

1 **First occurrence of the orectolobiform shark *Akaimia* in the Oxford Clay**
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3 **Formation (Jurassic, Callovian) of England**
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30 **ABSTRACT**
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33 The late Middle Jurassic (Callovian) Peterborough Member of the Oxford Clay Formation of
34 eastern England yields a rich variety of marine vertebrate fossils, including a diverse
35 assemblage of neoselachian elasmobranchs. Here we report the first record of the small
36 Jurassic orectolobiform shark *Akaimia* Rees, 2010, otherwise known only from Poland and
37 Germany, from the British Jurassic, together with an unusual, undetermined dermal denticle.
38 The material comes from exposures in Cambridgeshire, eastern England. We refer the new
39 specimens of *Akaimia* to the new taxon *A. myriacuspis* sp. nov., and provide a revised
40 diagnosis for the genus.
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54 **Keywords:** Jurassic, Callovian, Microvertebrates, Neoselachii, Orectolobiformes, England
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1. Introduction

The Callovian Oxford Clay Formation of England, best regarded for its vertebrate fauna of large marine reptiles and diverse and sometimes gigantic bony fishes (Woodward, 1890; Andrews, 1910-13; Brown, 1981; Martill, 1991; Liston, 2008), has also produced a diverse assemblage of elasmobranchs since sampling began in the mid-19th century (Woodward, 1889; Thies, 1983; Martill and Hudson, 1991). At least 25 elasmobranch species have been described to date (Thies, 1983; Rees and Underwood, 2008). These taxa range from large active predators such as *Hybodus* and *Asteracanthus* (Hybodontidae) to likely benthic animals such as *Synechodus* (Palaeospinacidae), the Angel shark *Pseudorhina* (Pseudorhinidae) (Carvalho et al., 2008; Klug and Kriwet, 2013) and a Guitar fish, *Spathobatis* (Rhinobatidae) (Thies, 1983). The latter two taxa represent groups which are still extant in oceans today, appearing to differ little from their Jurassic relatives (Thies and Leidner, 2011). Similar elasmobranch assemblages to those of the Oxford Clay Formation have been reported from the Callovian and Oxfordian of Poland and Germany (Thies, 1983, 1989; Kriwet and Klug, 2004; Rees, 2010). Here we describe the first record of the genus *Akaimia* (Rees, 2010) outside of mainland Europe, a genus unrelated to, but with traits similar to the extant Wobbegongs or Carpet sharks (Orectolobidae) of the Indo-Pacific region (Rees, 2010).

2. Geological setting

The Middle Jurassic Oxford Clay Formation is a sequence of organic-rich clays and shales deposited in a shallow epeiric sea during the Callovian, a time when much of Europe was submerged due to a global rise in sea level (Hudson and Martill 1994, Hallam 2001) with water column temperatures in the 11°C to 17°C range (Mettam et al., 2014). The basal Peterborough Member crops out extensively to the East of Peterborough where since the late-18th century it has been dug commercially for brick manufacture. Today only Must Farm pit

1 at Kings Dyke, Whittlesey, Cambridgeshire (National Grid reference TL237974) remains
2 operational, although it still yields a plethora of fossils (Fig. 1).
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5 FIGURE 1 HERE
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7 Historically this clay pit is one of several very important sites around the Fenland Town
8 and Whittlesey area for Oxford Clay fossils (Benton and Spencer 1995). Commercial
9 excavation of the Oxford Clay began in the late 1800's resulting in the discovery of hundreds
10 if not thousands of vertebrate skeletons, many collected by Alfred Nicholson Leeds (1847-
11 1917) and his elder brother Charles (born 1845) of Eyebury and Henry Keeping (1827-1924)
12 at Cambridge University between c. 1867 and 1917 (Leeds, 1956; Araujo et al., 2008).
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22 The Oxford Clay Formation sequence exposed at Whittlesey is incomplete. The lower
23 boundary of the Oxford Clay Formation is sometimes exposed in the pit bases, with the
24 underlying Kellaways Formation revealed in drainage ditches (Martill and Hudson 1991)
25 (Fig. 2). The main quarry face usually exposes the entire sequence of the Peterborough
26 Member, and the overburden may consist of weathered parts of the Stewartby Member.
27 However, the Stewartby Member is sometimes absent and replaced with Holocene Fen
28 gravels and peat deposits. The Peterborough Member spans the upper part of the Lower
29 Callovian and extends upwards into the base of the Upper Callovian (Hudson and Martill,
30 1991).
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46 2.1 Taphonomy 47

48 The teeth found in the Oxford Clay are well preserved, with little etching or abrasion
49 noted. Many teeth are missing cusps or roots, although these breakages may have occurred
50 post- fossilisation during collection and mechanical processing. Networks of micro-borings
51 (Underwood et al., 1999) belonging to the ichnotaxon *Mycelites ossifragus* (Roux, 1887) are
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1 noted on the lingual face of the indeterminate denticle and roots of many of the *Akaimia* teeth
2 (see section 5) as well as other teeth found during the taphonomic study.
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7 **3. Late Jurassic neoselachian sharks**

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10 Neoselachians embrace those groups of living sharks and rays which are represented in
11 modern seas, as well as their fossil relatives and some extinct families. As with all fossil
12 chondrichthyans, they are mostly represented by isolated teeth in the fossil record because the
13 high protein content of the cartilaginous skeleton is easily lost during decomposition, thereby
14 reducing the preservation potential of the elements of the endoskeleton. The dental character
15 that unites neoselachians is the presence of a triple-layered enameloid covering the surface of
16 the crown.
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27 Neoselachians seem to have had their origins in the Palaeozoic (Ginter et al., 2010), but do
28 not become diverse until the Mesozoic (Cappetta, 2012). Many of the late Triassic forms are
29 difficult to place with any certainty into higher taxonomic categories, other than identifying
30 them as neoselachians, and it is only in the Jurassic that members of extant orders can be
31 identified with any degree of confidence. A particularly important resource in this respect is
32 the occurrence of several conservation Lagerstätten in the Jurassic of Europe; articulated
33 whole-bodied chondrichthyan specimens are known, for example, from the Sinemurian of
34 Lyme Regis (Dorset, UK) and Osteno in Italy, the Toarcian of Holzmaden in Germany, and
35 the Kimmeridgian of Kimmeridge (Dorset, UK), plus the Tithonian lithographic limestones
36 of Nusplingen and Solnhofen in southern Germany, and Cerin in eastern France. These
37 spectacular deposits with their perfectly preserved faunas clearly indicate that the range of
38 modern chondrichthyan body forms was fully established in or by Jurassic times. Our
39 understanding of the intervening record of neoselachian orders necessarily depends on finds
40 of isolated teeth. Since many of these are in the sub-millimetric size range, it is necessary to
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1 concentrate and isolate them from enclosing sediments using a variety of mechanical and
2 chemical techniques. The Jurassic represents a particularly interesting time in the evolution of
3 the Neoselachii, but the bulk sampling necessary to elucidate the development of a true
4 picture of changing chondrichthyan faunal diversity throughout the Period is only in its early
5 stages.
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11 **4. Methods**

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14 Samples for microvertebrate processing were taken from beds 6, 7, 11, 13, 17 and 19 (Bed
15 numbers from Hudson and Martill 1994) as part of a taphonomic study examining the relative
16 abundances of otoliths and phosphatic skeletal fish remains. At least 2 kg of clay was
17 collected from each bed, and air dried prior to disaggregation in 10% hydrogen peroxide. The
18 resultant residues were sieved between 250 µm and 4 mm sieves to remove silt and clay,
19 while coarser shelly material was removed manually. Microvertebrate remains were picked
20 under a binocular microscope and mounted on aluminium SEM stubs for examination by
21 JEOL JSM-6100 scanning electron microscope at 10kv. Images were digitally processed. The
22 material described here has been accessioned into the collection of the Natural History
23 Museum, London numbers NHMUK PV P 73690 – P 73695.
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43 **5. Systematic palaeontology**

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46 The descriptive tooth terminology used here follows Cappetta (2012), which is also the
47 source for the higher taxonomic relationships of the Neoselachii. A key to the descriptive
48 terms used in the text is given for the sake of convenience in Fig. 3.
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FIGURE 3 HERE

66 *5.1 Euselachii indet.*

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Subclass ELASMOBRANCHII Bonaparte, 1838

1 Cohort ?EUSELACHII Hay, 1902

2 Euselachii indet.

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7 Material - One near complete undetermined dermal denticle or possible oropharyngeal
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9 denticle, NHMUK PV P 73695 (Fig. 4).

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12 Locality - Bed 17 of the Peterborough Member of the Oxford Clay Formation at Must
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14 Farm Pit, Whittlesey, United Kingdom. GR TL237974.

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17 Description - The asymmetrical denticle features a single large 'cusp' and four lateral
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19 'cusplets' (one vs three either side of the main cusp). Each cusp bears acute lateral margins and is
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21 curved labio-lingually. The lingual surface shows numerous borings of the possible fungus *Mycelites*
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23 *ossifragus* (Roux, 1887).

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26 Remarks - This dermal denticle is described here because of its somewhat unusual
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28 morphology and very small size. It is regarded as elasmobranchian on account of the morphology of
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30 the crown with major cusp and lateral cusplets and the texture of the basal body (root). Furthermore,
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32 chimaeroids, frequently represented by isolated tooth plates in the Oxford Clay Formation, lack
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34 denticles in the skin, apart from some specialised structures in the dorsal midline of the body. The
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36 denticle is identified as euselachian on somewhat negative grounds. Hybodontoids tend to have
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38 dermal denticles that are simple dome-like bodies with strongly buttressing ribs, quite unlike those of
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40 neoselachians (see figures in e.g. Brito and Ferriera 1989, Martill 1991). Although we regard this
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42 specimen to be of probable euselachian origin, its identification both as a euselachian and as a dermal
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44 denticle are tenuous. There is a superficial similarity of the form with oropharyngeal denticles seen in
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46 such widely divergent gnathostomes as hybodont sharks and placoderms (Johanson and Smith 2003),
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48 being strongly labio-lingually curved with a 'ctenoid' cusp arrangement.

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5.2 Akaimia

Subcohort NEOSELACHII Compagno, 1977

Superorder GALEOMORPHII Compagno, 1973

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Order ORECTOLOBIFORMES Applegate, 1972

Family indet.

Genus *AKAIMIA* Rees, 2010

Type Species - *Akaimia altucuspis* Rees, 2010 from the uppermost Callovian to lowermost Oxfordian of Southern Poland.

Revised diagnosis – A revised diagnosis for *Akaimia* includes the following characters 1: A high degree of monognathic heterodonty; 2: anterior teeth with a high and slender central cusp; 3: at least one pair of short lateral cusplets in anterior teeth; 4: lateral teeth considerably lower with a flattened, triangular cusp; 5: a single, strong, and centrally placed labial keel on the lower part of the tooth; 6: hemiaulacorhize root vascularisation.

5.3 *Akaimia myriacuspis* *sp. nov.*

Holotype - NHMUK PV P 73690 (Figs 5a-e), a complete anterior tooth.

Paratypes - NHMUK PV P 73691 (Figs 5f-h), mostly complete anterior tooth, missing one of the first pair of cusplets; NHMUK PV P 73692 (Figs 5i-k), a damaged tooth missing some of the lateral cusplets; NHMUK PV P 73693 (Figs 5l-o), a lateral tooth with worn cusplets).

Additional material - One additional damaged tooth (NHMUK PV P 73694, Figs 5p,q) is tentatively referred to *A. myriacuspis* here, based on the presence of additional carinae below the outermost cusplets despite appearing to lack the central ridge.

Derivation of name - The specific name *myriacuspis* derives from myriad (Greek, *myrios* = ten thousand, indicating ‘many’) and *cuspis* (Latin = point) alluding to the many cusps.

Type Stratum - Bed 17 (see Hudson and Martill, 1994) of the Peterborough Member of the Oxford Clay Formation.

Type locality - Must Farm Pit, Whittlesey, Cambridgeshire, United Kingdom. National Grid reference TL237974.

1 Differential diagnosis - *Akaimia myriacuspis* sp. nov. is differentiated from the type species
2 *A. altucuspis* by the possession of up to three pairs of lateral cusplets whose long axes are sub-parallel
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4 to that of the central cusp, a weaker labial apron, a stronger lingual uvula in lateral teeth, and the form
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6 of the vertical ridge ornamenting the labial face of the crown.
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9 Diagnosis - Orectolobiform shark known from three complete anterior teeth and one lateral
10 tooth. Characterised using the generic diagnosis revised above with the following additions for
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12 species level identification; 1: at least two pairs of short but well-developed lateral cusplets; 2: lateral
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14 cusplet axes sub-parallel to that of the central cusp in anterior teeth; 3: a well-developed lingual apron
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16 on the lateral tooth only; 4: ornamental ridges smaller than the central keel on the labial surface below
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18 the cusplets.
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22 Description – The holotype (NHMUK PV P 73690; Figs 5a-e) is an anterior tooth which
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24 measures 1 mm mesiodistally from tip to tip of the mesial and distal lobes of the root, and 1.67 mm
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26 from the labial margin of the labial apron to the central cusp apex on the crown. The tooth is slightly
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28 asymmetrical (Fig. 5b); the tall, relatively slender, sharply-pointed central cusp is angled slightly
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30 distally. It is flanked by two pairs of lateral cusplets, the heights of which decrease away from the
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32 central cusp (Figs 5a-b). The first lateral cusplet pair is around 40% of the height of the central cusp,
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34 while the second lateral cusplet pair is only around 17% of the central cusp height. Both lateral
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36 cusplet pairs are sharply pointed, and all of the cusps possess sharp cutting edges which descend the
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38 lateral margins of the cusp mesially and distally. The lateral cusplets are sub-parallel to central cusp,
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40 their axes diverging from that of the central cusp by only a few degrees. In cross-section, the cusps are
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42 slightly flattened labio-lingually. A moderate labial apron is developed on the crown margin beneath
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44 the central cusp base, and significantly overhangs the root (Figs 5d, e). Coronal ornamentation is
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46 restricted to the labial face of the crown. A prominent, short vertical ridge is developed above the
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48 labial apron at the level of the central cusp base (Figs 5b, e). A short uvula is developed lingually. The
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50 root has a V-shaped basal surface and a prominent lingual foramen is present on the baso-lingual
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52 margin beneath the central cusp. Lateral foramina are present midway up the root wall mesially and
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54 distally. The mesial and distal lobes of the root extend slightly beyond the mesial and distal heels of
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56 the crown.
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1 Further anterior teeth in the collection (NHMUK PV P 73691, NHMUK PV P 73692) show less
2 prominent labial aprons with much straighter labial margins and less significant overhang of the neck
3 or collar and the root (Figs 5g, h, I, k, p, q). The base of the central cusp may be somewhat inflated
4 mesiodistally (Figs 5f, i) and an incipient third pair of lateral cusplets may be developed (NHMUK
5 PV P 73692; Fig. 5i). The uvula is consistently weak in anterior teeth, but the available specimens
6 show some variation in labial ornamentation. The labial vertical ridge may be less prominent than is
7 the case in the holotype (Figs 5g-h, p-q), or it may be significantly stronger (Figs 5i-j). Short lengths
8 of vertical ridge may also be developed below the bases of the lateral cusplets (Figs 5i-k, p-q).

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FIGURE 5 HERE

A single lateral tooth, slightly wider (1 mm) than it is high, is present in the sample. This has a
much squatter, triangular, shorter central cusp which is a little more upright than in anterior teeth. The
mesial and distal cutting edges are consistently and strongly developed. The central cusp is flanked by
two pairs of lateral cusplets which are much shorter and possess a less acuminate, more rounded
outline than is the case in the holotype. The labial apron is prominent and the lingual uvula very
strongly developed. The labial vertical ridge is rather longer than in anterior teeth, extending from the
base of the central cusp almost half way to the cusp apex. There are no vertical ridges basal to the
lateral cusplets. The root is slightly deeper than in anterior teeth, and the flared mesial and distal lobes
extend well beyond the mesial and distal heels of the crown.

Heterodonty - There is clearly a high degree of heterodonty between the anterior and lateral teeth
of *A. myriacuspis*. Changes taking place distally through the dentition include a change in proportions
from anterior teeth which are one and a half to two times higher than wide to lateral teeth in which the
height and width are approximately identical. A long, slender central cusp flanked by up to three pairs
of lateral cusplets with their long axes sub-parallel to that of the main cusp in anteriors gives way to a
more squat, triangular central cusp flanked by relatively shorter, more rounded lateral cusplets in
laterals. The ornamentations also shows some changes with heterodonty; short but sometimes very
well developed in anterior teeth, the vertical ridge at the base of the central cusp becomes longer in
lateral teeth. Short vertical ridges beneath the lateral cusplet bases seems to be confined to some

1 anterior teeth. The rather weak uvula in anterior teeth is replaced by a strong and relatively high one
2 in laterals, and the labial apron, although quite variable irrespective of tooth position, tends to be more
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4 bulbous and prominent in lateral teeth.
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7 Remarks - The teeth of *Akaimia myriacuspis* and *A. altucuspis* are similar but clearly belong
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9 to two separate species. The most obvious difference is the presence of additional pairs of lateral
10 cusplets in *A. myriacuspis*; teeth of *A. altucuspis* possess a single pair of lateral cusplets in both
11 anterior and lateral teeth, while up to three pairs are present in *A. myriacuspis*. Furthermore, the long
12 axes of the lateral cusplets are sub-parallel to the central cusp in *A. myriacuspis*, but diverge strongly
13 from the central cusp axis in *A. altucuspis* (Rees, 2010 pl. 1 figs 4, 15, 16). The central cusp itself is
14 more elongate and gracile in *A. altucuspis*, and lacks the somewhat inflated base found in some
15 anterior teeth of *A. myriacuspis*. In lateral view, the central cusp may have a sigmoid flexure in some
16 specimens of *A. altucuspis* (Rees, 2010 pl. 1 figs 2, 7), a feature lacking in *A. myriacuspis*. The labial
17 apron in anterior teeth of *A. myriacuspis* is much reduced when compared to the condition in *A.*
18 *altucuspis*; the labial margin of the apron is almost straight in some specimens of *A. myriacuspis*
19 (NHMUK PV P 73691 and P 73692 Figs 5f-k), whilst it is prominent and very well developed with
20 parallel lateral margins in some specimens of *A. altucuspis* (Rees, 2010 pl. 1 figs 6, 7, 9). The lingual
21 uvula in lateral teeth of *A. myriacuspis* is much more strongly developed compared to that in *A.*
22 *altucuspis*.

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41 In terms of crown ornamentation, both *A. myriacuspis* and *A. altucuspis* display a vertical ridge in
42 the centre of the labial face of the crown, toward the base of the central cusp. In *A. altucuspis*, the
43 ridge is longer in anterior teeth, extending from part way up the central cusp to a point very close to
44 the labial margin of the labial apron. The teeth of *A. myriacuspis* are distinctive in that, although
45 relatively short, the vertical ridge is very strongly developed in some specimens (Figs 5 i-k).
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Furthermore, the presence of short lengths of vertical ridge beneath the bases of the lateral cusplets in
anterior teeth is a feature confined to some specimens of *A. myriacuspis*.

6. Discussion

There are a number of additional orectolobiform genera represented in Jurassic rocks, namely *Heterophorcynus* (Bathonian of England), *Dorsetoscyllium* (Bathonian of England), *Folipistrix* (Toarcian to Aalenian of Belgium and Germany), *Phorcynis* (Kimmeridgian to Tithonian of Europe), *Palaeobrachaelurus* (Aalenian to Barremian), *Annea* (Toarcian to Bajocian of Europe), and *Ornatoscyllium* (Bathonian of England) (Underwood and Ward, 2004; Thies 1983; Kriwet 2003; Kriwet and Klug 2004; Cappetta, 2012). Of these, only *Palaeobrachaelurus* has been assigned to a family (the Brachaeluridae); the remainder are currently *incertae familiae*. Of these, only *Annea* and *Ornatoscyllium* show any form of ornamentation on the labial face of the crown. In contrast to the condition in *Akaimia*, a vertical ridge descends the labial face of the central cusp in *Annea carinata* Thies (1983), originating at the cusp apex and bifurcating basally at a point around a third of the way down the cusp midline. In *Ornatoscyllium freemani* Underwood and Ward (2004), a somewhat curved vertical ridge extends for the greater part of the length of the central cusp midline, terminating before the cusp apex and just above the labial margin of the labial apron (Underwood and Ward 2008, pl. 8 figs 1, 6, 8). Short vertical ridges may be present at the bases of the lateral cusplets (Underwood and Ward, 2008, pl. 8 figs. 8, 11), especially in lateral teeth. The moderate labial apron has a more squared outline than is the case in teeth of *Akaimia*. It is quite possible that *Akaimia*, *Ornatoscyllium* and *Annea* will subsequently be shown to belong together in the same family of orectolobiform sharks.

When Rees (2010) originally erected the genus *Akaimia* he identified six distinguishing characters. As at that time *Akaimia* was considered monotypic, his diagnosis for the species was the same as that for the genus. However, the discovery of a species of *Akaimia* distinct from *A. altucuspis* requires minor modification to the generic diagnosis (see above). Our revised diagnosis for the type species *A. altucuspis* is as follows: 1, short cusplets that diverge laterally from the main cusp; 2, only one pair of cusplets in both anterior and lateral teeth; 3, a well-defined labial apron in anterior and lateral teeth.

A damaged tooth described by Thies (1989, fig. 12, referred to *Orectolobiformes* inc. fam., gen. et sp.) from the Callovian (Jason-zone) of the abandoned Hansa iron mine in Halingerode, Germany, is here referred to *A. altucuspis* based on the ridge on the labial surface and diverging, single pair of

1 lateral cusplets. The labial apron of this tooth is broken, but what remains suggests an apron more
2 similar to those of *A. altucuspis* than *A. myriacuspis*.
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4 The Oxford Clay has yielded a diverse range of elasmobranch taxa, whose discovery dates back to
5 the early years of Oxford Clay palaeontology (Woodward 1889). Elasmobranch taxa are known from
6 skeletal material, such as the archetypal Jurassic shark taxon *Hybodus* (Martill 1991) although the
7 majority of taxa, including *Akaimia myriacuspis* sp. nov., are known from microfossils. Of particular
8 interest here is the diversity of orectolobiform sharks, comprising the genera *Palaeobrachaelurus*,
9 *Ornatoscyllium* and now *Akaimia*.
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11 Today, the Orectolobiformes comprises 44 species belonging to 13 genera in 7 families of at least
12 519 known extant species belonging to 107 genera in 34 families (Compagno et al., 2005). The
13 Orectolobiformes present a range of sizes and modes of life, from animals such as the largest living
14 fish- the open-ocean filter feeding Whale Shark, *Rhincodon*, to bottom feeders such as the
15 Wobbegong (Orectolobidae) and Nurse Shark (Ginglymostomatidae).
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17 TABLE 1 HERE

18 Orectolobiformes comprise almost half of the known shark taxa in the Oxford Clay - 4 of 11
19 species reported (3 of 10 genera) (Table 1). A similar proportion is also seen in the Callovian-
20 Oxfordian of Poland (Rees 2010), from where the type species of *Akaimia* was described. These
21 comprise 5 of the 12 species (4 of the 9 genera). The Callovian-aged formation from which we refer
22 the tooth found by Thies (1989) is not mentioned and so we cannot compare the taxa known from the
23 formation, however we can instead look at the taxa described in Germany as a whole (as well as
24 England and Poland) during the Callovian and Oxfordian, although only one orectolobiform is known
25 from this period in Germany.
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27 Comparing the taxa themselves however, a number overlap between the Callovian-Oxfordian of
28 Germany, Poland and England. *Sphenodus longidens* has been found in all three countries, with 12
29 taxa being found in at least two of the countries, four of which are common to at least two of the
30 localities. Clearly, the epeiric seas of the northwest European platform contained a broadly
31 cosmopolitan selachian assemblage.
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FIGURE CAPTIONS

Fig. 1. Map showing location of Must Farm clay pit, near Whittlesey, Cambridgeshire. Currently this is the only working clay pit excavating the Peterborough Member of the Oxford Clay Formation.

Fig. 2. Simplified stratigraphic log for the Peterborough Member of the Oxford Clay Formation at Whittlesey, Cambridgeshire. Based on Martill and Hudson (1994).

Fig. 3. Diagram to show the key descriptive terms used in the text. *Akaimia myriacuspis* anterior tooth in (a) labial view and (b) oblique distal view. Lateral tooth of *Akaimia myriacuspis* in (c) labial view, and (d) lateral view.

Fig. 4. Indet. denticle showing *Myselites ossifragus* boring networks on the ‘lingual’ surface NHMUK PV P 73695. Orientation terms follow dental criteria. a, lingual view; b, labial view; c, lateral view; d, oblique view. Scale bar = 1 mm.

Fig. 5. Five examples of *Akaimia myriacuspis* sp. nov. a-e, holotype specimen NHMUK PV P 73690 in a, occlusal, b, labial, c, lingual, d, left lateral and e, right lateral views. f-h, paratype NHMUK PV P 73691 in f, labial, g, left lateral and h, right lateral views. i-k paratype NHMUK PV P 73692 in i, slightly oblique labial view, j, occlusal and k, right lateral views. l-o, lateral tooth paratype NHMUK PV P 73693 in l, labial, m, lingual, n, left lateral and o, right lateral views. p-q, additional specimen missing distal crown NHMUK PV P 73694 in p, labial and q, right lateral views. Scale bar = 1 mm.

Table 1. Distribution of elasmobranch taxa in the Callovian-Oxfordian of NW Europe. Based on data in Kriwet (2003), Kriwet and Klein (2004), Metcalf et al., (1992), Metcalf and Walker (1993), Rees (2005), Thies (1983), Underwood (2002), Underwood and Ward (2004).

Table

Systematics			Country			Locality		
Order	Family	Taxon	Germany	Poland	England	Hansa iron mine	Ogrodzieniec Quarry	Oxford Clay
Hybodontiformes	Hybodontidae	<i>Hybodus obtusus</i>	×		×			
		<i>H. dawni</i>			×			
		<i>Asteracanthus ornatissimus</i>	×		×			
		<i>A. acutus</i>			×			
		<i>A. medius</i>			×			
		<i>Planohybodus peterboroughensis</i>	×		×			×
		<i>Lissodus leiodus</i>				×		
Heterodontiformes	Heterodontidae	<i>Paracestracion falcifer</i>			×			
		<i>P. sarstedensis</i>			×			×
		<i>P. sp.</i>			×			
		<i>Heterodontus duffini</i>	×		×			×
Orectolobiformes	Indet.	<i>Ornatoscyllium pattersoni</i>			×			×
		<i>O. sp.</i>		×			×	
	Indet.	<i>Akaimia myriacuspis</i> sp. nov.			×			×
		<i>A. altuscuspis</i>	×	×		×	×	
	Indet.	<i>Palaeobrachaelurus bedfordensis</i>			×			×
		<i>Pb. alisonae</i>			×			×
	Hemiscyllidae	<i>Pb. sp.</i>			×			×
<i>Pseudospinax</i> sp. 1				×			×	
		<i>Psp</i> sp. 2		×			×	
Synechodontiformes	Palaeospinaciidae	<i>Paraorthacodus</i> sp.		×			×	
		<i>Synechodus riegrafi</i>	×		×			×
		<i>Syn. sp.</i>	×	×			×	
		<i>'Synechodus' prorogatus</i>		×			×	
	Orthacodontidae	<i>Sphenodus macer</i>	×					
		<i>Sph. longidens</i>	×	×	×		×	
		<i>Sph. nitidus</i>	×	×			×	
		<i>Sph. sp.</i>						
Pseudonotidanidae	<i>Welcommia cappetti</i>	×						
Hexanchiformes				×				
		<i>"Eonotidanus" serratus</i>						

	Hexanchidae	<i>Notidanus muensteri</i>	×		×			×
		<i>Notidanooides muensteri</i>	×					
		<i>Notidanooides</i> sp.		×			×	
		Hexanchidae indet.		×			×	
Squaliformes	Squalidae	<i>Squalogaleus</i> sp.		×				
Protospinaciformes	Protospinacidae	<i>Protospinax</i> annectans	×		×			
		<i>Prot. lochensteinensis</i>	×					
		<i>Prot. muftius</i>			×			
		<i>Prot. sp. 1</i>						
		<i>Prot. sp. 2</i>						
Squatiniformes	Squatinidae	<i>Pseudorhina</i> cf. <i>alifera</i>	×		×			×
		<i>Pseu. sp.</i>	×					
Rajiformes	Rhinobatidae	<i>Spathobatis weneri</i>			×			×

Figure 1

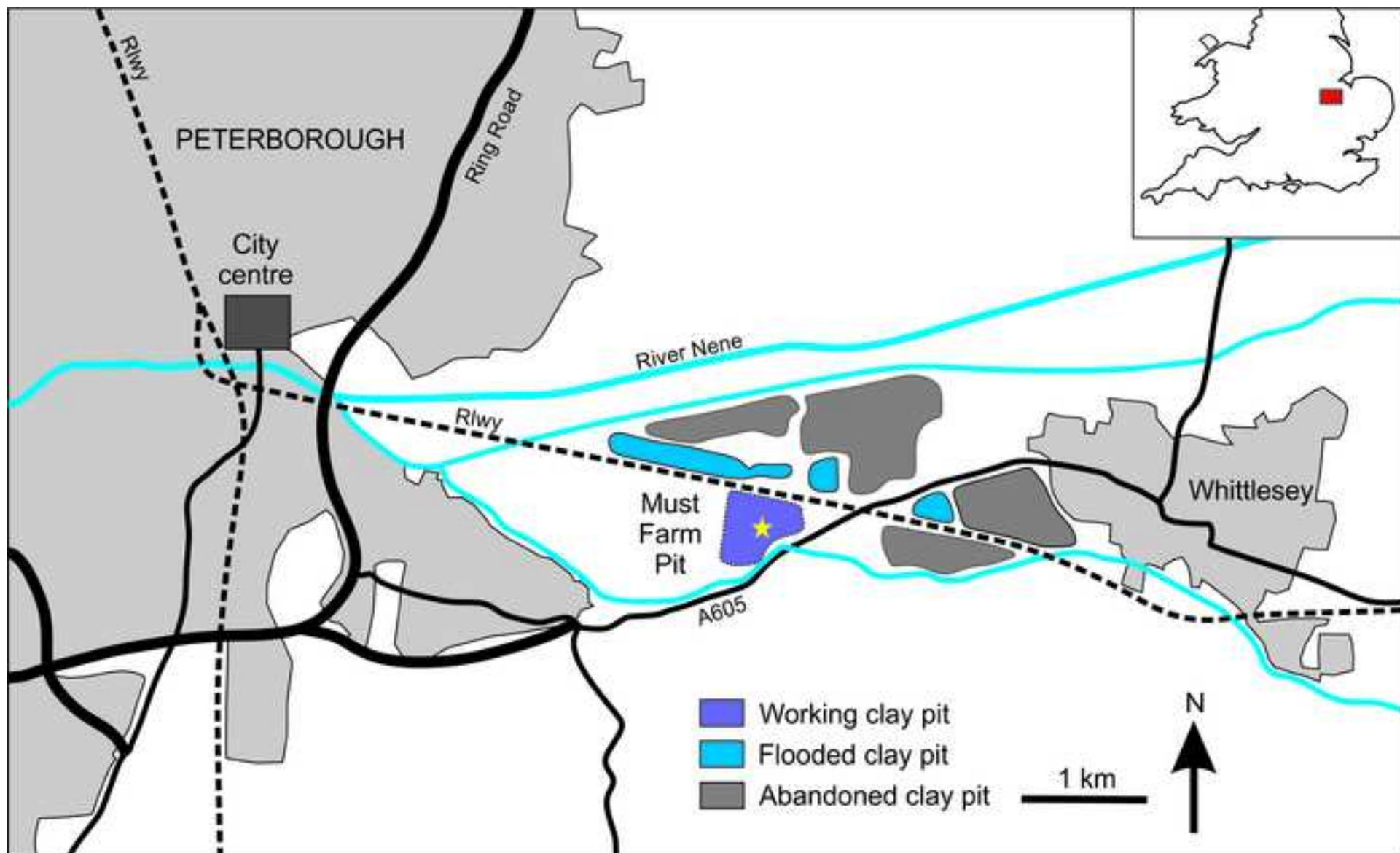


Figure 2

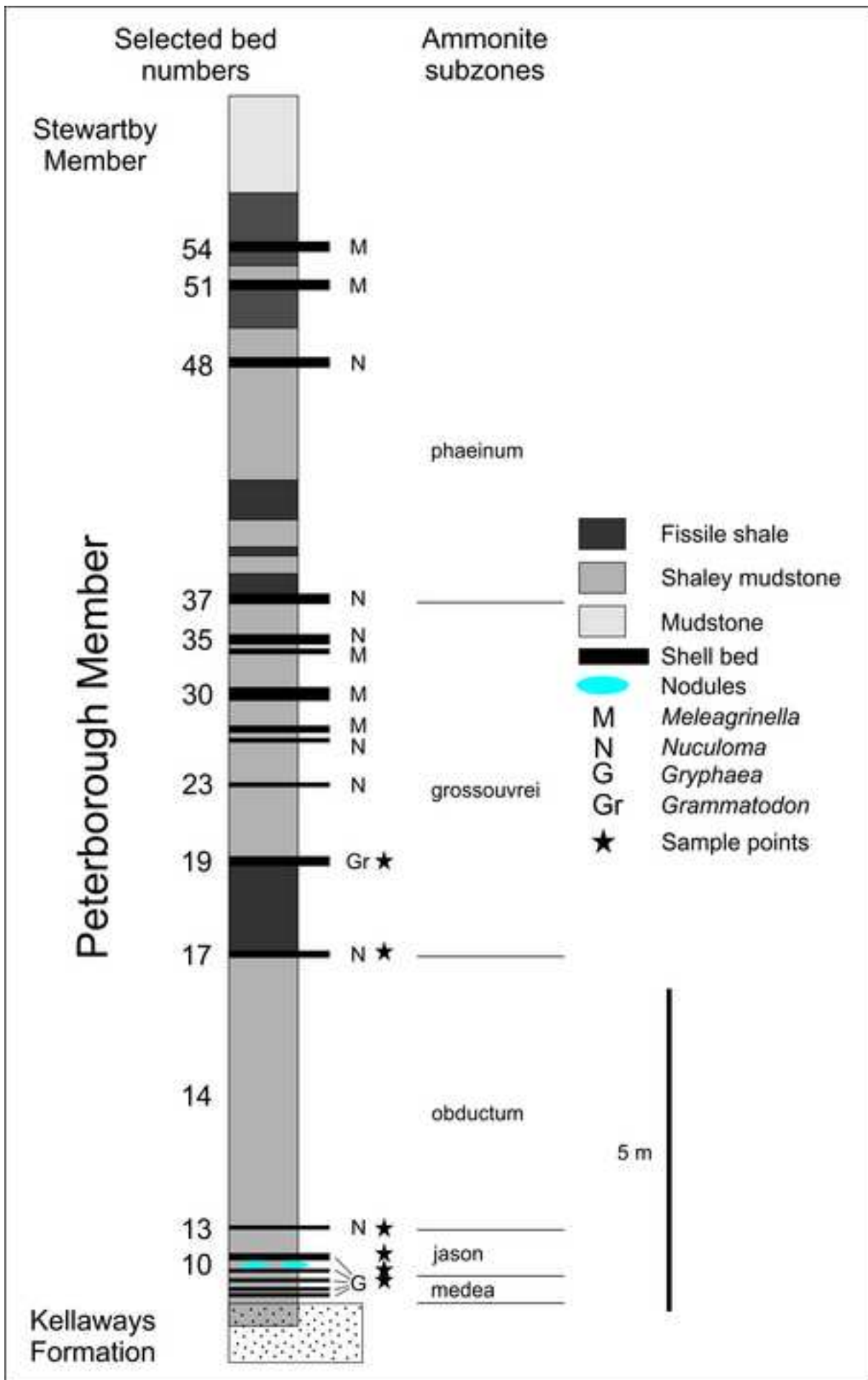


Figure 3

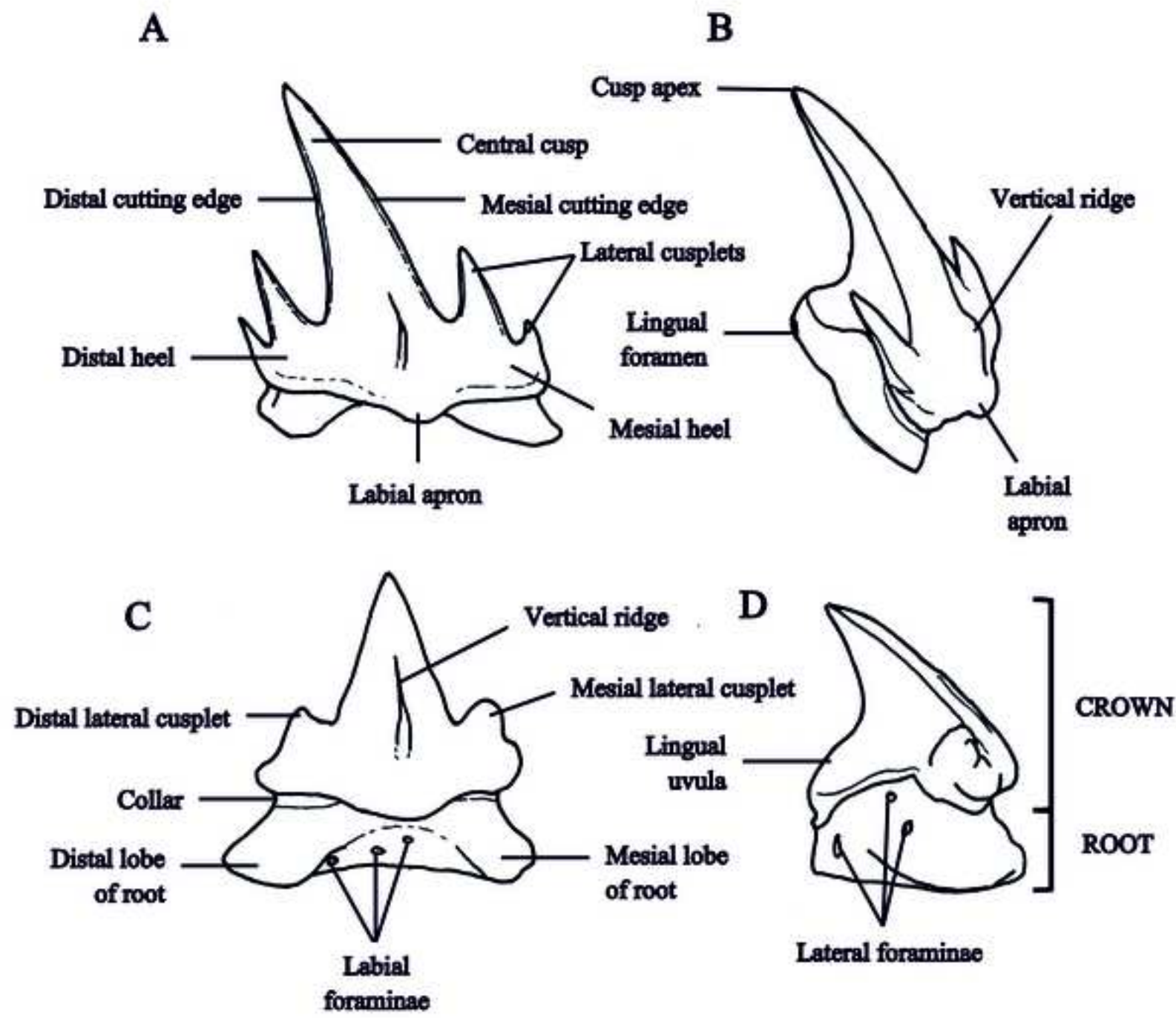


Figure 4



a



b



c



d



Figure 5

