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VERSITA

Palaeoecological implications of neoselachian shark teeth from the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland

JAN REES

Soldattorpet 48, SE-653 50 Karlstad, Sweden. E-mail: janrees71@gmail.com

ABSTRACT:

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Systematic sampling through the Middle and Upper Bathonian strata at Gnaszyn has resulted in the discovery of 13 neoselachian teeth. Systematically, the teeth represent five taxa including *Sphenodus* sp., *Protospinax* sp. 1, *Protospinax* sp. 2, *Palaeobrachaelurus* sp. and another, indeterminate orectolobiform. The presence of two species of the flattened and bottom-dwelling *Protospinax* and two different orectolobiforms that are likely to have lived near the bottom, is a strong indication of oxygenated bottom conditions at the time of deposition. The dietary preferences of these taxa included a wide variety of benthic invertebrates. The synechodontiform *Sphenodus* may have been the first pelagic predatory neoselachian in the Jurassic, equipped with high and slender piercing teeth that formed a tearing-type dentition. The diet of *Sphenodus* probably included bony fish, smaller sharks and cephalopods.

Key words: Neoselachii; Bathonian; Jurassic; Palaeoecology; Kraków-Silesia Homocline; Gnaszyn; Poland.

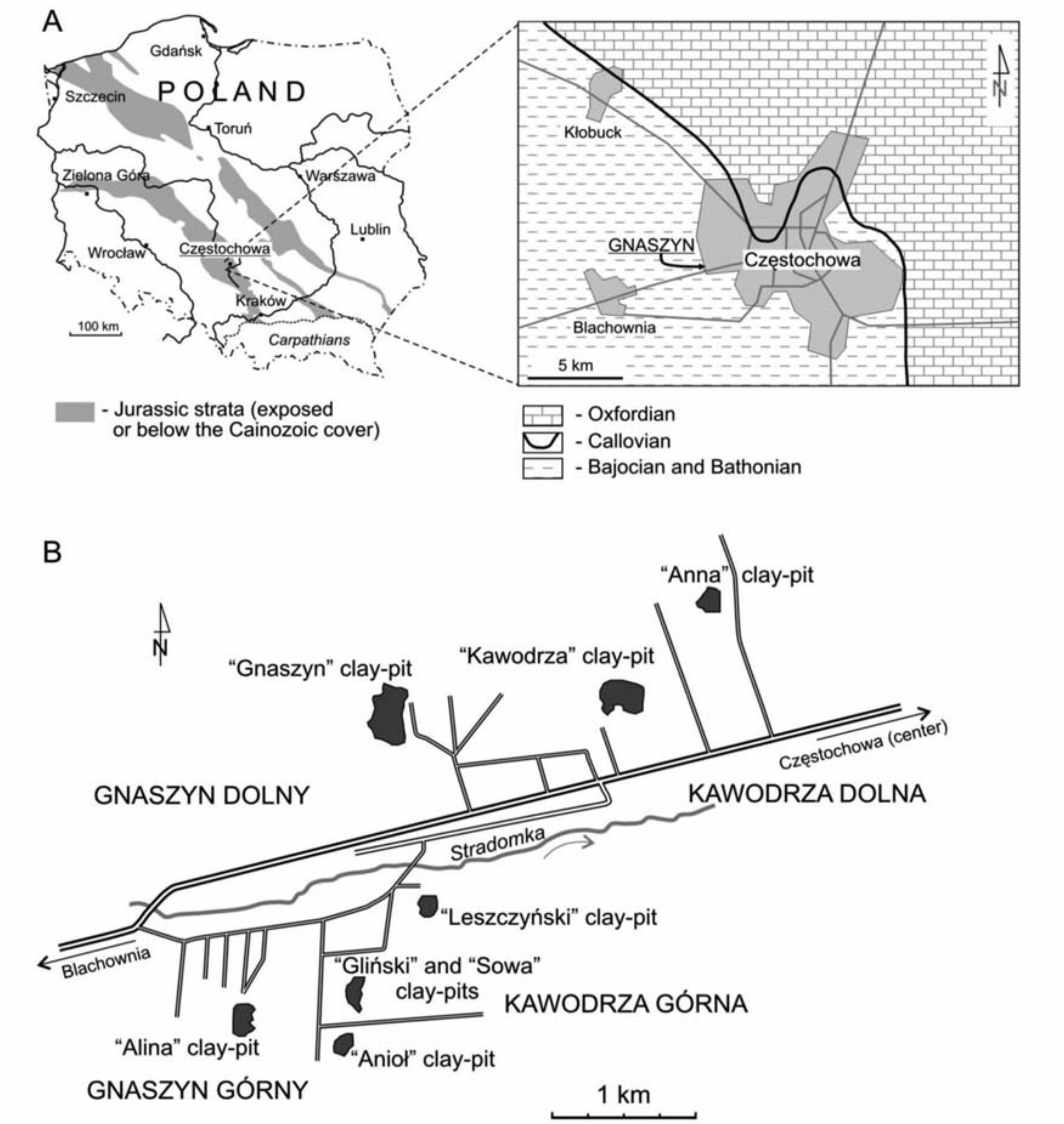
INTRODUCTION

The Neoselachii is a well defined clade which includes all extant sharks and rays. Although this is a diverse and important group in recent oceans, the early evolutionary history of the neoselachians is imperfectly known. The first representatives of the group occur in Permian strata (Ivanov 2005), but the first major radiation of stem-group taxa did not take place until the latest Triassic (e.g. Cuny and Benton 1999). The Middle Jurassic was a crucial period in the diversification of modern neoselachian sharks, a process that commenced in the later part of the Early Jurassic (Toarcian, see Rees 2000; Kriwet *et al*. 2009). Recent investigations (Underwood and Ward 2004; Kriwet 2003; Rees 2010) of Middle Jurassic faunas have revealed a major increase in neoselachian diversity, primarily in small-toothed carcharhiniforms, orectolobiforms and batoids. In a paper devoted to the environmental distribution of Bathonian neoselachians from Britain, Underwood (2004) concluded that the palaeoenvironmental specificity among neoselachians was already high in the Middle Jurassic. In previous investigations, where only a single palaeoenvironmental setting has been considered, this has resulted in a misleading impression of low diversity (Underwood 2004). Further increase of neoselachian diversity occurred in the later part of the Jurassic and the first half of the Cretaceous, the result being that Late Cretaceous faunas include most modern neoselachian groups.

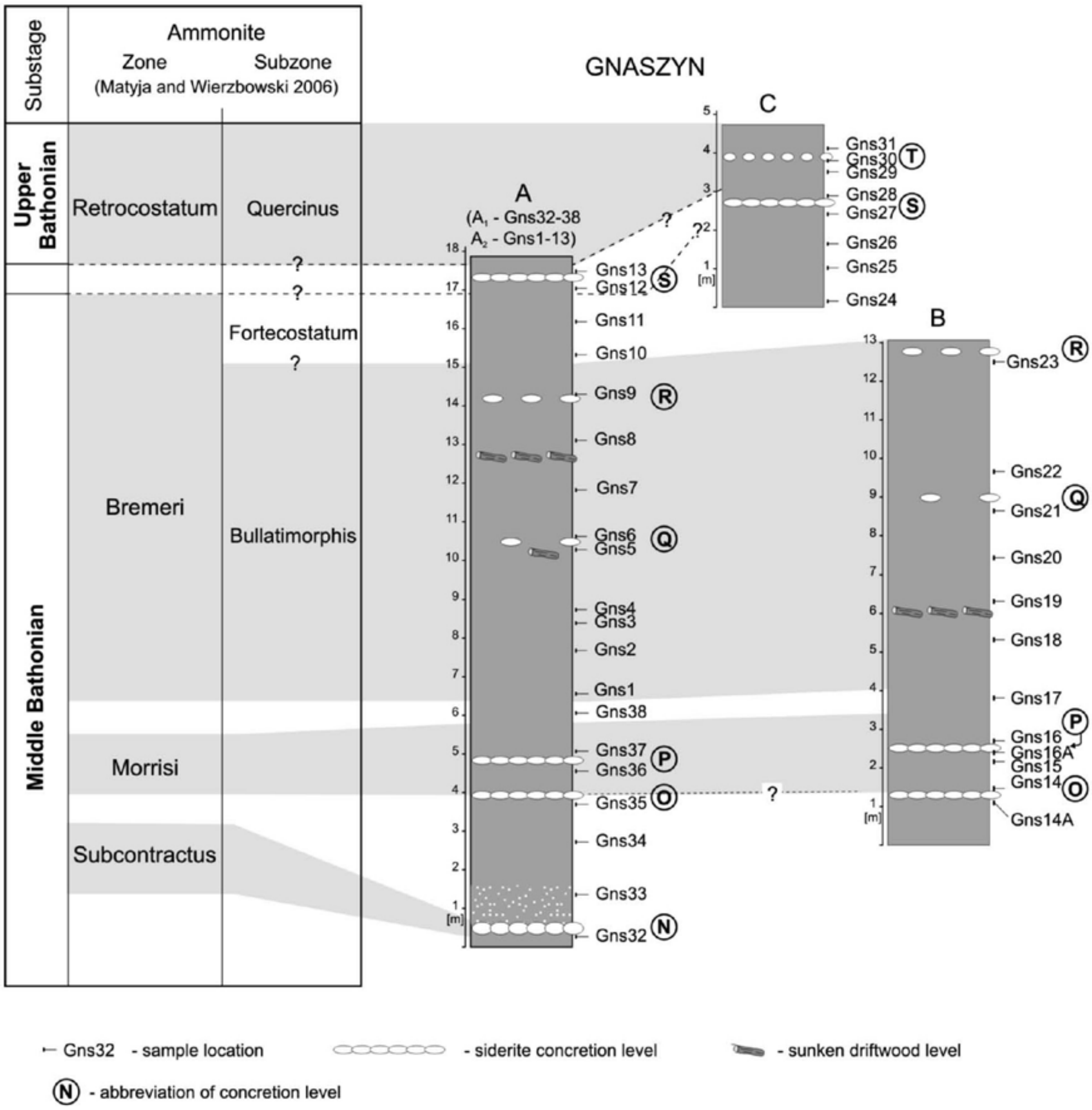
Selachian fossils of Jurassic age were virtually unknown in Poland until recent investigations (Kriwet 2003; Rees 2010) shed some light on the Callovian sharks from the country. The present note is an initial step towards a large scale investigation of the systematics and distribution of selachian faunas from the Middle Jurassic of the Częstochowa region in central Poland. It is intended, moreover, to place the scarce neoselachian teeth from Gnaszyn into their appropriate palaeoecological context, in light of recent advances in this field.

MATERIAL

The neoselachian teeth discussed herein were collected during systematic sampling of the entire section at the Gnaszyn clay pit (Text-figs 1, 2) as part of a multidisciplinary investigation of the palaeoecology and depositional environment thereof (see Gedl *et al*. 2003; Gedl and Kaim 2012). The exposed strata in this locality are dated to include the Middle and Upper Bathonian (Matyja and Wierzbowski 2006; Gedl and Kaim 2012). In total, the neoselachian material discovered includes 13 teeth of which none are complete, but several can be identified to generic level. Selachian teeth were often recovered in beds



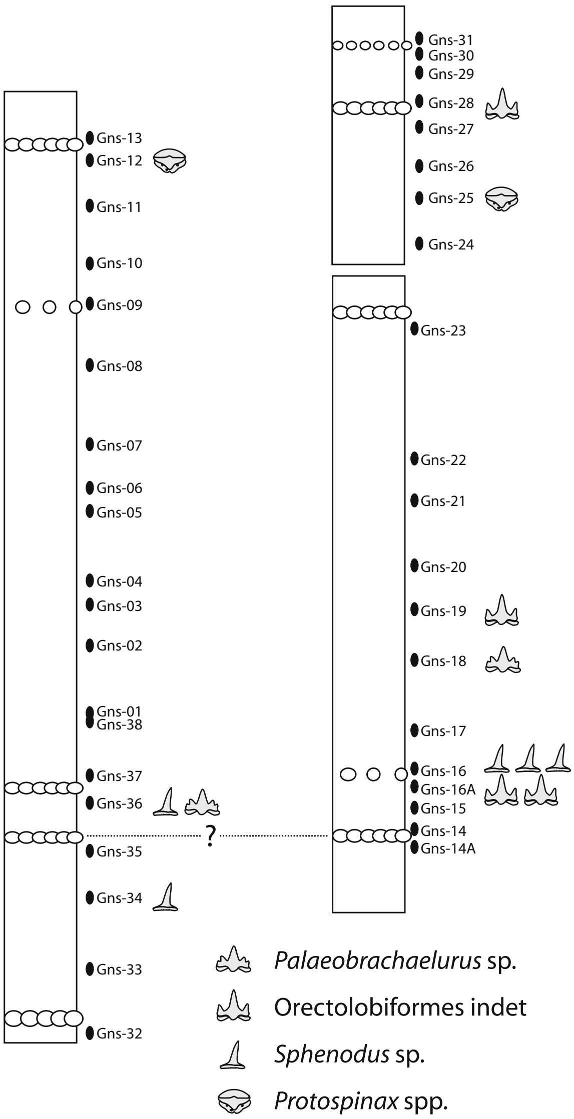
Text-fig. 1. Simplified geological map of the Częstochowa area (A – after Majewski 2000) and location of the studied Gnaszyn clay-pit (B – after Matyja and Wierzbowski 2006) close to levels where concretions are abundant (Text-fig. 3), indicating a decrease in sedimentation rate. Three synechodontiform teeth were found at horizon Gns16, including the two largest teeth in the material. In combination with the two teeth extracted from the underlying Gns16A, these two beds contained almost half of the teeth found. Additionally, single teeth were found in horizons Gns12, Gns18, Gns19, Gns25, Gns28, and Gns34, while Gns36 yielded two teeth (Table 1).



Text-fig. 2. Lithological logs of the studied Gnaszyn sections with indicated sample positions (by P. Gedl; from Gedl and Kaim 2012)

Taxon Sample (Gns)	12	16	16A	18	19	25	28	34	36
Indet orectolobiform			2		1		1		
Palaeobrachaelurus sp.				1					1
Sphenodus sp.		3						1	1
Protospinax sp. 1	1								
Protospinax sp. 2						1			

Table 1. Number of neoselachian teeth in different beds of the sampled sections



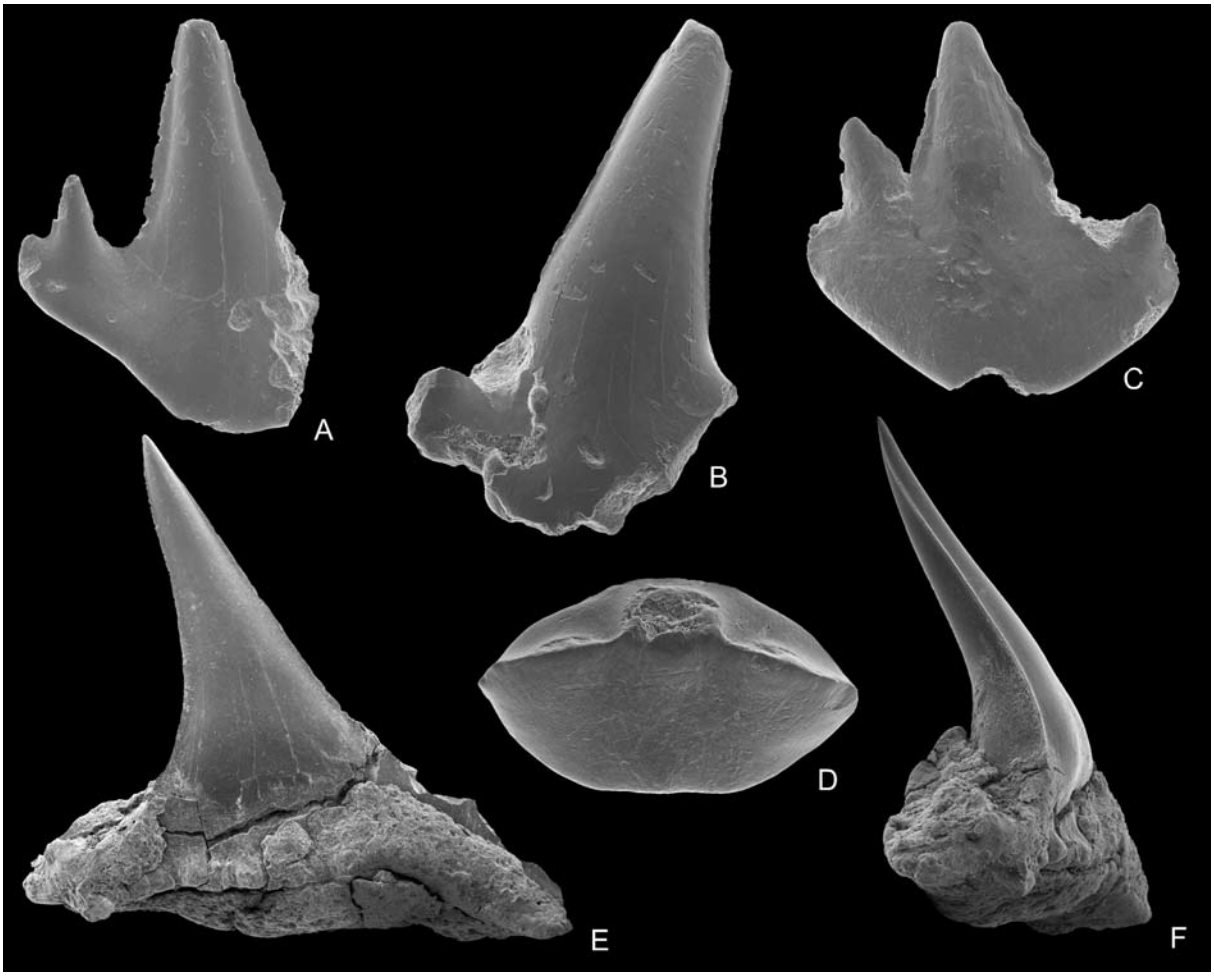
Text-fig. 3. Distribution of neoselachian taxa in the Gnaszyn sections. Log from Gedl and Kaim (2012)

SYSTEMATIC AFFINITY

The teeth from Gnaszyn represent three different neoselachian groups, the Orectolobiformes, Synechodontiformes and Protospinacidae. Six teeth can be assigned to the Orectolobiformes, and two of these (Text-fig. 4A) are sufficiently well preserved to be identified to generic level. These teeth are referred to *Palaeobrachaelurus* sp. as the general morphology is similar to contemporary species of this genus and in particular *P. mussetti* Underwood and Ward, 2004 from the Bathonian of England. The preserved lateral part of the crown in ZPAL P. 15.1 (Text-fig. 4A) is somewhat more delicate than that of figured teeth of *P. mussetti* (Underwood and Ward 2004, pl. 5) and is, in combination with the larger size of the tooth, an indication of other specific affinity. This tooth is also quite similar to teeth of *P. aperizostus* Thies, 1983 from the Toarcian and Aalenian of Germany, although apparently symmetrical and again more delicate. The second tooth, although less well preserved, is similar to ZPAL P. 15.1 but have a slightly more slender cusp. It is possible that some of the other orectolobiform teeth from Gnaszyn also originate from sharks of the genus *Palaeobrachaelurus* but their poor state of preservation does not allow a closer determination. The cusp of ZPAL P. 15.2 (Text-fig. 4B), however, is strongly lingually curved, indicating a different generic affinity. The synechodontiforms are represented by five teeth of *Sphenodus* sp. from horizons Gns6, Gns34 and Gns36 (Text-fig. 4E-F). The wide base of the cusp, in combination with remnants of small cusplets and the near absence of vertical folds, clearly demonstrate the generic affinity of ZPAL P. 15.3 and the other broken cusps. Teeth of *Sphenodus* are also present elsewhere in the Bathonian black clays of this area. Two different species of *Protospinax* have been recognized although neither can be identified as any previously described species. The large size and high cusplet preserved on ZPAL P. 15.4, herein referred to as *Protospinax* sp. 1 (Text-fig. 4C), in combination with a less rounded labial apron, may indicate that this tooth belongs to an undescribed species. Roughly contemporary species, including *P. annectans* Woodward, 1918, *P. bilobatus* Underwood and Ward, 2004, *P. carvalhoi* Underwood and Ward, 2004, and *P. magnus* Underwood and Ward, 2004 have teeth with lower cusplets and a smoothly rounded labial apron (see Thies 1983; Duffin 1993; Underwood and Ward 2004). The other tooth (ZPAL P. 15.5), referred to herein as *Protospinax* sp. 2 (Text-fig. 4D), is similar to teeth of *P. bilobatus* from the Bathonian of England in having a small cusp (lost in ZPAL P. 15.5) flanked by remnants of lateral cusplets. Further similarities include the shape of the labial apron, with a concave wear facet, and the slightly convex labial face. As there is only a single incomplete tooth in the Polish material, specific assignment is not possible.

PALAEOECOLOGICAL IMPLICATIONS

Apart from *Stegostoma* and the filter feeding *Rhincodon*, extant orectolobiform sharks are weak swimmers, being either nekto-benthic with a relatively elongated body shape or flattened bottom-dwellers, as in the Orectolobidae (Underwood 2004). As a result of the uncertain systematic position of many Jurassic orec-



Text-fig. 4. Neoselachian teeth from Gnaszyn. A, *Palaeobrachaelurus* sp. (ZPAL P. 15.1) from Gns 18 in labial view, × 40; B, Orectolobiformes indet. (ZPAL P. 15.2) from Gns16A in labial view, × 40; C, *Protospinax* sp. 1 (ZPAL P. 15.4) from Gns 12 in labial view, × 30; D, *Protospinax* sp. 2 (ZPAL P. 15.5) from Gns 25 in oblique labial view, × 40; E-F, *Sphenodus* sp. (ZPAL P. 15.3) from Gns16 in labial and lateral views (note mineral growth obscuring the texture of the root), × 8.5

tolobiforms, including *Palaeobrachaelurus*, it is difficult to interpret the habitat and life strategies of the orectolobiform taxa from Gnaszyn. It is nevertheless likely that these sharks were, at least partly, feeding near the bottom. The flattened body outline of *Protospinax annectans*, as inferred from complete skeletons recovered in the Upper Jurassic lithographic limestones of southern Germany (see Woodward 1918, fig. 3), approaches the morphology found in fossil and extant members of the neoselachian genus *Squatina*. This type of dorso-ventral flattening probably occurs in all species of *Protospinax* and is commonly associated with a bottom-dwelling lifestyle. The differences in tooth morphology in separate species of *Protospinax* may be the result of varied diets within the genus, where delicate, cuspidate teeth (as in *Protospinax* sp. 1) suggest a diet of non-shelled or thin-shelled invertebrates (see Duffin 1993), as well as other fishes. Other species, with lower and more robust teeth (as in *Protospinax* sp. 2), approaching the morphology of contemporary batoids like *Belemnobatis*, were possibly more specialized towards a diet of shelled invertebrates such as bivalves and crustaceans. In the Bathonian of England, different species of *Protospinax* appear to be environmentally restricted to certain habitats, and rare or lacking in other settings (Underwood 2004; Underwood and Ward 2004). The presence of orectolobiform and *Protospinax* teeth together is a strong indication of oxygenated bottom conditions, at least throughout parts of the investigated section.

The synechodontiform *Sphenodus* may have been the first pelagic neoselachian of the Jurassic, in competition with early hexanchiforms (Thies 1983). The large size of the teeth and the slender cusp with its sharp cutting edges and a minimum of ornamentation, imply the formation of a tearing-type dentition (of Cappetta 1987). The toothcrowns are similar to those of certain lamniforms and it is likely that *Sphenodus* adopted a similar mode of life as an active pelagic predator, feeding primarily on fish and cephalopods. This interpretation is further strengthened by the outline of the body (see Böttcher and Duffin 2000), similar to that of many extant pelagic sharks of the Carcharhiniformes, and the absence of *Sphenodus* teeth in the more near-shore Bathonian strata of England (see Underwood and Ward 2004).

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