

Discovery of the most ancient *Notidanodon* tooth (Neoselachii: Hexanchiformes) in the Late Jurassic of New Zealand. New considerations on the systematics and range of the genus

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Abstract: This paper describes the first hexanchid tooth from the Tithonian (Late Jurassic) of New Zealand. For the moment, this tooth represents the earliest representative of the fossil genus *Notidanodon* in the world and one of the most ancient neoselachians in the Southern Hemisphere. Despite the perfect state of preservation of the unique tooth, the species is left in open nomenclature, pending the discovery of additional specimens. Few nominal species have been assigned to the genus *Notidanodon*. Four from Cretaceous deposits: *N. antarcti* Grande & Chatterjee, 1987, *Notidanodon dentatus* (Woodward, 1886), *Notidanodon lanceolatus* (Woodward, 1886), *Notidanodon pectinatus* (Agassiz, 1843) and only two from Paleocene: *Notidanodon brotzeni* Siverson, 1995, and *Notidanodon loozi* (Vincent, 1876). Considering the important morphological variations observed between some of these species, it seems obvious that the genus *Notidanodon* is not monophyletic and will need a revision in the future.

Keywords: Chondrichthyes, Hexanchiformes, *Notidanodon*, Tithonian, New Zealand

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INTRODUCTION

Chondrichthyan remains are very uncommon in the New Zealand Mesozoic. The occurrence of elasmobranch teeth in the Mesozoic and Cenozoic deposits of New Zealand has been known since 1888, thanks to a monograph published by Davis, but the first described specimens from New Zealand are in fact the two *Notidanus dentatus* teeth figured by Woodward (1886) from the Maastrichtian of New Zealand. No Jurassic specimens have previously been formally reported, but ca. 15 Cretaceous species were recorded in the earliest studies of shark teeth from New Zealand (Woodward, 1886; Davis, 1888; Chapman, 1918).

After the publication by Woodward (1886) of the most ancient taxon, *Notidanus dentatus* from the Maastrichtian, on the basis of two teeth discovered in New Zealand, the selachians from this country were the subject of a series of papers. For the Cretaceous, one can cite Woodward (1886), Chapman (1918), Keyes (1977, 1984), Fordyce (1982), Consoli & Stilwell (2011). In a series of more recent articles, Cenozoic taxa were also described by Keyes (1979, 1982), Pfeil (1984), Anonymous (1987), Mannerling & Hiller (2005, 2008), or only cited by Cappetta (1987, 2012).

All these taxa were collected in Cretaceous or Cenozoic deposits. In fact, the most ancient selachian reported from New Zealand seems to be a fragment of fin spine from the Early Triassic of eastern Northland, probably belonging to a ctenacanth shark (Grant-Mackie *et al.*, 2014). Therefore, the hexanchid tooth reported herein, which was discovered in the Tithonian (Late Jurassic) represents the most ancient neoselachian known from the Southern Pacific ocean. Until now, the oldest hexanchiform shark from this geographical realm was

reported from the Early Cretaceous (probably Late Aptian) of Antarctica (Cione & Medina, 2009, p. 503), on the basis of a single tooth characterized by a mesial cutting edge devoid of serrations or cusplets. According to Cione & Medina (2009) this tooth could be related to a species close to the origin of *Hexanchus*. No Jurassic specimens have been reported before this discovery.

The aim of the present work is to describe the oldest specimen of *Notidanodon* so far known globally. We believe it unwise to give a species determination on the basis of a single tooth, even if it is very well preserved, although the likelihood of further specimens being discovered is probably unlikely, given the present lithology.

MATERIAL AND METHOD

The specimen that is object of this work is a single perfectly preserved tooth displaying its labial face, exposed on the surface of a brown calcareous siltstone slab covered with many fine manganese deposits. Even though the tooth is in a very good condition, its fragility, mainly some very thin cracks, prevents complete extraction from the slab. The specimen comes from the Waikorea Siltstone at the junction of the two main branches of the Huriwai River, about 800 m upstream from the Waikaretu Valley Road bridge (Fig. 1), Port Waikato area (New Zealand Fossil Record System locality R16/f6650, grid reference R16/650184) and is recorded as V463 in the Catalogue of Fossil Vertebrates and as part of collection AU9514 from that locality in the School of Environment, University of Auckland. It was collected by Anna V. Croad and David Wood in May 1983 during a field class of the then-Geology Department, University of Auckland.

The Waikorea Siltstone lies in the Murihiku Terrane, of dominantly marine volcanoclastics from a mainly shelf and slope environment (Edbrooke 2001) off the margin of the Gondwana continent. The locality from which this tooth came has also yielded a moderately diverse invertebrate fauna, including many specimens of the bivalve *Australobuchia plicata* (Zittel, 1864), confirming its age as within the *Plicata* Zone of the Waikatoan Substage of the Puroan Stage (Hikuroa & Grant-Mackie 2008), i.e., Late Tithonian, Late Jurassic, about 147 Ma (New Zealand Geological Timescale Project 2012).

ASSOCIATED FAUNA AND PALEOECOLOGY

As noted above, the locality yielded quite a varied invertebrate fauna, dominated by benthic bivalves (e.g., *Grammatodon (Indogrammatodon) fyfei* Marwick, 1953, *Otapiria masoni* Marwick, 1953, *Australobuchia plicata*, *Entolium* sp., *Retroceramus everesti* (Oppel, 1862), *Pseudolimea* sp., *Myophorella purseri* Fleming, 1987), worm tubes (*Rotularia* sp., *Pyrgopolon* sp.), and the nektonic cephalopods *Belemnopsis a. aucklandica* (Hochstetter, 1863), a belemnite, and ammonites *Subplanites huriwaiensis* and *Subdichotomoceras maraetaiense*, both of Stevens (1997).

The sequence to which the Waikorea Siltstone belongs has been described (Ballance & Campbell 1993) as consisting of immature proximal turbidites on the outer shelf-upper slope east of Gondwana, producing a belemnite-bivalve lutite facies (Li & Grant-Mackie 1988). Less commonly, buchias, including *Australobuchia*, occupy shallower coastal waters. The diverse fauna accompanying the *Notidanodon* tooth suggests this latter environment, representing perhaps a short shallowing period during deposition of the Waikorea Siltstone rather than the more offshore environs of the formation as a whole. However, the occurrence of *Notidanodon* would seem to be indicative of deeper waters, by reference to its association

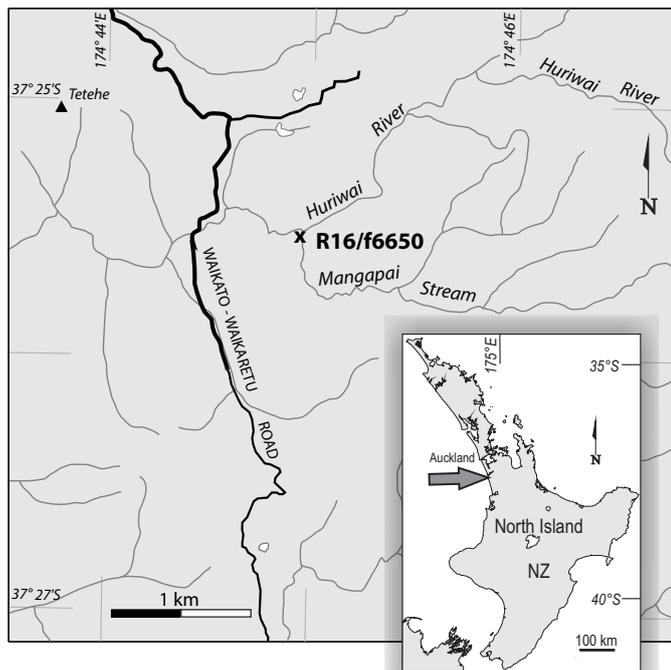


Figure 1. Location of the fossiliferous locality.

with deep-water elements elsewhere. For instance, teeth of *Notidanodon pectinatus* are associated with rather deep-water taxa (i.e. several species of *Chlamydoselachus*, *Echinorhinus lapaoui*, *Centrophoroides* sp., *Cretascymnus quimbalaensis*), in the Campanian/Maastrichtian deposits of Angola (Antunes & Cappetta 2002). If the deep-water character of some of them can be discussed, it remains however obvious that they do not characterize shallow water environments.

DESCRIPTION OF THE NEW ZEALAND NOTIDANODON TOOTH

The material consists of a single complete tooth on the surface of a rock slab.

Terminology (Fig. 2): before describing the New Zealand tooth, it is useful to define some terms used below. Most hexanchid teeth are characterised mainly by a rather strong labio-lingual flattening (except in some plesiomorphic genera like *Welcommeia* Cappetta, 1990, *Pseudonotidanus* Underwood & Ward, 2004, or, to a lesser extent *Crassodontidamus* Kriwet & Klug, 2011 or *Pachyhexanchus* Cappetta, 1990), mainly occurring in lower antero-lateral and lateral files and, to a lesser extent, in upper lateral files. The crown consists of a series of sharp triangular cusps that are more or less bent distally. The main cusp is usually in a rather mesial position, and is followed distally by a series of cusplets, variable in number according to the genus, but also with jaw position, and decreasing in size towards the distal part of the tooth. The base of the mesial cutting edge of the main cusp bears a series of serrations or cusplets, depending on their size. In fact, these size variations render difficult a very precise and indisputable terminology, and important intraspecific size variations are noted (see for example gradual changes in the teeth of figures 4G, H, D, F and E for teeth of *Notidanodon* « group » *loozi*. The number of these serrations or cusplets varies also according to the genus and species, as well as jaw position and even between individuals (in *Notorynchus* at least).

The main cusp (also named acrocone; see Cappetta, 1987; Siverson, 1995, 1997) is separated from the mesial and distal cusplets by a deep sharp notch. The mesial part of the tooth starts from the mesial edge to the mesial notch. The mesial notch corresponds to the notch separating the last mesial cusplet of the mesial part, from the mesial base of the main

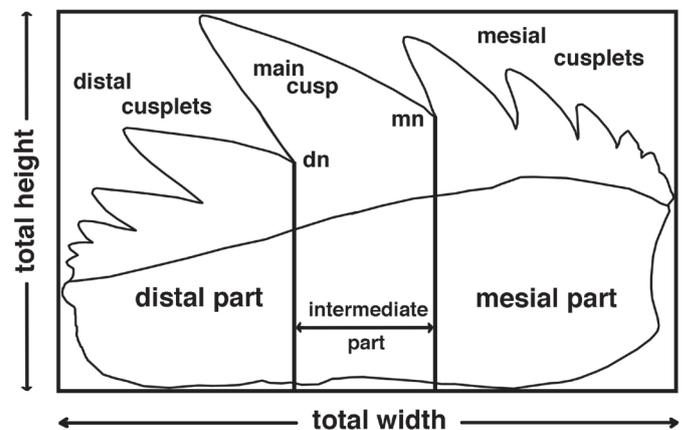


Figure 2. Schematic drawing of the *Notidanodon* tooth. dn: distal notch; mn: mesial notch.

cuspl. The distal notch corresponds to the notch separating the distal base of the main cusp from the first distal cusplet. The distal part of the tooth starts from the distal notch, separating the main cusp from the largest distal cusplet, to the distal edge of the tooth. The intermediate part corresponds to the region of the tooth below the base of the main cusp.

Description (Fig. 3): The tooth is about twice as broad as high (11 x 6.5 mm), with the distal part of the crown being more developed than the mesial one. The main cusp, or acrocone, is larger than the mesial or distal cusplet and bent distally at an angle of about 45° to the midline. The mesial cutting edge of this main cusp is very slightly convex, and the distal one practically straight. The labial face of this cusp is rather flat and the cutting edges are salient and thin, with a distinct height difference at the junction with the surface of the cusp. Mesially, there are five cusplets increasing in size towards the acrocone. These cusplets have a surface relatively more convex than that observed for the acrocone. Their tilt decreases toward the acrocone. The mesial cutting edge of each cusplet is much shorter than the distal one. The former edge is slightly convex whereas the latter is straight to barely concave. The most mesial cusplet is lower and slightly directed mesially, unlike the others. The mesial edge of the small cone extends by a very oblique and straight cutting edge joining the upper mesial part of the root margin.

The distal part shows five distal cusplets, the proximal one being larger than the biggest one of the mesial part. The mesial cutting edges of cusplets one and two (compared to the acrocone) are sigmoid, whereas the distal ones are straight. The two most distal cones are very small with a relatively less sharp apex. All the cusplets are separated from one another by deep sharp notches at their bases.

The root is about twice as high mesially compared to its distal margin. The mesial margin is slightly oblique and concave, the distal one is oblique and slightly convex. The basal edge is horizontal and rectilinear on the whole and joins the mesial and distal edges by a smooth curve.

The labial face of the root is rather flat, except for a transverse slightly depressed area in its median part. It is much higher mesially than distally. Many narrow vertical furrows run irregularly across the root. They are generally short and positioned at different heights, the longest below the mesial cusplets.

The crown-root boundary is rectilinear ascending up to the level of the second cusplets (from the mesial edge), then making a little marked convexity to join the mesial limit of the crown-root.

Discussion

By its general morphology, this tooth can be assigned without any doubt to a hexanchiform shark, and more precisely to the genus *Notidanodon sensu* Cappetta, 1975. The height/width ratio of the New Zealand tooth is close to 60%, falling in the values of the *Notidanodon pectinatus* teeth, on the basis of specimens previously published in the literature (Woodward 1886, Applegate 1965, Welton 1979, Antunes & Cappetta 2002, Hessin *et al.* 2007). Based on the little developed labial face of the root, and by comparison with extant hexanchids (for instance *Hepranchias*), this tooth is interpreted as an antero-lateral element of the upper jaw, but a lower element cannot be definitely excluded. The knowledge of Mesozoic Hex-



Figure 3. Tooth of *Notidanodon* sp., labial view.

anchiformes, and more precisely of hexanchids *s.l.*, rests on a very limited number of teeth for most of the species. Indeed, very few species are known by skeletons exhibiting complete dentitions. Only *Notidanoides muensteri* (Agassiz, 1835) from the Kimmeridgian of Germany and *Hexanchus gracilis* (Davis, 1887) from The Santonian of Sahel Alma, Lebanon, can be cited (Cappetta, 1980). The *Notidanoides muensteri* skeleton was described in detail by Maisey (1986) when he erected the genus *Notidanoides* and its dentition was figured and reconstructed later by Kriwet & Klug (2011).

Because strong dignathic and monognathic heterodonty characterizes most hexanchids (even though far weaker in *Notorynchus*, *Gladioserratus*, Jurassic genera and *Notidanodon* than in others), and the relative scarcity of fossil teeth, an assignment of isolated teeth to a precise species, and even genus, remains tricky and subject to discussion in some cases. For this reason, it seems better to leave the New Zealand specimen in open nomenclature, pending the discovery of additional material.

The genus *Notidanodon*, as originally defined by Cappetta (1975) on the type species *Notidanus pectinatus* Agassiz, 1843, includes Mesozoic and Cenozoic species with teeth that can reach a large size (up to at least 6 cm width, for lower teeth), and characterized by often large mesial cusplets, sometimes as large as the main cusp, and more or less bent distally.

On the basis of the previously published material it appears that teeth assigned to the genus *Notidanodon* do not exhibit homogeneous morphologies, some of them with very erect cusps and large and high mesial and distal cusplets (as in the type species), and others with a main cusp and mesial and distal cusplets clearly bent distally (as in the Cretaceous *Notidanus dentatus* Woodward, 1886 or in the Paleocene *Notidanus loozi* Vincent, 1876).

Therefore, it appears that the limits and content of the genus *Notidanodon* as defined by Cappetta (1975) and used so far, will need to be re-evaluated in the future.

It is worth noting that Adolfsen & Ward (2013) and Adolfsen *et al.* (2017) recognised morphological differences between the type species *N. pectinatus* and the other Cretaceous and Paleocene species assigned to *Notidanodon* (after a personal communication of Siverson 2014). Thus, it appears that the content and limits of the genus *Notidanodon* should be reconsidered.

A short review of the described « *Notidanodon* » species

The hexanchid sharks include a dozen genera extant, some represented also by fossils: *Hepranchias* Rafinesque, 1810, *Hexanchus* Rafinesque, 1810 and *Notorynchus* Ayres, 1855. Seven are only represented by fossil species: *Notidanodon* Cappetta, 1975, *Notidanoides* Maisey, 1986, *Pachyhexanchus* Cappetta, 1990, *Pseudonotidanus* Underwood & Ward, 2004, *Welcommia* Cappetta, 1990, *Weltonia* Ward, 1979, *Crassodontidanus* Kriwet & Klug, 2011 and *Gladioserratus* Underwood *et al.*, 2011.

Firstly, it seems useful to review the different described species assigned to the genus *Notidanodon*, highlighting mainly the Cretaceous species. Indeed, because the scarcity of teeth of some species, and also the poor state of preservation of many of them, the interpretation of their systematic status has varied according to the authors, introducing more confusion than clarification.

The genus *Notidanodon* Cappetta, 1975 is based on the Cretaceous species *Notidanus pectinatus* Agassiz, 1843 defined on a single but well preserved tooth according to Agassiz's figures. Few species currently assigned to *Notidanodon* have been described: four from Cretaceous deposits, *Notidanodon pectinatus* (Agassiz, 1843), *Notidanodon dentatus* (Woodward, 1886), *Notidanodon lanceolatus* (Woodward, 1886), *Notidanodon antarcti* Grande & Chatterjee, 1987 and two from Cenozoic deposits, *Notidanodon loozi* (Vincent, 1876) and *Notidanodon brotzeni* Siverson, 1995. Before 1975, the date of erection of the genus *Notidanodon* by Cappetta, most of those species were assigned to the genus *Notidanus* Cuvier, 1816, but also to *Notorynchus*, for instance *Notorynchus pectinatus* by Applegate (1965), which corresponds in fact to *Notidanodon dentatus*.

Leriche (1951, p. 494) advocated the use of the genus *Notidanus*, faced with the difficulty in distinguishing well-defined generic characters in the dentition.

Notidanodon pectinatus (Agassiz, 1843) (Fig. 4 A1-A2)

This species, assigned to *Notidanus* by Agassiz, is the type species of *Notidanodon* Cappetta, 1975. This unique but complete tooth came from the « craie blanche du Sussex », England, without more precise locality citation. The age is indicated as Late Cenomanian-Maastrichtian *vide* Ward 1979, but more probably from Campanian, according to the geology of the Sussex region; see Bailey *et al.*, 1983; GCR site account 216, 1980-2007). The species *pectinatus* was erroneously noted from the lower Cretaceous of England by Cappetta (1975, p. 119).

Range: Upper Cretaceous of England (Agassiz, 1843); Campanian of Antarctica (Grande & Chatterjee, 1987); Campanian/Maastrichtian of Angola (Antunes & Cappetta, 2002); Campanian of Hornby Island, British Columbia, Canada (Hessin *et al.*, 2007); Upper Cretaceous of Crimea, (Trikolidi, 2014); Maastrichtian of Denmark (Adolfson & Ward, 2013).

Notidanodon antarcti Grande & Chatterjee, 1987

This species comes from the Campanian/Maastrichtian (López de Bertodano Fm.) of Seymour Island, Antarctica. In Grande & Chatterjee (1987), the species is noted as new in the caption of figure 2, but without a designed type specimen, and not defined explicitly in the text where the teeth are named *Notidanodon* sp.

The type material is represented by two incomplete teeth and a third one preserved in matrix and showing some prismatic cartilage. This name must be regarded as a *nomen dubium*, and is probably a junior synonym of *Notidanodon pectinatus*.

Notidanodon dentatus (Woodward, 1886) (Fig. 4 B)

The two teeth figured by Woodward as *Notidanus dentatus* come from the Maastrichtian (Piripauan) of Amuri Bluff, New Zealand. They were again figured by Davis (1888), who added two well preserved additional teeth from the type locality. Those same four teeth were later illustrated by Chapman (1918).

Range: Campanian/Maastrichtian of New Zealand (Woodward, 1886; Davis, 1888 ; Chapman, 1918), of Angola (Antunes & Cappetta, 2002) ; Upper Cretaceous of California (Applegate, 1965; Welton, 1979) ; Campanian of Antarctica (Cione & Medina, 1987) ; Santonian/Campanian of Antarctica (Richter & Ward, 1990; Kriwet *et al.* 2006); Campanian of South Dakota, USA (Martin, 2014); Maastrichtian of Argentina (Bogan *et al.*, 2016); Upper Cretaceous of Japan (Kitamura & Kawasaki, 2001); Maastrichtian of Antarctica (Martin & Crame, 2006); Upper Cretaceous of Crimea, Europe (Trikolidi, 2014)

Notidanodon lanceolatus (Woodward, 1886) (Fig. 4 C)

The holotype and unique specimen is an incomplete tooth preserved on matrix from the Middle Albian, probably from Folkestone, Great Britain (Woodward, 1886). This tooth was figured and discussed repeatedly by Woodward (1886), Ward & Thies (1987), Smart (1990), and Bernard & Smith (2015). Since its original figuration by Woodward, the tooth has been damaged and has lost mesial serrations. Two serrations were present in the original description, whereas none is remaining currently. This species was not considered for decades until it was assigned to the genus *Notidanodon* by Ward & Thies (1987). Those authors attributed to the species *lanceolatus* a series of teeth of *Notidanodon* from the Lower Cretaceous of Germany and of Great Britain. However, these teeth, from their morphologies, can hardly be assigned to the species *lanceolatus* as illustrated by Woodward (1886) and probably correspond to a different species. In fact, the species *lanceolatus* has been broadly used so far and probably currently encompasses different species, at the light of the illustrated specimens (see Woodward 1886, Ward & Thies 1987, Long *et al.* 1993). In fact, this situation results from the poor state of preservation of the type specimen. A revision of this species, out of the scope of the present work, is necessary.

Range: Lower Barremian of Germany (Thies, 1987b; Ward & Thies, 1987; Ladwig, 2012; Frerichs, 2012); Albian of Great Britain (Woodward, 1886). The other occurrences of this species are considered as questionable, because resting on doubtful determinations.

In addition to the Cretaceous species, two Paleocene species are classically assigned to *Notidanodon*: *Notidanodon loozi* (Vincent, 1876) and *Notidanodon brotzeni* Siverson, 1995.

Notidanodon brotzeni Siverson, 1995 (Fig. 4 F-G)

This species is based on two incomplete teeth from the Danian of Limhamn quarry, Scania, Sweden. The root is very damaged on both specimens, but the crown of the holotype is well preserved enough, exhibiting the main diagnostic features concerning the mesial serrations, the acrocone and distal cusps.

Range: Danian (Sweden: Siverson, 1995).

Notidanodon loozi (Vincent, 1876) (Fig. 4 D, E)

The holotype, from the Selandian of Wanzin, Belgium, is a very incomplete lower tooth, showing the mesial serrations, the acrocone and the first distal accessory cone and a very small part of the root. The morphology of the type specimen, not figured since its publication by Vincent, is so close to that of the types of *N. brotzeni*, mainly at the level of the mesial serrations, that Siverson's species could be a junior-synonym of Vincent's species. The most striking difference concerns the distal notch separating the main cusp from the first distal cusplet, less deep in *N. loozi* than in *N. brotzeni*.

Range: Selandian-Thanetian: Europe (France, Belgium, Great Britain: Leriche, 1902; Priem, 1911; Leriche, 1951; Gurr, 1962; Casier, 1967; Herman, 1977; Hovestadt *et al.*, 1983; Cappetta, 1987, 2012; Russia: Glickman, 1964; central Asia, Kazakhstan: Kordikova *et al.*, 2001); Thanetian (North America, Dakota: Cvancara & Hoganson, 1993, under the name of *Notorynchus serratissimus* (Agassiz, 1843), *partim* figs. 2X, AA, non figs. 2W, Z).

CONCLUSIONS

Until now, the genus *Notidanodon* was unknown in Jurassic deposits. The *Notidanodon* sp. tooth from the Tithonian (Late Jurassic) of New Zealand constitutes the earliest record of the genus and the most ancient discovery of a Jurassic neoselachian remain in the Antarctic realm, at a moment where New Zealand was close to Antarctica. So far, the occurrence of the oldest hexanchiform shark in the southern hemisphere rested on a single tooth coming from Aptian deposits of Antarctica, and referred to *Hexanchus* sp. by Cione & Medina, 2009. This New Zealand hexanchid tooth discovery highlights the seniority of the genus *Notidanodon* and suggests the possibility of discovering older representatives of the genus.

However, despite the seniority of the genus *Notidanodon*, its species diversity remains low with only six nominal species described during a period spanning ca. 95 Myrs, between the Tithonian and the Thanetian (four between Tithonian and Maastrichtian: *Notidanodon antarcti*, *N. dentatus*, *N. lanceolatus*,

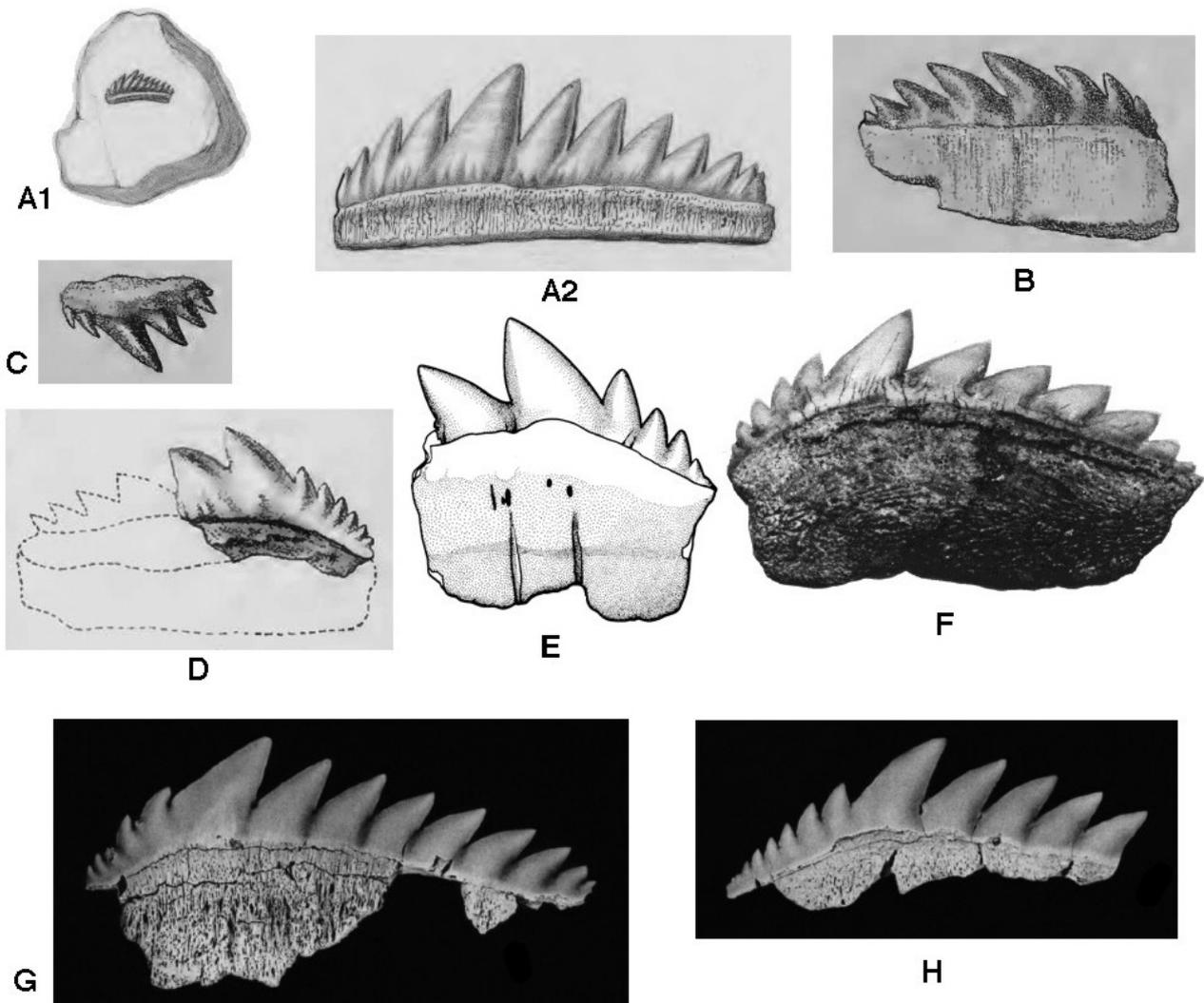


Figure 4. Type specimens (except fig. 4 E) of the species classically assigned to *Notidanodon*. **A1:** *Notidanodon pectinatus*, labial view, holotype; **A2:** same specimen, enlarged (after Agassiz, 1843). **B:** *Notidanodon dentatus*, lectotype (after Woodward, 1886). **C:** *Notidanodon lanceolatus*, lingual view, holotype (after Woodward, 1886). **D:** *Notidanodon loozi*, labial view, holotype (after Vincent, 1876). **E:** *Notidanodon loozi* (after Cappetta, 1987). **F:** *N. loozi*, lingual view (after Hovestadt *et al.*, 1983). **G:** *Notidanodon brotzeni*, labial view, holotype (after Siverson, 1995). **H:** *Notidanodon brotzeni*, labial view, paratype (after Siverson, 1995). (Note that the different specimens are not at the same scale. For the localities of the specimens, see the text).

and *N. pectinatus*; and two in a period covering the Danian, Selandian and Thanetian). Moreover, the number of available specimens is also low, mainly when considering the Mesozoic species.

This situation lead us to a short review of the previously described *Notidanodon* species, to discuss their status and to record precisely their stratigraphical and paleobiogeographical ranges. Concerning the different nominal species, it appears clearly that they can be combined in several morphological groups corresponding likely to different genera.

One group, corresponding to the type species *Notidanodon pectinatus*, is characterized by teeth with sharp, erect cusplets, those of the mesial part being particularly developed and directed mesially. By its general morphology, the New Zealand specimen seems to lie close to this group.

In a second group, corresponding to *Notidanodon dentatus*, the cusplets and the main cusp are clearly bent distally and the mesial part of the teeth is relatively less developed than in the *Notidanodon* type species, with a limited number of cusplets.

A third group includes the Paleocene species *N. loozi* and *N. brotzeni*, characterized by large-sized lower teeth with a high root, and a main cusp and cusplets bent distally. The distal cusplets are numerous (up to seven), as are the mesial ones (up to ten), which are more erect and even mesially directed in some teeth. It is interesting to note that this morphology is restricted to Paleocene species and that the tooth morphology of Cretaceous *N. dentatus* or *N. pectinatus* is not observed in Cenozoic taxa.

In the light of these observations, it appears obvious that the genus *Notidanodon* seems not to be homogeneous and will need a revision, beyond the scope of the present article.

Range of the genus *Notidanodon*

The following list is a summary of the range of the genus *Notidanodon*, illustrating its broad distribution despite the low number of described species.

Tithonian: the present work; **Valanginian:** Europe (France, Hérault, Lez spring: Cappetta, 2012); **Hauterivian, Barremian:** Europe, Germany (Ward & Thies, 1987); **Aptian:** North America (U.S.A., California: Long *et al.*, 1993); **Albian:** Europe (Great Britain: Woodward, 1886; Smart, 1990, 1995); **Cenomanian:** ? Asia (India, Tamil Nadu: Underwood *et al.*, 2011); Santonian (Asia, Japan: Kitamura & Kawasaki, 2001); **Campanian:** Antarctica (Richter & Ward, 1990; Kriwet *et al.* 2006); **Cenomanian/Campanian:** Europe (Great Britain: Agassiz, 1843); America (Canada, British Columbia: Hessin *et al.* 2007); **Maastrichtian:** Antarctica (Martin & Crame 2006); North America (USA, California: Applegate, 1965; Welton, 1979; South Dakota: Martin, 2016); South America (Argentina: Bogan *et al.*, 2016); New Zealand (Woodward 1886; Davis 1888); Europe (Denmark: Adolfsen & Ward, 2013); **Campanian/Maastrichtian:** Antarctica (Cione & Medina, 1987; Grande & Chatterjee, 1987); western Africa (Angola: Antunes & Cappetta, 2002); Europe, Crimea (Trikolidi, 2014); **Danian:** Europe (Sweden: Siverson, 1995); Russia (Glickman 1964); North Africa (Morocco: Gheerbrant *et al.*, 2003); North America (USA, Dakota: Cvanara & Hoganson, 1993); New Zealand (Mannerling & Hiller, 2008); **Selandian:** Europe (Belgium: Vincent, 1876; Hovestadt *et al.*, 1983); **Selandian/Thanetian:** Central Asia (Kazakhstan: Kordikova *et al.*, 2001); **Thanetian:** Europe (Great Britain: Gurr, 1962; Cappetta, 1987); North Africa (Morocco: Gheerbrant *et al.*, 2003; Cappetta, 2012).

According to Long *et al.* (1993), the evolution of the hexanchid dentition went through a sequence from teeth with smooth mesial edge [(*Notidanoides muensteri* (Agassiz, 1835)] towards teeth with dentate mesial edge (*Notidanodon lanceolatus* Woodward, 1886), with intermediate serrated forms like *Crassodontidanus serratus* (O. Fraas, 1855) and *Gladioserratus aptiensis* (Pictet, 1865). However, as some Jurassic species like *Notidanoides muensteri* possess weakly serrated mesial cutting edge (Cappetta, 1990) this conclusion seems debatable and cannot be retained with certainty, not to mention the occurrence of *Notidanodon* sp. exhibiting strong mesial cusplets as early as the Tithonian. Moreover, this hypothesis by Long *et al.* (1993) is in contradiction with the stratigraphic range of the taxa in their sequence. These authors have also considered the genus *Notidanus* (i.e. *Hexanchus*) as the ancestral stock of hexanchid sharks.

Thies (1987) suggested that Early Cretaceous cow sharks were distributed according to temperature: *Pachyhexanchus pockrandti* (Ward & Thies, 1987) and *Gladioserratus aptiensis* (Pictet, 1865) were presumably Tethyan faunal elements whereas *Notidanodon lanceolatus* would be a Boreal faunal form. Jurassic hexanchiforms were already occurring in these areas. Notwithstanding the Jurassic and Early Cretaceous elasmobranch record from the Southern Hemisphere is extremely poor (e.g. Siverson 1997, Cione 1996, Perea *et al.* 2001, Kriwet 2003, Cione & Medina 2009), the occurrence of *Notidanodon* in New Zealand (Woodward, 1886; Davis, 1888) is an argument confirming the bipolar biogeographical pattern for *Notidanodon* hypothesized by Cione (1996).

The type species *N. pectinatus* was the single occurrence of the genus *Notidanodon* in the northern Europe realm, until its recent discovery in Crimea (Trikolidi, 2014), which argues for great care in considering the range of fossil taxa, tributary from random field discoveries.

The discovery of a *Notidanodon* tooth in the Tithonian of New Zealand pushes back significantly the time-range of this genus and extends greatly its geographical range in the southern hemisphere. Kitamura *et al.* (1995) noted the occurrence of the genus *Notidanodon* in the Upper Cretaceous of Japan, on the basis of a lower tooth, which very likely does not belong to a hexanchiform but to a squaliform. Therefore, the presence of *Notidanodon* in Japan could not be confirmed on this occurrence. Later, Kitamura & Kawasaki (2001) cited *Notidanodon dentatus* in the Santonian of Japan, which thus confirms the presence of the genus in that country.

Finally, the geographical distribution of the genus *Notidanodon* is broad at a world scale despite a low species diversity. Indeed, it has been collected in practically all continents, but seems more represented in southern hemisphere than in the north, except maybe for the Palaeocene species. Concerning its stratigraphical range, besides the new Jurassic occurrence in New Zealand, *Notidanodon* is recorded practically continuously from the Valanginian to the Thanetian. However, it must be emphasised that in the Lower Cretaceous the number of collected teeth is low, mainly in Aptian and Albian deposits, making precise determinations often difficult. The same remark can be made for the period covering the Cenomanian to Santonian. The discovery of new *Notidanodon* teeth between the Tithonian and the Campano-Maastrichtian would be important for a better knowledge of its relationships among other hexanchid taxa and for more precise stratigraphical and paleobiogeographical ranges.

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