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LOST IN TRANSLATION – A HISTORY OF SYSTEMATIC CONFUSION AND COMMENTS ON THE TYPE SPECIES OF *SQUALODON* AND *PATRIOCETUS* (CETACEA, ODONTOCETI)

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Abstract: The two odontocete taxa *Squalodon grateloupii* and *Patriocetus ehrlichii*, both the type species of their respective genera, have been at the centre of a great deal of taxonomic confusion. Originally regarded to be conspecific, these two taxa have been the subject of a bewildering taxonomic debate lasting for more than a century, which recently led to the suggestion to abandon these widely used names and replace *S. grateloupii* with the similar, yet independently and later proposed name *S. gratelupi* as the type species of *Squalodon*. Here, we attempt to summarise the events leading to the current confused situation in the hope of resolving this issue once and for all and argue that the name *Squalodon grateloupii*, as originally proposed, should be reinstated.

Key words: Squalodontidae, Cetacea, Odontoceti, type species, *Squalodon*, *Patriocetus*.

SQUALODONTIDS and their relatives are an important and widely cited clade of odontocetes (e.g. Kellogg 1923; Rothausen 1965, 1968; Keyes 1973; Muizon 1994; Fordyce and Muizon 2001; Dooley 2003, 2005; Symeonidis *et al.* 2004; Cahuzac *et al.* 2005). Yet, despite intense study, some of the most fundamental aspects of the systematics of the group have been the subject of more than a century of debate and confusion. In particular, the historically and taxonomically important species *Squalodon grateloupii* von Meyer, 1843, usually regarded as the type species of the genus *Squalodon* Grateloup, 1840, and *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913, the type species of *Patriocetus* Abel, 1913, both have an unusually complex taxonomic history (Text-fig. 1). Originally described as the single species *Squalodon grateloupii* by von Meyer (1843), Van Beneden (1865) later divided this taxon into the two distinct species *Squalodon grateloupii* von Meyer, 1843 and *S. ehrlichii* Van Beneden, 1865 (later *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913). Subsequent doubts as to the correct application of either of these two names developed into a debate (e.g. Van Beneden 1865; Kellogg 1923; Rothausen 1965, 1968; Cahuzac *et al.* 2005), which ultimately culminated in the suggestion to abandon the widely used names *Squalodon grateloupii* and *Patriocetus ehrlichii* altogether (Kellogg 1923; Cahuzac *et al.* 2005), as well as the replacement of the former with the similar sounding, yet later and independently proposed *Squalodon gratelupi* Pedroni, 1845 as type species of the genus *Squalodon* (Cahuzac *et al.* 2005). Here, we argue that this suggestion was mainly based on a language-related misunderstanding of the original German publication that named *S. grateloupii* and attempt to settle this issue by showing *Squalodon grateloupii* von Meyer, 1843 to be the oldest available and clearly applicable name. We therefore reinstate the latter as the type species of the genus *Squalodon*.

MATERIAL

All specimens discussed in this text except the type specimen of *Squalodon grateloupii* von Meyer, 1843 (first described by Grateloup 1840) are housed in the Oberösterreichische Landesmuseen (OL), the Upper Austrian State Museums, formerly known as Museum Francisco-Carolinum. Previous authors have referred to these specimens using a catalogue numbering system no longer in use (following the general format 'Cet. XX'). The specimens were given new numbers in 1999 and listed online in the Catalogue of Palaeontological Types in Austrian

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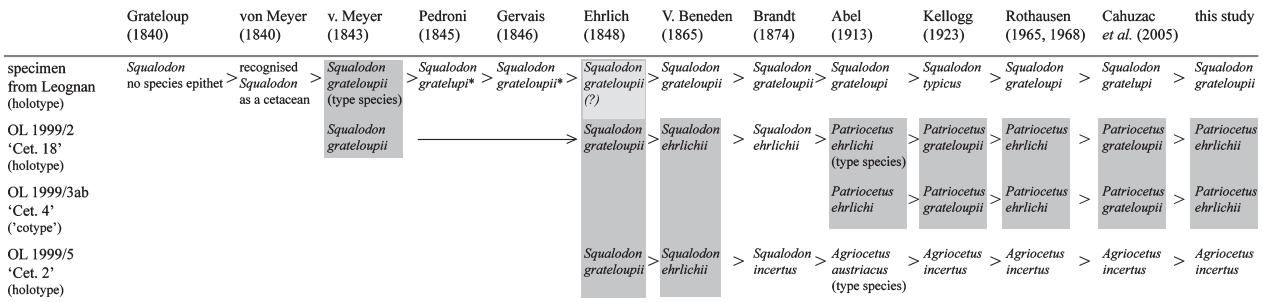

TEXT-FIG. 1. Overview of the changes in the names applied by different authors to the specimens discussed in the text. Specimens considered to belong to a single species by a given author are marked by a grey box. The two species names marked by an asterisk (*Squalodon gratelupi* Pedroni, 1845 and *Squalodon grateloupii* Gervais, 1846) were independently proposed as new taxa by their respective authors, despite their similarity to the earlier proposed name *Squalodon grateloupii* von Meyer, 1843. Ehrlich (1848) does not explicitly state his opinion regarding the specific affinities of the specimen from Léognan, and instead only recapitulates how *Squalodon* was named by Grateloup (1840), and shortly thereafter found to be a cetacean by von Meyer (1840). However, Ehrlich does propose a link between the Austrian and French specimens and makes it clear that his description follows the opinions of von Meyer published between 1840 and 1847.

Collections (OeTyp; http://www.oeaw.ac.at/oetyp/palhome.htm). Here, both the old and new numbers are given, to avoid confusion and enable exact cross-referencing in the future. According to Rothausen (1965), the fossil from Léognan described as the type specimen of *Squalodon grateloupii* by von Meyer (1843) seems to be lost, but casts still exist in a number of institutions, including the Institut Royal des Sciences Naturelles de Belgique in Brussels (catalogue no. R 2362).

A CONFUSING TAXONOMIC HISTORY

In 1840, Grateloup described the partial skull of a marine tetrapod from Lower Miocene bone-bearing molasse (molasse ossifère) deposits of Léognan, south-western France. Interpreting the specimen to be a previously unknown fossil reptile, he gave it the name *Squalodon*, but did not provide a species epithet. Almost immediately, von Meyer (1840) recognised the specimen from Léognan as a cetacean, but like Grateloup he did not name the species itself. This only changed when a few years later von Klipstein (1842) first mentioned the existence of another skull that had been found in the Upper Oligocene Linz Sands (OL 1999/2, formerly 'Cet. 18') of Upper Austria. Von Meyer (1843) interpreted the new skull from Austria to belong to the same taxon as the French specimen and decided to name the species *Squalodon grateloupii*. Apparently unaware of von Meyer's description, and disapproving of Grateloup's derivation of the name *Squalodon*, Pedroni (1845) re-described Grateloup's specimen as *Delphinoides* and gave the species the new name *gratelupi*. Just 1 year later, Gervais (1846), presumably without knowledge of either von Meyer's (1843) or Pedroni's (1845) work, also erected a new taxon for the French specimen. Confusingly, Gervais (1846) *also* chose the name *Squalodon grateloupii* Gervais 1846, which, despite its obvious similarity to the previous two suggestions, was still an entirely independently proposed taxon. However, despite Pedroni's (1845) and Gervais' (1846) renaming of the French specimen, most subsequent authors seem to have assumed that von Meyer (1843) intended his name *Squalodon grateloupii* to apply to both Grateloup's specimen *and* that from Linz (Van Beneden 1865; Abel 1913; Rothausen 1965, 1968) and hence accepted *S. grateloupii* von Meyer, 1843 as the oldest available name applied to the French skull.

However, in 1865, Van Beneden, having recognised that the two specimens did not belong to the same species, re-described the Linz specimen as *Squalodon ehrlichii*. He also referred the partial skull of another individual (OL 1999/5, formerly 'Cet. 2'), first mentioned and originally referred to *Squalodon grateloupii* von Meyer, 1843 by von Meyer (1847), to his new species; later, OL 1999/5 was removed from *S. ehrlichii* by Brandt (1874) to become the basis of yet another new species, *Squalodon incertus* Brandt, 1874 (subsequently renamed *Agriocetus austriacus* by Abel in 1913). Several years later, the new genus *Patriocetus* was erected by Abel (1913) for *Squalodon ehrlichii* (*sensu* Brandt 1874), after a second, nearly complete skull (OL 1999/3a, formerly 'Cet. 4') and mandible (OL 1999/3b, formerly 'Cet. 4') discovered in 1910 (König 1911) had been referred to the species in addition to the original specimen OL 1999/2 mentioned by von Meyer (1843) and Van Beneden (1865). There seems to have been some confusion in the literature about the taxonomic status of these two skulls, with the more complete specimen (OL 1999/3a) being referred to as both the holotype (Whitmore and Sanders 1977) and paratype (Rothausen 1965; Dubrovo and Sanders 2000) of

P. ehrlichii. It is likely that this typological uncertainty was partially caused by the description of OL 1999/3a as a 'cotype' of OL 1999/2 (the holotype of *P. ehrlichii*) by Abel (1913), a term formerly used to describe both syntypes and paratypes, but not recognised by the International Code of Zoological Nomenclature (ICZN 1999, Recommendation 73E). However, since OL 1999/3a was discovered long after Van Beneden's (1865) re-description of OL 1999/2 as *Squalodon ehrlichii*, it did not form part of the original type series on which the species name was based. It thus fails to meet the requirements for being designated a paratype (ICZN 1999, Article 72.4.5; Recommendation 73D) and should simply be regarded as referred material.

Van Beneden (1865), having re-described OL 1999/2 as *Squalodon ehrlichii*, retained the name *Squalodon grateloupii* von Meyer, 1843 for the French specimen originally described by Grateloup (1840). This use of the name *S. grateloupii* was disputed by Kellogg (1923), who, unlike most previous authors, considered von Meyer's (1843) original description of *Squalodon grateloupii* to apply to OL 1999/2 only. He thus considered *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913 to be a junior synonym of *P. grateloupii* (von Meyer, 1843) Abel, 1913. At the same time, Kellogg (1923) viewed *Delphinoides* (= *Squalodon*) *gratelupi* Pedroni, 1845 as either a misspelling of the name Grateloup or a typographical error and thus considered the name preoccupied by *Squalodon grateloupii* von Meyer, 1843. Convinced that, therefore, no valid name had ever been applied to Grateloup's original specimen, he proceeded to propose *Squalodon typicus* for the French species, which could be seen as the *de facto* type species of the genus *Squalodon*. However, Kellogg's (1923) new name *Squalodon typicus* was not accepted by subsequent workers, and *Squalodon grateloupii* von Meyer, 1843, as applied to the French specimen, continued to be used as the type species of the genus *Squalodon* (e.g. Colacicchi 1960; Rothausen 1965, 1968; Symeonidis *et al.* 2004). Similarly, *P. ehrlichii* remained in use as the name of the Austrian specimens (e.g. Rothausen 1965, 1968; Keyes 1973; Whitmore and Sanders 1977; Dubrovo and Sanders 2000).

The latest review of this issue was published by Cahuzac *et al.* (2005), who, like Kellogg, argued that von Meyer's (1843) name *Squalodon grateloupii* likely only applied to the Austrian specimen (OL 1999/2) and concluded that, because von Meyer (1843) had only mentioned the name in a letter without a proper description of the specimen, *Squalodon grateloupii* von Meyer, 1843 should be considered a *nomen nudum*. However, they discounted Kellogg's (1923) concerns regarding the misspelling of Grateloup's name by Pedroni (1845) based on linguistic arguments and regulations in the International Code of Zoological Nomenclature. As a consequence, they accepted *Squalodon gratelupi* Pedroni, 1845 as the oldest available and valid name for the French specimen first described by Grateloup (1840) and declared *Squalodon typicus* Kellogg, 1923 to be a junior synonym of the latter. Furthermore, they argued that the name *Squalodon grateloupii* was first properly used by Gervais (1846), who had applied it to the skull from Léognan. Following this line of reasoning, *Squalodon grateloupii* Gervais, 1846 becomes a junior synonym of *Squalodon gratelupi* Pedroni, 1845, whilst the first valid application of the name *Squalodon grateloupii* to the Austrian specimen by Ehrlich (1848), who did provide a proper description of the latter 5 years after it was first named by von Meyer (1843), created a homonym of *Squalodon grateloupii* Gervais, 1846. However, Cahuzac *et al.* (2005) accepted the name *Patriocetus grateloupii* (von Meyer in Ehrlich, 1848) Abel, 1913 instead of *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913 for the Austrian specimens following the revision of this taxon by Abel (1913), who had removed the species from its original genus (*Squalodon*) and placed it in a new genus (*Patriocetus*) and family.

LOST IN TRANSLATION

From the historic use of the names *Squalodon grateloupii*, *Squalodon gratelupi*, *Squalodon typicus* and *Patriocetus ehrlichii* and the recent arguments regarding their application, it becomes clear that the main issue at the heart of this controversy is the question whether von Meyer (1843) applied the name *Squalodon grateloupii* to the Austrian specimen (OL 1999/2) only, or whether he intended the new species to include both the French *and* Austrian specimens. If the former, as argued by Kellogg (1923) and Cahuzac *et al.* (2005), it is possible to disregard von Meyer's (1843) original proposal of the name *S. grateloupii*, as it was not accompanied by a sufficient description of the specimen (OL 1999/2) it was meant to apply to. However, if von Meyer (1843) regarded both specimens to belong to his new species, the situation would change dramatically, because in this case he would simply have added information to a description already provided by Grateloup in 1840, which in turn was accepted as appropriate by subsequent authors (e.g. Rothausen 1965; Cahuzac *et al.* 2005). The latter scenario was suggested by Rothausen (1965) in response to Kellogg's (1923) revision of *Patriocetus ehrlichii* as *P. grateloupii*, and, having read the original publication by von Meyer (1843), we also believe this to be the case. We further suggest that the argument that von Meyer (1843) only applied his name to the Austrian specimen may be a misconception possibly based on problems with the translation of the German text itself. Whilst it is true that von Meyer (1843) was not precise as to which of the two specimens he intended to

name, there are two clues that he had both in mind when he applied the name *Squalodon grateloupii*. First, von Meyer (1843, p. 704) stated that he believed that the partial skull found near Linz (OL 1999/2) 'belongs to the *Squalodon*, which Grateloup had thought to be a reptile close to *Iguanodon*' ('[…] woraus ich ersehe, dass derselbe dem *Squalodon* angehört, worin GRATELOUP (Jahrb.1841, 830) ein dem *Iguanodon* nahe stehendes Reptil vermuthet hatte […]'). Whilst this may sound as though von Meyer is simply referring the new skull to the genus *Squalodon*, it is important to remember that Grateloup (1840) had not provided a species epithet for his new taxon. Thus, unlike implicitly assumed by Kellogg (1923) and Cahuzac *et al.* (2005), it is impossible to distinguish whether von Meyer believed the Austrian fossil to belong to the same genus or species as the French one based on this statement alone. Secondly, it should be noted that von Meyer decided to name his new species *Squalodon grateloupii*. The clue here is in the name itself: species names given in honour of a person are usually applied either out of respect for someone else's work, or because of a certain connection of that person with the taxon in question. Given that von Meyer (1843) considered the Austrian specimen to 'belong to' the same taxon as the French one, the simplest assumption seems to be that von Meyer intended to name his new species after the person who had first described it – Jean Pierre Grateloup.

We thus concur with Rothausen (1965) and propose that von Meyer (1843) in fact based his new species *Squalodon grateloupii* on both the French *and* Austrian specimens. In doing so, he simply referred OL 1999/2 to the taxon already established by Grateloup (1840) and added information to Grateloup's generally accepted description of the French specimen. We believe that this confirms the validity of von Meyer's (1843) name despite the fact that he himself did not provide a detailed description of the specimens he was referring to. Von Meyer (1843) thus created two syntypes, one of which (OL 1999/2) was later recognised as a separate taxon and re-described as the new species *Squalodon ehrlichii* by Van Beneden in 1865 (= *Patriocetus ehrlichii* (Van Beneden) Abel, 1913). This view of the line of events is further supported by the fact that Van Beneden (1865) also retained the name *S. grateloupii* von Meyer, 1843 for the French specimen. Ehrlich (1848) thus simply treated *Squalodon grateloupii* as appropriate for the Austrian material, and hence his publication did not contain any novel uses of the name. On the other hand, as was also argued by Van Beneden (1865) and Cahuzac *et al.* (2005), Pedroni (1845) and Gervais (1846) most likely were simply not aware of von Meyer's (1843) original proposal, making *Delphinoides* (= *Squalodon*) *gratelupi* Pedroni, 1845 and *Squalodon grateloupii* Gervais, 1846 junior synonyms and, in the latter case, even a homonym, of *S. grateloupii* von Meyer, 1843. As a result, *S. grateloupii* von Meyer, 1843 is reinstated as the type species of *Squalodon*.

In addition to the question which names should be considered appropriate, some confusion seems to exist in the literature as to whether *Patriocetus ehrlichii* and *Squalodon grateloupii* should be spelt with *-i* or *-ii* (e.g. von Meyer 1843; Van Beneden 1865; Abel, 1913; Kellogg 1923; Dubrovo and Sanders 2000; see Rothausen 1965 for a comprehensive overview of the use of both forms up to 1965). In their original descriptions of these taxa, both von Meyer (1843) and Van Beneden (1865) spelt the new names they proposed with *-ii*. According to Article 31.1.1 of the International Code of Zoological Nomenclature (ICZN, 1999), this is deemed valid if the original modern name from which the species epithet was formed was latinised as part of the naming process. The Code (Art. 33.4) further states that 'the use of the genitive ending *-i* in a subsequent spelling of a species-group name that is a genitive based upon a personal name in which the correct original spelling ends with *-ii*, or vice versa, is deemed to be an incorrect subsequent spelling, even if the change in spelling is deliberate'. Whilst we cannot be certain that von Meyer (1843) and Van Beneden (1865) intended to use the names Grateloup and Ehrlich in their latinised forms, we also lack any evidence that they did not and hence propose that an emendation of their original names is both largely inconsequential and against the regulations of the Code. We therefore consider *Patriocetus ehrlichi* and *Squalodon grateloupi* to be incorrect subsequent spellings of *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913 and *Squalodon grateloupii* von Meyer, 1843, respectively.

CONCLUSIONS

In summary, our main conclusions are the following:

1. *Squalodon grateloupii* von Meyer, 1843 is the type species of *Squalodon*, and the appropriate name for the specimen form Léognan is described by Grateloup (1840).
2. *Delphinoides gratelupi* Pedroni, 1845 and *Squalodon grateloupii* Gervais, 1846 are junior synonyms (and, in the latter case, also a homonym) of *Squalodon grateloupii* von Meyer, 1843.
3. OL 1999/2 (formerly 'Cet. 18') is the type specimen of *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913; OL 1999/3a (formerly 'Cet. 4'), referred to as a 'cotype' of *P. ehrlichii* by Abel (1913) does not constitute a paratype of this taxon, but is instead regarded as referred material.
4. *Patriocetus ehrlichi* and *Squalodon grateloupi* are incorrect subsequent spellings of *Patriocetus ehrlichii* (Van Beneden, 1865) Abel, 1913 and *Squalodon grateloupii* von Meyer, 1843, respectively.

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