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RESEARCH PAPER

The bipolar bivalve *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) in the Upper Pliensbachian of Germany

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Abstract The morphologically conspicuous bivalve *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822), known for its palaeogeographically bipolar distribution, from a limestone bed in the boundary "Belemniten–Schichten"/Amaltheenton formation, Lower Jurassic, in N Germany is described. The occurrence of this palaeoceanographically significant bivalve points to an influx of cool seawater from the Arctic to the North-German Basin at the base of the Upper Pliensbachian, just before the deposition of the Amaltheenton formation. A review of previously reported occurrences on the NW European Shelf indicates two distinct stratigraphic intervals of occurrence of this taxon: the Rhaetian–Hettangian boundary and the Upper Pliensbachian. Whereas the former interval of occurrence may be related to short-term cooling in the course of the end-Triassic extinction event, the latter is interpreted as reflecting the influx of a cool water current to the eastern part of the NW European Shelf, which continued southwards parallel to the coast of the Bohemian–Vindelician High.

Keywords Bivalvia · Germany · Triassic–Jurassic boundary · Pliensbachian · Boreal

Kurzfassung Die morphologisch markante, bipolar verbreitete Muschel *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) wird von einer Kalksteinbank an der Grenze "Belemnitenschichten"/Amaltheenton-formation, Unterer Jura, Norddeutschland beschrieben. Das Auftreten dieser paläoozeanographisch bedeutsamen Muschel deutet auf einen Einbruch kühlen Meerwassers aus der Arktis in das Norddeutsche Becken an der Basis des Oberen Pliensbachiums hin, knapp vor der Ablagerung der Amaltheenton-formation. Eine Übersicht bisher publizierter Vorkommen auf dem NW-Europäischen Schelf belegt, daß dieses Taxon auf zwei stratigraphische Intervalle beschränkt ist, und zwar den Rhaetium-Hettangium-Grenzbereich und das Obere Pliensbachium. Während das Vorkommen des ersteren Intervals mit einer kurzfristigen Abkühlungsphase im Zuge des Aussterbeereignisses am Ende der Triaszeit stehen könnte, wird das letztere Vorkommen als Resultat einer Kaltwasserströmung auf den östlichen Teil des NW-Europäischen Schelfs gedeutet, welche dann weiter südwärts parallel der Küste des Böhmisch-Vindelzischen Landes verlief.

Schlüsselwörter Bivalvia · Deutschland · Trias–Jura-Grenze · Pliensbachium · Boreal

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Introduction

Oxytoma (Palmoxytoma) is one of the morphologically most conspicuous Jurassic bivalves. The bivalve resembles "a stretched wing of a bat" (Wetzel in Hölder 1953) and is "one of the most beautiful morphotypes of England, showing the inequality of valves so conspicuous" (Quenstedt 1867: 616). *Oxytoma (Palmoxytoma)* is regarded as dwelling in cool-water habitats and has a striking bipolar palaeogeographic distribution pattern in the Hettangian, with restriction to the Boreal Realm later in the Sinemurian and Pliensbachian (Damborenea 1993, 2002). At that time, i.e., the Sinemurian–Pliensbachian, the NW European Shelf underwent significant palaeoceanographic changes with the opening of a marine strait connecting the Arctic Ocean in the North with the Tethys in the South (Ziegler 1988, 1990; Bjerrum et al. 2001). Although the exact timing of the opening of the Transcontinental Laurasian Seaway is under discussion (Ziegler 1988; Richards 1990; Steel and Ryseth 1990; Dore 1991; Bjerrum et al. 2001), there is clear evidence from palynomorphs of cool water ingression into the Spinatum Zone of the Late Pliensbachian (van de Schootbrugge et al. 2005).

In this paper, we report the discovery of the bivalve *Oxytoma (Palmoxytoma) cygnipes* (Young and Bird, 1822) in the lowermost Margaritatus Zone of the Upper Pliensbachian in Beierstedt, Northern Germany. Although previously found in the Lower Jurassic of Northern Germany by von Seebach (1864) and Brauns (1871), this species is documented for the first time from a distinct stratigraphic horizon of a detailed section, and its palaeoceanographic significance is discussed.

Materials and methods

Five valves of *Oxytoma (Palmoxytoma) cygnipes* (Young and Bird, 1822) have been recovered during a sampling campaign in August 2006. Bivalve specimens were prepared using a variety of pneumatic preparation chisels and pens. Seventeen thin-sections (7.5 × 10 cm), together covering the complete limestone beds and concretions, were prepared.

Repository: The material is stored in the Museum and Collection of the Geoscience Centre, University of Göttingen (GZG).

Location and geological overview

The investigated section at Beierstedt (sheet 3931 Jerxheim R: 36 27 000; H: 57 71 650) is located 20 km southeast of Braunschweig, south of the abandoned railway Börßum-Hedeper-Jerxheim (Fig. 1). The area is located at the eastern margin of the Lower Saxony Basin, a 300 km long and 65 km wide depression with a sedimentary succession from the Lower Permian Rotliegend Group to Tertiary formations (Ziegler 1990) up to 5 km thick. Salt cushions and diapirs rising from the Upper Permian Zechstein Group resulted in numerous salt anticlines and synclines, with a number of unconformities, mainly in the Buntsandstein Group and between Cretaceous formations. The Beierstedt section is located on the southern slope of the Asse-Heeseberg salt anticline (Fig. 1). There, Hettangian to Pliensbachian strata, which are unconformably overlain by Hauterivian strata, dip with an angle of approximately 5° to the SW. To date, no formal formation names have been established for the North-German Lias Group (Mönnig 2005), so traditional, informal lithostratigraphic units are used in this paper.

The Pliensbachian section at Beierstedt

More than 60 cm of unfossiliferous, bluish–dark grey claystones of the Upper Sinemurian "Raricostaten–Schichten" (equivalent to the South German Obtususton Formation) are exposed at the base of the section at Beierstedt (Fig. 2; Table 1). The total thickness of the "Raricostaten–Schichten" at this locality is approximately 21 m, as demonstrated by the Wetzleben drill core (Thomas 1924).

Above, the Pliensbachian starts with the 45–50 cm thick "Belemniten–Schichten" (equivalent to the South German

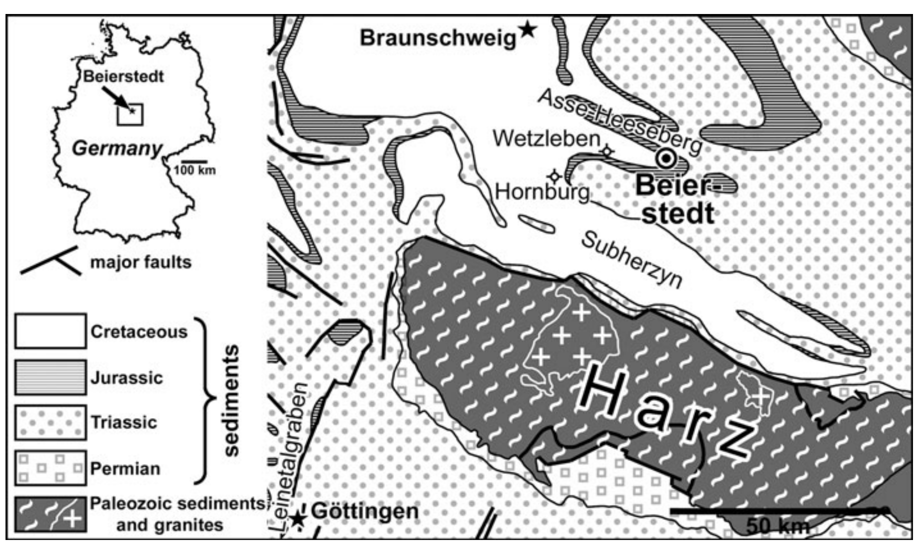


Fig. 1 Geological map of the study area showing the location of the section Beierstedt and further locations mentioned in the text

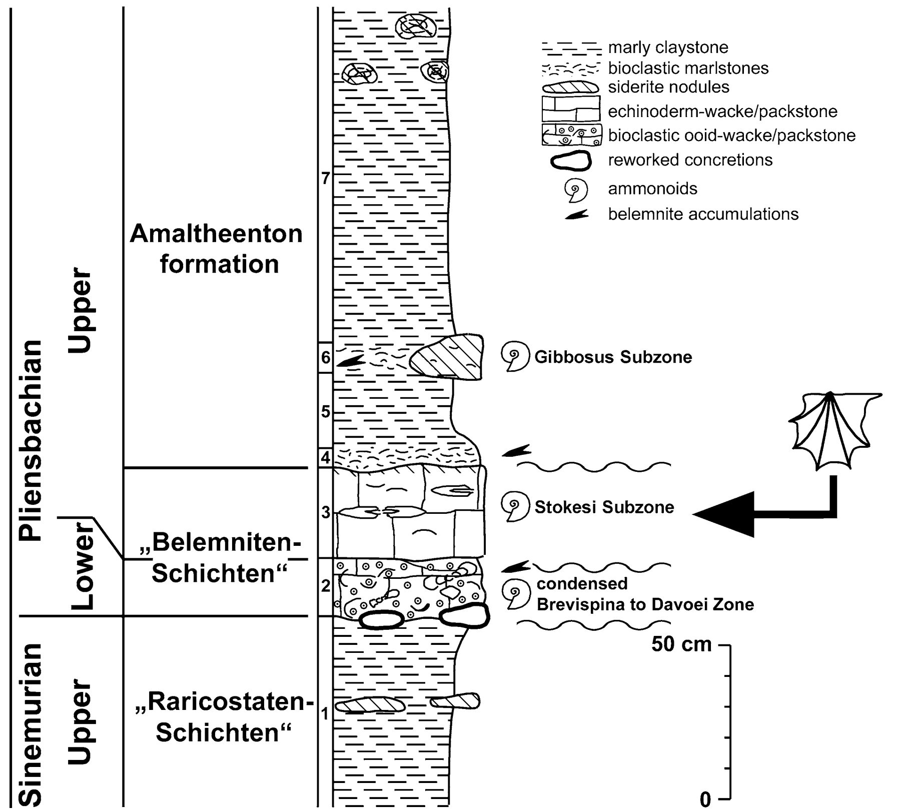


Fig. 2 Columnar section of the “Belemniten–Schichten” at Beierstedt, with the position of *Oxytoma (Palmoyxtoma) cygnipes* (Young & Bird, 1822)

Numismalismergel Formation). The lower part of this highly condensed formation is formed by a 15–20 cm thick, highly fossiliferous limestone bed, a bioturbated bioclastic iron-ooid wackestone to packstone (Fig. 3a, b). It contains abundant echinoderm clasts, brachiopod and bivalve shell fragments (among them inoceramid shell fragments with prismatic structure), rotaliid foraminifera, and belemnite rostra bioeroded by endoliths. The 300–400 μm sized ooids have siderite-replaced nuclei with limonitic cortices; locally calcitic cortices with radial crystallites also occur. Most conspicuous are cm to dm-sized grey micritic concretions with round borings 8–10 mm in diameter. These concretions are reworked from the underlying “Raricostaten–Schichten” and indicate a discontinuity at the base of the formation. Besides abundant belemnites, bivalves, gastropods, and brachiopods, well preserved ammonoids occur, which indicate the Brevispina to Maculatum Subzones, with a possible lack of the Taylori to Polymorphus Subzones (Fig. 2; Table 1). The upper part of the “Belemniten–Schichten” is formed by a 26–30 cm thick limestone bed, composed of a bioturbated echinoderm packstone with scattered other bioclasts and rotaliid foraminifera (Fig. 3c, d). Generally, the bioclasts are smaller than in the bed below, and more corroded. Locally, cm-sized, matrix-supported patches occur, indicating bioturbation. Macrofossils (ammonites, belemnites, bivalves) are generally well preserved, with only minor signs of corrosion, and embedded subhorizontally.

The lower bedding plane shows *Amaltheus stokesi* (Sowerby, 1818), *Androgynoceras maculatum* (Young & Bird, 1822), and *Prodactylioceras davoei* (Sowerby, 1822) representing the condensed Maculatum and Stokesi Subzones, whereas major parts of the bed contain *Amaltheus stokesi* (Sowerby, 1818) and *Lytoceras salebrosum* Pompeckj, 1896 indicating the Stokesi Subzone. The upper surface of the bed shows limonite impregnation and sharp, discontinuous contact with the overlying marl.

The Amaltheenton formation starts with a marly packstone consisting of shell debris, belemnites, and echinoderm bioclasts, followed by claystones with thin shell debris layers, and a second shell debris packstone with siderite nodules (Fig. 2). The latter contain *Amaltheus gibbosus* (von Schlotheim, 1820), the index fossil of the Gibbosus Subzone; together, these shell-debris-rich marls are 40–50 cm thick; there is no indication of the Subnodosus Subzone, and a corresponding discontinuity is assumed for the base of the Amaltheenton formation. Of the remaining approximately 65 m of Amaltheenton (drill core Hornburg; Thomas 1924), only the lowermost 110 cm of bluish–grey, marly claystones with siderite concretions have been exposed in this section (Fig. 2).

The three formations were deposited in an open-marine mid-shelf environment, with higher siliciclastic supply in the “Raricostaten–Schichten” and Amaltheenton formation, and strongly reduced siliciclastic influx in the

Table 1 Lithologic description of the section Beierstedt

Formation	Bed No.	Thickness	Lithology
Amaltheenton	7	>110 cm	Bluish–grey shaly claystone with disseminated pyrite; topmost 30 cm with reddish–brown siderite nodules
	6	10 cm	Grey shaly marlstone rich in mollusc and echinoderm debris, numerous belemnites, lignified driftwood; locally reddish-brown siderite nodules up to 10 × 30 cm in size; layer of cm-sized black phosphorite nodules at the top of the bed; *Amaltheus gibbosus* (von Schlotheim), *Ptychomphalus expansus* (Sowerby), *Harpax spinosa* (Sowerby), *Myoconcha (Modiolina)* sp.
	5	20–30 cm	Grey shaly clayey marlstone with numerous layers of mollusc and echinoderm debris and slightly corroded small belemnites of the *Subhastites* group; bioturbated fabric because of small branching burrows
	4	5–10 cm	Grey shaly marlstone rich in mollusc and echinoderm debris, numerous belemnites; *Amaltheus* sp.; *Harpax spinosa* (Sowerby)
"Belemniten–Schichten"	3	26–30 cm	Grey, weathering yellow–brown, bioturbated bioclastic limestone, divided by a joint into an upper and lower part; upper part with *Amaltheus stokesi* (Sowerby) and *Lytoceras salebrosum* Pompeckj; middle joint plane with *Amaltheus stokesi* (Sowerby), *Pleurotomaria* sp., *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird), *Eopecten velatus* (Goldfuss), *Camptonectes subulatus* (Münster in Goldfuss), *Pseudopecten equivalvis* (Sowerby), *Myoconcha (Modiolina) decorata* (Münster in Goldfuss), lignified driftwood; lower bedding plane with numerous ammonoids; *Amaltheus stokesi* (Sowerby), *Androgynoceras maculatum* (Young & Bird), *Prodactylioceras davoei* (Sowerby), *Liospiriferina rostrata* (von Schlotheim), *Pseudopecten equivalvis* (Sowerby)
	2	15–20 cm	Grey, weathering yellow–brown, bioturbated oolitic limestone; ferruginous ooids dominate at the base, calcareous ooids in top parts; highly fossiliferous; lowermost part clayey; erosive undulating lower boundary; *Androgynoceras maculatum* (Young & Bird) abundant within one lense at the top, *Beaniceras luridum* (Simpson), *Liparoceras (Liparoceras) cheltiense* (Murchison); *Uptonia* sp., *Platypleuroceras brevispina* (Sowerby. (5 cm above base); *Lytoceras fimbriatum* (Sowerby), *Tragophylloceras loscombi* (Sowerby), *Liospiriferina rostrata* (von Schlotheim), *Pseudokatosira* cf. *undulata* (Benz), *Pinna hartmanni* Zieten, *Parainoceramus ventricosus* (Sowerby), *Entolium lunare* (Roemer), *Pseudopecten equivalvis* (Sowerby), *Camptonectes subulatus* (Münster in Goldfuss), *Eopecten velatus* (Goldfuss), *Chlamys textoria* (von Schlotheim), "*Avicula*" *calva* (Schloenbach), *Terquemia difformis* (von Schlotheim), *Antiquilima succincta* (von Schlotheim), *Plagiostoma gigantea* (Sowerby), *Pseudolimea pectinoides* (Sowerby), *Gryphaea gigantea* (Sowerby), *Myoconcha (Modiolina) decorata* (Münster in Goldfuss), *Astarte* sp., *Cardinia rugulosa* Tate, *Pholadomya ambigua* (Sowerby), *Pleuromya costata* (Young & Bird), *Pleuromya ovata* (Roemer), *Pleuromya meridionalis* Dumortier
"Raricostaten–Schichten"	1	>60 cm	Bluish–grey shaly claystone with one layer of reddish-brown siderite nodules ca. 25 cm below top, no macrofossils observed

"Belemniten–Schichten". Contrary to previous assumptions (Thomas 1924), there is no indication of a high-energy shallow water or coastal environment. A detailed description of the section is given in Table 1.

Systematic palaeontology

Order Pterioida Newell, 1965
Family Oxytomidae Ichikawa, 1958
Genus *Oxytoma* Meek, 1864
Subgenus *Palmoxytoma* Cox, 1961

Type species: *Pecten cygnipes* Young & Bird, 1822, from the ironstone bands of the aluminous strata, Yorkshire, by original designation.

Oxytoma (Palmoxytoma) cygnipes (Young & Bird, 1822) (Fig. 4a–g)

*1822 *Pecten cygnipes*; Young & Bird: 235, pl. 9/fig. 6
1828 *Pecten cygnipes*; Young & Bird: 236, pl. 9/fig. 3
1829 *Avicula cygnipes*; Philipps: 162, pl. 14/fig. 3
1839 *Avicula longicostata*, Stutch.; Stutchbury: 163, fig.
1856 *Avicula cygnipes*; Oppel: 179
1857 *Avicula cycnipes* (Phillips); Dumortier: 7–10, pl. 4/figs. 1–4
1864 *Avicula cygnipes* Young and Bird; von Seebach: 103
1867 *Avicula cygnipes* Phill.; Quenstedt: 616, pl. 59/fig. 5
1869 *Avicula cycnipes* (Phillips); Dumortier: 294–297, pl. 35/figs. 6–9
1871 *Avicula cygnipes*; Brauns: 359
1876 *Monotis cygnipes* Young and Bird; Tate and Blake: 370–371
1881 *Avicula (Oxytoma) magnifica* n.sp.; Lundgren: 19, pl. 5/figs. 2–5

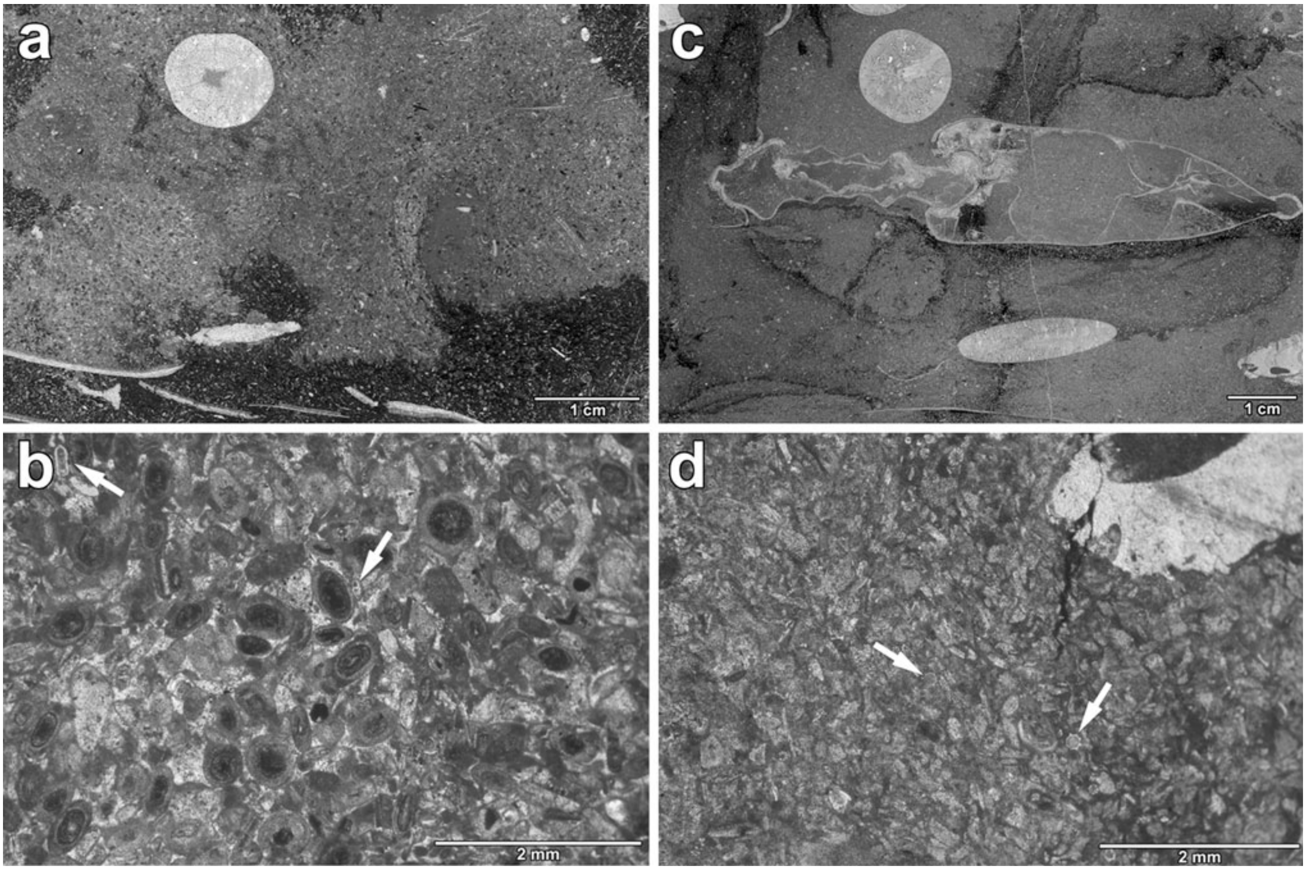
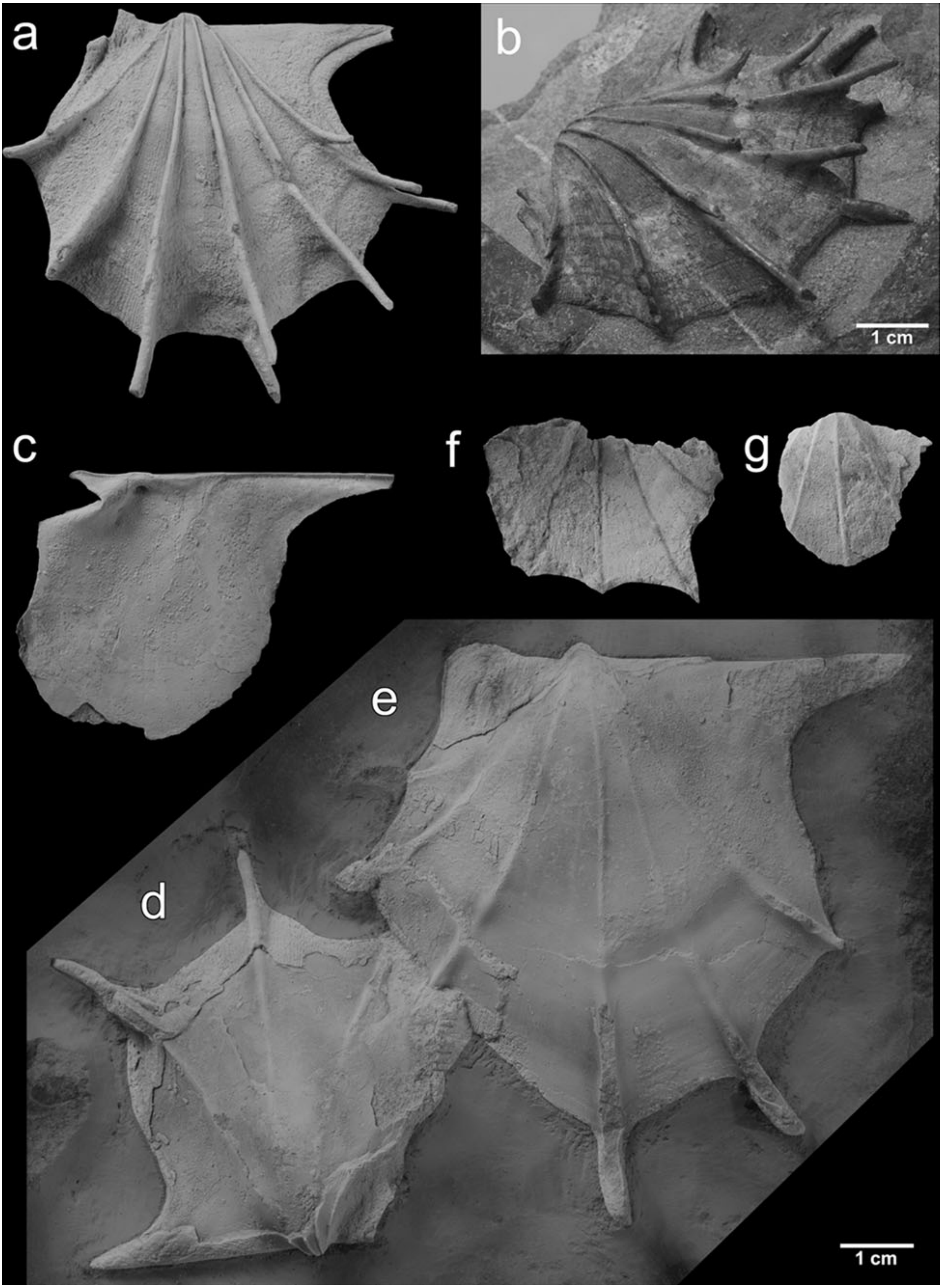


Fig. 3 Microfacies of the "Belemniten–Schichten", condensed Lower Pliensbachian and Stokesi Subzone of Beierstedt. **a** Overview of bioclastic iron-ooid wackestone to packstone of bed 2, Lower Pliensbachian, with belemnite rostra and bivalve shells. Note intense bioturbation. **b** Detail of **a** showing ooids with ferrugineous inner and calcareous outer cortices, bioclasts, and rotaliid foraminifera (*arrows*). **c** Overview of bioturbated echinoderm packstone of bed 3. Note cross-section of several belemnite rostra and an *Amaltheus stokesi* (Sowerby, 1818). **d** Detail of **c** showing densely packed echinoderm clasts, a corroded belemnite fragment, and scattered rotaliid foraminifera (*arrows*)

1888 *Avicula scanica* L.; Lundgren: 18
1888 *Avicula anserina* n. sp.; Moberg: 38, pl. 3/fig. 18
1891 *Avicula cygnipes*; von Gümbel: 379
1891 *Avicula cygnipes* Phill.; von Ammon in von Gümbel: 690
1906 *Avicula cygnipes* Phil.; Fugger: 231
v 1907 *Avicula cygnipes* Phill.; von Koenen: 44
non 1911 *Oxytoma inaequivalve* Sow. aff. *cycnipes* Phill. (Y. & B.); Hahn: 541, pl. 20/fig. 2
1913 *Avicula (Oxytoma)* cf. *cycnipes*, Phill.; Jeannet: 367, fig. 25
? 1923 *Oxytoma* sp.; Trechmann: 272, pl. 12/figs. 6–7
1933 *Oxytoma longicostata* (Strickland); Arkell: 602, pl. 29/fig. 1
? 1934 *Oxytoma* cf. *cygnipes* Y. et B.; Rosenkrantz: 51, 117
1934 *Oxytoma cygnipes* Y. et B.; Rosenkrantz: 112
v 1935 *Oxytoma* cf. *longicostata* Strickl.; Kuhn: 2, pl. 2/fig. 6
1951 *Oxytoma scanica* (Lundgren); Troedsson: 201, pl. 10/fig. 15
v 1953 *Oxytoma scanica* (Lundgren 1888); Hölder: 359, fig. 1
1957 *Oxytoma cygnipes* Phillips; Frebold: 67, pl. 16/figs. 1–5
1961 *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird 1822); Cox: 593
1964 *Oxytoma* cf. *cygnipes* (Phillips); Hölder: 432, fig. 126
1967 *Oxytoma (Palmoxytoma) cygnipes* (J. Sow.); Hallam: 400
1968 *Oxytoma cygnipes* (Young et Bird), 1822; Efimova et al.: 46, pl. 22/figs.11–12
1976 *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird); Milova: 53, pl. 4/fig. 6, pl. 5/figs. 2–5
1991 *Oxytoma (Palmoxytoma) cygnipes* (Young and Bird); Poulton: 26, pl. 11/figs. 14–16
? 1991 *Palmoxytoma* sp.; Riccardi et al.: 166, fig. 4/14


a
b
1 cm
c
f
g
e
d
1 cm

◀ **Fig. 4** *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) from the top of the "Belemniten–Schichten", Stokesi Subzone, Lower Saxony. **a**, **b** External view of left valve showing spines. Bed 3, Beierstedt. GZG.INV. 31004. **c** Internal view of right valve. Bed 3, Beierstedt. GZG.INV. 31005. **d** Internal mould of left valve with spine-like rib projections. Bed 3, Beierstedt. GZG.INV. 31002. **e** Internal mould of left valve with spine-like rib projections. Bed 3, Beierstedt. GZG.INV. 31001. **f**, **g** Fragmentary internal mould and negative imprint of left valve. Top of "Belemniten–Schichten", Göttingen-Geismar. GZG.INV. 30576 a & b

? 1992 *Palmoxytoma* sp.; Damborenea and Mancenido: 132, pl. 1/fig. 1

1992 *Oxytoma (Palmoxytoma) cygnipes*; Sey et al.: 228

1994 *Oxytoma (Palmoxytoma)* cf. *cygnipes*; Aberhan: 35, Text-fig. 16

1997 *Palmoxytoma* sp.; McRoberts et al.: 82, 87

1998 *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird 1822); Aberhan: 95, pl. 9/fig. 15–16, 18–19

2002 *Palmoxytoma* cf. *cygnipes* (Young & Bird 1822); Damborenea: 23, pl. 1/figs. 6–8

? 2002 *Palmoxytoma* n. sp.; Damborenea: 23, Text-fig. 9

2004 *Oxytoma (Palmoxytoma) ussurica* Voronetz; Konovalova and Markevich, pl. 21/figs. 1–7

2007 *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird); Rulleau: 82, pl. 52/5

Material: One right complete, three left complete, and one left incomplete valves from bed 3 (Upper Pliensbachian, Stokesi Subzone) of the "Belemniten–Schichten" at Beierstedt. One incomplete internal mould and corresponding external imprint of a left valve from the "Gamma-Delta-Grenzbank" (Upper Pliensbachian, Stokesi Subzone), top of "Belemniten–Schichten" of Göttingen-Geismar.

Description: Shell medium-sized, very inequivalve with left valve convex and right valve almost flat. Shape suborbicular, equilateral to slightly opistocline. Hinge long and straight, with a wing-like posterior auricle and a small anterior auricle. Right valve anterior auricle triangular and separated from valve by deep byssal notch. Ligament groove long and narrow. Right valve with umbo not protruding and slightly prosogyrous, faint ornamentation consisting of fine radial striae. Left valve with umbo slightly protruding and ornamentation consisting of 4–6 prominent radial ribs separated by areas with fine radial riblets. Main ribs with ovoid to circular cross-section resting upon a thin ridge. At major growth lines, ribs grade into spines up to 15 mm long and projecting at the disc margin.

Measurements These are provided in Table 2.

Remarks: The species *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) is derived from the Carnian-Norian ancestor *Oxytoma mojsisovicsi* Teller, 1886 (Damborenea 1987: 160, 2002: 22). Early Hettangian representatives have been referred to as *Oxytoma (Palmoxytoma) longicostata* (Stutchbury, 1839) (e.g., Arkell 1933; Kuhn 1935). However, the morphological differences between *O. (P.) longicostata* and *O. (P.) cygnipes* are gradual, and reflect largely preservational effects (Fig. 4a–g). Specifically, within limestones (e.g., Psilonotenkalk; Hölder 1953) internal moulds and inside views of shells are obtained, and the spiny outer surface remains hidden within the attached matrix. This is true for our specimens also; the long projections and spines are observed only after laborious preparation (Fig. 4a, b).

Apart from that, *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird) has, indeed, some variability with regard to the density of ribs and the shape of the disc. *Oxytoma cygnipes* (Young et Bird) from Eastern Siberia described

Table 2 Measurements of *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822)

Specimen	Location	Material	*L* (mm)	*H* (mm)	*I* (mm)	*R*
GZG.INV. 31001	Beierstedt, Northern Germany	LV, internal mould	65	65	9	6
GZG.INV. 31002	Beierstedt, Northern Germany	LV, internal mould	50	50	9	4
GZG.INV. 31003	Beierstedt, Northern Germany	LV, incomplete negative	(40)	(42)	(5)	(4)
GZG.INV. 31004	Beierstedt, Northern Germany	LV, shell	50	47	9	6
GZG.INV. 31005	Beierstedt, Northern Germany	RV, shell	35	37	2	–
GZG.INV. 30576 a & b	Göttingen, Northern Germany	LV, internal mould & negative imprint	(18)	(21)	(3)	4
GZG.INV. 30577 a	Whitby, Yorkshire	LV, internal mould	75	73	8	5
GZG.INV. 30577 b	Whitby, Yorkshire	LV, internal mould	56	58	7	5
GZG.INV. 30577 c	Whitby, Yorkshire	LV, internal mould	(50)	50	6	5
GZG.INV. 30577 d	Whitby, Yorkshire	RV, external mould	48	(42)	2	–
SMNS 17361 (Kuhn 1935)	Nellingen, Southern Germany	LV, internal mould	52	(48)	8	7
GPIT 1028/53 (Hölder 1953)	Bebenhausen, Southern Germany	LV, internal mould	55	54	7	6

Numbers in brackets are approximations

L length, *H* height, *I* inflation, *R* number of ribs by Efimova et al. (1968) has only four prominent ribs. The umbo is slightly prosogyrous, and the valves are otherwise identical with the specimens described in this paper. Three left valves of *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird) published by Poulton (1991) are comparatively small, and hence have only four ribs. Apart from that, they are identical with our specimens in shape and ornamentation, including spine-like rib projections. A variety with seven ribs with rather close spacing has been described as *Oxytoma (Palmoxytoma) ussurica* Voronetz by Konovalova and Markevich (2004). The specimens have slightly prosogyrous umbones but the general shape and ornamentation, including spine-like rib projections, is almost identical with those of *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird).

More pronounced differences from the specimens from the NW European Shelf can be seen in specimens from South America and New Zealand. The internal mould of a right valve of *Palmoxytoma* cf. *cygnipes* (Damborenea 2002: pl. 1/8a and Riccardi 1991: fig. 4/14) from Argentina has a very deeply incised byssal notch, not observed in our specimen with shell preservation. An extreme variety from New Zealand, a specimen with only three prominent ribs and curved spines, has been illustrated by Damborenea (1993: fig. 3b, 2002: text-fig. 9) as *Palmoxytoma* n. sp. In addition, the disc margins between the prominent ribs are curving outward, and are not concave as in the NW European specimens with their umbrella-like appearance (cf. Troedsson 1951: 201). Further specimens of this *Oxytoma (Palmoxytoma)* variety are required to decide whether the low rib number is a constant feature enabling definition of a new species.

Taking these variations into account, the currently available data are consistent with the interpretation of the mentioned specimens as a single species, with morphological variations between specimens from the northern and southern hemispheres.

Biogeography of *Oxytoma (Palmoxytoma) cygnipes* (Young and Bird) on the Lower Jurassic NW European Shelf

On the NW European Jurassic Shelf *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) occurs at two distinct stratigraphic intervals. These are the Rhaetian–Hettangian boundary strata (Pre-Planorbis beds to Planorbis bed) and the Upper Pliensbachian (base of Marlstone Rock Formation, Staithes Sandstone, and Cleveland Ironstone Formation, Amaltheenton formation) (Table 3).

Rhaetian/Hettangian. From the British Lower Jurassic, one of the stratigraphically oldest records of *Oxytoma (Palmoxytoma) cygnipes* is that of Stutchbury (1839) from the Saltford Shale (Blue Lias Formation), a long-spined variety initially described as *Avicula longicostata* Stutchbury, 1839. A precise bed has not been identified, but the Saltwick Shale is confined to the Planorbis to lower Angulata Zones (Ambrose 2001).

Hodges in Cope (1991) mentioned *Palmoxytoma* from the Pre-Planorbis Beds, i.e. the basal part of the Blue Lias Formation. The precise position below or above the Rhaetian–Hettangian boundary is not clear. In addition, the Bath Royal Literary and Scientific Institution hosts several specimens of *O. (P.) longicostata* from “Lower Lias clay with White & Blue Lias Lst.”, Montpelier, Bristol (collection C. Moore). From the same location, *Oxytoma longicostata* has been illustrated by Arkell (1933) as a characteristic fossil of the Pre-Planorbis beds.

A further occurrence from the Rhaetian–Hettangian transition is represented by *Palmoxytoma* sp. from the Upper Schattwald Shales of Lorüns/Vorarlberg (McRoberts et al. 1997), above the negative $\delta^{13}C$ excursion preceding the Triassic–Jurassic boundary (von Hillebrandt et al. 2007). Again, it is not clear whether the specimen is still latest Rhaetian or earliest Hettangian.

Of lowermost Hettangian age seems to be *Avicula (Oxytoma)* cf. *cycnipes* Phill. described and illustrated by Jeannet (1913). He obtained four valves of this taxon from approximately 6 m below the “Niveau à Planorbis” but still 20 m above typical Rhaetian limestones. Again, the precise position of the Rhaetian–Hettangian boundary is not evident from currently available information.

Clearly of Hettangian age are the reports of *O. (Palmoxytoma)* from the Swabian Jurassic (South Germany), i.e. findings from the Psilonoten Limestone. These are one fragmentary internal mould assigned to *Oxytoma* cf. *longicostata* Strickl. from Nellingen (Kuhn 1935) and one internal mould described as *Oxytoma scanica* (Lundgren, 1888) from Bebenhausen (Hölder 1953). The latter specimen is associated with *Psiloceras plicatulum* (Quenstedt, 1883). Recently, Schweigert and Klaschka (2011) discovered a further specimen comparable with *Oxytoma (Palmoxytoma)* from the Psilonoten Limestone of Bebenhausen. The Psilonoten Limestone is a 30–40 cm thick, condensed transgressive bed including ammonites of the lower Planorbis Zone, Psilonotum and Plicatulum horizons, locally underlain by a Neophyllites horizon (Bloos 1999). These ammonite horizons rest unconformably upon Rhaetian marine-deltaic sandstones.

Possibly younger but still within the Planorbis Zone are the youngest published occurrences from the Hettangian of the Northern Calcareous Alps. From top parts of the Hettangian Kendlbach Formation (still below *Psiloceras calliphyllum* (Neumayr, 1879) and *Psiloceras costosum* Lange, 1952) at the Ochsentaljoch section, Karwendel, von

Table 3 Occurrences of *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) on the NW European Shelf and adjacent areas

Chronostratigraphic unit	Lithostratigraphic unit	Location	Ref.
Rhaetian–Hettangian boundary	Pre-Planorbis Beds	England, Bristol	Arkell (1933): Pre-Planorbis beds, Montpelier, Bristol
Rhaetian–Hettangian boundary	Pre-Planorbis Beds	England	Hodges in Cope (1991)
Rhaetian–Hettangian boundary or Hettangian	Blue Lias Fm., Saltford Shale Mbr.	England, Somerset	Stutchbury (1839): lias shales at Saltford, between Bristol and Bath, Somersetshire
Rhaetian–Hettangian boundary	Fm. de Plan Falcon	Switzerland, Préalpes	Jeannet (1913): Hettangien inferieur, Plan-Falcon sur Corbeyrier, Préalpes
Rhaetian–Hettangian boundary	Kendlbach Fm.	Austria, Austroalpine	McRoberts et al. (1997): Upper Schattwald Shale, Lorüns/ Vorarlberg
Lower Hettangian, Planorbis Zone	Kendlbach Fm.	Austria, Austroalpine	Fugger (1906) "graue Hornsteinkalke der Psilonoten-Schichten, Glasenbachklamm bei Salzburg
Lower Hettangian, Planorbis Zone	Psilonotenton Fm.	Germany, Baden-Württemberg	Kuhn (1935): Psilonotenkalk, Nellingen
Lower Hettangian, Planorbis Zone	Psilonotenton Fm.	Germany, Baden-Württemberg	Hölder (1953): Planorbis-Bank, Hettangium, Bebenhausen
?Upper Pliensbachian	Neill Klinter Group, Gulehorn Fm.	Greenland, Jameson Land	Rosenkrantz (1934): Charmouthian, East Greenland
Condensed Low. Pliensbachian plus Stokesi Subzone	"Belemniten–Schichten"	Germany, Niedersachsen	Brauns (1871): Niveau des Amm. centaurus bei Scheppenstedt, in der Gegend von Oker, bei Jerxheim - und des Amm. Davoei bei Lüerdissen am Ith
Condensed Low. Pliensbachian plus Stokesi Subzone	"Belemniten–Schichten"	Germany, Göttingen, Niedersachsen	von Koenen (1907): Mittlerer Lias, sämtlich oder doch größtenteils aus der Zone des Amm. Davoei
Lower/Upper Pliensbachian boundary	"Belemniten–Schichten"	Lower Saxony, Hils syncline	von Seebach (1864): Schichten des Am. capricornus bei Lürdissen am Ith
Upper Pliensbachian, Margaritatus Zone	Cleveland Ironstone Fm.	England, Yorkshire	Philipps (1829): Marlstone Series, Bilsdale, Wilton Castle/ Yorkshire
Upper Pliensbachian, Margaritatus Zone	Cleveland Ironstone Fm.	England, Yorkshire	Oppel (1856): Basis des Marlstone, unter Amm. margaritatus, Robin Hoods Bay
Upper Pliensbachian, Margaritatus - Spinatum Zone	Staithes Sandstone Fm., Cleveland Ironstone Fm.	England, Yorkshire	Tate and Blake (1876) Zones of Am. margaritatus, Staithes, Rockcliff, Hummersea, Huntcliff, Bilsdale, bottom seam of ironstone, Slapewath, Grosmont, Glaizedale; Am. spinatus, Staithes, Eston, Upleatham, Guisbro'.
Upper Pliensbachian, Margaritatus - Spinatum Zone	Amaltheenton fm.	Germany, Bavaria, Bodenwöhr	von Gümbel (1891): Sohlerz des mittleren Lias mit Am. margaritatus und spinatus, Bodenwöhrer Becken
Upper Pliensbachian, Spinatum Zone	Cleveland Ironstone Fm.	England, Yorkshire	Young and Bird (1822, 1828): from the ironstone bands of the aluminous strata
Upper Pliensbachian, Spinatum Zone	Lias Group	Yorkshire, Midlands, England, Hebrides	Hallam (1967): Spinatum Zone, Yorkshire (common), Midlands (occurs), SW-England (occurs), Hebrides (occurs)
Upper Pliensbachian, Spinatum Zone	Lumachelle à Harpax	France, Rhône, Isère	Dumortier (1857): St. Fortunat au Mont d'Or/Rhône, Chamagnieu/ Isère, la partie superieur du lias moyen
Upper Pliensbachian, Spinatum Zone	Lumachelle à Harpax	France, Rhône	Dumortier (1869): Giverdy, zone du Pecten aequivalvis
Upper Pliensbachian, Spinatum Zone	Lumachelle à Harpax	France, Rhône	Rulleau (2007): Domérien supérieur, Croix Rampaud, Poleymieux-au-Mont-d'Or

Table 3 continued

Chronostratigraphic unit	Lithostratigraphic unit	Location	Ref.
Upper Pliensbachian	Brandsberga sandstone	Sweden, Scania	Lundgren (1881, 1888): I den marina Hörssandstenen, Brandsberga ö om Gellaberg
Upper Pliensbachian	Brandsberga sandstone	Sweden, Scania	Moberg (1888): Liasmorän vid Rödmölla
Upper Pliensbachian	Brandsberga sandstone	Sweden, Scania	Troedsson (1951): Brandsberga sandstone (Pebble), Kolleberga
Toarcian	Neill Klinter Group, Ostreaelv Fm.	Greenland, Jameson Land	Rosenkrantz (1934): Toarcian, East Greenland

Hillebrandt et al. (2007: fig. 9) illustrated an "*Oxytoma*", which can be identified as the left valve of *O. (Palmoxytoma) cygnipes*. In addition, Fugger (1906) mentioned *Avicula cygnipes* Phil. from Lower Hettangian siliceous limestones with cherts at the Glasenbachklamm near Salzburg.

Taking all these published occurrences into account, *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) seems to have been widespread in the Rhaetian–Hettangian boundary strata of the NW European Shelf and its margin to the Tethys. By contrast, the following Upper Hettangian to Lower Pliensbachian deposits of this area appear to be devoid of this species.

Pliensbachian. The type species of Young and Bird (1822) comes from the Upper Pliensbachian Cleveland Ironstone Formation ("hard bands in the alum shale"), where it is most abundant in the "Avicula seam" (i.e., top of the Subnodosus Subzone; Howarth 1955; Rawson and Wright 1996: 206). This coincides with the descriptions of Harries and Little (1999), who mention *Palmoxytoma cygnipes* from the upper Staithes Sandstone and Cleveland Ironstone Formations (Stokesi to Apyrenum Subzone) of the Yorkshire coast (Staithes Harbor and Saltwick Nab). Similarly, Hallam (1967) reports *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) from the Spinatum Zone of Yorkshire (common), in addition to the Midlands (occurs), SW-England (occurs) and the Hebrides (occurs).

From East Greenland, *Oxytoma cygnipes* Y. et B. is reported by Rosenkrantz (1934: 112) from the Pliensbachian (Charmouthian), though without illustration. From the sections described and the few ammonites found, it seems possible that the fossil-bearing strata range into the Upper Pliensbachian.

Also, the early reports of *Oxytoma (Palmoxytoma)* from southern Sweden (Lundgren 1881, 1888) apparently show specimens from the Pliensbachian. The fine-grained sandstone that contained the *Oxytoma (Palmoxytoma)* specimen of Moberg (1888) is also most likely Pliensbachian in age (cf. Reyment 1959; Ahlberg et al. 2003). However, a more precise biostratigraphic designation is not available, because the material is derived from glacial till deposits (Brandsberga sandstone, Middle Liassic; Sivhed 1984).

In Northern Germany the Lower–Upper Pliensbachian boundary strata yield *Palmoxytoma* specimens, as noted by von Seebach (1864) and Brauns (1871). These authors mention *Avicula cygnipes* Young and Bird from the "Belemniten–Schichten" of the Hils syncline and Subhercynian syncline and from the margin of the Asse-Heeseberg anticline (von Seebach 1864; Brauns 1871). Unfortunately, these reports are without illustration and without described sections, so the precise stratigraphic position (Davoei Zone or Stokesi Subzone), crucial for

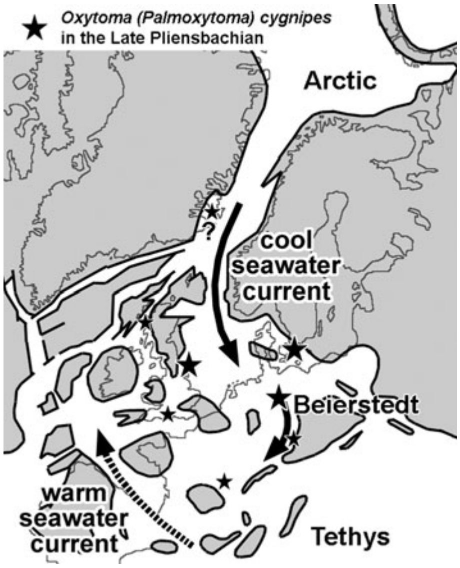


Fig. 5 Possible seawater current pattern on the NW European Shelf based on the occurrences/non-occurrences of *Oxytoma (Palmoyxtoma) cygnipes* (Young & Bird, 1822) and model calculations of Bjerrum et al. (2001). Palaeogeography based on Ziegler (1988)

palaeoceanographic interpretations, in these condensed beds remains unclear. Similarly, the precise biostratigraphic level of *Avicula cygnipes* Phill. of von Koenen (1907: 44) from the Middle Lias of Göttingen is not clear from this publication. However, the corresponding specimen is in the GZG collection ("*Avicula cycnipes* Phill., M. Lias, d d [donum dedit] Wolf, Göttingen-Geismar"; Fig. 4f, g), preserved within an echinoderm packstone, which is likely to be derived from the top of the "Belemniten–Schichten", i.e. the Stokesi Subzone.

From Southern Germany, von Ammon (in von Gümbel 1891: 690) lists *Avicula cygnipes* from the Upper Pliensbachian iron ores of Bodenwöhr, Eastern Bavaria. These highly condensed, 0.2–1.5 m thick fissile goethite-haematite deposits comprise the Margaritatus and Spinatum Zones (von Gümbel 1891; Meyer and Bauberger 1998). This is currently the southeasternmost occurrence of *Oxytoma (Palmoxytoma) cygnipes*. Unfortunately, no corresponding specimen exists in the Gümbel collection of the Bavarian Geological Survey.

Further specimens have been discovered in southeastern France, as already described and illustrated by Dumortier (1857) from the upper part of the Pliensbachian east of Lyon (St Fortuna), and from the Upper Pliensbachian ("Zone du Pecten aequivalvis") of Giverdy in the Mont d'Or area (Dumortier 1869). In the region of Lyon, *Oxytoma (Palmoxytoma) cygnipes* occurs within a highly condensed limestone bed (Calcaire à Harpax) together with *Gryphaea (Bilobissa) sportella* (Dumortier, 1869), *Cardinia crassissima* (Sowerby, 1817) and rare *Pleuroceras spinatum* (Bruguiere 1789) and *Pleuroceras solare* (Phillips, 1829), pointing to the top parts of the Apyrenum Subzone of the Spinatum Zone (Louis Rulleau, personal communication).

In summary, Late Pliensbachian occurrences of the bivalve *Oxytoma (Palmoxytoma) cygnipes* (Young & Bird, 1822) are evident for England, southern Sweden to southeastern Bavaria, and southeastern France (Fig. 5) whereas specimens are rare or absent on the western shelf parts of NW Europe and the Mediterranean region.

Toarcian. The only published occurrence in the Toarcian known to the authors is *Oxytoma* cf. *cygnipes* Y. et B. of Rosenkrantz (1934) from Jameson Land, East Greenland, but the taxon has not been illustrated.

Discussion

The Lower Jurassic sedimentary pattern on the NW European Shelf has predominantly been interpreted on the basis of sea-level changes being the major controlling factor (Brandt 1985; de Graciansky et al. 1998; Hesselbo and Jenkyns 1998). However, changes in the current systems may have played an equally important role. Specifically, the palaeogeographic situation of the NW European Shelf, with a narrow seaway to the North (Viking Corridor: Westermann 1993; Transcontinental Laurasian seaway: Bjerrum et al. 2001) implies that the sedimentary system of the shelf was susceptible to changes in current direction, dependent on the density differences between Arctic and Tethyian seawater (Bjerrum et al. 2001).

The Late Pliensbachian has been interpreted as a relatively cool period in NW Europe, mainly as a result of general climatic cooling in the Northern Hemisphere (Price 1999; Guex et al. 2001). Alternatively, cool water conditions, as reflected in palynomorph assemblages and $\delta^{18}O$ values from belemnites, were considered to reflect influx of cool water masses from boreal regions (Riding and Hubbard 1999; van de Schootbrugge et al. 2005). In addition, there is increasing geochemical evidence that changes in current directions occurred on the NW European Shelf during the Early Jurassic (Dera et al. 2009).

In Germany, major parts of the Upper Pliensbachian are represented by the comparatively thick, monotonous succession of dark marly claystones, the Amaltheenton formation, which is dominated by macrobenthos assemblages of comparatively low diversity (see, e.g., Paleobiology Database collection numbers 23624–23628 and 23812–23818), although species listings by Brauns (1871), Monke (1889) and Kuhn (1936) give a contrary impression. By contrast, the Lower Pliensbachian of Germany contains calcareous sediments (marlstone–limestone alternations), with iron–oolitic intercalations in the north and phosphoritic intercalations in the south. The macrobenthos shows more diverse bivalve assemblages (Wollemann 1892). Although these differences in macrobenthos assemblages may be partly explained by substrate changes, the—albeit scattered—occurrence of coralline sponges in the Numismalismergel Formation suggest an influx of warmer seawater from Tethyan regions in the Early Pliensbachian.

In this context, the new finds of the bivalve *Oxytoma (Palmoxytoma)* are of palaeozeanographic significance. This taxon has been extensively reviewed by Damborenea (1993, 2002) as a bivalve with a pronounced bipolar distribution, including occurrences from southern South America and New Zealand, and from northern boreal areas (NE Siberia, far-east Russia, Japan, Canada) and England, Sweden, and France.

Accordingly, the occurrence of *Oxytoma (Palmoxytoma)* at the top of the "Belemniten–Schichten" in Northern Germany may indicate an influx of cool seawater to the eastern part of the NW European Shelf at the base of the Upper Pliensbachian (Fig. 5), i.e. just before the onset of the Amaltheenton formation. This carbonate top bed of the "Belemniten–Schichten" consists of echinoderm wacke/packstones with reduced macrobenthos species richness. Indeed, at Beierstedt this condensed bed contained only five bivalve species, compared with 20 bivalve species in the condensed Lower Pliensbachian carbonate bed below (Table 1). Certainly, these species counts provide only a first hint, and quantitative benthos analysis of sections less affected by time-averaging (Fürsich and Aberhan 1990) are required to verify this trend. This supposed cool water current may have extended (during the upper Margaritatus to Spinatum Zones) farther south to eastern Bavaria and southeastern France, as suggested by the specimens reported by von Ammon in von Gümbel (1891), by Dumortier (1857, 1869) and by Rulleau (2007) (Fig. 5).

Continuing cool water conditions during deposition of the Amaltheenton formation in Northern Germany are evident from glendonites, which have been reported from the upper part of the Amaltheenton formation (motorway A 39 at Wolfsburg; Luppold and Teichert 2007), although their significance as an indicator of low temperatures has subsequently been questioned by the same authors (Teichert and Luppold 2009). However, the temperature–pressure stability field of ikaite, the precursor of glendonites, is well constrained, and the significance of the associated species-rich and supposed thermophile microfauna mentioned by these authors must be verified.

For the Rhaetian–Hettangian boundary, the palaeoenvironmental implications of the *Oxytoma (Palmoxytoma)* occurrences are more difficult to determine. Assuming a cool water preference of *Oxytoma (Palmoxytoma)* for this time interval also, the occurrences within the Alpine region may point to a cool deeper-water setting, or alternatively to a global cooling interval. Although the causes of the Triassic–Jurassic boundary extinction event are still under discussion (Tanner et al. 2004), climatic fluctuations with a short-term cooling period (induced by aerosols) immediately after the negative δ^{13}C excursion, followed by a warming period (induced by increased atmospheric CO_2) seem well constrained (reviewed by, e.g., Wignall 2001; Guex et al. 2004; Pieńkowski et al. 2008). Also, the higher extinction rate of tropical than non-tropical genera in the Rhaetian point to a palaeoclimatic factor in the end-Triassic mass extinction (Kiessling and Aberhan 2007). A short-term cooling interval may hence be assumed for the English Pre-Planorbis beds and the Southwest German Psilonotenkalk, both deposited in shallow-water settings on the NW European Shelf. However, the occurrence of the coral *Isastrea* in the Psilonotenkalk (Schweigert et al. 2010), a zooxanthellate warm-water coral rather than an azooxanthellate cool-water coral, challenges this hypothesis. Here, further investigations are required to assess faunal mixing by reworking of stratigraphically older material into the transgressive Psilonoten Limestone.

Conclusions

Oxytoma (Palmoxytoma) cygnipes (Young & Bird, 1822) from the Lower Jurassic of Northern Germany (to be precise, from the basal Upper Pliensbachium), is described and illustrated for the first time. Comparison of published specimens of *Oxytoma (Palmoxytoma)* suggests there is only one species in the Lower Jurassic, i.e. *cygnipes* (Young & Bird, 1822). This species ranges from the Rhaetian–Hettangian boundary to the Upper Pliensbachian, probably extending into the Toarcian. A review of published occurrences on the Early Jurassic NW European Shelf indicates two distinct stratigraphic intervals: the Rhaetian–Hettangian boundary and the Upper Pliensbachian. The occurrence of *Oxytoma (Palmoxytoma) cygnipes* at the base of the Upper Pliensbachian, just before the onset of the Amaltheenton sedimentation, is interpreted as reflecting an influx of cool water from the Boreal Ocean on to the eastern NW European Shelf. This cool water current may have extended southwards as far as Southern Germany, with a possible counter current on the western shelf parts. For the occurrences of the species at the Triassic–Jurassic boundary of the NW European Shelf, a short-term cooling interval at the same time as the extinction event might provide an explanation.

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