planus* – AGASSIZ 1845a: 47; [England]; de l'argile de Londres [Lower Eocene].—*Phyllodus planus* – AGASSIZ 1847: 128; [England]; London-Thon [Lower Eocene].—*Phyllodus planus* – COCCHI, 1864: 30–32, pl. 1, figs 4, 4a, 5, 6, 6a, 6b (Tooth plates); dalle argille di Londra [England; Lower Eocene].—*Phyllodus* cf. *planus*, L. AGASSIZ – LERICHE 1908: 251–253, pl. 6, fig. 1 (“Pharyngien”); Builly (Marne) [France]; Landénien [Upper Paleocene].—*Phyllodus* cf. *planus* L. AGASSIZ – LERICHE 1923: 195 (no indication); Bassin de Paris [France]; Landénien [Upper Paléocene].

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus polyodus AGASS. – AGASSIZ 1843, 2/2: 240, 2/Atlas: pl. 69a, figs 6–7 (Tooth plate); Sheppy [England]; De l'argile de Londres [Lower Eocene].—*Phyllodus* – OWEN 1840–45: 138–140, pl. 47, figs 1–2 (Tooth plate).—*Phyllodus polyodus* – AGASSIZ 1845a: 47; [England]; de l'argile de Londres [Lower Eocene].—*Phyllodus polyodus* – AGASSIZ 1847: 128; [England]; London-Thon [Lower Eocene].—*Phyllodus* – GIEBEL 1855: 106, pl. 45, fig. 9 (Tooth plate).—*Phyllodus polyodus* – COCCHI 1864: 43–44, pl. 3, fig. 8, 8a (Tooth plate; the same specimen as in OWEN 1840–45: pl. 47, figs 1–2)); dall'isola di Sheppy [England; Lower Eocene].—*Phyllodus polyodus*, AG. – DAIMERIES 1892: XIV; Calevoet [and] Schaerbeek [Belgium]; Système bruxellien [Middle Eocene].—*Phyllodus polyodus* – WOODWARD 1901: 548, 547, fig. 19 (Tooth plate); Sheppey [England; Lower Eocene].

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus secundarius – COCCHI 1864, 38–40, pl. 2, fig. 7, 7a, pl. 6, fig. 3, 3a (Tooth plates); dall’Isola di Sheppy e non ne conosco di altra provenienza [England; Lower Eocene].—*Phyllodus secundarius*, COCCHI, 1864 – LERICHE 1905: 166; Uccle (Calevoet) [and] Schaerbeek, Belgique; Bruxellien, [Middle Eocene].—*Phyllodus secundarius*, COCCHI, 1864 – LERICHE 1906b: 262 (no indication); Uccle-Calevoet [and] Schaerbeek, Belgique; Bruxellien [Middle Eocene]; 270 [and] 272 [and] 295 [and] 332 (no indication); Belgique; Lutétien [Middle Eocene].

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus – GIEBEL 1855. – see: *Phyllodus polyodus* AGASSIZ.

Phyllodus – WYMAN 1850: 234, 232, fig. 9a, 9b (“The palatine or pharyngeal plates”; tooth plate); Richmond, Virginia [USA]; medial pliocene [or] Miocene [or] Eocene [Eocene].—*Phyllodus* – COCCHI 1864: 57.

Remarks: EASTMAN (1901: p. 113) took WYMAN’s figure 9a, determined as *Phyllodus*, into the synonymy of his *Phyllodus hipparionyx*, see above. – Placed by LERICHE (1942: p. 40) in synonymy with *Ph. toliapicus*, see below.

? ***Phyllodus* sp.** – BASSANI 1899: 36, pl. 3, figs 56–65 (Isolated teeth); Gassino, Piemonte [Italy]; Eocene.

***Phyllodus*, sp.** – LERICHE 1905: 167; Uccle (Calevoet), Saint-Josse-ten-Noode, Schaerbeek, [Belgique]; Bruxellien, [Middle Eocene].—*Phyllodus*, AG. – LE HON 1862: 812 (no indication); Bruxelles [Belgium]; système bruxellien [Middle Eocene].—*Phyllodus* sp. – LERICHE 1906b: 262 (pharyngiens); Uccle-Calevoet [and] Saint-Josse-ten-Noode [and] Schaerbeek, Belgique; Lutétien [Middle Eocene]; 270 [and] 273 [and] 295 [and] 332: (Belgique); Lutétien [Middle Eocene].

***Phyllodus* sp.** – LERICHE 1906b: 348 (no indication); Cuise-Lamotte (Oise), Bassin Parisien [France]; Yprésien [Lower Eocene]; 351 [and] 376: Bassin de Paris [France]; Yprésien [Lower Eocene].—*Phyllodus marginalis* ? – GERVAIS 1848–52, Explication des planches 67 a 70, Poissons (1): 2, pl. 67, figs 5, 5a (Tooth plate), 6, 6a, 6b (Isolated tooth); Cuise-la-Motte [Paris Basin, France; Lower Eocene].

Remarks: In 1906 LERICHE (1906b: p. 348) put GERVAIS 1852’s *Phyllodus marginalis* ? in a separate species but without a species name.

Phyllodus – LERICHE 1906b: 348 (“dents isolées et fragments de pharyngiens”); Margival (Aisne), Bassin parisien [France]; Yprésien [Lower Eocene].

***Phyllodus* sp.** – LERICHE 1923: 196 (no indication); Sables de Cuise, Bassin de Paris [France]; Yprésien [Lower Eocene].

***Phyllodus* sp.** – LERICHE 1923: 190 [and] 196 (“dents isolées”); Chaumont-en-Vexin (Oise), Bassin de Paris [France]; Calcaire grossier, Lutétien [Middle Eocene].

***Phyllodus* sp.** – PRIEM 1908: 101; Pierrefonds, Hérouval (Oise), Margival (Aisne), Bassin Parisien [France], Yprésien; 115, fig. 58 (Tooth plate, part); Cahaigues (Eure), Bassin Parisien [France], Lutétien inférieur; 128; Bassin Parisien [France]; Yprésien [and] Lutétien [Lower and Middle Eocene].

***Phyllodus* sp.** – LERICHE 1927b: 18 (no indication); Quenast, Belgique; Yprésien [Lower Eocene].

Remarks: Should probably be placed into the synonymy of *Ph. toliapicus*; see also CASIER (1946: p. 139).

Phyllodus (two species) – SALTER & YOUNG 1906: 107 (no indication); new road cut from Well Hall Station to Eltham Church, near London [United Kingdom]; Blackheath Beds, which rise from under the London Clay [Lower part of Lower Eocene or earlier].—variants of *P. toliapicus* AGASSIZ – WHITE 1931: 12 (“dismembered plate”); Well Hall Road, Eltham, Kent; Blackheath Beds, Lower Ypresien [Lower Part of Lower Eocene].
Remarks: WHITE (1931: p. 12) studied a part of the mentioned material of SALTER & YOUNG (1906) and the result was that the material “refer to variants of *P.[hyllodus] toliapicus*”. We think it is the best to agree with WHITE’s determination and place this material *Phyllodus toliapicus* below.

Phyllodus speciosus – COCCHI 1864: 32–34, pl. 1, figs 7, 7a, 8, pl. 2, figs 5, 6 (Tooth plates); London clay [resp.] rimanegiato nel Red Crag [resp.] Red Crag di Sutton, ma provengono originalmente dall’argilla di Londra [England; Lower Eocene].—*Phyllodus speciosus* COCCHI – PRIEM 1908: 101, 128; Cuise-la-Motte (Oise), Bassin Parisien [France]; Yprésien [Lower Eocene].—*Phyllodus speciosus* COCCHI – GILDERSLEEVE 1933: 387, 382, figs 7–10 (Pharyngeal tooth plate); Virginia [USA]; Eocene.

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus submedius – COCCHI, 1864: 54–56, pl. 2, fig. 13, 13a, 13b (Tooth plate); e proviene dal Red Crag [England; dislocated from Eocene].

Remarks: Placed by WHITE (1931: p. 95) and LERICHE (1942: p. 40) into synonymy with *Ph. toliapicus*, see below.

Phyllodus trigonella: see below in Perciformes, ? Sciaenidae, *Diaphyodus trigonella* SCHAFHÄUTL.

in Beryciformes, in Holocentridae

Gillidia antiquus (AGASSIZ, 1833–1844) – BLOT 1980: 377 (imperfect fish); Monte Bolca, Province de Verona, [Italy; Lower Eocene].

Remarks: Personal communication by BLOT cf. BLOT (1986): this species should be placed in synonymy with *Eoholocentrum macrocephalum* (DE BLAINVILLE), see SORBINI & TIRAPELLE (1974: p. 208); it is therefore placed in the Holocentridae.

in Perciformes, in Centropomidae

in *Cyclopoma gigas* AGASSIZ

(already by AGASSIZ 1835: pp. 294, 299, 310, 312)

Labrus turdus – VOLTA, 1796: 202–204, pl. 49 (imperfect fish); Monte Bolca [Italy; Lower Eocene].

Remarks: The specific names given by AGASSIZ (1835) replace the names given by VOLTA (1796); these replacements do not follow the rules of nomenclature. All names need to be carefully checked.

in Perciformes, Sparidae

Phyllodus depressus [see below: *Phyllodus umbonatus*].

Phyllodus umbonatus – MÜNSTER, 1846: 10, 28, 66, pl. 1, fig. 8a (Fragment of a bone with one tooth); Neudörfel bei Wien [Devinska Nova Ves (Neudorf an der March), [Slovakia]; Middle – Upper Badenien, Middle Miocene].—*Phyllodus depressus* – MÜNSTER, 1846: 10–11, 28, 66, pl. 1, fig. 8b–c (called “*Phyllod. depressi*”: isolated tooth); Neudörfel bei Wien [Devinska Nova Ves (= Neudorf an der March), [Slovakia]; Middle – Upper Badenien, Middle Miocene].—*Phyllodus umbonatus* MÜNSTER – HÖRNES 1848: 14, Nr. 47; Neudorf [a.d.March = Devinska Nova Ves, [Slovakia]; Badenien, Middle Miocene].—*Phyllodus depressus* MÜNSTER – HÖRNES 1848 14, Nr. 48; Neudorf [an der March = Devinska Nova Ves, [Slovakia]; Badenien, Middle Miocene].—*Phyllodus umbonatus*, MUNST. – COCCHI 1864: 56.—*Sparoides umbonatus* MÜNSTER sp. – PROBST 1874: 291–292, pl. 3, figs 16–19 (Bones with teeth and isolated teeth); Molasse von Baltringen [Württemberg, FRG; Obere Meeresmolasse, Lower Miocene].—*Sparus umbonatus* (MÜNSTER, 1846) – SCHULTZ 2013: 311–315, pl. 68, figs 1, 2a+b [provides an extensive list of localities yielding sparid material in Austria and elsewhere: Upper Oligocene to Middle Miocene].

in Perciformes, ? in Sciaenidae [see WHITE 1931: 89]

Genus *Eodiaphyodus* CASIER in DARTEVELLE & CASIER, 1949

- 1943 *Eodiaphyodus* – CASIER in DARTEVELLE & CASIER: 90. [the name only]
 * 1949 *Eodiaphyodus* nov. – CASIER in DARTEVELLE & CASIER: 226.
 1952 *Eodiaphyodus* DARTEVELLE & CASIER 1949 – ARAMBourg: 252.
 1959 *Eodiaphyodus* – CASIER in DARTEVELLE & CASIER: 425; Crétacique supérieur.

Type species: *Eodiaphyodus lerichei* CASIER in DARTEVELLE & CASIER, 1949.

***Eodiaphyodus lerichei* CASIER in DARTEVELLE & CASIER, 1949**

1943 *Eodiaphyodus lerichei* nov. gen., nov.sp. – CASIER in DARTEVELLE & CASIER: 90. [the name only]

* 1949 *Eodiaphyodus lerichei* nov. sp. – CASIER in DARTEVELLE & CASIER: 226–229, fig. 67 B, pl. 18, figs 1–8 (Lower and upper pharyngeal plates); Manzadi IV, Bas Congo [Central Africa]; Crétac, supérieur.

1959 *Eodiaphyodus lerichei* DART. et CASIER, 1949 – CASIER in DARTEVELLE & CASIER: 360 (no indication); Weka qu'à Manzadi [and] Kama M'Bote, Enclave de Cabinda [Central Africa]; 374: Manzadi, pt. IV [and] Weka, Bas-Congo; 384: Manzadi IV, Bas-Congo; Sénomien [Upper Cretaceous]; 384–385: Weka, Bas-Congo; Maestrichtien [Upper Cretaceous]; 388: Manzadi, Point IV, Base; 414: Congo et régions voisines; Maestrichtien [Upper Cretaceous], 425, pl. 18, figs 1, 4–6 (“Plaque pharyngienne supérieur incomplète [or] fragment”), figs 2 [and] 7 (“Plaque pharyngienne inférieur”), 3 (“Fragment de plaque pharyngienne”), and 8 (“Fragment de plaque dentaire supérieur”); Manzadi, Point IV, Bas-Congo.

Type locality: Manzadi IV, Bas Congo, Central Africa.

Age of type species: Crétacé, supérieur.

Type material: Lower and upper pharyngeal plates.

Remarks: The new genus *Eodiaphyodus* was placed by CASIER in DARTEVELLE & CASIER (1949) in the family Sciaenidae (?) according to WHITE (1931), who put *Diaphyodus* into the Sciaenidae with (?). By contrast ARAMBOURG (1952) put *Eodiaphyodus* in the Labridae. CASIER in DARTEVELLE & CASIER (1959: p. 360) is of the opinion that *Eodiaphyodus* should be placed within the “Sciaenidae (?)”. We tentatively agree.

Additional species:

Eodiaphyodus granulosis nov. sp. – ARAMBOURG 1952: 252–254, pl. 37, figs 45 (“Dentition(s) pharyngienne, série supérieure”), 46 (“Faces orales, section verticale d'un fragment”), 47 (“probablement une dentition pharyngienne inférieure”), and 48–51 (“Éléments dentaires isolées”); Ouled Abdoun et des Ganntour [Morocco]; Maestrichtien [Upper Cretaceous].—*Eodiaphyodus granulosis* – CASIER in DARTEVELLE & CASIER 1959: 414 (no indication); Maroc; Maestrichtien [Upper Cretaceous].—*Eodiaphyodus granulosis* – ARAMBOURG 1976: 66 (no indication); Ouled Abdoun [and] Ganntour [and] Meskala, Maroc occidental; Maestrichtien [Upper Cretaceous, and] Montien [Paleocene].

in Perciformes, ? in Sciaenidae [see WHITE 1931: p. 89]

Genus *Diaphyodus* SCHAFHÄUTL, 1863

* 1863 *Diaphyodus* – SCHAFHÄUTL: 246.

1931 *Diaphyodus* SCHAFHÄUTL (emend.) – WHITE: 89–90.

Type species: *Diaphyodus trigonella* SCHAFHÄUTL, 1863.

***Diaphodus trigonella* SCHAFHÄUTL, 1863**

1863 *Phylloodus trigonella* mihi – SCHAFHÄUTL: 246. [the name only]

* 1863 *Diaphodus trigonella* mihi [resp.] SCHAFH. – SCHAFHÄUTL: 246–247, 284, pl. 65c, fig. 15a, b.

Type locality: Maximiliansflötz [Kressenberg, Bavaria, FRG].

Age of the type species: [Middle Eocene]

Type material: Tooth plate.

Remarks: SCHAFHÄUTL (1863) probably used first the name “*Phylloodus trigonella*” but later he erected the new genus *Diaphodus*. – WHITE (1931: p. 89) erected the new subfamily Diaphyodontinae for *Diaphodus* and placed it within the “Sciaenidae (?)”.

Additional species:

Diaphodus ovalis mihi – SCHAFHÄUTL 1863: 247, 284, pl. 64, fig. 3a, b (Isolated tooth stuck); Achthaler Bergbau [resp.] Josephsflötz [near Kressenberg, Bavaria, FRG; ? Eocene].

Nummopalatus Sauvagei, nov. sp. – LERICHE 1900: 177–178, 194, pl. 1, fig. 2, 2a (Upper pharyngeal bone); Cuis, environs d’Epernay (Marne) [Paris Basin France]; sables a Unios et Térédines [Upper Ypresien, Lower Eocene].—*Labrodon Sauvagei*, LERICHE, 1900 – LERICHE 1906b: 349 (no indication); Cuis (Marne), Bassin parisien [France]; Yprésien [Lower Eocene]; 351 [and] 376: Bassin du Paris [France]; Yprésien [Lower Eocene].—*Labrodon Sauvagei* LERICHE – PRIEM 1908: 101, 128 (“plaques pharyngiennes supérieures”) Cuis (Marne), sables a Unios et Térédines; environs d’Epernay (Agéien); Pourcy (Marne); Bassin Paris; Yprésien sup. [Lower Eocene].—*Diaphodus sauvagei* (LERICHE) – WHITE 1931: 90–95, figs 146–149 (“Upper pharyngeal plates”, figs 150–156 (“Lower pharyngeal plates”), and 157 (Restoration of the lower and upper pharyngeal dentition); Abbey Wood, E London, Kent [United Kingdom]; Blackheath Beds, Ypresian [Lower Eocene]; 29 (no indications); England; Landenian [Upper Paleocene, and] Blackheath Beds, *etc.* [and] London Clay, Ypresian [Lower Eocene].

Remarks: Perhaps also add “*Nummopalatus trapezoidalis*” and of “Embiotocidae ? indéterminés” given below, see the remarks there.

Nummopalatus trapezoidalis, nov. sp. – LERICHE 1900: 178–179, 194, pl. 1, figs 3–5, 3a–5a (Upper pharyngeal bone); Cuis, environs d’Epernay (Marne) [Paris Basin, France]; sables a Unios et Térédines [Ypresien, Lower Eocene].—*Labrodon trapezoidalis*, LERICHE, 1900 – LERICHE 1906b: 349 (no indication); Cuis (Marne), Bassin parisien [France]; Yprésien [Lower Eocene]; 351 [and] 376: Bassin de Paris [France]; Yprésien [Lower Eocene].—*Labrodon trapezoidalis*, LERICHE – LERICHE 1908: 255–257, pl. 6, figs 3–5 (“Pharyngien supérieurs), fig. 6 (“Pharyngien inférieur”); Pourcy (Marne) [France]; Yprésien [Lower Eocene].—*Labrodon trapezoidalis* LERICHE – PRIEM 1908: 101, 128 (“plaques pharyngiennes supérieures”); Cuis (Marne), sables a Unios et Térédines; environs d’Epernay; Pourcy (Marne), Bassin Parisien [France]; Ypresien

[Lower Eocene].—*Labrodon trapezoidalis* LERICHE – LERICHE 1923: 190, 196, 200, pl. 8, fig. 23 (“pharyngien supérieur droit”), fig. 24 (“pharyngien inférieur”); Limay (Seine-et-Oise), Bassin de Paris [France]; Gravier de base du Calcaire grossier, Lutétien [Middle Eocene]; 196 [additionally]; Faluns de Pourcy; Sables à Unios et Térédines, Yprésien [Lower Eocene].

Remarks: WHITE (1931) was of the opinion that *Nummopalatus trapezoidalis* should be placed in synonymy with *Diaphyodus sauvagei* LERICHE.

Embiotocidae ? indéterminés – PRIEM 1901: 499–500, figs 7–10 (“Plaques pharyngiennes”); Cernay, environs de Reims [Paris Basin, France]; Eocène inférieur [Thanetien, Upper Paleocene].—Embiotocidés ? indéterminés – PRIEM 1908: 86, 87, 128; Bassin Parisien [France]; Thanetien [Upper Paleocene].

Remarks: WHITE (1931: p. 90) placed the above material, in synonymy with *Diaphyodus sauvagei* (LERICHE).

in Perciformes, *incertae sedis*

Eolabroides szajnochae (DE ZIGNO, 1887) – BLOT 1980: 377 (imperfect fish); Monte Bolca, Province de Verona, [Italy; Lower Eocene].—*Crenilabrus Szajnocha*, ZIGNO. – DE ZIGNO, 1887: 17–19, pl. [1], fig. 3 (imperfect fish); Monte Bolca [Italy; Lower Eocene].—*Crenilabrus (?) Szajnochae*, DE ZIGNO, 1887 – LERICHE 1906b: 386 (no indication); Monte Bolca [Italy]; Eocène.

Remarks: BELLWOOD (1999) noted that this species was not pharyngeognath, precluding inclusion in the Labroidei or Labridae. BANNIKOV & ZORZIN (2012: p. 7) agreed and placed it in the genus *Bradyurus* GILL, 1904.

in Perciformes, *incertae sedis*

in *Pterygocephalus paradoxus* AGASSIZ

(already by AGASSIZ 1835: pp. 295, 300, 312, 313):

Labrus malapterus – VOLTA 1796: 228–229, pl. 55, fig. 3 (imperfect fish); Monte Bolca [Italy; Lower Eocene].

in Perciformes, *incertae sedis*

in *Pygaeus gigas* AGASSIZ

(already by AGASSIZ 1835: pp. 294, 295, 302, 312, 313):

Labrus ciliaris – VOLTA 1796: 279–281, pl. 66 (imperfect fish); Monte Bolca [Italy; Lower Eocene].—*Labrus punctatus* – VOLTA, 1796: 189–191, pl. 46 (imperfect fish); Monte Bolca [Italy; Lower Eocene].—*Labrus rectifrons* DE BLAINVILLE 1818: 351.

in Perciformes, Scombridae

in *Thynnus propterygius* AGASSIZ

(already by AGASSIZ 1835: pp. 294, 305, 312, 315):

Labrus bifasciatus – VOLTA 1796: 204–205, pl. 50, fig. 1 (imperfect fish); Monte Bolca [Italy; Lower Eocene].

unknown

Otolithus (Crenilabrus) simplicissimus sp. nov. – SCHUBERT 1906: 652–653, 688, 695, pl. 4, figs 43, 44; (Otolith); Neudorf an der March [Devinska Nova Ves, [Slovakia]; Middle – Upper Badenien, Middle Miocene].—Espèce rejetée – NOLF 1981: 143 (Otolith); Neudorf [an der March = Devinska Nova Ves, Slovakia]; Badenien (Miocène) [Middle – Upper Badenien, Middle Miocene].

Pseudosphaerodon antiquus sp. nov. – CASIER 1966: 223–225, fig. 48, pl. 15, figs 6–9 (Tooth bearing bones, ? pharyngeal bones and isolated teeth); Sheppey (Kent) [England]; London Clay [Lower Eocene]

Remarks: see remarks for the type species of *Pseudosphaerodon*, *P. hilgendorfi* below.

“Auchenilabrus frontalis” AGASSIZ, 1845: 308 (nomen nudum) – CASIER 1966: 226.

Remarks: Primarily written *Anchenilabrus*, see also in: Labridae indet.

Pseudosphaerodon Hilgendorfi sp.n. – NOETLING, 1885: 104–106, pl. 11, figs 1–8 (Isolated teeth and tooth plates); Im samländischen Tertiär, Zone A1 [Late Eocene to Early Oligocene].

Remarks: *P. hilgendorfi* is the type species of *Pseudosphaerodon* NOETLING, 1885. WOODWARD (1901: p. 552) wrote for *Pseudosphaerodon*: “An extinct genus, possibly *Labroid*”. JORDAN (1963: p. 222) thought the same.

Pseudosphaerodon navicularis (WINKLER, 1878): *Gyrodus navicularis* WINKLER – WINKLER, 1878: 30–31, pl. 2, figs 19–21 (Isolated tooth); Uccle, [Belgium]; terrain bruxellien [Middle Eocene].—?: *Pseudosphaerodon*, WINKL. sp. – DAIMERIES 1889: XLIII–XLIV: Le Helmét [Belgium], Système paniselien [Lower/Middle Eocene]; Dieghem [and] Woluwe-Saint-Lambert [Belgium], Système bruxellien [Middle Eocene]; Saint-Gilles [and] Ixelles [Belgium], Système laekenien [Middle Eocene]; Wommel [Belgium], Système wommelien [Middle Eocene].—*Pseudosphaerodon navicularis* WINKLER, 1874 – LERICHE 1905: 167 (dents isolées); Bruxelles, Dieghem, Ixelles, Uccle, Woluwe-Saint-Lambert, Belgique; Bruxellien, [Middle Eocene], 196; Forest, Ixelles, Saint-Gilles, Uccle, Belgique; Laekenien [Middle Eocene], 212; Wommel, Belgique; Wommelien [Middle Eocene].—*Pseudosphaerodon navicularis*, WINKLER, 1874 – LERICHE 1906b: 262–263 (“dents isolées”); Bruxelles [and] Dieghem [and] Ixelles [and] Uccle [and] Woluwe-Saint-Lambert [and] Forest [and] Saint-Gilles, Belgique; Bruxellien resp. base du Laekenien, both Lutétien [Middle Eocene]; 270 [and] 273: Belgique; Lutétien [Middle Miocene]; 295 [and] 332: Belgique; Bruxellien [and] Laekenien

[Middle Eocene, and] Wemmeliën, Bartonien [Upper Eocene].—*Pseudosphaerodon navicularis* (T.C. WINKLER, 1874) – LERICHE 1951: 543 (molaires isolées); Schaerbeek, Uccle-Calevoet, Uccle, Woluwe-Saint-Lambert, Belgique; Bruxellien [Middle Eocene]; and Bruxelles, Ixelles, Saint-Gilles, Uccle, Woluwe-Saint-Lambert, Belgique; Ledien [Middle Eocene].

Remarks: See remarks for the type species of *Pseudosphaerodon*, *P. hilgendorfi* above. LERICHE (1906b) put *Pseudosphaerodon*, sp. of DAIMERIES (1889) in synonymy with *Pseudosphaerodon navicularis*.

Pseudosphaerodon pycnoides E.I.WH. – CASIER in DARTEVELLE & CASIER 1959: 398 (no indication); Nigeria; Eocene.

Remarks: See remarks for the type species of *Pseudosphaerodon*, *P. hilgendorfi* above.

kein Labroide. *Labrus parvulus* HECK. – KNER 1862: 487.—*Labrus parvulus* HECK. – HÖRNES 1848: 14; Margarethen in Ung. [St. Margarethen, Burgenland, E Austria]; Leithakalk [Upper Badenien, Middle Miocene].—*Labrus parvulus* – HECKEL 1856: 271, pl. 15, fig. 5 (imperfect fish); Margarethen [St. Margarethen, Burgenland, E Austria; Upper Badenien; Middle Miocene].—? *Labrus parvulus* HECK. – SCHUBERT 1906: 695; Margarethen [St. Margarethen, Burgenland, E Austria]; Mittelmiocän [Upper Badenien, Middle Miocene].—*Labrus parvus* HECK. – SCHULTZ in BRZOBOHATÝ & SCHULTZ 1978: 445 (tho quotation of HECKEL 1856 only); St. Margarethen, Bgld., Eastern Austria; [Upper Badenian, Middle Miocene].—“*Labrus parvulus*” HECKEL, 1856 – SCHULTZ 2013: 338, Abb. 46 (St. Margarethen, Burgenland, E Austria); Mittelmiocän [Upper Badenien, Middle Miocene].

Remarks: WOODWARD (1901: p. 540) noticed that the systematic position of this fish is “very doubtful” and “probably not Labroid”.

in Tetraodontiformes, Diodontidae

Phyllodus – GERVAIS 1867–69: 237, 239, pl. 48, fig. 5, 5a (Oral tooth plate); Castries, Hérault [S France]; Miocene.

Phyllodus corsicanus. LOCARD – LOCARD 1877: 11–12, pl. 1, figs 1–2 (Tooth plate); Bonifacio, Corse, France; Tertiaire [Miocene].—*Diodon corsicanus* LOCARD, sp. – PORTIS 1889: 379 (the quotation of LOCARD only); Elveziano o Tortoniano [Middle or Upper Miocene].

Scaroides gatunensis – TOULA 1909: 687–688, 738, fig. 3a–c (Oral tooth plate); Gatun, Panamakanal; Jungtertiär [Neogene].—aff. *Scaroides gatunensis* TOULA – SURARU & SURARU 1966: 72–73, 77, figs 12–15 (Oral tooth plates); V[alea] Plesca, Cluj [and] V[alea] Satului-Turnul Rosu (Porcesti) [Transylvanian Basin, Romania]; Eocène.—*Scaroides gatunensis* TOULA – SURARU, STRUSIEVICI & LASZLO 1980: 179–180, pl. 1, figs 4–11 (Oral tooth plates); “an der Wehre”, Cluj-Napoca [Transylvanian Basin, Romania];

Eozän.—*Scaroides gatunensis* TOULA – SURARU & SURARU 1987: 129, pl. 1, fig. 2a–c (Oral tooth plate); Baciú, [Transylvanian Basin, Romania]; Horizont des oberen Grobkalkes (= Clujer Kalkstein), Eozän.—*Chilomycterus hilgendorfi* (DAMES) – DICA 2002: 40, figs 1, 2 (Somes Dam, Plesca Valley, Baciú quarry (Cluj Napoca area) Varatecului Valley, Turbuta (Salaj district) [Romania]: Cluj Limestone [Late Eocene]. – Turnu Rosu (Sibiu district) [Romania]: Nisului Valley Formation [Late Eocene]).

Diodon incertus MICHELOTTI sp. – BASSANI 1899: 31–35, pl. 3, figs 66–68 (Tooth plate); Gassino, Piemonte [Italy]; Eocene.—*Phyllodus incertus* – MICHELOTTI, 1861: 355 (Tooth plate); Gassino [Italy].—*Diodon Rovasendae*, nov. sp. – PORTIS 1889: 371–375, 379 (Tooth plate); Gassino [N-Italy]; Bartoniano [Upper Eocene].

Concluding Discussion

One of the greatest benefits of the fossil record is the ability to place taxa in both place and time. Fossils are facts while phylogenies must always remain hypotheses. However, these facts are invariably constrained by our ability to identify forms and place them within a coherent phylogenetic or evolutionary framework. This is no more apparent than in the Labridae. With no morphology-based cladistic analysis of the family it is not possible to place many of the fossil taxa within known taxonomic groups. However, there are a few exceptions. The scarine (parrotfish) material can often be placed within extant lineages (BELLWOOD & SCHULTZ 1991), likewise the pseudodacine material (SCHULTZ & BELLWOOD 2004). However, perhaps the most striking of all records examined herein are those of hypsigenyine for consistency fossils. United by a unique pharyngeal morphology (phyllodont dentition; Fig. 1) the hypsigenyine fossil evidence offers a rare picture of the evolution of reef fishes based exclusively on fossil evidence. Unlike many fish groups, where the first (and often only) record in the fossil record is from Monte Bolca in Italy at 50 Ma (BELLWOOD 1996; BANNIKOV 2014; CARNEVALE *et al.* 2014), the Hypsigenyini have a relatively complete fossil record. The Hypsigenyini, and *Labrodon* in particular, offers a clear picture of a major (and readily identified) reef fish lineage with evidence of its form and distribution from the first record (in Bolca again) and throughout both the Eocene and Miocene (Fig. 3).

The fossil record of the Hypsigenyini offers strong support for patterns inferred from phylogenies. The suggestion that the Hypsigenyini is the earliest diverging lineage within the Labridae (COWMAN *et al.* 2009) is supported by the first record of the lineage in the Eocene with *Phyllopharyngodon* in Monte Bolca, one of the oldest descriptions of a labrid based on articulated material. The relatively widespread occurrence of this lineage during the Eocene points to a period of expansion in the Tethys, when western Europe was the cradle of evolution for tropical lineages (RENEMA *et al.* 2008). Remarkably, by the mid Eocene there are already records of the Hypsigenyini from Nigeria; presumably reflecting the extensive spread of tropical conditions at this time along the West African coast, facilitating the spread of tropical taxa along the African coast from the central Tethys (in the region where the Mediterranean lies today) (DILLEY 1973). By

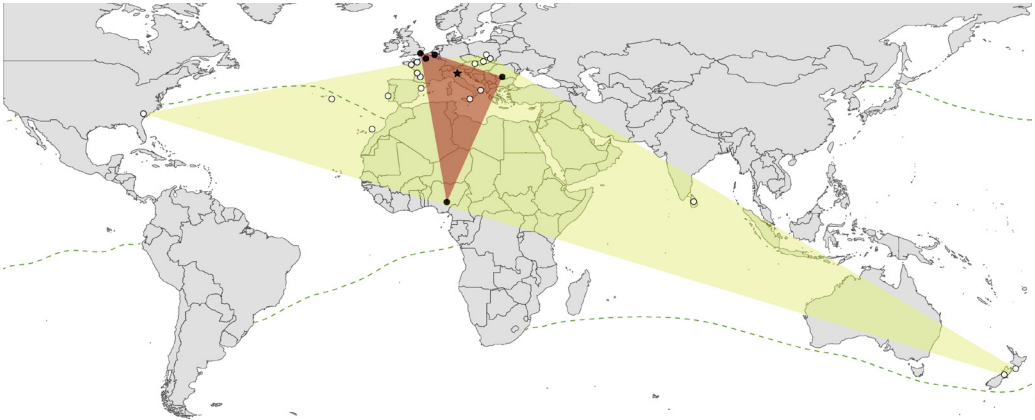


Fig. 3. The biogeography of the Hypsigenyini. The earliest record is in the Eocene of Monte Bolca (50 Ma), Italy (*Phyllopharyngodon*, marked with a star), later Eocene records of *Labrodon* (solid dots) show a central Tethys distribution, while the Miocene distribution (open dots; multiple records from central Europe not included for clarity) extends from the USA to New Zealand. Today the lineage is circum-tropical, often extending into temperate waters (dashed line delineates the extant geographic extent).

the Miocene, range expansion resulted in the geographic extent of the lineage extending from South-Eastern North America, across the Indian and SE Asian regions to Australia and New Zealand (Fig. 3). A pattern that strongly reflects both the expansion of reef fish lineages over time (COWMAN & BELLWOOD 2013; COWMAN *et al.* 2017) and the west to east relocation of the marine biodiversity hotspot (RENEA *et al.* 2008).

Although only based on fragmentary remains, the history of the Hypsigenyini, and *Labrodon* in particular, is one of success that mirrors reef fishes in general. This is marked by the earliest origins in the central Tethys, followed by major expansion in the Miocene and pan-tropical distributions today (BELLWOOD *et al.* 2017; COWMAN *et al.* 2017). Yet even in this successful group there is evidence of range reductions, with an apparent loss of the Hypsigenyini from the northern part of the East Atlantic and Mediterranean (Fig. 3).

In the remaining labrid groups, the fossil record offers a more fragmented view with the usual pattern of exceptional representation of taxonomic diversity in the Lagerstätte deposits of Monte Bolca in Italy, with 5 labrid genera to date (BANNIKOV & BELLWOOD 2017), and the Miocene deposits of St. Margarethen in Burgenland, Austria, with four genera, at least one of which represents an extant lineage (*Calotomus*) and an extinct genus *Trigonodon* which is sister to the extant *Pseudodax* (in the Hypsigenyini) (BELLWOOD & SCHULTZ 1991; CARNEVALE 2015). The remaining material is very hard to place within specific groups but it does exhibit a comparably wide biogeographic spread to that seen in *Labrodon*. Given the inability to reliably separate labrid pharyngeal material from other pharyngognath taxa, definitive conclusions about the history of the Labridae are not possible. These problems with the identity of pharyngeal fragments are reflected

by the extensive list of material, formerly placed in the Labridae, that needs reassignment. This material is almost invariably fragmentary and, although their placement in other groups must remain tentative, in many cases it is clear that they do not belong in the Labridae. In conclusion, the fossil record of the Labridae offers considerable challenges but, as with many groups, the fossils are able to offer invaluable insights. In the Labridae, the phyllodont hypsigenyine *Labrodon* offers a unique fossil-based view of the evolutionary history and biogeography of an important reef fish lineage.

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