FIRST MENTION OF THE FAMILY PSEUDONOTIDANIDAE (CHONDRICHTHYES: NEOSELACHII) IN THE JURASSIC OF NORMANDY

by Gilles CUNY (1) and Jérôme TABOUELLE (2)

ABSTRACT

The discovery of a tooth of cf. *Pseudonotidanus* sp. is reported from the Bathonian of Normandy. Its morphology supports the transfer of the species *terencei* from the genus *Welcommia* to the genus *Pseudonotidanus*. It also supports the idea that Pseudonotidanidae might be basal Hexanchiformes rather than Synechodontiformes.

KEYWORDS

Normandy, Arromanches, Jurassic, Bathonian, Chondrichthyes, Elasmobranchii, Synechodontiformes, Hexanchiformes, Pseudonotidanidae.

RÉSUMÉ

La découverte d'une dent de cf. *Pseudonotidanus* sp. est signalée dans le Bathonien de Normandie. Sa morphologie soutient le transfert de l'espèce *terencei* du genre *Welcommia* au genre *Pseudonotidanus*. Elle soutient également l'idée que les Pseudonotidanidae pourraient appartenir aux Hexanchiformes basaux plutôt qu'aux Synechodontiformes.

MOTS-CLEFS

Normandie, Arromanches, Jurassique, Bathonien, Chondrichthyes, Elasmobranchii, Synechodontiformes, Hexanchiformes, Pseudonotidanidae.

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1 – INTRODUCTION

In 2004, Underwood and Ward erected the new family Pseudonotidanidae for sharks showing teeth with a hexanchid-like crown (compressed labio-lingually with several cusps) and a Palaeospinacid-like root (lingually expanded and flat based), hence offering an opportunity to better understand the phylogenetic relationships between the Hexanchiformes and the Synechodontiformes, which might be closely related (Duffin & Ward, 1993; Underwood, 2006).

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(1) Université Claude Bernard Lyon 1, Campus de la Doua, Bâtiment Géode
2, rue Raphaël Dubois 69622 VILLEURBANNE CEDEX, France
Email: gilles.cuny@gmail.com

(2) Museum Elbeuf – La Fabrique des Savoirs
7, cours Gambetta 76500 ELBEUF, France
Email : jerome.tabouelle@la-crea.fr

Pseudonotidanidae were first included into Synechodontiformes (Underwood & Ward, 2004), an idea accepted by Klug & Kriwet (2008, 2010), Klug *et al*. (2009), Klug (2010) and Kriwet & Klug (2011), but this family may as well belongs to the Hexanchiformes according to other authors (Underwood, 2006; Cappetta, 2012; Maisey, 2012). Based on enameloid microstructure, Guinot & Cappetta (2011) also considered *Welcommia* to be a Hexanchiformes. So far, the family Pseudonotidanidae is represented by two genera, encompassing three and two species respectively (*Pseudonotidanus politus, P. semirugosus, P. terencei, Welcommia bodeuri, W. cappettai).* Cappetta (2012) considers indeed that the species *terencei* is better attributed to the genus *Pseudonotidanus* than to *Welcommia.* The genus *Pseudonotidanus* has been reported from the Toarcian of Germany and Belgium, the Bathonian and Callovian of England and the Oxfordian of France, whereas the genus *Welcommia* is known from the Oxfordian of Germany and Valanginian of Southern France (Underwood & Ward, 2004; Klug and Kriwet, 2010; Cappetta, 2012). We add here a report of this family in the Bathonian of Normandy.

2 – GEOLOGICAL SETTING

The specimen, housed in the collection of Elbeuf Museum with the number 2013.5.1 ME, was surface collected on the intertidal zone at Arromanches (Fig. 1), at the top of the lower member of the Port-en-Bessin Marls Formation (*Tenuiplicatus* zone, Lower Bathonian, Arromanches 2 surface). To the East of Port-en-Bessin, the rocky intertidal zone is made of the last beds of the Porifera Limestone (Calcaire à spongiaires). In the background, the cliff is made of three parts. The basal part is a vertical cliff made of a series of greyish marlstone, the Port-en-Bessin Marls (Marnes de Port-en-Bessin). The middle part is a gently sloping scree measuring 25 m and showing sediment slides with some marls outcropping. This slope is covered by vegetation. Near the top, the cliff becomes stiff again and is made of a series of marls and limestones, the limestone beds becoming thicker to make the massive yellowish limestone, called Saint-Pierre-du-Mont Limestone (Calcaire de Saint-Pierre-du-Mont). The stratigraphic log of the cliff (log of the « Tour Vauban ») is thus as follows:

1. Saint-Pierre-du-Mont Limestone (12 m): Middle Bathonian.
2. Port-en-Bessin Marls (35-40 m): Lower to Middle Bathonian.
3. Porifera Limestones (outcropping thickness: 2 m): Upper Bajocian.

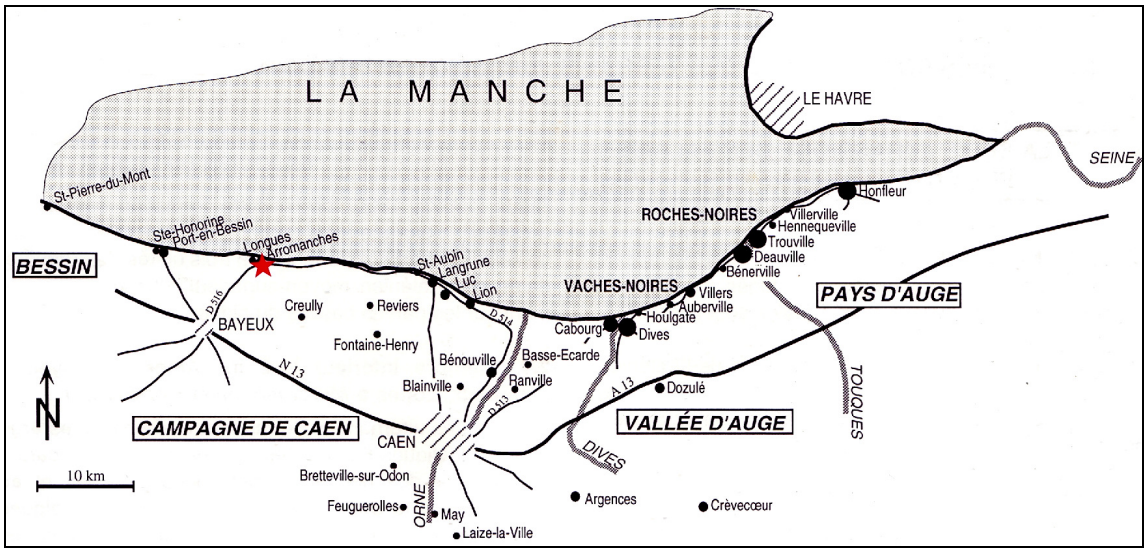

Fig. 1: Geographical location of Arromanches (red star) (France, Calvados) (Dugué *et al*., 1998).

Only the upper part of the Porifera Limestone and the lower part of Port-en-Bessin Marls are easily accessible. A detailed log of the Bajocian/Bathonian transition has been published by Rioult & Fily (1975, 1980) and Rioult *et al.* (1991) (Fig. 2).

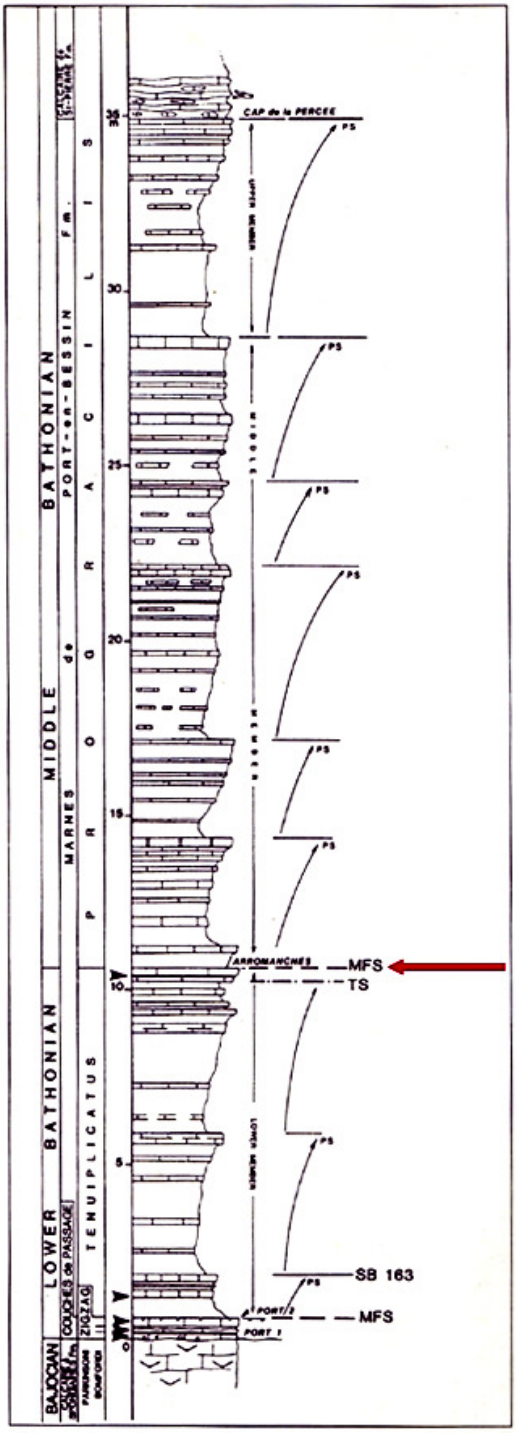

Fig. 2: Log and sequence stratigraphy of the eastern cliff at Port-en-Bessin (Lower and Middle Bathonian). The red arrow marks the Arromanches 2 surface, where 2013.5.1 ME was found. From Rioult *et al.* (1991).

The top of the Porifera Limestone is made of a white limestone with lumps of clay and pyrite, the latter often hydrated into limonite. It is bioturbated and ends with an erosion surface, the Port-en-Bessin 1 surface. This surface is overlain by three thin beds of hard, argillaceous limestone, called beds a, b and c of the transition zone (Guillaume, 1927), which makes the transition between the Bajocian Porifera limestone and the Bathonian Port-en-Bessin Marls. Each of these beds corresponds to one of the three sub-zones of the *Zigzag* zone (Lower Bathonian).

The Port-en-Bessin Marls (*Tenuiplicatus* and *Progracilis* zones, Lower Bathonian to lowermost Middle Bathonian) are made of a series of grey marls and argillaceous limestones that outcrop in many places around the Bessin area, but more particularly in the coastal cliffs between Grandcamp and Arromanches (Fig. 3). Three units are distinguished in the Port-en-Bessin Marls (Rioult & Fily, 1975 ; Fily *et al.*, 1989), but only the lower one (10 to 12 m, *Tenuiplicatus* zone, Lower Bathonian) is accessible in the cliffs. It is made of a series of decimetric marly beds grading into argillaceous limestone. The latter appears often discontinuous, without a clear upper boundary. Their thickness and coarseness raise regularly through two parasequences, reflecting the progradation of a shelf prism. The upper boundary of this unit is marked by two beds of limestone (0.5 m thick at Port-en-Bessin, 1 m thick at Arromanches) with more bioturbations, often overhanging in the cliffs. These two beds are interpreted as a thin transgressive interval. This lithology marker holds at its base the transgressive surface Arromanches 1 and at its top the Arromanches 2 surface, a sedimentary discontinuity characterized by mineralogical changes, where smectite replaces kaolinite, as well as by faunistic changes, with the disappearance of the endofauna and explosion of plankton. It marks the maximum flooding surface (MFS) and the boundary between the Lower and Middle Bathonian.

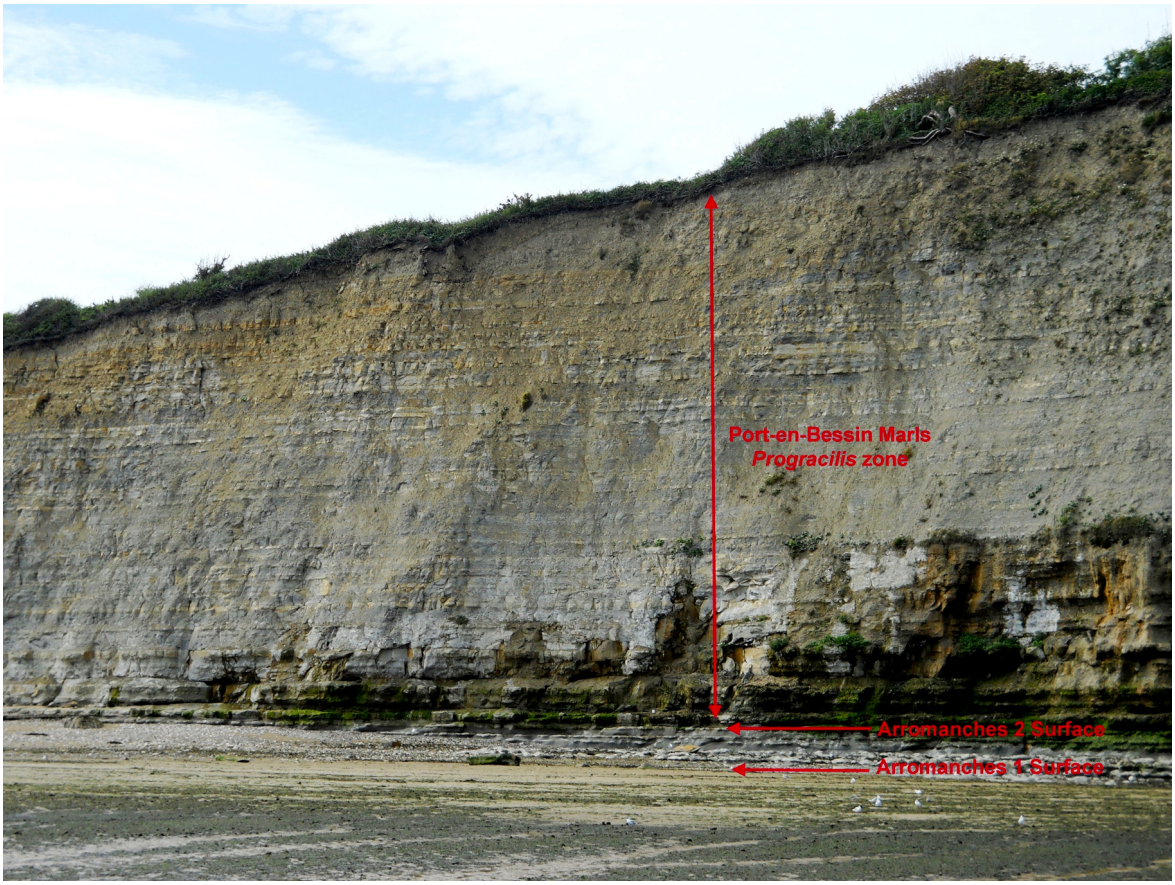

Fig. 3: The cliff at Arromanches, displaying the Lower and Middle Bathonian Port-en-Bessin Marls with the Arromanches 1 and Arromanches 2 surfaces.

3 – DESCRIPTION

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Subcohort Neoselachii Compagno, 1977
Order ?Hexanchiformes Buen, 1926
Family Pseudonotidanidae Underwood & Ward, 2004
Genus *Pseudonotidanus* Underwood & Ward, 2004
cf. *Pseudonotidanus* sp.

Material: 1 tooth (2013.5.1. ME, fig. 4)

The tooth 2013.5.1 ME measures 10 mm mesio-distally, 4 mm labio-lingually and is 8 mm high. It is almost complete, although the mesial extremity of the tooth is missing. It shows a main cusp flanked by 6 cusplets distally, the sixth one being incipient and 5 cusplets mesially. The main cusp and first distal cusplets are inclined distally. The distal cusplets are larger than the mesial ones. They show, like the main cusp convex labial and lingual faces whereas the mesial ones are more flattened. Lateral cusplets decrease regularly in size towards the mesial and distal extremities of the crown. The first and third mesial cusplets show a small extra cusplet mesially. There is a well developed cutting edge, which is continuous from the main cusp to the most distal and mesial cusplets. The enameloid is smooth on both sides of the crown, but there is a band devoid of enameloid at the base of the lingual face of the crown (lingual neck, fig. 4C).

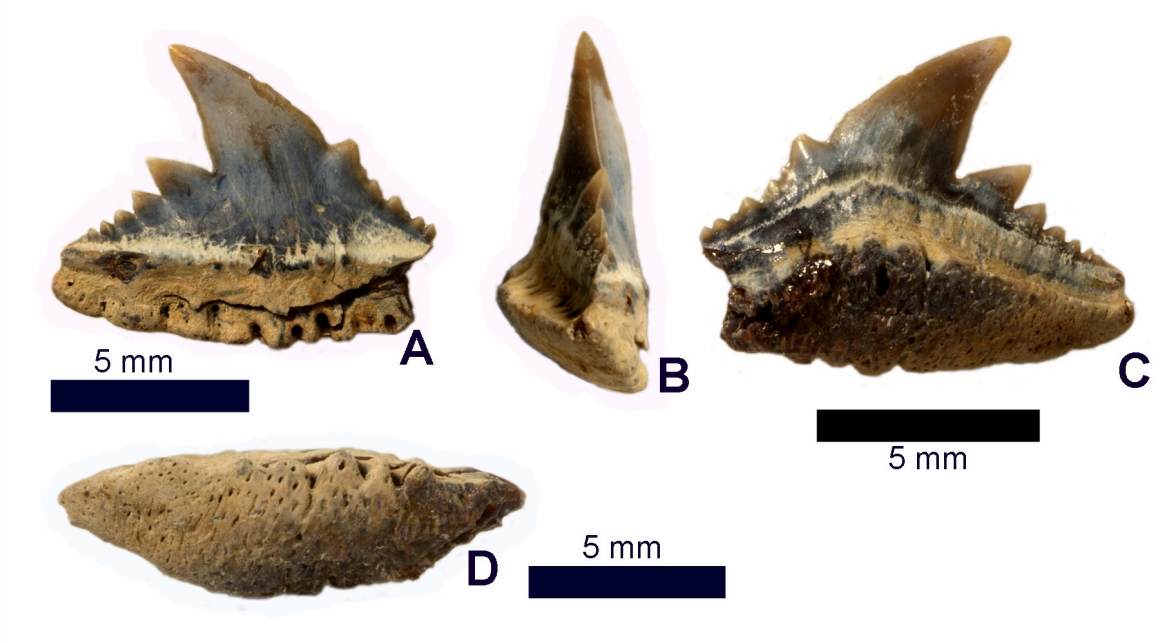

Fig. 4: Tooth of cf. *Pseudonotidanus* sp. from Arromanches in A: labial, B: distal, C: lingual, and D: basal views.

The root is quite deep in labial view and shows foramina mainly restricted to its lower part (Fig. 4A). There are three enlarged foramina at the base, just below the main cusp, with a partially open basal wall, thus forming three short grooves on the labial part of the basal face of the root (Fig. 4D). The root is slightly projected lingually with a concave face showing a row of slit-like foramina in its middle part. There is also one enlarged foramen in the basal part, just below the main cusp. It is flanked distally by a rather large, slit-like foramen, again lacking part of its basal wall. The basal face of the root is lozenge-shaped and show many foramina randomly distributed. Its basal face forms with the axis of the crown an angle of approximately 50° (Fig. 4B).

4 – DISCUSSION

The shape of the crown of 2013.5.1. ME is quite similar to that of the teeth of Crassonotidae (*Crassodontidanus, Notidanoides* and *Pachyhexanchus*), except for its cuspidate mesial part and its relatively small first distal cusplet (Kriwet & Klug, 2011; Cappetta, 2012). The main difference with the teeth of Crassonotidae is, however, seen at the level of the root, which is shallower, especially in labial view, and pseudopolyaulacorhize (Kriwet & Klug, 2011; Cappetta, 2012). 2013.5.1 ME is better attributed to the family Pseudonotidanidae based on the following characters: cusps compressed, not curved lingually, and devoid of ornamentation; crown does not overhang root; tooth strongly asymmetrical with main cusp and distal cusplets inclined distally; root peudopolyaulacorhize and expanded lingually (Underwood & Ward, 2004; Cappetta, 2012). 2013.5.1 ME shares with the teeth of *Welcommia bodeuri* a similar angle between root and crown (Cappetta, 1990, fig. 5b), but this angle is more acute in the teeth of *W. cappettai* (Klug & Kriwet, 2010, fig. 2b). Anyway, 2013.5.1 ME differs from the ones of *Welcommia* in possessing more than four distal cusplets and a cuspidate mesial heel (Klug & Kriwet, 2010; Cappetta, 2012). It shares with the genus *Pseudonotidanus* the presence of numerous distal and mesial cusplets, all considerably shorter than main cusp and a well-developed cutting edge continuous along the apical edge (Underwood & Ward, 2004).

The presence of a cuspidate mesial heel is, according to Cappetta (2012) an important character of *Pseudonotidanus,* and according to this character, the latter author proposes to transfer the species *terencei* to *Pseudonotidanus.* In their original diagnosis of the genus *Pseudonotidanus,* Underwood & Ward (2004) wrote that "Basal face of root flat, at right angles to crown…" (Underwood & Ward, 2004, p. 476). On the contrary, we measured an angle of approximately 50°. Cappetta (2012) stated, however, that "The basal angle of the root is obtuse" (Cappetta, 2012, p. 104). The basal angle of the root corresponding to the angle between the lingual face of the crown and the lingual face of the root, an obtuse angle correspond to an acute angle between the basal face of the root and the axis of the crown, as we measured. Delsate & Godefroit (1994) mentioned that the basal angle of the root of anterior and antero-lateral teeth of *P. terencei* was around 120°, and we measured a similar angle of 140° in 2013.5.1 ME. The crown of 2013.5.1 ME appears to be intermediate in shape between that of *P. semirugosus* and that of *P. terencei.* If indeed the tooth from Arromanches belongs to *Pseudonotidanus,* that would support the transfer of the species *terencei* from *Welcommia* to *Pseudonotidanus.*

The wide band devoid of enameloid at the base of the lingual face of the crown (lingual neck) is more developed in 2013.5.1. ME than in any other Pseudonotidanidae (Underwood & Ward, 2004; Klug & Kriwet, 2010; Cappetta, 2012) and such a feature is closer to what can be observed in Crassonotidae (Rees, 2010; Kriwet & Klug, 2011; Cappetta, 2012). Similarly, although the root of 2013.5.1 ME is pseudopolyaulacorhize, showing a series of basal foramina partially open basally, it lacks the labial depression normally seen in basal view in Pseudonotidanidae. The flat basal surface of the root is actually more reminiscent to the condition seen in Crassonotidae (Kriwet & Klug, 2011). The presence of a broad lingual neck and a flat basal face of the root in 2013.5.1 ME tends to blur the boundary between teeth of Pseudonotidanidae and Hexanchiformes and would support the inclusion of this family into the Hexanchiformes.

No dignathic heterodonty has been reported among Pseudonotidanidae (Cappetta, 1990; Delsate & Godefroit, 1994; Underwood & Ward, 2004; Klug & Kriwet, 2010), indicating that these sharks possessed a cutting dentition, whereas Hexanchidae and Heptranchidae show a cutting-clutching dentition with a strong dignathic heterodonty (Cappetta, 2012). Crassonotidae, on the other hand, displays a weak dignathic heterodonty (Kriwet & Klug, 2011; Cappetta, 2012), most developed in *Notidanoides* (Schweizer, 1964). The cutting dentition is considered more primitive than the cutting-clutching dentition (Cappetta, 2012) so that the succession Pseudonotidanidae – Crassonotidae – (Hexanchidae – Heptranchidae) witnesses the different steps of the acquisition of a cutting-clutching dentition in Hexanchiformes. That would suggest basal Hexanchiformes possessed a pseudopolyaulacorhize root vascularization. In turn, that would hint to the fact that Synechodontiformes might be paraphyletic.

Pseudonotidanus politus is the only Pseudonotidanidae known from a partial skeleton found in connection and possessed at least one posterior dorsal fin with a spine (Reif, 1974; Thies, 1992). As the part where the possible anterior dorsal fin could have been situated is not preserved, it cannot be demonstrated that it possessed two dorsal fins and spines (Klug, 2010). This assertion probably came from the fact that the species *P. politus* was originally described as a species of *Palaeospinax* (Thies, 1992). If Pseudonotidanidae are indeed basal Hexanchiformes, it would, however, demonstrate that basal Hexanchiformes possessed a fin spine in front of their dorsal fin, subsequently lost during the evolution of the clade.

5 – CONCLUSION

We report from the Bathonian of Normandy a tooth of cf. *Pseudonotidanus* sp. The morphology of this tooth supports, as suggested by Cappetta (2012), the transfer of the species *terencei* from the genus *Welcommia* to the genus *Pseudonotidanus,* mostly based on its cuspidate mesial heel. It also supports the idea that Pseudonotidanidae might be basal Hexanchiformes rather than Synechodontiformes. Basal Hexanchiformes would have then possessed a pseudopolyaulacorhize root vascularisation and a dorsal fin spine. The discovery of the tooth from Arromanches calls therefore for more studies to decipher the phylogenetic relationships between Hexanchiformes and Synechodontiformes, which are beyond the scope of the present work.

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