A new Jurassic cow shark (Chondrichthyes, Hexanchiformes) with comments on Jurassic hexanchiform systematics

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Abstract A new taxon, †Crassodontidanus gen. nov. of Hexanchiformes (cow sharks) from the Jurassic of Germany is described. It is characterized by peculiar teeth combining apomorphic (serrated mesial cutting edge of the main cusp) and plesiomorphic features (deep root with convex mesial and distal margins in labial and lingual views; protruding lingual root bulge). This character combination readily distinguishes members of the new taxon from all other known extant (Heptranchias, Hexanchus, Notorynchus) and extinct (†Gladioserratus, †Notidanodon, †Notidanoides, †Pachyhexanchus, †Paraheptranchias, †Weltonia) hexanchiforms. Currently, two species, †C. serratus (type species; Late Jurassic, Late Kimmeridgian of Nusplingen, South Germany) and †C. wiedenrothi (Early Jurassic, Early Pliensbachian of Gretenberg (Hanover), North Germany) are assigned to this taxon. †Crassodontidanus gen. nov. is member of †Crassonotidae fam. nov. and sister to †Notidanoides MAISEY, 1986 and †Pachyhexanchus CAPPETTA, 1990. We consider †Notidanus amalthei Oppel, 1854 from the Pliensbachian of South Germany, †Notidanus insignis Seguenza, 1887 from the Oxfordian of Sicily (Italy) and †Notidanus wagneri AGASSIZ, 1843 from the Early Tithonian of Solnhofen (South Germany) nomina dubia and nomina nuda, respectively. The family †Crassonotidae comprises plesiomorphic hexanchiforms

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Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK ranging from the Sinemurian (Early Jurassic) to the Hauterivian (Early Cretaceous).

Keywords *Notidanus serratus · Hexanchus*? wiedenrothi · Crassodontidanus gen. nov. · Crassonotidae fam. nov. · Jurassic · Nusplingen Plattenkalke

Institutional abbreviations

State Museum of Natural History Stuttgart, **SMNS**

Germany

GPIT Palaeontology Department and Museum,

Institute of Geosciences, Eberhard-Karls

University Tübingen, Germany

Natural History Museum, London, NHMUK PV

United Kingdom

Introduction

Cow sharks (the Hexanchiformes) form a monophyletic group of plesiomorphic squalomorph neoselachians. The three living oceanic genera, which represent mid-water predators, are conspicuously characterized by additional gill arches (one in Hexanchus; two in Heptranchias and Notorynchus), a single dorsal fin, imperfectly calcified vertebral centra and very characteristic dignathic dentitions comprising labio-lingually flattened saw-like teeth in the lower jaws. Their fossil record is dominated by isolated teeth extending back into the Jurassic (e.g., Thies 1983; Kriwet and Klug 2004; Underwood 2006). Articulated skeletal remains only occur in the Late Jurassic of southern Germany (e.g., Maisey 1986; Kriwet and Klug 2004) and Late Cretaceous of Lebanon (e.g., Cappetta 1980).

The earliest fossil occurrences consisting of few isolated teeth are from the Early Jurassic of Switzerland S108 J. Kriwet, S. Klug

(†Notidanus arzoėnsis Beaumont, 1960), SW Germany (†Notidanus amalthei Oppel, 1854) and NW Germany (†Hexanchus? widenrothi Thies, 1983). A single species, †Notidanus contrarius Münster, 1843, was reported from the Middle Jurassic (Bajocian) of Bavaria (Cappetta 2006). Underwood and Ward (2004) additionally figured a partial hexanchid tooth from the Bathonian of England.

Late Jurassic records are more numerous and different species have been described mainly based on isolated teeth. Two species, †Notidanus huegeliae Münster, 1843 and †Notidanus serratus FRAAS, 1855 were reported from the Kimmeridgian of Baden-Württemberg (SW Germany). Cappetta (1990) tentatively assigned †Notidanus huegeliae to †Pachyhexanchus. However, the holotype of †Notidanus huegeliae deposited in the State Museum of Natural History Stuttgart, Germany under collection number SMNS 86237 represents a very incomplete tooth lacking useful characteristics for its taxonomic assignment. Tithonian species represented by isolated teeth only are †Notidanus eximius Wagner, 1862 and †N. intermedius Wagner, 1862, which were recovered from the Lithographic Limestones of Bavaria. The latter species is based on a symphyseal tooth that most likely belongs to †Notidanoides. The only Jurassic species represented by an articulated skeleton is †Notidanoides muensteri (AGASSIZ, 1843) from the Late Kimmeridgian of Nusplingen (SW Germany). However, isolated teeth of the same species occur in the Oxfordian of Switzerland, and in Germany in the Kimmeridgian of Baden-Württemberg and Tithonian of Bavaria.

Different taxonomic and systematic concepts of extinct and extant hexanchiforms were presented in the last decades. For instance, Pfeil (1983) introduced the genus †Eonotidanus based on †Notidanus contrarius to include †N. muensteri and all other Jurassic hexanchids. This taxonomic concept, however, was refuted by Maisey (1986), Ward and Thies (1987), and Cappetta (1990) due to the incompleteness of the holotype of $\dagger N$. contrarius. Maisey (1986) consequently transferred †N. muensteri to †Notidanoides based on skeletal aspects. Additional skeletal fossil selachians from the Tithonian of Bavaria subsequently were assigned to this species based on the presence of a single dorsal fin as it occurs in extant forms (e.g., Kriwet and Klug 2004). A comprehensive revision of Jurassic sharks and rays, however, provided sound evidence that the hitherto known Bavarian specimens characterized by a single dorsal fin mostly (if not all) belong to synechodontiforms (Klug, pers. obser.). Consequently, the number and arrangement of paired and unpaired fins and the number of gill arches in Jurassic hexanchiforms remain ambiguous. The Late Jurassic taxa †N. arzoënsis, †N. eximius, †N. huegeliae and †N. daviesi were considered to be junior synonyms of †N. muensteri by Kriwet and Klug (2004). This, however, needs further analyses of teeth assigned to these taxa, which is not the focus of this study.

Ward and Thies (1987) assigned †Hexanchus? wiedenrothi from the Early Jurassic and †Notidanus serratus from the Late Jurassic to a new genus, †Paranotidanus. Both taxa are represented by isolated teeth only, which are characterized by serrations at the base of the mesial cutting edge of the principle cusp. This name, however, represents a nomen nudum according to the rules of zoological nomenclature (ICZN, paragraphs 10, 11, and 15), because no holotype and diagnosis was represented despite the assumption of Underwood and Ward (2004). Consequently, Kriwet and Klug (2004) continued to use †"Eonotidanus" for †N. serratus and two hexanchiforms in the Late Jurassic of South Germany and northern Switzerland can be distinguished: †Notidanoides muensteri from the Oxfordian of Switzerland, Kimmeridgian of Baden-Württemberg and Tithonian of Bavaria, and †"Eonotidanus" serratus from the Kimmeridgian of Nusplingen. The intention of this paper is to establish a new genus for Jurassic hexanchiforms characterized by teeth with serrated mesial cutting edges and a new family, †Crassonotidae fam. nov., to discuss its systematic composition.

Systematic palaeontology

The dental terminology used herein follows that of Applegate (1965) and Kemp (1978). The taxonomic scheme adopted here is based on Kriwet and Klug (2004), Cappetta (2006) and Cione and Medina (2009). However, we use the term 'main cusp' instead of 'acrocone'.

Class Chondrichthyes Huxley, 1880 Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902 Subcohort Neoselachii Compagno, 1977 Superorder Squalomorphii Compagno, 1973 Order Hexanchiformes Buen, 1926

Family †Crassonotidae nov.

Etymology

Derived from the genus name †*Crassodontidanus* gen. nov., which displays the characteristic tooth root morphology of members of this family and the subfamily name Notidanini Bonaparte, 1838.

Remarks

Bonaparte (1838, p. 208) introduced the subfamily Notidanini (family Squalidae) for the extant hexanchiforms

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Heptranchias (type) and Notidanus (=Hexanchus). The name Notidanini subsequently often was used incorrectly as family name Notidanidae (=Notodanidae; Owen (1846)) for extinct and/or extant hexanchiforms in the past. Gray (1851) allocated both living hexanchiforms to the family Hexanchidae, which is the correct systematic assignment. Consequently, no appropriate family name is available to comprise only extinct hexanchiforms, which do not belong to any extant taxon.

Included taxa

†Crassodontidanus gen. nov. (syn. †Notidanus Cuvier, 1816 in partem), †Notidanoides Maisey, 1986 (syn. †Aellopus Münster, 1836; Notidanus Cuvier, 1816 in partem) and †Pachyhexanchus Cappetta, 1990 (syn. †Eonotidanus Pfeil, 1983).

Genus †Crassodontidanus nov.

Etymology

Derived from the Latin word 'crassus': 'fat, thick' in allusion to the massive tooth root, the Greek word 'odontosi' $(o\delta \delta v \tau \omega \sigma \eta)$: 'jagged, serration' in allusion to the serrated mesial cutting edge and the ending 'idanus' derived from *Notidanus*.

Type species †Notidanus serratus Fraas, 1855. Included species †Hexanchus? wiedenrothi Thies, 1983.

Stratigraphic distribution

Early Pliensbachian (*Davoi* zone), Early Jurassic (†*C. wiedenrothi* nov. comb.); Late Oxfordian (*Bimammatum* and *Transversarium* zones) and Early Kimmeridgian (*Beckeri* zone, *Ulmense* subzone) (†*C. serratus* nov. comb.).

Geographic distribution

†*C. wiedenrothi* nov. comb.: Gretenberg near Hanover, Lower Saxony, NW Germany; †*C. serratus* nov. comb.: Lochen near Balingen, Stuifen near Reichenbach and Nusplingen, Baden-Württemberg, SW Germany (Fig. 1).

Diagnosis

Hexanchiform shark based on the following combination of dental characters: upper and mesial teeth multicuspid; only weak dignathic and monognathic heterodonties; mesial cutting edge of main cusp serrated; no mesial cusplets; main cusp stout and massive; up to seven accessory cusplets decreasing gradually in size distally; crown neck well-developed; root thick and high with convex outline in labial and lingual views; lingual root bulge prominent; basal root face oblique in profile views forming an acute angle; basal root face broad and slightly convex.

Differential diagnosis

The character combination of a main cusp with serrated mesial cutting edge and deep and rounded root with oblique basal face readily distinguishes †Crassodontidanus gen. nov. from all other hexanchiform sharks although great similarities to other taxa exist (e.g., serrated mesial cutting edge of main cusp in †Gladioserratus, Hexanchus and Notorynchus spp.; root morphology similar in †Notidanoides and †Pachyhexanchus). The dentition of living and fossil members of Heptranchias, Hexanchus and Notorynchus (=Notidanion JORDAN AND HANIBAL, 1923) differs from that of †Crassodontidanus gen. nov. in being strongly dignathic. Additionally, the root of their multicuspid lower teeth is rectangular and strongly compressed labio-lingually with the basal root face being almost vertical conversely to the condition in †Crassodontidanus gen. nov., in which the root is very deep and basal root face forms an angle to the crown.

†Paraheptranchias Pfeil, 1981 is characterized by a strongly dignathic dentition and lower multicuspid teeth, in which larger and smaller cusps alternate. These are arranged into sets consisting of three cusps starting mesially with the largest one decreasing in size distally. Teeth of †Weltonia Ward, 1979 easily can be distinguished by their very enlarged and sigmoidal curved slender main cusp and rectangular root outline.

The serrated mesial cutting edge of the main cusp distinguishes teeth of †*Crassodontidanus* gen. nov. conspicuously from those of †*Notidanoides* Maisey, 1986, †*Notidanodon* Cappetta, 1975 and †*Pachyhexanchus* Cappetta, 1975 (=*Eonotidanus* Pfeil, 1983). The differences in serration of the main cusp are not related to ontogenetic changes since juveniles of the extant *Notorynchus* and the extinct †*Gladioserratus* Underwood et al. 2011 lack serrated mesial cutting edges of the main cusp that are present in adults. Teeth of †*Notidanodon* Cappetta, 1975 furthermore vary in having sub-rectangular root outlines and additional mesial cusplets.

Description of holotype of $\dagger C$. serratus nov. comb.

The holotype of †*C. serratus* nov. comb. (SMNS 3695/10; Fig. 2a, b), representing the type-species of the new taxon, is a single tooth. It measures 18 mm in mesio-distal width and 12 mm in height. The crown is labio-lingually compressed without any ornamentation. The lingual face is flat, whereas the labial one is markedly convex. It consists of six cusps. The main cusp is massive, comparably low and stout

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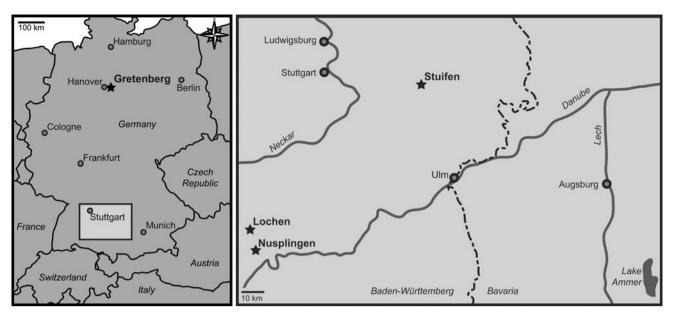


Fig. 1 Geographical maps showing the occurrence of †*Crassodontidanus* gen. nov.: Gretenberg near Hanover (Early Pliensbachian, Early Jurassic) and three Late Jurassic localities in SW Germany—Nusplingen (Late Kimmeridgian), Stuifen and Lochen (both Late Oxfordian)

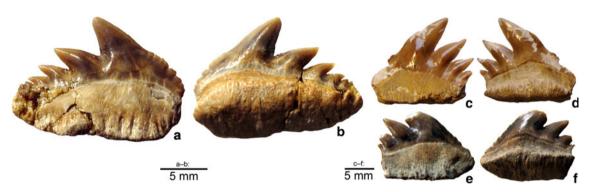


Fig. 2 †*Crassodontidanus serratus* nov. comb. from the Late Jurassic of Germany. Holotype SMNS 3695/10 from the Late Kimmeridgian of Nusplingen, upper lateral tooth in labial (a) and lingual (b) views. Upper antero-lateral tooth (SMNS 52097) from the

Late Oxfordian of Stuifen in labial (c) and lingual (d) views. Lower lateral tooth (SMNS 95824/1) from the Late Oxforidan of Lochen in labial (e) and lingual (f) views

widening basally. It is distally inclined and forms an angle of ca. 30° with the base of the crown. The mesial cutting edge is slightly sigmoidal with a shallow central convexity. It bears characteristic serrations extending from the base almost two-thirds up the mesial cutting edge with the serrae decreasing gradually in size upwards. There is no mesial heel. The distal cutting edge is straight and almost vertical. The cross-section of the main cusp is flattened oval.

The accessory cusplets are strongly bent distally. The angle between main cusp and first accessory cusp is about 62°. The first cusplet is considerably smaller and more delicate than the main cusp. It has an acute apex. The second and third accessory cusplets become gradually more inclined distally and decrease in size. The fourth and

fifth cusplets are very reduced with erect apices. The cross section of the accessory cusplets is sub-rounded.

The root neck separating the crown from the root is well developed, broad and bears very faint vertical striations labially. In both labial and lingual views, the tooth neck is concavely curved.

The root is rather low but deep. The outline is convex with rounded mesial and distal edges but almost straight basal aspect in labial and lingual views. The distal edge tapers and is very low below the last two accessory cusplets. The lingual root bulge is prominent and almost shelf-like below the main cusp. The basal angle is acute and the basal root face is broad and slightly convex in profile view. Labially, slit-like, vertical foramina are arranged along the

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basal margin. Lingually, a very narrow, also slit-like foramen is located below the main cusp.

Variability and heterodonty

The new taxon is known from only a few teeth, which makes it difficult to establish heterodonty patterns. The single upper antero-lateral tooth (SMNS 52097) from Stuifen (Fig. 2c–d) and the only known specimen from Lochen, a lower lateral tooth (SMNS 95824/1; Fig. 2e–f) show both the typical serrated medial cutting edge and the

deep and rounded root in combination with several cusplets distal to the main cusp. The small sample of teeth from Nusplingen (Fig. 3) represents predominantly adults implying that teeth of the upper and lower jaws most likely had comparable numbers of cusps conversely to the condition found in extant hexanchiforms. Heterodonty patterns also are less developed compared to those found in living hexanchiforms. In †*Crassodontidanus* gen. nov., weak monognathic as well as dignathic heterodonty patterns seemingly were developed. In the upper and lower jaw, teeth are multicuspid. The number of cusps increases from



Fig. 3 Associated tooth set of †*Crassodontidanus serratus* gen. nov. from the Late Kimmeridgian (Late Jurassic) Nusplingen Plattenkalke (SW Germany). a Complete preserved plate with 18 isolated teeth of the right lower dentition (GPIT 81512). b Sketch of 17 numbered teeth, not to scale. c Tooth 1 in lingual view. d Tooth 2 in lingual

view. **e** Tooth 3 in lingual view. **f** Tooth 5 in lingual view. **g** Tooth 10 (*left*) and 11 (*right*) in labial (10) and lingual (11) views. **h** Tooth 6 in lingual view. **i** Tooth 8 (*bottom*) and 9 (*top*) in labial views. **j** Tooth 14 (*left*), 13 (*middle*) and 12 (*right*) in lingual (14) and labial (12–13) views

six (or less) mesially to eight (or more) distally. Additionally, teeth of the lower jaw are mesio-distally broader than those of the upper jaw. Nevertheless, more material including articulated dentitions is necessary to establish the whole range of heterodonty patterns.

Geographic range

The geographic range of †*Crassodontidanus serratus* nov. comb. is restricted to SW Germany according to our current knowledge. The single specimen (NHMUK PV P.35667) from the Oxford Clay of Scarborough (England) assigned to †*Notidanus serratus* by Woodward (1886) is characterized by small denticles at the mesial base of the main cusp despite a serrated cutting edge and probably represents a different genus, which also occurs in the Bajocian of Germany (pers. obser.). Taxonomic identification of this hexanchiform, however, requires further analyses. The known geographic distribution of †*Crassodontidanus* gen. nov. currently is restricted to Germany.

Remarks

The fossil record of hexanchiforms mainly consists of isolated teeth. Skeletal remains, conversely, are very rare and have been recovered so far only from Late Jurassic Lithographic Limestones of South Germany (two skeletons from Nusplingen (Late Kimmeridgian; Schweizer 1964) and Solnhofen (Late Tithonian; Beyrich 1849), respectively) and Late Cretaceous (Early Santonian) calcareous sediments of Lebanon (few incomplete skeletal remains; e.g. Cappetta 1980). The rather large articulated skeleton from Solnhofen figured by Beyrich (1849) was included in †*Notidanus muensteri* by Wagner (1862) but has been lost during World War II. Thus, it is not possible to establish its taxonomic assignment.

Originally, all Jurassic hexanchiforms have been collectively assigned to the genus †*Notidanus* Cuvier, 1816 (=*Hexanchus* Rafinesque, 1810 and *Heptranchias* Rafinesque, 1810) (e.g., Cuvier 1816; Woodward 1886, 1889; Arambourg 1952; Schweizer 1964) regardless of obvious morphological differences between fossil and extant taxa. The oldest hexanchiform teeth known to date are from the Sinemurian of Switzerland (Canton Ticino) and were described as †*Notidanus arzoėnsis* by Beaumont (1960). In their morphology, these teeth resemble those of †*Notidanus muensteri* to some extent.

In the Late Jurassic, hexanchiforms seemingly became more diverse and numerous species based on few or single isolated teeth were described in the past. Among these, Agassiz (1833–1844) defined the Late Jurassic hexanchiform †*Notidanus muensteri*. The almost complete specimen from Nusplingen assigned to this species was described in

detail by Schweizer (1964) and Maisey (1986). The latter author based the genus †*Notidanoides* on this specimen and included †*N. arzoënsis* in this taxon. †*Notidanus serratus*, which forms the focus of this study, is another Late Jurassic hexanchiform, which was based on a single tooth embedded in a calcareous matrix from Nusplingen by Fraas (1855: 98). Quenstedt (1858: 784, pl. 96, fig. 44) subsequently presented a calcareous slab from Nusplingen with 14 disarticulated teeth of a single dentition of this species. Schweizer (1964), nevertheless, was the first and only author up to now to present a detailed study of this species based on the material described by Fraas (1855) and Quenstedt (1858) and few additional teeth from Nusplingen.

†Notidanus serratus is widely assumed to be a member of †Notidanoides although Maisey (1986) did not include this species in †Notidanoides. Subsequently, Cappetta (1990) indicated that this species should be included in a different taxon pending a revision of Late Jurassic hexanchiforms. We agree with both and consequently introduce a new taxon, †Crassodontidanus. Momentarily, two species, †C. serratus (Fraas, 1855) and †C. wiedenrothi (Thies, 1983) are referred to this genus. †C. wiedenrothi is known by a single tooth so far with complete tooth crown displaying the characteristic serrated mesial cutting edge and an incompletely preserved but typically massive tooth root (compare Thies 1983: pl. 3, fig. 1).

The tooth crown morphology of the neoselachian stem-lineage †Synechodontiformes (Klug 2010), especially of the family †Pseudonotidanidae, resembles that of hexanchiform sharks including †Crassonotidae fam. nov. to some extent, but the teeth are readily distinguishable by different features. The tooth root of synechodontiforms, which is comparably low, is characterized by a pseudopolyaulacorhize vascularization pattern, and displays a labial depression in basal view, which is lacking in hexanchiforms (Klug 2010). Additionally the morphology of the tooth crown of pseudonotidanids presents a divergent pattern of the main cusp and the first distal cusplet (Klug and Kriwet 2010).

Conclusions

Hexanchiformes represents a plesiomorphic group of squalomorph sharks with a fossil record extending back into the Early Jurassic. The re-evaluation of Jurassic and Cretaceous hexanchiforms herein confirms previous assumptions that hexanchiform teeth from the Late Jurassic characterized by serrated mesial cutting edges of the main cusp and massive, rounded roots with oblique basal root faces represent a genus different from all other hitherto known hexanchiform taxa. Therefore, the new taxon, †*Crassodontidanus* gen. nov. with two species, †*C. serratus* (Fraas, 1855) and †*C. wiedenrothi* (Thies, 1983) is introduced.

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Currently, four families, Chlamydoselachidae, †Crassonotidae fam. nov., Heptranchidae and Hexanchidae, are recognized within Hexanchiformes. All identified Jurassic hexanchiform sharks are assigned to the extinct family, †Crassonotidae fam. nov. by us (conversely to the taxonomic scheme of Cappetta 2006). The main uniting character is the morphology of the root. Based on dental characters, this family is considered the most plesiomorphic taxon within Hexanchiformes.

Although crassonotids have their greatest taxonomic diversity in the Jurassic, a single taxon assigned to †*Pachyhexanchus*, †*P. pockrandti*, is restricted to the Early Cretaceous. The assignment of †*P.? huegeliae* Münster, 1843 to †*Pachyhexanchus* by Cappetta (2006) remains doubtful. Based on Maisey (1986), Cappetta (1990, 2006) and Kriwet and Klug (2004) and the results of this study we propose the following taxonomic arrangement of crassonotids sharks:

Order Hexanchiformes Buen, 1926

Family † Crassonotidae nov.

Stratigraphic range Sinemurian (Early Jurassic)-Hauterivian (Early Cretaceous).

Genus †Notidanoides MAISEY, 1986

Type species †Notidanus muensteri AGASSIZ, 1843; Late Kimmeridgian, Late Jurassic, Nusplingen, Baden-Württemberg, SW Germany

Included species †N. arzoënsis (Beaumont 1960); Sinemurian, Early Jurassic; Canton Ticino, Switzerland

†*N. daviesii* (Woodward, 1886); Oxfordian, Late Jurassic; Oxford, England

†N. eximius (WAGNER, 1862); Early Tithonian, Late Jurassic; Franconian Alb, South Germany

†N. muensteri (AGASSIZ, 1843); Kimmeridgian, Late Jurassic; Franconian Alb, South Germany; Kimmeridgian, Late Jurassic, Canton Schaffhausen, Switzerland (=† N. intermedius WAGNER, 1862, symphyseal tooth)

Genus †Crassodontidanus gen. nov.

Type species †Notidanus serratus Fraas, 1855; Late Kimmeridgian, Late Jurassic, Nusplingen, Baden-Württemberg, SW Germany

Included species †C. wiedenrothi (THIES, 1983); Early Pliensbachian, Late Jurassic, Lower Saxony, Northern Germany

Genus †Pachyhexanchus CAPPETTA, 1990

Type species Notidanoides pockrandti WARD AND THIES, 1987; Early Hauterivian, North Germany

Included species †P. nikitini (Chabakov and Zonov, 1935); Tithonian, Late Jurassic, Province of Moscow, Russia †P. pockrandti (Ward and Thies, 1987); Hauterivian, Early Cretaceous, North Germany

Inc. sed.

†*Notidanus huegeliae* Münster, 1843; Kimmeridgian, Late Jurassic, Baden-Württemberg, SW Germany

Nomina dubia/nuda

†*Notidanus amalthei* Oppel, 1854; Pliensbachian (Lias Delta), Early Jurassic, Mössingen, Baden-Württemberg, SW Germany

†"Notidanus" contrarius Münster, 1843; Bajocian (Dogger Delta), Middle Jurassic, Bavaria, South Germany †Notidanus insignis Seguenza, 1887; Oxfordian, Late Jurassic, Sicily, Italy

†*Notidanus wagneri* AGASSIZ, 1843; Early Tithonian, Late Jurassic, Solnhofen, South Germany

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