

# The systematic position of the European Squalodontidae (Odontoceti, Mamm.)

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## 1. Introduction

The inventory of all, including the European, “shark-toothed Cetacea” by Kellogg (1923) is the most important publication on the Squalodontidae in recent decades. Simpson (1945) placed these Odontoceti in the superfamily Squalodontoidea.

The last inclusive survey of European finds was long ago; it was done by Brandt (1873/1874). Therefore all the material of European museums must be reviewed, because the bases are lacking for knowledge of the essential evolutionary tendencies in the morphological modification of the characters in the Squalodontoidea, which can only be achieved through extended, comparative morphological investigation.

Even for the dentition, which in other mammals deviates strongly, the attempt to comprehend characteristic features broke down at the beginning. This has led to many false conclusions, because one proceeded from incorrect assumptions, especially with regard to the meaning of the number of teeth and the number of roots; on these however the infrageneric taxonomy was mainly built.

Likewise the very variable relicts of the insertion of the third root in the upper molar region, which illustrate the reduction of the protocone portion of the tooth, are no generic characteristic. Also a sharp boundary between one- and two-rooted molars cannot be drawn. A separation of P & M on this basis is also not possible as Abel (1905) and Giorgio dal Piaz (1916) have already perceived without explaining it (cf. Colacicchi 1960).

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Thus once forms which belonged to different groups of species - with sub- genus rank - were collected in one species, and on the other hand genera and species were based on supposed differences, which in part did not exist or had narrow taxonomic meaning.

Hitherto almost only Miocene Squalodontidae have been described from the European area – dominantly from the Burdigalian to Tortonian – while for the Oligocene a widespread gap in the records appears to exist, as with all cetaceans. However, the Oligocene is one of the most important time gaps for the phylogeny of whales.

Even Aquitanian\* Squalodontidae long appeared to be lacking. In 1960 Thenius reviewed the little described Oligocene finds. He emphasized then the apparent Aquitanian age of a find from the upper Melker Sand at Oberitzberg (Lower Austria), as well as the Aquitanian age of the *Squalodon* find from Bolzano-Belluno in northern Italy (dal Piaz 1901, 1916), which previously had been placed in the Burdigalian.

The present revision and new description also points out Oligocene Squalodontidae, so that the Oligocene gap in the record of the history of the small toothed whales is smaller than hitherto supposed. For the others it appears that a connection to the Agorophiidae exists, contrary to the assumptions of several authors. Therewith were the essential tendencies and stages of the morphological modification of the Squalodontoidea comprehensible for the time from the lowermost Oligocene to the Tortonian and Messinian respectively (Deurnian, cf. Anderson, 1961:169, Table).

## 2. Terminology, Measurements, Indices

Up to now a compulsory terminology has been lacking for the description of the teeth of the Squalodontoidea. Therefore there must be a short introduction to it here. The anterior 3 or 4 molars

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\* Lower Miocene

are single-rooted, with higher, sharper, bilaterally moderately flattened crowns. Farther caudally they are 2-rooted, in the upper jaw often with relict third, lingual root sockets. In the sketch is shown last a 3-cornered, bilaterally strongly flattened crown with tips in the form of small conical “toothlets” on the anterior and posterior edges. These first-order tips will be called denticuli (*denticulus* -i, m. Lat. = toothlet) (denticulus anterior = dentic. ant. for the anterior edge, dentic. post. for the posterior). Most difficult to describe are two small enamel papillae that more or less border the (papillated) enamel edges on the flanks of the crown and will here be called cristae rugosae (*crista*, f., Lat., = edge; *rugosus* - a - um, Lat. = rough) (= cr. rug.).

The following dimensions of teeth are important:

a = ant.-post. dimension of the base of the crown;

ad = base dimension of the largest dentic. post. measured along the edge of the tooth (Fig. 1).

Apical angle = angle, which is included if one subtends the side from the apex of the tooth crown to the oral and caudal endpoints of the base of the crown, and at the same time produces an index for the proportion a: crown height.

cr-density = number of cr. rug. in 5 mm (about 5 mm apicalward from the base of the crown, close caudal from the middle of the labial side).

One of the most important indices is the Index Denticulorum:

$$ID = \frac{ad * 100}{a}$$

All molars will be numbered from anterior to posterior and accordingly designated as buccal tooth 1, 2 etc. (= B<sup>1</sup>, B<sup>2</sup>, and B<sub>1</sub>, B<sub>2</sub> etc.). The problems of homologizing the B with the P & M of other mammals will be discussed in another place.

### 3. Taxonomic part

#### Superfamily Squalodontoidea Simpson, 1945

The superfamily Squalodontoidea was set up by Simpson (1945:100, 215) without demarcation. It includes the oldest and most primitive hitherto known Odontoceti. The “telescoping” process, through which primarily in the Odontoceti the nasal opening and in the following part the maxillae (Max; cf. also Fig. 2) and intermaxillae (premaxillae) (Imx) were displaced under increasing compression of the cranium on the skull, has also in the most ancient known forms already been clearly established. The Imx have teeth, as in normal mammalian dentition. All forms have heterodont and – as far as is known – already polyodont dentition. The B are bilaterally flattened and show in the lateral view somewhat triangular crown outline. The sharp edges ant. & post. are in the caudal B more or less trimmed with denticles. The lingual part of the tooth, homologous to the protocone part of the tribosphenic plan of the upper B of the Theria is sometimes completely, sometimes extensively, reduced, as is the third, lingual root.

This superfamily includes two developmental stages of the Odontoceti, which are combined in the ancestral Agorophiidae Abel, 1913, and the more progressive Squalodontidae Brandt, 1873. The previously assumed range of these two families, which in part are insufficiently defined, is shifted somewhat. Thus the phylogenetic position is precisely defined. Both families are demonstrated as developmental stages, and especially the early stage, which the Agorophiidae represent, would run through all Odontoceti lines. In any case one cannot say that the Agorophiidae stand apart, as many authors, e.g. Slijper (1936:545, 1962:75), believe. Only certain genera of the Agorophiidae – within this evolutionary stage – could stand aside from the main line of evolution that is not yet recognizable at this time.

Fam. Squalodontidae Brandt, 1873

The Squalodontidae are distinguished from the Agorophiidae especially by progressive “telescoping.” The nares (Nar) have migrated farther on the cranium, so that the caudal border of the external nares lies clearly behind the level of the middle of the orbits. Because at the same time the insertion for the musculus maxillonasolabialis (Lawrence & Schevill 1956:136, 137, 148) was enlarged and displaced backward, as a result of the displacement of the nares the maxilla and premaxilla are moved far back on the cranium. The so-called supraorbital plate of the maxilla therefore reaches the caudal border of the supraorbital process of the frontal. The frontals are thus in part covered over, so that their connection with the cranial root as far as the supraorbital process is no longer visible. The pushing up of the maxilla is expressed in an index (ratio of the amount of pushing up to the length of the cranium), which for the Squalodontidae amounts to 50%–76.5% against 17.6%–40% for the Agorophiidae.

In the drawing of the “telescoping” process the parietals on the cranial root already have lost their medial contact with each other, whereas in the Agorophiidae they still show the normal condition.

Also the postorbital intertemporal constriction of the cranium is strongly formed again through the “telescoping,” whereas the Agorophiidae also here show quite the normal relation in mammals.

The ancestral family shows also in the lateral view yet an attenuated cranial outline (margin) and a higher rostral base, characters that stand nearer to the proportions in land mammals and Archaeoceti.

On the other hand the Squalodontidae already are substantially more progressive, with gradually increasing compression of the cranium and a rounding off of the rostral base.

Within the Squalodontidae it is possible to distinguish two further evolutionary stages, which will be considered as subfamilies and are illustrated by upper Oligocene finds. In the Miocene only the more progressive of these stages is yet represented.

According to Abel (1913) the forms of the ancestral subfamily were separated from the line (Kreis) of the Odontoceti. Now will the gap between the evolutionary stages of the Odontoceti, which appear to split in the Oligocene, through the upper Oligocene forms be considerably reduced.

#### Subfamily Patriocetinae Abel, 1913

The forms *Patriocetus ehrlichi* (V. Beneden, 1865) and *Agriocetus incertus* (Brandt, 1874) considered by Abel (1913) as Archaeoceti and forerunners of the Mysticeti and placed in a single family from a subfamily of the Squalodontidae. They should be labeled with the family name employed by Abel (1913) as Patriocetinae. This subfamily represents a stage in the evolution of the Squalodontoidea that I might label as protosqualodontid (Fig. 2a). The nominal genus is *Patriocetus* Abel, 1913 with the type species *P. ehrlichi* from the Linz sands of the Chattian, upper Oligocene, of Linz/Donau Austria.

Diagnosis: The parietals are separated from each other, but participate still to a considerable extent in the structure of the cranial roof part. The parietals still separate the maxillae from the supraoccipital. The intertemporal constriction is strongly marked.

Remarks: According to our present knowledge, only *Patriocetus ehrlichi* (V. Beneden, 1865) and *Agriocetus incertus* (Brandt, 1874) from the upper Oligocene of Linz belong in this subfamily. Abel's conclusions depend obviously on erroneous hypotheses and observations. Here ancestral forms are provided with a mosaic ground-plan, in which the supraorbital plates of the maxillae are shoved up on the cranium in the normal odontocete manner. Abel considered fractures

as boundaries of bones, and for that reason was especially convinced that here representatives of the Archaeoceti and forerunners of the baleen whales existed previously whose maxillae were not shoved back. In the Patriocetinae the parietals are in the process of “telescoping” already separated from each other, but still participate in the structure of the cranial root. Thus they are clearly distinguished from the second subfamily of the Squalodontidae.

Subfamily Squalodontinae n. subf.

The subfamily Squalodontinae includes most of the known Squalodontidae and is clearly progressive. It represents a stage of evolution that is essentially recognizable by the progressive “telescoping,” which I may label as eusqualodontid (Fig. 2b, c). The nominal genus is *Squalodon* Grateloup, 1840.

Diagnosis: A subfamily of Squalodontidae with the following peculiarities: the parietals are excluded from the structure of the cranial roof, and the maxillae and supraoccipital are no longer separated from one another by these bones. The intertemporal constriction is extensively eliminated.

Remarks: Three European genera belong to this subfamily, both well-known genera: *Squalodon* Grateloup, 1840 and *Neosqualodon* dal Piaz, 1904 as well as a new, ancestral genus, *Eosqualodon* n.g.

*Eosqualodon* n.g.

Derivatio nominis: *Eos* f., Gr. = dawn; *Squalodon*.

Type species: *Eosqualodon langewieschei* n. sp., whose holotype comes from the upper Oligocene of Bunde (Westphalia) (p. 90, Pl. 11, Fig. 1; Fig. 2b). The holotype of the type species of this new genus was found in 1911 through the attention of gymnasium Professor Langewiesche.

Diagnosis: Longirostrine genus of the subfamily Squalodontinae n. subf. in the family Squalodontidae, with the following characters: the base of the rostrum is still relatively wide. The caudal border of the external nares (blowhole) lies at the height of the caudal part of the orbits. The maxillae are with their supraorbital plates shoved farther back on the cranium than in the less progressive genera belonging to the Patriocetinae and Agorophiidae; they have completely overlapped the frontals and reached the supraoccipital. In the region of the orbit (facial skull) the intermaxillae are only moderately widened. The intertemporal constriction is only weakly developed, but the width of the skull remains here still clearly less than the width of the supraoccipital, which is broadly rounded. In outline the cranium appears faintly trapezoidal, in lateral view it exhibits a slightly extended, box-shaped elevation. The base of the rostrum is moderately high, but shows a distinct, if also weak contraction of the ventral lateral border.

The pterygoid sinuses (Sin. pt.) are small and short. The choanae (Cho.) lie far caudally.

Remarks: This genus is closely related to the genus *Squalodon*. But in *Squalodon* many characters are modified in a progressive direction. Thus the base of the rostrum is relatively narrower, and the caudal border of the external nares lies distinctly farther back over the apex of the zygomatic process (Proc. zyg.). Also the maxillae are shoved farther backward, and the intertemporal constriction is more strongly eliminated, so that the width of the supraoccipital is reached or overlapped. The Sin. pt. are larger and longer and the Cho. lie distinctly farther rostral.

These are characters of a more progressive phase of the eusqualodontid stage than in *Eosqualodon* n.g. With *Eosqualodon* is present the earliest hitherto known phase of eusqualodontid

stage in the evolution of the Squalodontidae. Here are the essential steps, especially in the “telescoping” process, as they would be mentioned in the characterization of the subfamily, but several ancestral characters are still retained.

Within the genus *Eosqualodon* two species can be included:

*Eosqualodon langewieschei* n.g. n.sp.

Plate 11, Fig. 1

Derivation nominis: Compare p. 88; Langewiesche, Friedrich, gymnasium Professor 1897–1960. Founder of the Bünde District Native Land and Tobacco Museum; he was responsible for the preservation of the holotype. The specific name serves as a *nomen nudum*.

Holotype: Quite complete skull (Plate 11, Fig. 1), atlas, axis, several dorsal and caudal vertebrae. Storage: Bünde District Native Land and Tobacco Museum (Westphalia), No. 326.

Paratypes: Distal rostral fragment, 531-1, Geol.-Pal. Institut Göttingen; right proximal lower jaw fragment, A540, Geol.-Paläontol. Institut Münster (Westphalia); lower back tooth, 7, 1 private collection of Dipl.-Ing. Witte, Bünde (Westphalia), Herforder Strasse 25.

Not completely certain is the species membership for: *Eosqualodon langewieschei* n.g. n.sp.? Two teeth of the proximal left lower jaw (?), Ter. 4, Geol. Landesamt Nordrhein-Westfalen, Krefeld (Rothausen, 1958: 370, 371, 373; Fig. 4).

Locus typicus: Doberg bei Bünde (Westphalia).

Stratum typicum: Chattian, Oligocene.

Diagnosis: A species of the genus *Eosqualodon* n.g. with the following specializations: the premaxillae form a sharp, accentuated prenasal constriction of the dorsal opening of the rostral canal, and the end caudally probably bluntly on the apex of the nasal-frontal suture. The surface of

the forehead plate is flat and lacks sculpture. The zygomatic processes of the malar are curved along a short arc. The incisura antorbitalis (Inc. *antorb.*) is slit-like. Moderately high crowns with a high degree of symmetry with low values for  $\underline{a}$  and narrow apical angles are characteristic of the buccal teeth. The edges of the buccal teeth have a maximum of 4 large denticles, the index denticulorum is 22-28% – apparently high. Very heavy cr. rug. with strong papillae are present (thickness of cr. = 7–9 for the upper buccal teeth).

Remarks: In the same genus is also to be placed the form mentioned by Capellini (1904: 445, Fig. 1, 2) as “*Squalodon bariensis* Jourd. var. *latirostris* Cap.” from the supposed Miocene (or) from the upper Oligocene *Arenaria calcifera* of Schio in northern Italy. It represents an additional species, *Eosqualodon latirostris* (Capellini, 1904) and is distinguished among other things by gradual and slight contraction of the dorsal opening of the rostral canal, by abruptly ending premaxilla caudal to the nasal-frontal suture, and by a relatively wide sculptured forehead plate with raised middle part.

These are distinguishing characteristics which characterize two groups of species in *Squalodon* (pp. 91, 92).

#### *Squalodon* Grateloup, 1840

Type species: *Squalodon grateloupi* von Meyer, 1843.

Of the genus names cited by Simpson (1945:100), *Rhytisodon* Costa, 1852 (erroneously attributed by Simpson to Paolo, 1897) and *Trirhizodon* Cope, 1890 fall into synonymy with *Squalodon*. The most important advanced relationships are to *Eosqualodon* n.g. (pp. 89, 90). Table 1 gives a summary of the European species of the genus in chronological order.

Table 1. Chronologic and geographic distribution of the European species of *Squalodon*.

<i>Squalodon</i> a n. sp.	Tortonian/Messinian, NW Belgium
<i>S. antverpiensis</i> V. Beneden, 1861	Tortonian/Messinian, NW Belgium
<i>S. servatus</i> (V. Meyer, 1841)	Helvetian, S. Germany
<i>S. dalpiazii</i> Fabiani, 1949	Upper Burdigalian, Sicily
<i>S. zitteli</i> Paquier, 1893	Burdigalian, S Germany
<i>S. bariensis</i> (Jourdan, 1861)	Burdigalian, SE France
<i>S. melitensis</i> (Blainville, 1840)	Burdigalian, Malta
<i>S. kelloggi</i> n. sp.	Lower Burdigalian, SW France
<i>S. grateloupi</i> V. Meyer, 1843	Lower Burdigalian, SW France
<i>S. bellunensis</i> Dal Praz, 1916	Aquitanian (somewhat higher) N. Italy
<i>S. catulli</i> Zigno, 1876	Aquitanian, N. Italy

Two groups of species can be distinguished within the genus *Squalodon*, which doubtless belong to subgeneric rank. However, part of the species fall outside of both groups and is insufficiently known or solitary. Thus these species also cannot be placed in subgenera. Therefore assignment of both well-defined groups to subgenera will be made on a taxonomic basis.

The first of the two species groups will be named the *catulli*-group after the most primitive species, the second the *bariensis*-group after the best classical species. They are defined here only by several differences characteristic of these groups in skull structure and dentition. The *catulli*-group exhibits premaxillae whose caudal ends, pointed and long drawn out, end caudal to the nasal-frontal suture, while those in the *bariensis*-group are usually blunt, but in any case short, and end at the apex of the nasal-frontal suture. In the first species group the frontal plate exhibits an arched,

rostrally round-ended middle part, with a nearly cigar-shaped little bone element of unknown position in the median suture between the nasals and with irregular, rostrally converging furrowing. In the second group, on the other hand, the frontal plate is flat and smooth (Fig. 2b, c; corresponding to the above-mentioned relation of *E. langewieschei* to the *bariensis* group; p. 92).

In lateral view the first group displays a dorsally rounded outline of the frontal plate and a strong facial depression, the second a more triangular rounded outline and an extensively eliminated depression. Also the dentition is clearly different. Chief differences are: the lack of the homologue of the fifth buccal tooth of the *bariensis*-group in the *catulli*-group, higher value of  $a$  (anterior-posterior length of base of crown) for the teeth of the latter through lengthening of the caudal part of the tooth crown and thus stronger asymmetry as well as a greater apical angle, more numerous denticles, smaller value for the index denticulorum, and higher number of crista rugosa per 5 mm in the *catulli*-group.

In these morphological characteristics the group around *Squalodon catulli* connects closely to *Eosqualodon latirostris* (Capellini), and the group around *Squalodon bariensis* just as closely to *Eosqualodon langewieschei* n. sp.

The *catulli*-group is named after the oldest and most primitive species from the Aquitanian of Libano (northern Italy), which was for a long time assigned to *S. bariensis*, because Giorgio dal Piaz (1901, 1916) saw no essential difference from this species. However *S. catulli* Zigno, 1876 (Plate 11 Fig. 2) shows characteristics outside of the group characteristics, which must be considered as ancestral within the genus.

To this belong a still relatively wide rostral base and clearly emphasized widening in the malar region. In lateral view appears, first through moderately strong reduction of the ventrolateral borders, the rostral base to be relatively little leveled off. It could be that the Squalodontoidea

clearly underwent a development from rostra with a wider and higher base of quite a land-mammal type to those with a narrower, flatter base. This process has already progressed far in *Squalodon*, but not yet completed within the genus. The cranial ground-plan is slightly trapezoid in *S. catulli*, also a distinct characteristic – with attenuated cranium – to be found in older Squalodontoidea and which appears in land-mammal-like lines.

In younger Squalodontoidea, especially in younger species of *Squalodon*, the ground-plan takes on an increasingly rectangular form.

Corresponding tendencies of the supraorbital process to ascend rostrally and dorsally, and of the antorbital process and the postorbital process to thickening, are also first clearly defined in *S. catulli*.

A hitherto undescribed rostral fragment with narrow part of the facial portion of the skull and part of the facial portion of the skull and part of the mandibular ramus is to be considered as a paratype on this species, which is preserved without a number in the Instituto di Geologia dell'Università di Torino (Italy). The specimen also comes from the Aquitanian of Bolzano-Belluno (Plate 11, Fig. 2).

In the same group belongs *S. bellunensis* dal Piaz, 1916 from a higher level of the Aquitanian of the same collecting area with clearly progressive development of the just-mentioned characteristics.

Also the type species through later fixation (von Meyer 1843: 704), *S. grateloupi* von Meyer, 1843 from the lower Burdigalian of Leognan near Bordeaux belongs here and displays a progressive status in the above-mentioned characteristics. The oldest published discovery of a representative of the Squalodontidae (Scilla 1670: 61, 165: Plate 12, Fig. 1) comes from the Burdigalian of Malta and also represents a species, *S. melitensis* (Blainville, 1840), which must be

placed in the *catulli*-group according to the form of the tooth crowns (see above). Contrary to the conception of Fabiani (1949: 28) “*S. scillae* (Agassiz)” falls into synonymy.

A new species will be provisionally designated, for lack of adequate material, as *Squalodon* a. It will be separated from the species *S. antverpiensis* van Beneden, 1861, whose peculiarities it lacks, while definite tooth characteristics of the *catulli*-group are recognizable.

*Squalodon* a.

Plate 12, fig. 4

Proximal right rostral fragment, with fourth upper buccal tooth from the back (B<sup>8</sup> or B<sup>9</sup>?), root remains of the third from the back, and double alveolae of both the upper posterior buccal teeth (Pl. 12, fig. 4). – Location: Ct.M.505., 1T, Institut Royal des Sciences Naturelles de Belgique, Brussels.

Locus typicus: Fort No. 4 at Vieux-Dieu near Antwerp, Belgium.

Stratum typicum: Lower sands, Aversian, Tortonian, Miocene.

Diagnosis: An apparently separate species of *Squalodon* with tooth characteristics of the species-group of *S. catulli*.

Special characteristics are probably the complete lack of relict third roots on the upper posterior buccal teeth, the very small caudal root branches, the extensive re-forming of the anterior denticles and the relatively large apical angle.

The relationship to the *catulli*-group is uncertain for a remarkably unique lower jaw. This discovery certainly represents a new species:

*Squalodon kelloggi* n. sp.

Pl. 11, Fig. 3

Derivatio nominis: This species is named after Dr. Remington Kellogg, whose contributions are known and who in 1923 conjectured on the existence of this form.

Holotypus: Damaged right lower jaw section with B<sub>5</sub> and B<sub>8</sub>. – Fischer, *Melanges cetologiques*: 12, Plate 2, Fig. 3, 1868; (Plate 11, Fig. 3).

Location: Number illegible, Museum d'Histoire Naturelle Bordeaux, (label: “*Squalodon grateloupi* Leognan, 1876, Soc. Linn. XXVII, p. 12, pl. 2, Fig. 3”; a label is missing).

Locus typicus: Leognan, S. Bordeaux, Graves, Dept. Gironde.

Stratum typicum: osseous Molasse, Faluns de Leognan, lower Burdigalian, Miocene.

Diagnosis: A species of the genus *Squalodon* with the following characters (of the only known lower jaw): the lower jaw is remarkably short and sturdy with very low development of the tooth-bearing part in contrast to the caudal tooth-free part. The apex of the lower jaw curves – in contrast to all other species – distinctly dorsally, and the symphyseal part is unusually wide. The bilateral dimension of the alveolae are – especially in the symphyseal part – in contrast relatively very narrow. In the teeth the measurement of a corresponds to that of the *catulli*-group, but the apical angle is through the higher, slimmer crown shape of the teeth, which also have a higher degree of symmetry, smaller than that.

For the second species-group the species is plainly characteristic, having been long combined with the *S. catulli*-group, *S. bariensis* (Jourdan, 1861) from the Burdigalian of Barie at Saint-Paul-Trois-Châteaux (France). This species is clearly more progressive than *S. catulli*, as the analysis on p. 92 has adduced, which pointed out progressively modified characters within the genus.

In the *bariensis*-group also belongs *S. zitteli* Paquier, 1893 from the Burdigalian of Bleichenbach at Passau. This species demonstrates, in contrast to *S. bariensis*, further progressive modification of several characters.

*S. servatus* (V. Meyer, 1841) is known from the Helvetian of Baltringen at Ulm, a poorly illustrated species, which one must however place in this group.

Of European species there remain two certainly outside the above-mentioned groups: *S. dalpiazii* Fabiani, 1949 and *S. antverpiensis* V. Beneden 1861.

The first species, from the upper Burdigalian of Tabuna at Ragusa (Sicily), is only well known by its tooth characteristics. In these it deviates clearly from both groups. The anterior buccal teeth are relatively stubby while the posterior ones have relatively high triangular crowns. Denticles are found only far caudal in strongly reduced number and modified form. Crista rugosa are almost completely absent.

To be considered as paratype is a specimen from the same beds, placed by Colacicchi (1960) in *S. bariensis* (in the sense of Dal Piaz).

*S. antverpiensis* must, aside from the separation from *Squalodon* a, be split into two subspecies. Thus the definition of this species will be made precise, as it was already known indistinctly by V. Beneden (1865: 25, 27; 1868: 11) and Brandt (1873: 321, 322; 1874, 33).

*Squalodon antverpiensis antverpiensis* V. Beneden, 1861

Plate 12, Fig. 5

Lectotypus: Maxillary fragment with three upper buccal teeth and a remnant of the premaxilla. – Beneden: Mammifère nouveau...: 24, 28 (partim), 1861, (Plate 12, Fig. 5). – Location: Ct. M.517, 2T, Inst. Roy. Sci. Nat. Belgique, Brussels.

Paralectotypes: Right rostral point with three teeth, Ct.M. 502, 3898., Institut Royal des Sciences Naturelles de Belgique, Brussels. Beneden, Recherches sur les ossements ...: 28, Pl. 1, (partim), 1865; broken maxillary fragment with one buccal tooth, Ct. M. 503, 3898, in the same museum.

Locus typicus: Fort No. 4 at Vieux-Dieu, near Antwerp, Belgium.

Stratum typicum: Black sands, lower sands of Antwerp, Aversian, Tortontian, Miocene.

Diagnosis: A subspecies of *S. antverpiensis* with laminated course of the crista rugosa without papillization and with lower crista thickness (8-10). A crenellation of the backs of the anterior teeth is almost completely absent. Moderately strong anterior denticles are formed, and the ID is less (21–23%) than in the other subspecies, whose posterior denticles are also relatively smaller.

*Squalodon antverpiensis papillatus* n. subsp.

Pl. 12, figs. 6 & 7

Derivatio nominis: *papillatus* -a, -um, Latin = provided with tubercles; on account of the strongly papillate crista rugosa.

Lectotypus: Lower Jaw fragment of the symphyseal region with a part of the teeth. – Beneden, Recherches sur les Squalodons, Suppl.: 3-12, Plate without number, Fig. 1, 2, 1868. (Pl. 12, fig. 6). – Location: Ct.M. 508 A (left), Ct. M. 508B (right), Institut Royal des Sciences Naturelles de Belgique, Brussels.

Paralectotypus: Double-rooted upper left? buccal tooth of middle position, Series PX No. 213, Institut Royal des Sciences, Naturelles de Belgique, Brussels (Pl. 12, Figs. 7, 7a).

Locus typicus: Neighborhood of Antwerp, Belgium.

Stratum typicum: same as for the lectotype of the type subspecies.

Diagnosis: A subspecies of the species *S. antverpiensis* with the following characteristics: anterior teeth with very strong and irregularly rugose enamel, as well as with very strongly crenellated blades. The posterior teeth show lingually a similar – characteristic of the species – converging course of the crista rugosa toward the middle as in the other subspecies, but the cristae rugosae are less dense and have strong papillae. The anterior denticles are very strongly formed and the ID is very high (25%).

For several finds of single teeth of *Squalodon* from the south German Molasse is a sufficient indication not possible. They can be assigned to no known species for want of comparable renditions. The assignment of such teeth to *S. catulli*, *S. servatus*, etc., as would often be undertaken, is not tenable. However, since some of these teeth can belong to previously described species, in which the count is insufficiently known, mutually definable groups of such teeth must be named in open nomenclature, in order not to hinder an eventual later possible classification.

A group of smaller teeth from the south German Helvetian Molasse will be designated *Squalodon* b, a group showing somewhat larger measurements as *Squalodon* c, and a third with still larger size as *Squalodon* d.

The characters of the periotics and bullae of the family are now as far known, that ear bones are recognizable without difficulty as those of Squalodontidae. On account of the small number of finds in situ it is however so far not possible to define systematically the characters of genera, species groups and species. Single finds from the Helvetian Molasse or South Germany may be placed in *Squalodon*.

*Neosqualodon* Dal Piaz, 1904

This genus would be considered for the most part as a progressive form, which was derived from *Squalodon*. However, Fabiani (1949: 22) conjectured correctly that here is a genus derived independently from the Agorophiidae.

These little Squalodontidae show several ancestral characters, which are combined with the nearest most striking progressive habitus properties in a mosaic manner. The length of the rostrum and the numerous teeth fall more as ancestral characters than for instance the thin supraorbital process, which hardly forms an angle on the skull axis, or the symmetrical, low form of the buccal teeth with large denticles.

Quite unique is the strongly elongated antorbital process, on whose ventral side the jugal is directly attached. Such an independent genus must certainly stay in a separate family, but so long as a “horizontal” classification must be retained, one cannot depart from it in this case.

With regard to the general stage of evolution this is an eosqualodontid form, which is to be classified in the Squalodontinae.

Within the genus hitherto three species have been distinguished. They must however be reduced to two, while the ancestral species, *N. gastaldii* (Brandt, 1873) is divided into three subspecies.

The form distinguished by Fabiani (1949: 6, Pl. 1, Figs. 5–8) as “*N. gemmelaroi*” belongs accordingly as a subspecies of *N. gastaldii*. (The indication of the subspecies follows in another place.) The type species of *Neosqualodon*, *N. assenxae* Dal Piaz, 1904 from the upper Burdigalian of Schio at Modica (Sicily) is distinguished from the other species by a broader skull and rostrum, as well as relatively broader premaxilla, and also through the parallel arrangement of the denticle axes on the axes of the tooth crowns. In *N. gastaldii* the denticle axes diverge strongly.

In *N. assenzae* must be placed a find as paratype, which Fabiani (1949: 11) placed in his species "*N. gemmelaroi*": rostral and facial fragments of the skull, tooth impressions, right dental canal mold, without catalog number, Istituto e Museo di Geologia dell'Universita, Palermo (Pl. 12, fig. 8).

#### 4. Conclusions

The oldest hitherto known remains of Odontoceti come from the Jackson group of South Carolina, which according to Cooke & MacNeil (1952:27) is to be assigned to the lower Oligocene.

The forms found there belong, like all known pre-Aquitania Odontoceti, to the Squalodontoidea, and indeed to the ancestral family, the Agorophiidae, which are considered by many authors as a separate group (Slijper 1936: 545, 1962: 75; Thenios & Hofer 1960: 183).

From the middle Oligocene there are only isolated Squalodontoidea remains, whose position is uncertain. From positive upper Oligocene there are known only a few unequivocal Squalodontidae remains and isolated Squalodontoidea of uncertain position.

First with the lower Miocene, together with all modern superfamilies of Odontoceti, there was also well-marked a short time of flowering of coming Squalodontidae, culminating in the Burdigalian.

Through the revision it appears that the temporal, morphological, and phylogenetic distance between the oldest and next younger well-preserved finds is substantially smaller than hitherto assumed. Of course there are in the Oligocene new and probably meaningful finds only in the Chattian. These throw some light not only on the upper Oligocene time segment, important for the phylogeny of the Odontoceti, but also indirectly on that of the middle Oligocene.

The general scarcity of finds brings with it, that only stages of the general phylogenetic development can be known, but not evolutionary lines. Such stages correspond to the customary horizontal taxonomic classification of the Squalodontoidea into the two, in their extent now sharply distinguished, families of the Agorophiidae and the Squalodontidae.

The Patriocetinae n. subf., an ancestral group within the Squalodontidae, with the taxa *P. ehrlichi* and *A. incertus*, form the bridge in the proportions of the skull structure between the Agorophiidae on one side and the younger Squalodontidae as well as the modern Odontoceti on the other side. That is expressed especially in the stage, which the “telescoping” process has reached in these taxa. Here the parietals take – in contrast to the Agorophiidae – already separated in the middle from each other, contrary to the structural plan in all other Odontoceti still in essential extent in the formation of the divided skull roof. On the other hand the supraorbital plates of the maxillae have already fully overlapped the supraorbital processes of the frontals as in the modern Odontoceti. They are however separated from the supraoccipital by the parietals as in the Agorophiidae. Also the nares reach with a position of the nostril-caudal border caudal to the height of the middle of the orbits a stage of displacement, which clearly exceeds that of the Agorophiidae. However the stage of displacement of the more progressive Odontoceti is not reached.

On the other hand the intertemporal constriction is still clearly present and the braincase in lateral view is still stretched out in the shape of a box. Also the base of the rostrum still remains wide and high. These are characters, which divide these forms from the Agorophiidae (p. 87).

Here certainly are present upper Oligocene *Superstites*<sup>\*</sup> of a protosqualodontid<sub>stage</sub> of evolution probably distributed in the younger middle Oligocene, which at least with regard to *Patriocetus* must remain somewhat aside from lines leading farther, and preserve several archaeocetoid traits.

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\* Can't find this in dictionary [Translator's note]

Archaeocetes, as they were seen by Abel (1913), Slijper (1936: Table 253; 1962: 70, 417, Lavocat (1955: 412), and ancestors of the Mysticeti, as Abel (1913), Marples (1956: 566) and Deschaseaux (1961: 878) believed them to be, are not here under consideration in any case.

The eusqualodontid stage, represented by the Squalodontinae n. subf. has, like *Eosqualodon* n.g., sprung from progressive forms in the upper Oligocene (*Prosqualodon davidi* Flynn, 1923, upper Oligocene or lower Miocene of Tasmania; “*Prosqualodon*”? *hamiltoni* Benham, 1937, upper Oligocene of New Zealand).

In the essential traits of the “telescoping” these forms correspond extensively to the modern Odontoceti. Here the parietals are completely separated from the structure of the roof of the braincase, and the maxillae are pushed farther onto the braincase. The intertemporal constriction is thus completely eliminated, and the base of the rostrum begins to be narrowed and flattened. In the early phases of the eusqualodontid stage the stretched out, box-shaped outline of the braincase is preserved, which here would have led to substituting for primitive characters of these early forms.

Interesting in contrast to the younger Squalodontinae, modern Odontoceti, and above all land mammals, is the far caudal position of the choanae in the older Squalodontinae. That is established distinctly in *Archaeodelphis patrius* Allen, 1921, a form which is to be placed in the most primitive Agorophiidae, just as in *Microzeuglodon* aff. *caucasicus* Riabinin, 1938. Emlong established the upper Oligocene species *Aetiocetus cotylavens* (*sic*) Emlong, 1966 (1966: 12), which he assigns to the near-mysticete Archaeoceti. One of his arguments for this assignment, farther posterior-lying choanae not being present in Odontoceti (1966: 48), does not at all correspond to the given facts.

The oldest known example of the Archaeoceti, *Protocetus atavus* Fraas, 1904, also exhibits very far caudally situated choanae.

That is the opposite to what was to be expected, if one proceeded from the normal situation in land mammals. The choanae also lay farther caudal in ancestral forms; in younger as well within the Archaeoceti, as also the Odontoceti, in general they lay farther rostral. Possibly this indicates that in early amphibious stages of evolution – perhaps in a preprotocetid stage – similar to the Crocodylia a functionally improved combination of breathing and eating process was achieved through elongation of the bony palate. That the choanae then are once more anteriorly shifted in more progressive forms, could be functionally connected with the progressive backward shift of the nares in the “telescoping” process. This same tendency in the different suborders speaks rather for a direct derivation of the Odontoceti as well as the Archaeoceti from preprotocetid forms.

In the younger eusqualodontid forms, many characters are further modified in a progressive manner and the remaining ancestral traits are eliminated.

*Squalodon catulli* Zigno, 1876 – for a long time synonymized with *Squalodon bariensis* (Jourdan, 1861) – is as an Aquitanian species the oldest and most primitive hitherto known representative of this genus. *Squalodon* is essentially representative of the flowering or the family in the Miocene, together with the derived genera *Neosqualodon* and – in the southern hemisphere – *Prosqualodon* Lydekker, 1893, which are independent of the Agorophiidae.

*S. catulli* and *S. bellunensis* Dal Piaz, 1916, are the best known representatives of a species group, which contrasts with another, in many ways conservative group around *S. bariensis*. Both groups should have subgenus ranks but several isolated European and extra-European species cannot be adequately classified, so that first of all we should speak without taxonomic fixation of only two species groups, the *catulli*-group and the *bariensis*-group.

The early eusqualodontid forms *E. langewieschei* n.g. n.sp. and *E. latirostris* (Capellini, 1904) allow clear connections to both species groups. So the taxon from Bunde stands near the *bariensis*-group, that of Schio near the *catulli*-group.

The younger species of *Squalodon* show tendencies in the modification of the characters, which clearly make, that one derivation of modern Odontoceti from the terminal Squalodontidae is not possible. One of these characters is the complete filling of the premaxilla with teeth, which in the younger forms remain even stronger and completely functional, quite in contrast to the situation in modern Odontoceti. So the younger Squalodontinae must be regarded as a blind branch of evolution, which still proceeds a bit far against the other Odontoceti, and then ends in the Tortonian or Messinian.

A comparison of the skull characters of Recent Odontoceti with those of the Squalodontidae and the tendencies established of the modification lies near a phylogenetic tree of the Odontoceti, which is presented in Fig. 3 and elsewhere will be more closely substantiated.

The complex, partly furthermore unclear relationships of the dentition deserves a detailed discussion. Here only a few conclusions can be produced: the evolution of the teeth in the Squalodontoidea is only partly understandable in general outlines and as modification process of a single organ. The correlation with the mosaic modification of the structure of the rest of the skull is, especially because of the lack of skulls to accompany the middle Oligocene tooth finds, only partly possible within the Squalodontidae. The earliest Squalodontoidea back teeth allow one to think most of a primitive tooth type, which – according to the above-mentioned retrogressive metamorphosis of the protocone part and the lingual root of the upper buccal teeth – exhibits a symmetrical, high triangular, bilateral, moderately flattened crown with convex edges. The edges were occupied with three large denticles each, with a high ID (ca. 23%). The enamel must have

assumed quite smooth, with few laminated cristae rugosae. The tendency went then among the best known large Squalodontidae especially in two directions: retention of an extensive conservative habitus characterizes the *bariensis*-group under inclusion or *E. langewieschei*. The *catulli*-group shows an asymmetrical conformation through caudal elongation of the basal part of the crown of the buccal teeth. This causes a stretching of the caudal cutting edge and at the same time an increase in the posterior denticles by a smaller ID (about 20%) as well as a posterior movement of the enlarged crista rugosa. In other forms are progressive and ancestral characters mosaically combined with each other, similar to the case of the skull, and as we know it in other mammal groups (Tobien, 1960: 581).

Latest from the middle Oligocene on is polydonty evident. The very difficult question of the way of eruption of the supplemental teeth is still not clearly answered. As Abel (1905: 31–33) conjectured, it appears possible also according to my research that it was only an insertion in the middle, functionally on the strongest required part of the dentition. In all Squalodontoidea known to me the caudal part of the dentition is progressively reduced, so that probably the primitive molars of the eutherian dentition were fully lost at the latest in *Eosqualodon*. Concerning an insertion in one of the most mobile parts of the tooth row, namely between P and M of the eutherian dentition is rather to be regarded as one between P<sup>3</sup> and P<sup>4</sup> as Abel (1905: 33) conjectured. In any case the quantitative conclusions favor this, just as does the presence only from caudal upper B (terminalward) to B5 of established relics of a lingual root. According to these relics of the lingual root one can rather regard an increase in number of molars rather than in the number of premolars. That would make explainable in *Eosqualodon langewieschei* n.g. n.sp. and in the *bariensis*-group in addition a 5<sup>th</sup> back tooth as the last rostrally intercalated molar (instead of a 5<sup>th</sup> premolar, as most interpret it).

The morphologic analysis of the skull of the Squalodontoidea allows the assumption of a common preprotocetid root of the three suborders of Cetacea.

This is supported by the great similarity of certain agorophiid forms with early Cetotheriidae as the first certain representatives of the Mysticeti. Especially, however, the evolutionary tendency in the modification of the skull morphology points to early Odontoceti, which presupposes archaeocetoid ancestors.

The morphologic analysis of the axial skeletons of Cetacea by Slijper (1936) contradicts this idea in part. The rare existing postcranial skeletal material of the Squalodontoidea still needs to be studied.

The comparison of the modification of the skull morphology during the phylogenetic evolution of the Squalodontoidea with the skull morphology of recent Odontoceti and Delphinoidea are independently derivable from different agorophiid stages. A similar conception is shown by the phylogenetic tree of Thenius in Thenius & Hofer (1960: 177). These groups have independently gone through a protosqualodontid stage.

On the other hand the Platanistoidea could very well have branched off first in the protosqualodontid stage.

To the ontogenesis is to be determined that the often taxonomically evaluated, now and again present, overlapping position of the posterior buccal teeth is to be provided, in which the longitudinal growth of the rostrum still was not concluded.

The combination of catcher-, carnivore-, and bottom-feeding dentition gives a hint of a perhaps dominant littoral environment. This does not mean, that these animals were not also high seas swimmers, as is exemplified for modern Odontoceti (Gewalt, 1967: 67, 82) by the bottom-

feeding Recent *Delphinapterus leucas* (Pallas, 1776). Pelagic habitat is only possible for a few large forms like *S. antverpiensis*.

The geographic distribution of the localities confirms the earlier represented conception (Rothausen, 1958: 381, 382, Fig. 7), that these Odontoceti were restricted to the range a little equatorward of the 20 annual isotherm and retreated farther equatorwards with the Tertiary climatic deterioration (Rothausen, 1968). The basis for this is also the isotherms for the early Tertiary, as Schwarzbach (1946: 356; 1961: 158) stated. Berg (1965: 331) recently demonstrated quite similar tendencies for terrestrial vertebrates. Oligocene Squalodontidae are of course now found somewhat farther equatorward than previously, namely in northern north Italy. In any case the earlier drawn conclusion (Rothausen, 1958: 381, 382) could, lacking larger relative motions of the continents since the Oligocene, also be supported from this point of view.