

Batoids (Rajiformes, Torpediniformes, Myliobatiformes) from the Sülstorf Beds (Chattian, Late Oligocene) of Mecklenburg, northeastern Germany: a revision and description of three new species

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Abstract: Bulk-sampling of fossil-rich tempestites from the Chattian Sülstorf Beds of Mecklenburg, north-eastern Germany, yielded a rich selachian fauna in which batoids predominate by the abundance of teeth but are subordinate by the number of taxa. Thirteen taxa are identified, among which rajiform batoids are the most diverse (six species). One genus and three species are newly described: *Raja thiedei* sp. nov., *Oligoraja pristina* gen. et sp. nov., and *Torpedo chattica* sp. nov. Two species are reallocated: *Atlantoraja ceciliae* (Steurbaut & Herman, 1978) new comb., and *Dipturus casieri* (Steurbaut & Herman, 1978) new comb. Ontogenetic heterodonty is documented for the first time in the dental pattern of *Myliobatis* sp. Stratigraphical ranges of batoid taxa in the period from Rupelian to Langhian are presented and partly discussed in context with the palaeoclimatic evolution and palaeogeographic situation of the North Sea Basin.

Keywords: Batoids, Elasmobranchii, Chattian, Oligocene, North Sea Basin

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INTRODUCTION

After a short episode of strong cooling and concomitant sea-level lowering at the Rupelian-Chattian boundary (e.g. Van Simaeyns *et al.*, 2004, 2005), the earliest Chattian in the North Sea Basin (NSB) initiated an extended episode of major climate warming (De Man & Van Simaeyns, 2004; Van Simaeyns *et al.*, 2004), corresponding to the global “Late Oligocene Warming Event” (Zachos *et al.*, 2001). The warming caused the widespread appearance of thermophilic marine invertebrates and vertebrates in the southern shelf ranges of the basin (e.g. Janssen, 1986; Rothausen, 1958, 1986; Schwarzahns, 1994; Müller, 1996; De Man & Van Simaeyns, 2004).

Although in the NSB many taxa of chondrichthyan fishes, e.g. *Alopias*, *Araloselachus*, *Carcharhinus*, *Carcharoides*, *Galeocerdo*, *Isurolamna*, *Keasius*, *Notorynchus*, *Carcharocles*, *Parotodus*, *Pristiophorus*, *Squalus*, and *Squatina*, persisted from the Rupelian to the Chattian, the early Chattian also saw the appearance of myliobatiform and rajiform batoids, as well as of lamniform and small carcharhiniform sharks (genera *Galeorhinus*, *Isurus*, *Mitsukurina*, *Pachyscyllium*, *Raja*, *Dasyatis* and *Scyliorhinus*, Von der Hocht, 1986; Reinecke *et al.*, 2005; Gille *et al.*, 2010; Reinecke, 2014) which were either uncommon or apparently absent during extended periods of the colder temperate Rupelian (Boom Clay and Rupel Formations). Their teeth are mainly detected in the siliciclastic sediments of the Sülstorf Beds of Mecklenburg, north-eastern Germany (Reinecke *et al.*, 2005; Reinecke, 2014), and Grafenberg Formation of the Lower Rhine area (Von der Hocht, 1986, and personal communication), less commonly also in the Kassel Formation of northern Hesse (Müller, 1996; Gille *et al.*, 2010), and Doberg Formation of Lower Saxony (Weiler, 1943,

1957; Reinecke *et al.*, 2005). The rich material of batoid teeth obtained from the Sülstorf Beds includes species of the genera *Raja*, *Atlantoraja*, *Sympterygia*, *Dipturus*, *Dasyatis*, *Gymnura*, *Torpedo*, *Myliobatis*, and *Mobula*, most of which are hitherto poorly characterized or unknown. With complementary observations from Rupelian and Early/Middle Miocene deposits the stratigraphical range of batoids in the NSB can be documented and updated for the time interval from Rupelian to Langhian.

GEOLOGICAL SETTING

The Sülstorf Beds, Chattian, late Oligocene, of Mecklenburg, eastern Germany, are a ca. 80 m thick sequence of calcareous, glauconite- and white mica-bearing silts, coarsening upwards into well sorted fine sands, that were deposited on the upper shelf of the south-eastern NSB. A detailed representation of the Paleogene and Neogene regional geology and stratigraphy, which was largely explored from drillings, is given by Von Bülow (2000) and Von Bülow & Müller (2004). Fig. 1 presents the Chattian chrono-, litho- and biostratigraphy, the latter being based on benthic foraminiferal assemblages.

Conglomeratic layers in the Sülstorf Beds with elongate sand/siltstone intraclasts, well-rounded quartz and lithic pebbles, pieces of wood, large molluscs, shark teeth and rare bones of marine vertebrates represent proximal tempestites that are characterized by normal graded bedding and sharp, erosional contacts with the silty basis (Suhr & Braasch, 1991). Sandy and conglomeratic layers are locally solidified by calcite cement, forming discontinuous layers in the largely unconsolidated deposits. The depositional regime of the Sülstorf Beds inferred from mollusc and ostracod associations was the upper

sublittoral zone (Janssen, 1986; Endler & Herrig, 1995; Moths *et al.*, 1998). The diverse mollusc fauna includes many thermophilic taxa and therefore points to a warm-temperate to subtropical climate. Relatively high bottom-water temperatures during the early to middle Chattian were inferred also from benthic foraminiferal assemblages in the south-western regions of the NSB (Kohnen, 1995; De Man & Van Simaey, 2004; Van Simaey *et al.*, 2004).

Except for core drillings, the Sülstorf Beds are almost exclusively accessible as glaciofluvial drift (pebbles and cobbles commonly 3-15 cm, rarely more than 25 cm in diameter; Schulz, 1972). All samples collected for this study come from the sandpit in Kobrow, near Sternberg (Fig. 2). A northwest-southeast extending salt dome in the surroundings of Sternberg raised the Chattian deposits to the shallow underground (Schulz, 1972: text-fig. 5) were they have been eroded by ice advances of the Weichselian glacial. The upper Sülstorf Beds (Fig. 1) contain a characteristic shallow-marine assemblage with large, benthic foraminifera (*Palmula*, *Lenticulina*, *Cyclamina*, *Fronicularia*, *Astacolus*, *Dentalina*) which can be easily recognized on the weathered, sandy surfaces of many pebbles and in coarser sieve fractions as well. On the other hand, marine clastic sediments of late Chattian age (Rogahn Beds, Fig. 1) or Early/Middle Miocene sediments are very exceptionally observed in the glaciofluvial drift at the sample locality, because these sediments were deposited only further to the west (i.e. west of a line extending from Wismar to Schwerin and the river Elbe; Fig. 2; and Von Bülow & Müller, 2004: figs. 3.9.1-6 and 3.9.2-1). Hence, faunal mixtures are very unlikely to exist in the elasmobranch assemblage investigated in this study.

MATERIAL AND METHODS

Over the last 10 years more than two tons of calcite-cemented mollusc-rich sandstones were dissolved in dilute formic or acetic acid. The silt and fine sand fraction of the acid-insoluble residue was removed with a 0.5 mm mesh sieve and the remaining volume split into the >3 mm, 1-3 mm, and 0.5-1 mm fractions. In the 0.5-1 mm fraction, yielding the largest amount of residue, fish remains were further concentrated with an isodynamic magnetic separator. Most batoid teeth (> 95%) occur in the 1-3 mm fraction, whereas the 0.5-1 mm

fraction contains a low amount of rajoid teeth but many dermal denticles. Tooth diameters are measured with a digital calliper under the binocular.

Photographs of teeth shown in Figures are obtained with a Novex RZB-SF stereo trinocular equipped with a 5 megapixel USB camera. 15-30 images sequentially taken at different levels of focus are combined into a single image with the Euromex Image Focus Stacking Software. Teeth of the very common species *Dasyatis* aff. *delfortriei* Cappetta, 1970 which were already illustrated in detail (Reinecke *et al.*, 2005: 69) are not re-examined in this study.

All figured specimens are deposited in the palaeontological collections of the Senckenberg Research Institute and Natural History Museum (abbreviated: SMF P). Synonymy lists are mainly referring to publications dealing with Rupelian and Chattian batoid dental material. The classification largely follows Compagno (2005). According to White (2014: 149), the family Myliobatidae Bonaparte, 1835 includes only the eagle rays with the genera *Aetobatus* Blainville, 1816; *Aetomylaeus* Garman, 1908; and *Myliobatis* Cuvier, 1816, and the two described species of *Pteromylaeus* Garman, 1913 have to be reallocated to the genus *Aetomylaeus* Garman, 1908. The dental terminology for rajiform, torpediniform and myliobatiform species is adopted from Cappetta (2012), except for the tooth and tooth plate terminology of Myliobatidae which is from Hovestadt & Hovestadt-Euler (2013: text-fig. 2). Valid names and publication dates of extant species are taken from www.fishbase.org, version 08/2014 (Froese & Pauly, 2014).

SYSTEMATIC PALAEONTOLOGY

The type location, type stratum and age of all species, first described in this study are:

Type location. Sandpit of “Thomas Beton” in Kobrow, near Sternberg, Mecklenburg-Vorpommern, Germany. UTM coordinates (WGS84/ETR89): 32N 686283 5951456.

Type stratum. Sülstorf Beds: calcite-cemented, fine-grained sandstones and siltites with cm- to dm-thick layers of shell detritus and endoclasts; occurring as glaciofluvial drift (vernacular name: “Sternberger Gestein”), see Von Bülow (2000) and Gürs (2005).

Age. Early to middle Chattian (“Eochattian”), Late Oligocene; benthic foraminiferal *Palmula oblonga* Zone (Müller, 2000).

Oligocene						Miocene	
Rupelian		Chattian				Aquitainian	Stages
28.1		23.0					Time (Ma)
Rupel Clay	Plate Beds	Sülstorf Beds lower	Sülstorf Beds upper	Rogahn Beds	Brook Beds	Regional lithostratigraphy	
<i>Rotalia</i> <i>bulimoides</i> - Zone	<i>Siphonia</i> <i>reticulata</i> - Zone	<i>Asterigerinoides</i> <i>guericchi</i> - Zone	<i>Palmula</i> <i>oblonga</i> - Zone	<i>Almaena</i> <i>osnabrugensis</i> - Zone	<i>Saracenaria</i> <i>magna</i> - Zone	<i>Quinqueloculina</i> <i>disparilis</i> - Zone	
Regional benthic foraminiferal zones of western Mecklenburg (Müller, 2000)							

Figure 1. Late Rupelian and Chattian (Oligocene) to Aquitanian lithostratigraphy, chronostratigraphy, and biozones of benthic foraminifera in north-eastern Germany (modified from Von Bülow & Müller, 2004 and Müller, 2000). The time scale of Rupelian/Chattian and Chattian/Neogene stage boundaries is from Vandenberghe *et al.* (2012).

Order RAJIFORMES Berg, 1937

Family ARHYNCHOBATIDAE Fowler, 1934

Genus *Atlantoraja* Menni, 1972

Atlantoraja ceciliae (STURBAUT & HERMAN, 1978) new comb.
(Figs. 3a and 6b)

v* 1978 *Raja ceciliae* n. sp., Steurbaut & Herman, 1978, p. 306, pl. 2, fig. 4.

v 1978 *Raja terhagenensis* n. sp., Steurbaut & Herman, p. 307, pl. 2, fig. 3.

v 1978 *Raja heinzeli* n. sp., Steurbaut & Herman, p. 306, pl. 2, fig. 2.

. 1996 *Raja* cf. *heinzeli* Steurbaut & Herman, 1978 - Müller, p. 40, pl. 1, fig. 9a-b.

. 1996 *Raja* aff. *terhagenensis* Steurbaut & Herman, 1978 - Müller, p. 40, pl. 1, fig. 8a-d.

v 2005 *Raja ceciliae* Steurbaut & Herman, 1978 - Reinecke *et al.*, p. 63, pl. 52, pl. 53, figs. 2, 4, 5; pl. 54; pl. 59, fig. 7.

v 2008 "*Raja*" *ceciliae* Steurbaut & Herman, 1978 - Haye *et al.*, p. 71, text-fig. 7, pl. 10, figs. 1-3.

. 2010 *Raja ceciliae* Steurbaut & Herman, 1978 - Gille *et al.*, p. 23, figs. 22a-f.

Material. ca. 2000 teeth of male morph, ca. 2200 teeth of low-crowned, female/juvenile morph (in part referable to *Raja thiede* sp. nov., see below).

Measurements

high-crowned anterolateral teeth of male morph (n = 27)

height: 0.9 – 2.0 mm (average 1.6 mm)

width*: 0.6 – 1.0 mm (average 0.8 mm)

length*: 0.6 – 1.5 mm (average 1.0 mm)

high-crowned lateroposterior teeth of male morph (n = 21)

height: 0.7 – 1.4 mm (average 1.0 mm)

width*: 0.5 – 0.8 mm (average 0.7 mm)

length*: 0.5 – 1.1 mm (average 0.8 mm)

low-crowned teeth of female/juvenile morph (n = 21)

height: 0.6 – 1.1 mm (average 0.9 mm)

width*: 0.8 – 1.3 mm (average 1.0 mm)

length*: 0.7 – 1.2 mm (average 0.9 mm)

* mesio-distal (width) and labio-lingual (length) diameter of the crown basis.

Remarks and discussion

The taxa *Raja terhagenensis* Steurbaut & Herman, 1978 (anterolateral male teeth), *Raja heinzeli* Steurbaut & Herman, 1978 (anterolateral and lateroposterior female teeth), and *Raja ceciliae* Steurbaut & Herman, 1978 (lateroposterior male teeth) are different morphs of a single valid species, *R. ceciliae*, and are related to each other by sexual and gradient monognathic heterodonty (Hovestadt & Hovestadt-Euler, 1995). Represented by 29, 23, and 5 type specimens, respec-

tively, they were first recovered and described from beds 41, 49, and 58 of the Boom Clay Formation, Rupelian, of northern Belgium (Steurbaut & Herman, 1978). The Chattian Sülstorf Beds have produced a much larger number of well preserved teeth, which likely covers all jaw positions. This sample may be suitable to construct an artificial tooth set.

The sample was split into low-crowned and higher-crowned teeth. The first fraction includes teeth with a rather flat labial crown face and a distinct but low transverse crest, sometimes equipped with a slightly pointed cusp (Hovestadt & Hovestadt-Euler, 1995: pl. 7, figs. 1a-c; pl. 8, figs. 1a-c; Reinecke *et al.*, 2005: pl. 54), as well as many, very small and rather unspecific rajoid teeth (typically less than 1.2 mm in width; e.g. Steurbaut & Herman, 1978: pl. 2, fig. 2). These

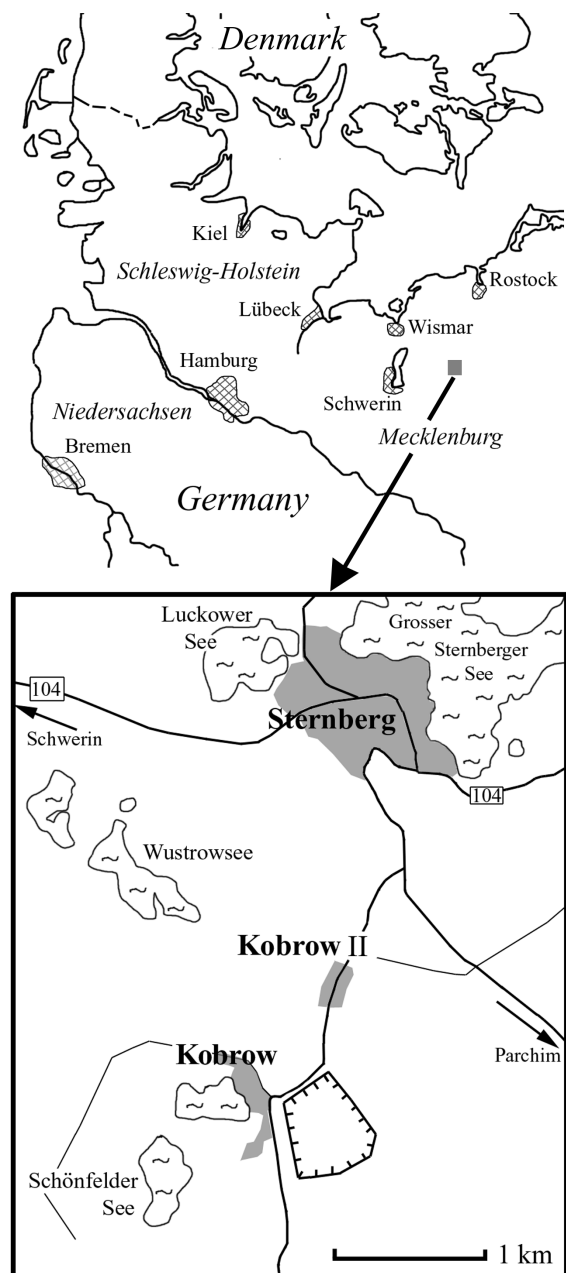


Figure 2. Location of the sandpit at Kobrow near Sternberg, Mecklenburg-Vorpommern, Germany, which is the type locality of the new batoid species described herein.

likely represent female and juvenile male specimens of the taxon *cecilae*, but in small number also the female teeth of other species, e.g. *Raja thiedei* sp. nov. and *Sympterygia* sp. (see below).

High-crowned (male) teeth are used in the construction of the artificial tooth set illustrated in Fig. 3a. They are sorted by size, lingual/distal inclination and crown shape/asymmetry and arranged according to gradient heterodont patterns known for male individuals of the type species of the extant genera *Sympterygia* Müller & Henle, 1837 (type species: *Sympterygia bonapartii* Müller & Henle, 1841); *Atlantoraja* Menni, 1972 (type species: *Atlantoraja cyclophora* (Regan, 1903)); and *Rioraja* Whitley, 1939 (type species *Rioraja agassizii* (Müller & Henle, 1841) (Herman *et al.*, 1994: pl. 39, 53-54; Herman *et al.*, 1996: pl. 33-34). These genera are chosen for comparison, because their dental characteristics appear to be morphologically closest to the taxon *cecilae* (see also Hovestadt & Hovestadt-Euler, 1995). The number of teeth per half jaw shown in Fig. 3a is 14, but this is largely hypothetical and may deviate from actual numbers. Regan (1903: 60) reports the presence of 36-38 teeth in the upper jaw of the 480 and 410 mm long type specimens of *Atlantoraja cyclophora*, and Norman (1937) and Hildebrand (1946) mention 30-44 files of teeth in different species of *Sympterygia*.

If we are examining the tooth set in detail, teeth of anterior files (first two files in Fig. 3a) have erect, elongate cusps (labial view in first row) which are strongly curved in lingual direction (profile in second row). Mesial and distal cutting edges are weakly developed and extend from the apex to the lower third

of the cusp. In anterolateral files (files 3 to 7), the crown is getting more oblique, the labial keel shifts to a more distal position, and the root lobes develop more asymmetrically, while the width and length of the crown basis and length of the mesial and distal cutting edges is remaining almost constant. Teeth of the lateral to lateroposterior files (files 8-14 in Fig. 3a) are decreasing in height towards the commissure. Teeth of files 8-11 have a shallow labial keel which gets lost in more posterior teeth developing a flat labial crown face. The lateral cutting edges of the crown in the most posterior files extend closer to the crown basis and finally form a convex transverse crest (files 12-14 in Fig. 3a).

Apparently, the dental pattern is not smoothly gradient. If the discontinuity after the seventh file is an artefact and due to lack of intermediate specimens, remains unresolved. Among the specimens with male morphology, very few teeth do not follow the pattern described above. These are specimens with an upright, eccentric cusp, markedly displaced from the axial position (Figs. 5F-H), which are morphologically closer to *Sympterygia* sp. and/or *Rioraja* sp. (see below).

The artificial tooth set proposed and illustrated in Fig. 3a may also contribute to the generic affiliation of the taxon *cecilae*. Hovestadt & Hovestadt-Euler (1995) first pointed out the close correspondence of the three nominal species *terhagenensis*, *heinzelini*, and *cecilae* with the sexual and male gradient heterodonty of *Sympterygia bonapartii* Müller & Henle, 1841 (for spelling of species name, see Froese & Pauly, 2014, Fishbase). Different from our male tooth set of *cecilae*, male teeth in anterior files of *S. bonapartii*, the type species

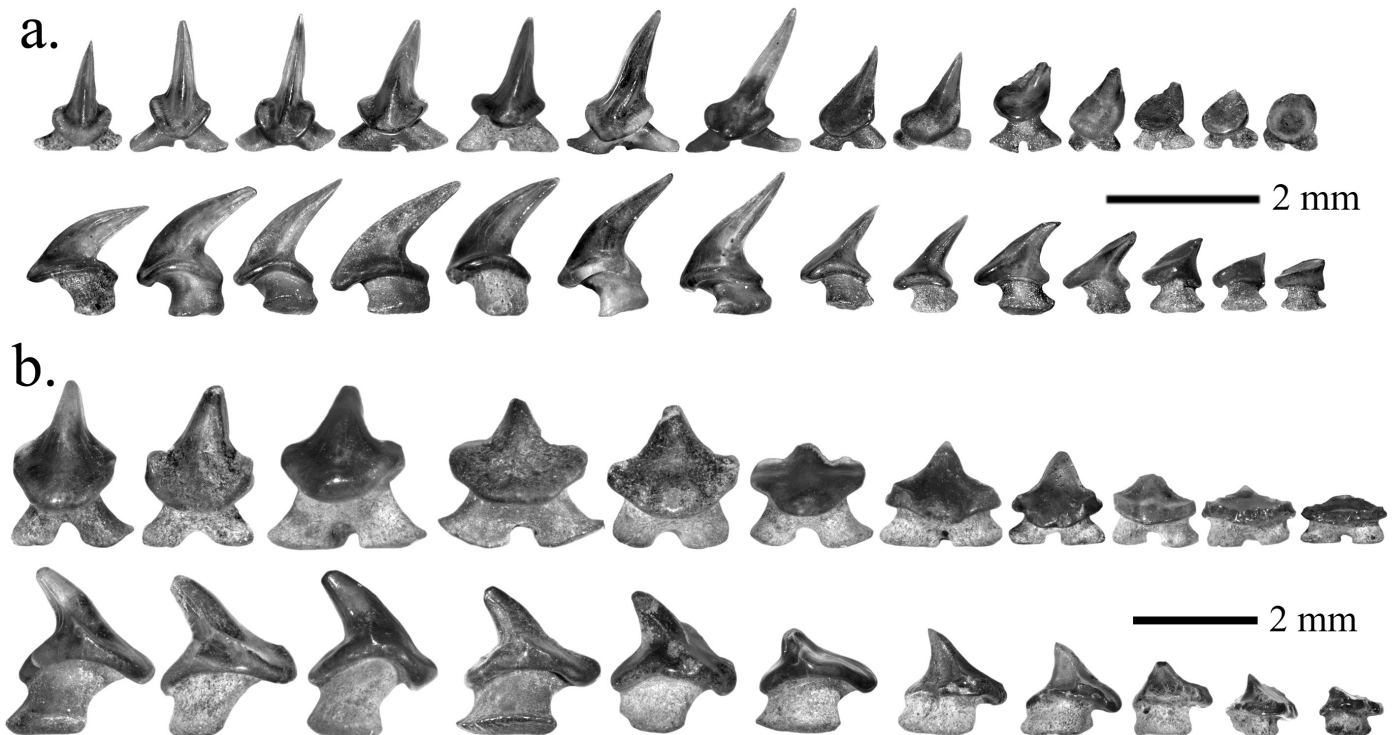


Figure 3a. Artificial male tooth set (half jaw) of *Atlantoraja cecilae* (Steurbaut & Herman, 1978) new comb., assembled from the largest teeth referable to morphologically different dental files. The number of teeth per half jaw is actually unknown. Dignathic heterodonty is not observed. Illustrations of some teeth are reversed left to right, SMF P 9818. **3b.** Artificial male tooth set (half jaw) of *Dipturus casieri* (Steurbaut & Herman, 1978) new comb., assembled from the largest available teeth. The apex of the sixth tooth from left is shortened by wear. Dignathic heterodonty is not observed. Some illustrations are reversed left to right, SMF P 9819.

of *Sympterygia* Müller & Henle, 1837, have a distorted cusp, eccentrically placed on the crown basis (Herman *et al.*, 1996: 190, group 2). The same feature occurs in male teeth of *Rioraja agassizii* (Müller & Henle, 1841), the type species of *Rioraja*, which also distinguishes from *cecilae* (and *S. bonapartii*) by a secondary hemiaulacorhizid root and weak sexual heterodonty (Herman *et al.*, 1996: 190). Only in *A. cyclophora* (Regan, 1903), the type species of *Atlantoraja*, an undistorted, narrow, elongate cusp is observed in anterior male teeth (Herman *et al.*, 1996: 190), a character which is combined with distinct sexual heterodonty, and the presence of a holaulacorhize root, a labial keel in anterolateral male teeth and convex mesial and distal cutting edges in lateroposterior male teeth. Obviously, the dental characters of male teeth of the genus *Atlantoraja* are morphologically closest with the taxon *cecilae*, which is therefore combined with *Atlantoraja* into *A. cecilae* new comb.

Dermal denticles recovered from the Sülstorf Beds include a number of thorns with the characters described and illustrated by Reinecke *et al.* (2005: 64 and pl. 59, fig. 7). These represent specialized alar thorns derived from the latero-external region of the pectoral fins in mature male rajoids. McEachran & Konstantinou (1996: 169, fig. 10c) illustrate a morphologically identical thorn of an extant species of *Atlantoraja*. It differs from those of *Sympterygia* and *Rioraja* by the anterior rather than central position of the barbed cusp over the narrow, elongate base.

The vascularization of several male *cecilae* teeth, submerged in anise oil and examined microscopically in transmitted light, does not provide further evidence for their generic allocation. All teeth have an elongate pulp cavity situated in the lower crown and root area, with short extensions into the root lobes, the external foramen of the nutrient groove, and the cusp (Fig. 6b). A vascular vessel extends into the apical cusp region. Feathery tubes of circumpulpar dentine emanate from the pulp cavity into the crown basis and the upper regions of the cusp. Marginolingual foramina are not present. A very similar vascularization is documented for *Atlantoraja*, *Sympterygia*, and *Rioraja* (Herman *et al.*, 1995, 1996).

The genus *Atlantoraja* includes three species which are restricted to the upper-middle shelf of the south-western Atlantic (Froese & Pauly, 2014). The common presence of *Atlantoraja* during the early-late Oligocene and early Miocene in the NSB, marginal to the northern Atlantic, points to a much wider distribution of the genus in the geological past.

Genus *Sympterygia* Müller & Henle, 1837

Sympterygia sp.

(Figs. 5F-H)

Material. 14 teeth (male morph).

Measurements (mm):

height:	1.2	1.4	1.7
width*:	0.8	0.8	0.9
length*:	1.1	0.8	0.9

* mesio-distal (width) and labio-lingual (length) diameter of

the crown basis.

Description

A few teeth, rarely occurring in the Sülstorf Beds, differ from male anterolaterals of *Atlantoraja cecilae* by their more asymmetrical crown shape. The cusp is noticeably shifted towards the distal side of the crown base, the labial keel is slightly more curved, and its basal projection meets the labial visor more distally (Figs. 5G3 and 5H1) than in male teeth of *A. cecilae* (Fig. 3a). The three teeth illustrated are considered to partially reflect the gradient monognathic heterodonty of this species, ranging from anterior (Fig. 5H) to more lateral jaw positions (Figs. 5G, 5F). The anterior tooth (Fig. 5H, and other specimens not illustrated) has an erect, lingually curved cusp, with indistinct mesial and distal cutting edges, extending from the apex to the mid of the cusp, and a much sharper labial keel that extends to near the basal labial crown margin. Crown ornamentation is absent. Whereas the distal crown margin is vertical and slightly flexuous (in labial view), the mesial crown margin is subvertical and slightly convex in the apical region but widens in basal direction to a shallow, oblique heel (Fig. 5H1). The labial visor distinctly overhangs the labial root face, but does not form an apron. An uvula is not observed. The holaulacorhize, low root has well separated lobes, where the distal lobe is much wider than the mesial lobe. Two teeth from more lateral files (Figs. 5G, 5F) develop gradually lower cusps and less inclined (subhorizontal) mesial heels than the anterior specimen.

Discussion

An attempt to fit the present teeth into the gradient monognathic dental pattern of male *Atlantoraja cecilae* (Sturbaut & Herman, 1978) is seemingly problematic (Fig. 3a). In addition, their relative uncommonness in the batoid tooth assemblage would be incompatible with the hypothesis that these specimens document dignathic heterodonty of the taxon *cecilae*. Our observations rather suggest relationships with a genus different from *Atlantoraja*. As outlined above, batoid species in the extant genera *Sympterygia* Müller & Henle, 1837 and *Rioraja* Whitley, 1939 have male anterolateral teeth with a moderately high principal cusp asymmetrically displaced in distal direction (Herman *et al.*, 1994: pl. 39, 53-54). Only *Sympterygia* (represented by *S. bonapartii*), however, has a holaulacorhize root. I therefore place the present specimens in the genus *Sympterygia*.

Family RAJIDAE Blainville, 1816

Genus *Dipturus* Rafinesque, 1810

Dipturus casieri (Sturbaut & Herman, 1978) new comb.

(Figs. 3b, 4, 5A-E, and 6A)

v* 1978 *Raja casieri* n. sp., Sturbaut & Herman, p. 305, pl. 2, fig. 1.

. 1991 *Raja* cf. *casieri* Sturbaut & Herman, 1978 - Freess, p. 160, pl. 6, fig. 11.

. 1995 *Raja casieri* Steurbaut & Herman, 1978 - Hovestadt & Hovestadt-Euler, p. 265, pl. 2, fig. 1a-d.

v 2005 *Raja casieri* Steurbaut & Herman, 1978 - Reinecke *et al.*, p. 65, pl. 55-56.

v 2008 *Raja casieri* Steurbaut & Herman, 1978 - Haye *et al.*, p. 73, pl. 9, figs. 1-2.

. 2010 *Raja casieri* Steurbaut & Herman, 1978 - Gille *et al.*, p. 23, figs. 23A-c.

. 2012 *Raja casieri* Steurbaut & Herman 1978 - Cappetta, p. 360.

Material. 108 teeth (male and female morph).

Measurements

high-crowned teeth of male morph (n = 65)

height: 0.8 – 2.8 mm (average 1.8 mm)

width*: 1.1 – 2.5 mm (average 1.7 mm)

length*: 0.9 – 2.3 mm (average 1.7 mm)

low-crowned teeth of female and juvenile/subadult morph (n = 6)

height: 1.1 – 1.7 mm (average 1.4 mm)

width*: 1.6 – 2.5 mm (average 1.8 mm)

length*: 1.1 – 1.6 mm (average 1.3 mm)

* mesio-distal (width) and labio-lingual (length) diameter of the crown basis.

Remarks and discussion

The dental morphology of this species was previously described by Steurbaut & Herman (1978: 305), Hovestadt & Hovestadt-Euler (1995: 265), Reinecke *et al.* (2005: 65) and Bor *et al.* (2012: 65). The material recovered from the Sülstorf Beds represents the largest sample of *casieri* teeth hitherto collected from a single deposit and thus provides the chance to assemble an artificial tooth set (Fig. 3b) and document sexual and ontogenetic heterodonty.

A large part of the tooth sample, affiliated to adult male individuals, has dimensions (height, width) near to 2 mm, with a maximum height ranging up to 2.8 mm and a width up to 2.5 mm. Gradient heterodonty is documented by the widening and lowering of the cusp (i.e. decreasing height-to-width ratio) in anterolateral files (Figs. 4E-4G) and the rapidly decreasing crown height in lateroposterior files (Figs. 4H-4K and Fig. 3B). In labial view, cusp orientation is upright and crown shape more

or less symmetrical. Very few teeth have an oblique cusp (Fig. 4I) and these represent rare variations that do not match the characteristic dental pattern (Fig. 3b). Observations supporting digonathic heterodonty are not made.

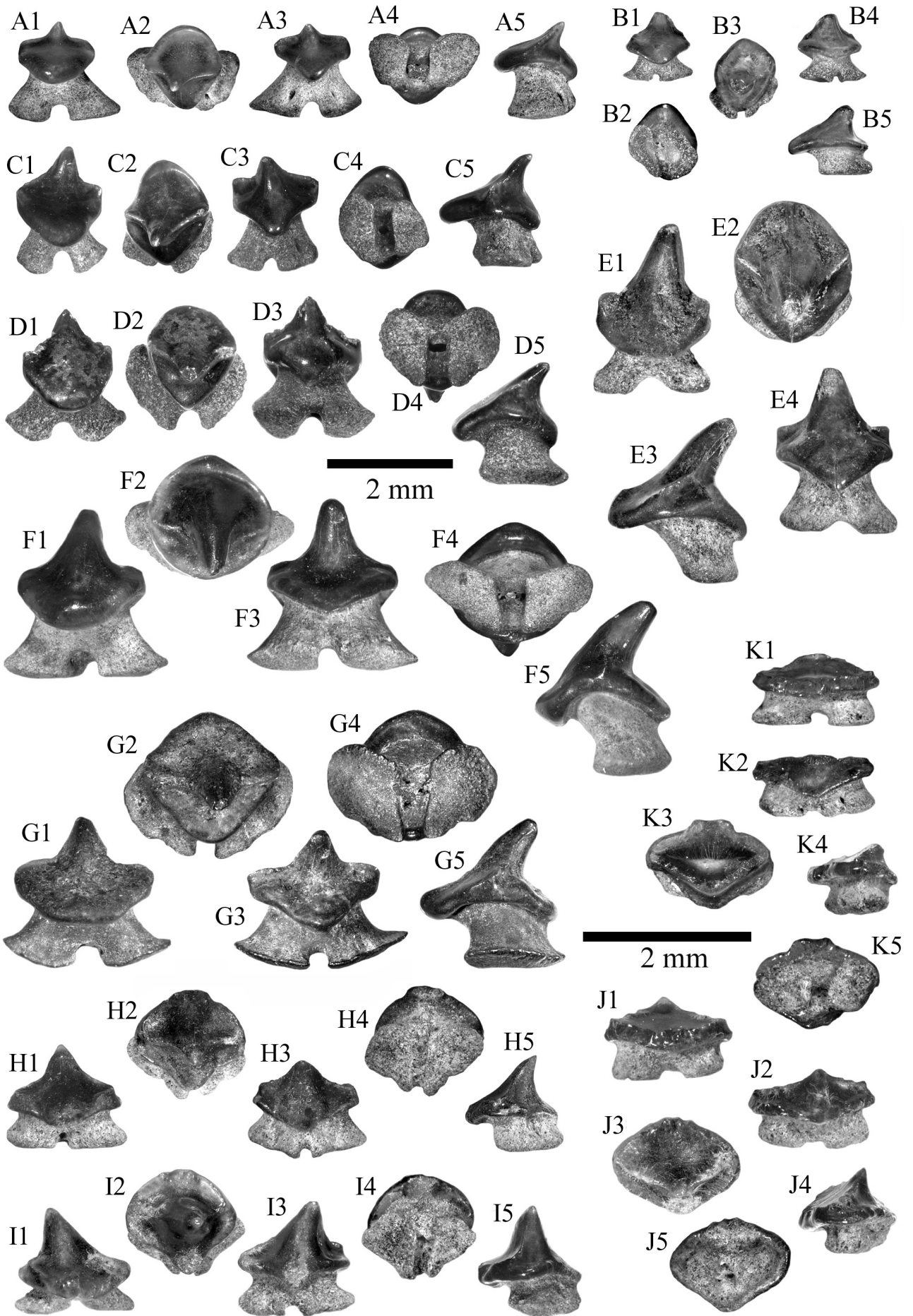
Whereas anterior to lateral teeth have smooth crown faces and lack an apron, lateroposterior teeth develop a distinct apron (Figs. 4H2, 4H4 and Figs. 4K3, 4K5) and a transverse ridge on the basal labial crown face ornamented with short ridges (Figs. 4J1, 4K1; Reinecke *et al.*, 2005: pl. 55, fig. 5). Lateroposterior teeth have a low principal cusp and their V-shaped transverse crest extends across the full tooth width (Figs. 4J3, 4K3).

Vascularization is similar in all teeth: The holaulacorhize root shows 1-3 larger foramina centred in the wide nutrient groove. Marginolingual foramina, rarely present in a few small (subadult) teeth of the male (Fig. 4A3) and female morph (Fig. 5D5), are absent in most specimens. A single specimen was cut along the axial plane extending from the apex to the nutrient groove (Fig. 6a). It shows a low pulp cavity (filled with dark sediment grains) which opens basally to the nutrient groove. Vascular vessels extend from the pulp cavity into the cusp and the labial crown region and narrow tubes of circumpulp dentine are radiating from the pulp cavity and the vascular vessels (terminology after Herman *et al.*, 1995).

Small teeth with similar crown and root morphology as larger specimens may derive from juvenile/subadult individuals (Figs. 4A-4D). Typically, they have an apico-basally more compressed crown with proportionally lower central cusp than in alike adult teeth (compare Fig. 4A with Fig. 4G and Fig. 4B with Fig. 4F). Hence, a moderate extent of ontogenetic heterodonty is established.

Teeth with low or missing central cusp and a straight to slightly arched transverse crest (seen in occlusal view) (Figs. 5A-5E; Reinecke *et al.*, 2005: pl. 56) can be most probably allocated to subadult and adult females, as suggested in previous studies (e.g. Reinecke *et al.*, 2005; Bor *et al.*, 2012). Different from the dimensionally similar lateroposterior male teeth, the basal labial crown face of female specimens is smooth and lacks a ridge, and the transverse crest, seen in occlusal view, is less arched in lingual direction (compare Figs. 5B3-5D3 and 5E2 with Figs. 4J3, 4K3). Largest teeth of the female morph have a similar width and length (labio-lingual diameter) as large male specimens (see above), but do not fit their gradient monognathic pattern (Fig. 3b). Their combined characteristics exclude the hypothesis that they might represent

Figure 4. *Dipturus casieri* (Steurbaut & Herman, 1978) new comb., Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. The upper 2 mm scale bar refers to Figs. A-H, the lower right to Figs. I-K. **A**, anterolateral tooth, H (height) = 1.6 mm, W (width) = 1.2 mm, L (length) = 1.4 mm, A1 labial view, A2 occlusal view, A3 lingual view, A4 basal view, A5 profile view, SMF P 9812. **B**, anterolateral tooth, H = 1.1 mm, W = 1.0 mm, L = 1.2 mm, B1 labial view, B2 occlusal view, B3 lingual view, B4 basal view, B5 profile view, SMF P 9820. **C**, anterolateral tooth, H = 1.9 mm, W = 1.4 mm, L = 1.7 mm, a. labial view, b. occlusal view, c. lingual view, d. basal view, e. profile view, SMF P 9821. **D**, anterolateral tooth, H = 1.9 mm, W = 1.9 mm, L = 1.6 mm, D1 labial view, D2 occlusal view, D3 lingual view, D4 basal view, D5 profile view, SMF P 9822. **E**, anterolateral tooth, H = 2.6 mm, W = 1.8 mm, L = 2.2 mm, E1 labial view, E2 occlusal view, E3 profile view, E4 lingual view, SMF P 9823. **F**, anterolateral tooth, H = 2.7 mm, W = 2.1 mm, L = 2.1 mm, F1 labial view, F2 occlusal view, F3 lingual view, F4 basal view, F5 profile view, SMF P 9824. **G**, lateral tooth, H = 2.4 mm, W = 2.3 mm, L = 2.2 mm, G1 labial view, G2 occlusal view, G3 lingual view, G4 basal view, G5 profile view, SMF P 9825. **H**, lateral tooth, H = 1.7 mm, W = 1.9 mm, L = 1.7 mm, H1 labial view, H2 occlusal view, H3 lingual view, H4 basal view, H5 profile view, SMF P 9826. **I**, lateral tooth, H = 1.3 mm, W = 1.4 mm, L = 1.3 mm, I1 labial view, I2 occlusal view, I3 lingual view, I4 basal view, I5 profile view, SMF P 9827. **J**, posterior tooth, H = 1.0 mm, W = 1.5 mm, L = 1.2 mm, J1 labial view, J2 lingual view, J3 occlusal view, J4 profile view, J5 basal view, SMF P 9828. **K**, posterior tooth, H = 0.8 mm, W = 1.5 mm, L = 1.0 mm, K1 labial view, K2 lingual view, K3 occlusal view, K4 profile view, K5 basal view, SMF P 9829.



juvenile/subadult ontogenetic stages of *D. casieri*.

While until the 80's of the last century most species of rajoid batoids described from Tertiary deposits were referred to the genus *Raja* Linné, 1758, the detailed studies on rajoid teeth of all living supraspecific taxa presented by Herman *et al.* (1994, 1995, 1996) first allowed a closer approach to the taxonomy of fossil skates in the families Rajidae and Arhynchobatidae.

Comparison of the *casieri* dental pattern (Fig. 3b) with dentitions of extant rajoid genera (Herman *et al.*, 1994, 1995, 1996) indicates a closer affinity only with the genera *Dipturus* Rafinesque, 1810, *Raja* Linné, 1758 and *Rostroraja* Hulley, 1972. Similar to *casieri* teeth, adult male and female anterolateral teeth of the type species *Dipturus batis* (Linné, 1758) and *Rostroraja alba* (Lacépède, 1803) have bulky crowns with an upright to slightly oblique cusp and variably broad heels with cutting edges extending from the apex to the mesial and distal crown margins. In adult male teeth of *Raja clavata* Linné, 1758, the cusp is stouter, the crown heels much narrower, and cutting edges shorter, i.e. not reaching the crown margins (Herman *et al.*, 1995: pls 29-30), than in male *casieri* teeth. The apron is distinct (*Rostroraja alba*) or missing (*Dipturus batis*, *Raja clavata*), and the uvula weak to absent in all three type species.

The low-crowned lateroposterior teeth of *R. alba* and *D. batis*, as well as our male *casieri* teeth, have a mesio-distally more expanded crown and wider root lobes than corresponding teeth of *Raja clavata* (and other extant species of this genus). Although having a similar overall shape as the lateroposterior teeth of *casieri*, corresponding teeth of *R. alba* and *D. batis* lack the transverse ridge and ornamentation of the labial crown basis observed in specimens of *casieri*. Another species of the genus *Dipturus* with well-documented dentition, i.e. *D. nidarosiensis* (Storm, 1881), shows a distinct labial crown ornamentation in anterolateral to lateroposterior teeth, consisting of irregular folds and prickles, and a distinct transverse basal ridge (Herman *et al.*, 1996: pl. 35-36). Sexual heterodonty is pronounced in adult teeth of *Raja clavata* and appears to be less developed in *Dipturus batis* and *D. nidarosiensis*, but is absent or weak in *Rostroraja alba* (Herman *et al.*, 1995: 243, 244, 247; Herman *et al.*, 1996).

The root lobes are more massive and basally broader in anterolateral teeth of *D. batis*, *D. nidarosiensis*, and *casieri* than in male and female teeth of *Rostroraja alba* and particularly of *Raja clavata*. All type species have holaulacorhize roots, with marginolingual foramina being commonly absent. The vascularization of the taxon *casieri* closely resembles that of *Dipturus batis*. The rounded shape of the pulp cavity and the length and orientation of the vascular strings of *Dipturus casieri* (Fig. 6a)

is very similar to that of *Dipturus batis* (Herman *et al.*, 1995: text-fig. 5). By comparison, the pulp cavity of *Rostroraja alba* is much higher and labio-lingually more expanded (Herman *et al.*, 1995: text-fig. 11). Male teeth of *Raja clavata* have a smaller, apico-basally more elongate pulp cavity than male specimens of *casieri* and lack the string of vascular vessels radiating from the pulp cavity in labial direction (compare Herman *et al.*, 1995: text-fig. 7 with Fig. 6a in this study).

In conclusion, the taxon *casieri* seems to be much closer to *Dipturus* by dental morphology and vascularization than to *Raja* or *Rostroraja* and is therefore combined with the genus *Dipturus*. The genus *Dipturus* comprises about 49 extant species (Froese & Pauly, 2014). Five species of *Dipturus* are living in the North Atlantic, accepting a wide range of benthic substrates, temperatures, and depths (Ebert & Stehmann, 2013). Recent studies indicate that *Dipturus batis* is actually a composite species, and can be split into two species, *Dipturus* sp. cf. *flossada* (Risso, 1826) and *D.* sp. cf. *intermedia* (Parnell, 1837), which differ among other features also in tooth morphology (see Ebert & Stehmann, 2013).

Lowermost records of *Dipturus casieri* are from the Kerniel and Berg Members of the Bilzen Formation (Taco Bor, personal communication 2014), and the Terhagen (beds S35, S39, S41) and Putte Members (bed S47, yielding the type material) of the Boom Clay Formation, Belgium (Steurbaut & Herman, 1978; Hovestadt & Hovestadt-Euler, 1995: 62). The species is also present in the Winterswijk Member of the Rupel Formation, late Rupelian, of The Netherlands (Bor *et al.*, 2012: 66) and in the Böhlen Formation, Rupelian, of Saxony, Germany (Freess, 1992). In addition to the Sülstorf Beds, *D. casieri* is uncommon but widespread in early to late Chattian deposits of the southern NSB, e.g. the Kassel Formation and the Chattian Silt (Haye *et al.*, 2008; Gille *et al.*, 2010), the Doberg Formation at Astrup near Osnabrück (Reinecke *et al.*, 2005) and the Grafenberg Formation of the Lower Rhine Embayment (Von der Hocht, pers. communication, 2014). Preferred habitats comprise sandy to clayey bottoms in near-coastal to deeper shelf environments.

Genus indeterminate

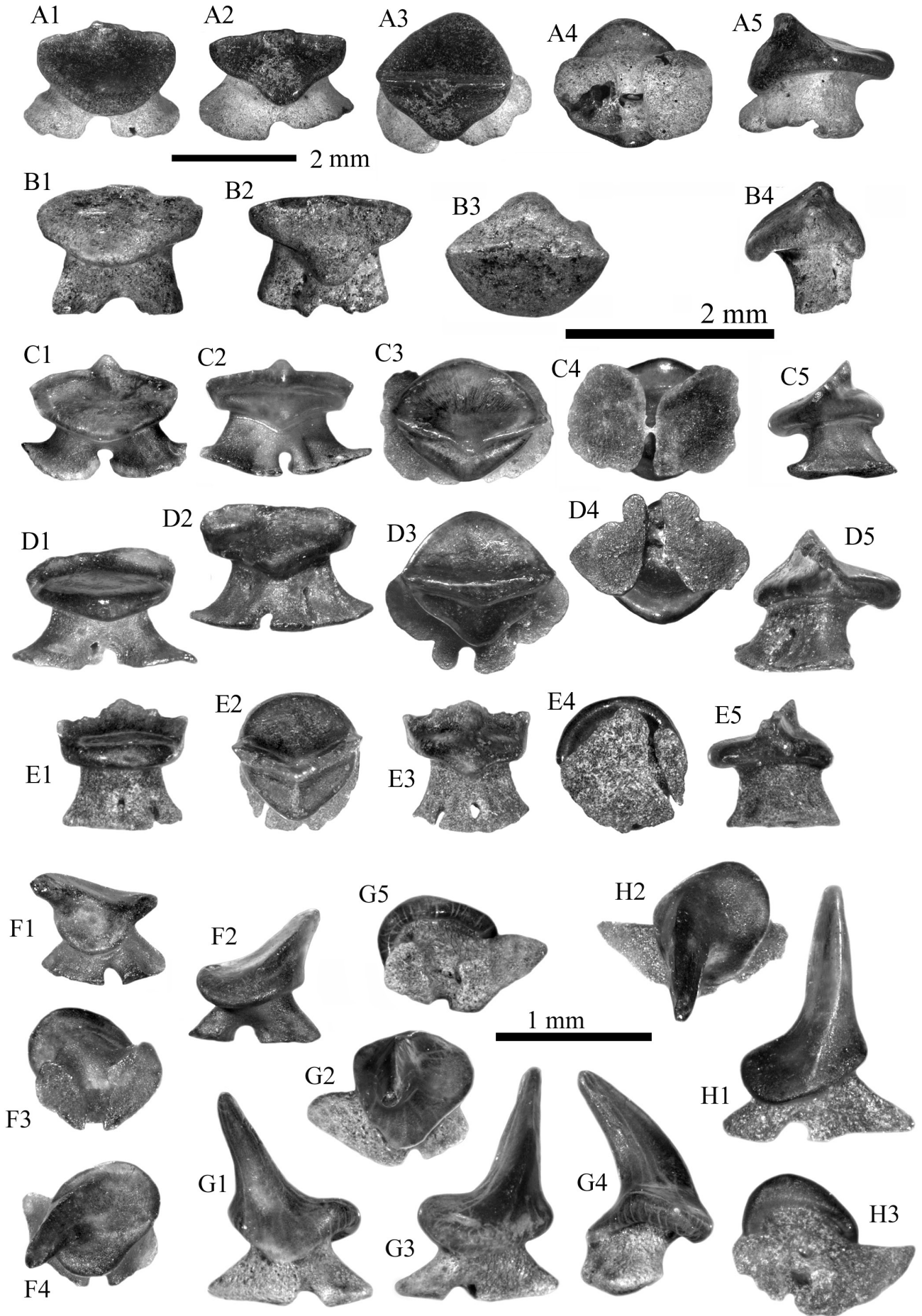
“*Raja*” *holsatica* Reinecke, Von der Hocht & Gürs, 2008

(Fig. 7)

v 2005 *Raja* sp. 3 - Reinecke *et al.*, p. 67, pl. 57, figs. 7-8; pl. 58, figs. 1-2.

v* 2008 *Raja holsatica* sp. nov., Reinecke *et al.*, p. 19 and 32, pl. 8.

Figure 5. A-E, *Dipturus casieri* (Steurbaut & Herman, 1978) new comb., teeth of female morph, Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany, The upper 2 mm scale bar refers to Fig. A, and the lower right to Figs. B-E. **A**, anterolateral tooth, H = 1.7 mm, W = 2.5 mm, L = 2.1 mm, A1 labial view, A2 lingual view, A3 occlusal view, A4 basal view, A5 profile view, SMF P 9830. **B**, anterolateral tooth, H = 1.2 mm, W = 1.6 mm, L = 1.2 mm, B1 labial view, B2 lingual view, B3 occlusal view, B4 profile view, SMF P 9831. **C**, anterolateral tooth, H = 1.1 mm, W = 1.6 mm, L = 1.2 mm, C1 labial view, C2 lingual view, C3 occlusal view, C4 basal view, C5 profile view, SMF P 9832. **D**, anterolateral tooth, H = 1.2 mm, W = 1.8 mm, L = 1.3 mm, D1 labial view, D2 lingual view, D3 occlusal view, D4 basal view, D5 profile view, SMF P 9833. **E**, ?lateroposterior tooth, H = 1.3 mm, W = 1.3 mm, L = 1.2 mm, E1 labial view, E2 occlusal view, E3 lingual view, E4 basal view, E5 profile view, SMF P 9834. **F-H, *Sympterygia*** sp., teeth of male morph, Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. 1 mm scale bar. **F**, lateral tooth, H = 1.2 mm, W = 0.8 mm, L = 1.1 mm, F1 lingual view, F2 labial view, F3 basal view, F4 occlusal view, SMF P 9835. **G**, anterolateral tooth, H = 1.4 mm, W = 0.8 mm, L = 0.8 mm, G1 lingual view, G2 occlusal view, G3 labial view, G4 profile view, G5 basal view, SMF P 9836. **H**, anterolateral tooth, H = 1.7 mm, W = 0.9 mm, L = 0.9 mm, H1 labial view, H2 occlusal view, H3 basal view, SMF P 9837.



v 2008 *Raja holsatica* Reinecke *et al.*, 2008 - Haye *et al.*, p. 75, text-fig. 9, pl. 9, fig. 3.

Material. 73 teeth.

Measurements (n = 25):

height: 0.8 – 2.1 mm (average 1.2 mm)

width*: 1.0 – 2.7 mm (average 1.6 mm)

length*: 1.0 – 2.6 mm (average 1.6 mm)

* mesio-distal (width) and labio-lingual (length) diameter of the crown basis.

Remarks

This species is characterized by low-crowned teeth that reveal moderate gradient monognathic heterodonty, but apparently do not indicate dignathic, ontogenetic, and/or sexual heterodonty (for description of the type material see Reinecke *et al.*, 2008: 32). The characteristics and dimensions of teeth from the Sülstorf Beds are undistinguishable from the sample recovered from the type deposits of “*Raja*” *holsatica*, the Vierlande Finesands (Aquitanian to early Burdigalian) of northern Germany, where “*R.*” *holsatica* represents more than 50% of the batoid teeth (Reinecke, 2013: table 1).

From the Chattian to early Middle Miocene teeth of “*Raja*” *holsatica* have retained almost constant morphological characters. These are the globular crown with the convex labial crown face (e.g. Figs. 7A4, 7B4, 7D5), the angular to smoothly convex curvature of the labial visor in profile and basal views (Figs. 7A4, 7B4), and the low transverse crest lacking cutting edges (Figs. 7A4, 7C4). Only anterior teeth display a sharper and higher transverse crest (Fig. 7D5). Teeth with apron-like protuberance of the labial visor (Fig. 7E2) are very rarely encountered. In all teeth except those from anterior files the crown height is lower than the crown width and length (labio-lingual diameter). The labial face and transverse crest of many specimens is flattened by wear (Fig. 7B2) which indicates

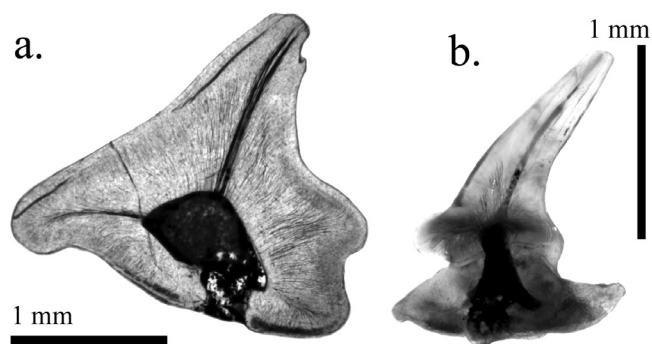


Figure 6 a. axially cut, 60–63 μm thin section of a tooth of *Dipturus casieri* (Steurbaut & Herman, 1978) new comb., and b. male tooth of *Atlantoraja ceciliae* (Steurbaut & Herman, 1978) new comb., submerged in anise oil. Both specimens are photographed in transmitted light. The *casieri* tooth has an apico-basally low pulp cavity, which opens basally to the nutrient groove. Vascular vessels (dark strings) extend from the pulp cavity into the cusp and the labial crown region. The *ceciliae* tooth shows an elongate pulp cavity with extensions to the root lobes and the lower cusp. A vascular vessel extends into the apical cusp region. Dark and bright fillings in both teeth are composed of iron oxyhydroxide and quartz grains, respectively. Specimens are from the Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany.

preference for a hard-shelled diet like crustaceans, small molluscs, and other invertebrates with calcareous exoskeleton.

Allocation of this species to the genus *Raja* Linné, 1758 was provisional (Reinecke *et al.*, 2008: 20) and its generic affiliation still remains unresolved. Extant species of *Raja* display a marked sexual heterodonty with variably high, cuspidate crowns in male dentitions and lower crowns with distinct transverse crest in female dentitions, as established in the type species *Raja clavata* Linné, 1758 and other species, e.g. *Raja montagui* Fowler, 1910 (Herman *et al.*, 1995; and own collection). It could be supposed that low-crowned (female) *holsatica* teeth in the batoid assemblage of the Sülstorf Beds are related to high-crowned (male) teeth of *Raja thiedei* sp. nov. (see below). This hypothesis, however, can be rejected, because the male morph of *Raja thiedei* sp. nov. does not occur in batoid tooth assemblages of the Vierlande Finesands (Aquitanian) and of late Burdigalian and Langhian deposits (see below), in which the low-crowned teeth of “*Raja*” *holsatica* are much more frequent than in the Sülstorf Beds.

“*Raja*” *holsatica* is unknown in the Rupelian and earliest Chattian of the NSB and uncommon in the Sülstorf Beds, but commonly occurs from the late Chattian (Haye *et al.*, 2008) to the Langhian (Miste Bed, Aalten Member; Antwerpen Sand Member, Berchem Formation; Bislich Beds; Reinecke & Wienrich, 2009; Bor *et al.*, 2012).

Genus *Raja* Linné, 1758

Raja thiedei sp. nov.

(Fig. 8)

v 2001 *Raja ceciliae* Steurbaut & Herman, 1978 - Moths, p. 7, pl. 4, fig. 4.

v 2005 *Raja* sp. 1 - Reinecke *et al.*, p. 66, pl. 53, figs. 1, 3.

v 2008 *Raja* sp. 1 - Haye *et al.*, p. 76, pl. 9, fig. 4.

Derivation of name. named after Karina and Nils Thiede from Parchim, Germany, who provided a large part of rock samples for this study.

Holotype. Senckenberg Research Institute and Natural History Museum, SMF P 9845 (Fig. 8C).

Paratypes.

1. SMF P 9843, Fig. 8A.
2. SMF P 9844, Fig. 8B.
3. SMF P 9846, Fig. 8D.
4. SMF P 9847, Fig. 8E.
5. SMF P 9848, Fig. 8F.

Material. 59 teeth.

Measurements (mm):

	<u>height</u>	<u>width*</u>
SMF P 9845 holotype	2.0	1.5
SMF P 9843 paratype 1	1.9	1.3

	<u>height</u>	<u>width*</u>
SMF P 9844 paratype 2	2.0	1.3
SMF P 9846 paratype 3	1.9	1.3
SMF P 9847 paratype 4	1.5	1.1
SMF P 9848 paratype 5	0.9	0.8

width*: 0.8 – 1.5 mm (average 1.2 mm)
 length*: 0.8 – 1.6 mm (average 1.2 mm)
 * mesio-distal (width) and labio-lingual (length) diameter of the crown basis.

Description

The description of this species is based on specimens that display the male morph. These are teeth with a variably high,

height: 0.9 – 2.2 mm (average 1.7 mm, n = 25)

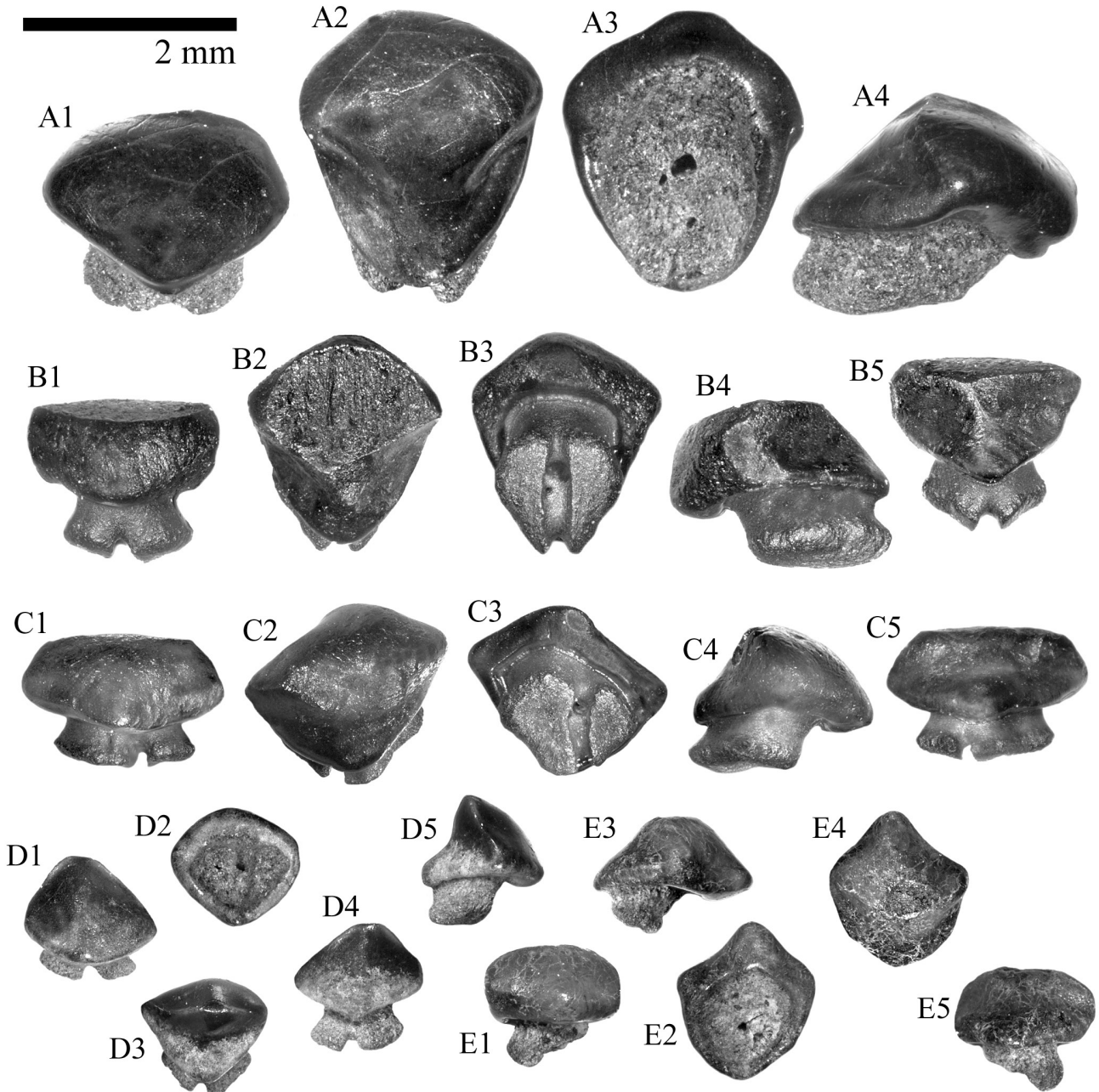


Figure 7. “*Raja*” *holsatica* Reinecke, Von der Hocht & Gürs, 2008, Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. **A**, anterolateral tooth, H = 1.8 mm, W = 2.3 mm, L = 2.6 mm, A1 labial view, A2 occlusal view, A3 basal view, A4 profile view, SMF P 9838. **B**, anterolateral tooth, H = 1.5 mm, W = 1.9 mm, L = 1.9 mm, B1 labial view, B2 occlusal view, B3 basal view, B4 profile view, B5 lingual view, SMF P 9839. **C**, anterolateral tooth, H = 1.3 mm, W = 1.9 mm, L = 1.6 mm, C1 labial view, C2 occlusal view, C3 basal view, C4 profile view, C5 lingual view, SMF P 9840. **D**, anterior tooth, H = 1.3 mm, W = 1.2 mm, L = 1.2 mm, D1 labial view, D2 basal view, D3 occlusal view, D4 lingual view, D5 profile view, SMF P 9841. **E**, anterolateral tooth, H = 1.1 mm, W = 1.3 mm, L = 1.5 mm, E1 labial view, E2 basal view, E3 profile view, E4 occlusal view, E5 lingual view, SMF P 9842.

pointed cusp. Anterolateral teeth have a slender cusp resting on a circular or elliptical crown basis (Figs. 8A-8D). The cusp steadily increases in width from the sharp apex to near the crown basis. It is upright or slightly inclined distally and always curved in lingual direction. The crown faces are smooth. Weak cutting edges, that are displaced to the marginolingual region of the cusp, extend from the apex to the half cusp length and never reach the lateral basal crown extensions. A labial keel is absent. In labial and profile view, the crown basis has the shape of a warped disk. It possesses subhorizontal extensions on mesial and distal sides, and a basally declining labial face with a smoothly convex visor (lacking an apron). The lingual crown basis shows a broad, flattened uvula. The lateral and anterior margins of the crown basis are much wider than the root stem and strongly overhang the anterolateral root faces. Lateroposterior teeth (Figs. 8E, 8F) show a significant crown and root asymmetry. The cusp is lower, displaced in distal direction, and more distally and lingually inclined than the cusp in anterolateral teeth.

The height of the root is less than one third of the total height. It is lingually displaced with respect to the crown axis (Figs. 8A5, 8B5, 8C4, in profile view). The wide, wedge-shaped nutrient groove divides the root into two short lobes which have flat basal faces and are mesio-distally widened in basal direction. 1-3 small foramina occur in the centre of the nutrient groove. Marginolingual foramina are absent.

The holotype (Fig. 8C), an anterolateral male tooth, and the five paratypes (Figs. 8A, 8B, 8D, 8E, 8F) reflect the range of morphological variation.

Differential diagnosis

Rajoid species reported from Oligocene deposits of Europe and North America are *Dipturus casieri* (Sturbaut & Herman, 1978), *Atlantoraja ceciliae* (Sturbaut & Herman, 1978), "*Raja*" *holsatica* Reinecke *et al.*, 2008, and *Raja mccollumi* Cicimurri & Knight, 2009. Teeth of *Raja thiedei* sp. nov. are much smaller and less massive than teeth of *D. casieri* (up to 3 mm high and 2.5 mm wide; Figs. 3B and 4) and have a relatively higher and narrower cusp. Different from *Raja thiedei* sp. nov., *D. casieri* has distinct lateral cutting edges that are extending to the mesial and distal crown margins. *R. thiedei* nov. sp. differs from male anterolateral teeth of *Atlantoraja ceciliae* by having a proportionally wider and labio-lingually shorter crown basis and a well rounded labial visor, by lacking a labial keel, and having root lobes that are commonly narrower than those of *Atlantoraja ceciliae* (compare Fig. 8 with Fig. 3A). Different from *Raja thiedei* sp. nov., teeth of "*Raja*" *holsatica* have a low, globular crown with a weak transverse crest, and commonly lack cutting edges (Fig. 7). Teeth of *R. thiedei* sp. nov. are quite similar in size and morphology to the male holotype of *Raja mccollumi* from the Chattian of South Carolina (Cicimurri & Knight, 2009: figs. 7C1-C4), but differ from it in having a basally wider, labio-lingually thinner cusp, shorter cutting edges which less closely approach to the crown basis, and a well rounded rather than slightly concave labial visor.

Raja thiedei nov. sp. can be well distinguished by its combined characters from the small number of valid rajoid species that have been described from Paleocene and Eocene deposits, i.e.

"*Raja*" *lousi* Cappetta, 1972 (Thanetian of Niger), *Raja harrisi* Ward, 1984 (Ypresian of SE England), *Raja* (*Malacoraja*, *Cruriraja*) *marandati* Adnet, 2006 (Lutetian of SW France), *Raja* (*Malacoraja*, *Cruriraja*) *michauxi* Adnet, 2006 (Ypresian/Lutetian of SW France), and *Smithraja forestensis* Herman, 1986 (Ypresian of Belgium). *R. thiedei* nov. sp. also differs significantly from the few, well defined rajoid species occurring in the Neogene, i.e. *Rostroraja olisiponensis* (Jonet, 1968), *Raja gentili* Joleaud, 1907-1912, and *Raja clavata* Linné, 1758. The latter three species have a wider cusp than *R. thiedei* nov. sp. (for *R. gentili*, see Ward & Bonavia, 2001: pl. 2, figs. c-e; for *R. clavata*, see Herman *et al.*, 1995: pl. 29-30), and additionally *Rostroraja olisiponensis* is characterized by a strong gradient monognathic heterodonty which is not reflected in the sample of *Raja thiedei* nov. sp. from the Sülstorf Beds.

Discussion

Dentitions of extant species of the genus *Raja* Linné, 1758 invariably exhibit sexual heterodonty (see above: Remarks on "*Raja*" *holsatica*), in which the female teeth are often difficult or sometimes impossible to distinguish between different species. Correspondingly, low-crowned teeth of female individuals, referable to *R. thiedei* sp. nov., should be also present in the tooth assemblage of the Sülstorf Beds. Indeed, it includes a large number of low-crowned, morphologically similar rajoid teeth in the 0.8-1.5 mm width range which may derive from female dentitions of different taxa (see above: Remarks and Discussion on *Atlantoraja ceciliae*). Altogether, they are characterized by a sharp transverse crest (partly equipped with a low, pointed cusp); a shallow labial crown face that is larger than the lingual face and lacks a labial keel; absence of crown ornamentation; a low root with narrow nutrient groove; and root lobes that are commonly not wider than the crown base; Reinecke *et al.*, 2005: pl. 54).

Although rajoid teeth were often described in open nomenclature, there are only a few reports from Oligocene deposits: Müller (1999: figs. 18-7 to 10) illustrates teeth of *Raja* sp. 1 from the Late Oligocene Ashley and Old Church Formations, North Carolina and Virginia, USA, of which the male morph has a thicker, more robust cusp and narrower heels than corresponding teeth of *R. thiedei* nov. sp. Specimens similar to Müllers *Raja* sp. 1 were documented by Cicimurri & Knight (2009: fig. 7a: *Raja* sp.) also from the Chattian Chandler Bridge Formation, South Carolina. Moths (2001: pl. 4, fig. 4) denoted a millimetre-sized tooth from the Rupel Formation at Malliß, Mecklenburg, north-eastern Germany, as "*Raja ceciliae* Steurbaut & Herman, 1978". The specimen, however, lacks a labial keel and has a rather wide crown base. It may be identified as *Raja thiedei* nov. sp. *R. thiedei* nov. sp. is present also in the Winterswijk Member of the Rupel Formation, late Rupelian, at the clay pits "De Vlijt", Winterswijk, The Netherlands (Reinecke, unpublished).

In addition to the Sülstorf Beds and the Rupel Formation, *R. thiedei* nov. sp. rarely occurs in the Chattian Silt, latest Chattian, at Johannistal, Schleswig-Holstein, northern Germany (Haye *et al.*, 2008: pl. 9, fig. 4), but could not be found in Early to Middle Miocene deposits of northern Germany and The Netherlands in spite of extensive bulk-sampling for microteeth.

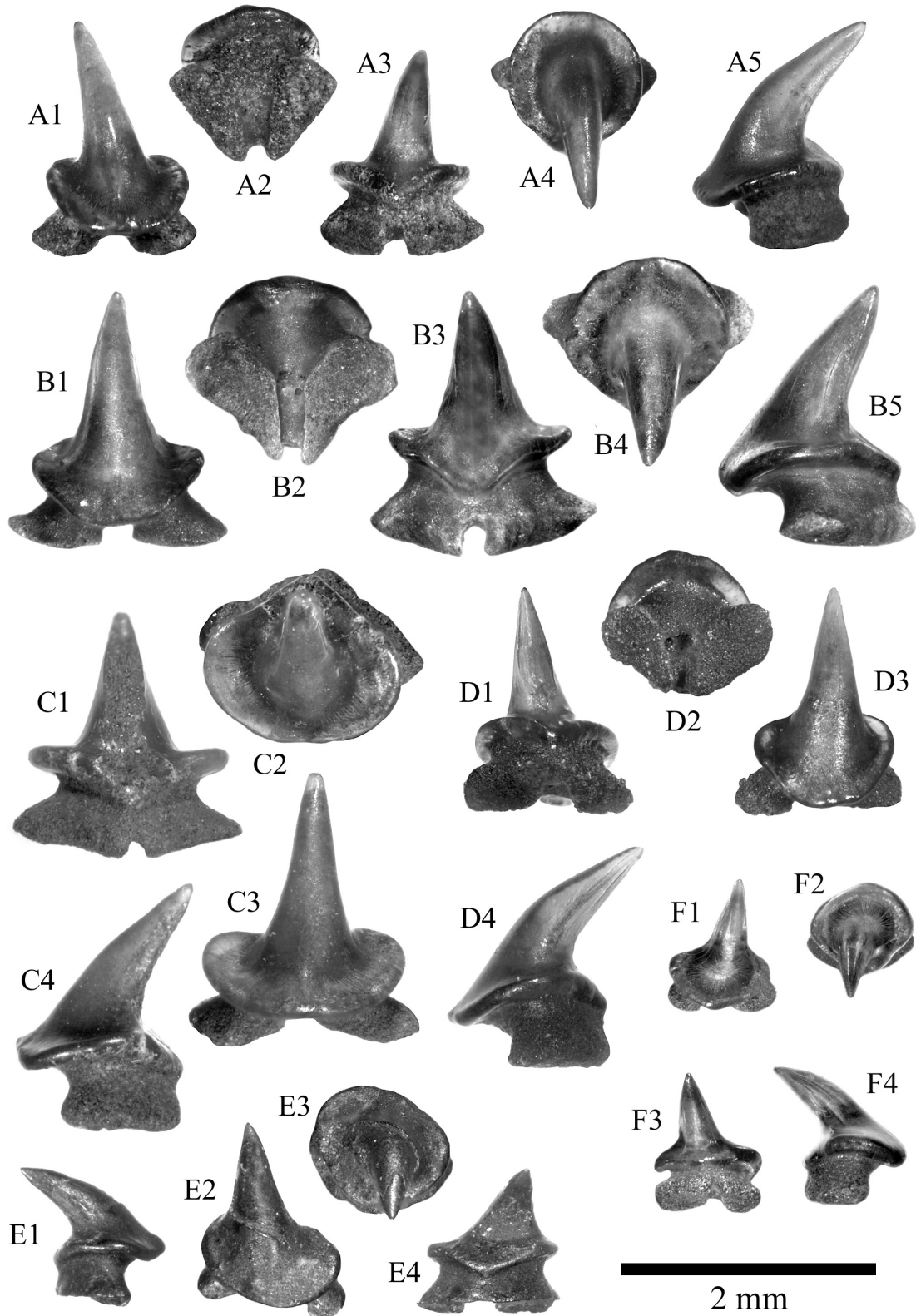


Figure 8. *Raja thiedei* sp. nov., Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. **A.** anterolateral tooth, H = 1.9 mm, W = 1.3 mm, L = 1.2 mm, A1 labial view, A2 basal view, A3 lingual view, A4 occlusal view, A5 profile view, SMF P 9843, paratype 1. **B.** anterolateral tooth, H = 2.0 mm, W = 1.3 mm, L = 1.4 mm, B1 labial view, B2 basal view, B3 lingual view, B4 occlusal view, B5 profile view, SMF P 9844, paratype 2. **C.** anterolateral tooth, H = 2.0 mm, W = 1.5 mm, L = 1.3 mm, C1 lingual view, C2 occlusal view, C3 profile view, C4 labial view, SMF P 9845, holotype. **D.** anterolateral tooth, H = 1.9 mm, W = 1.3 mm, L = 1.1 mm, D1 lingual view, D2 basal view, D3 labial view, D4 profile view, SMF P 9846, paratype 3. **E.** lateroposterior tooth, H = 1.5 mm, W = 1.1 mm, L = 0.9 mm, E1 profile view, E2 labial view, E3 occlusal view, E4 lingual view, SMF P 9847, paratype 4. **F.** lateroposterior tooth, H = 0.9 mm, W = 0.8 mm, L = 0.7 mm, F1 labial view, F2 occlusal view, F3 lingual view, F4 profile view, SMF P 9848, paratype 5.

Genus *Oligoraja* gen. nov.

Type species. *Oligoraja pristina* gen. nov., sp. nov.

Derivation of name. Referring to the occurrence of this rajoid in the Oligocene.

Diagnosis of genus

The following characters are collectively specific of the genus:

- anterior and lateral teeth less than 1.5 mm high and wide; crown faces smooth; labial keel lacking; holaulacorhize root, typically up to 1/2 of the total tooth height; root lobes as wide or wider than basal lateral crown margins; nutrient groove typically wedge-shaped in basal view.

- anterior teeth with compact, lingually inclined, triangular cusp; short, laterolingually displaced cutting edges; and mesio-distally and labio-lingually widened crown basis; labial visor bulging; crown tip sharp and pointed in very anterior teeth, and blunter (i.e. mesio-distally widened) in anterolateral teeth.

- lateral teeth with symmetrical crown; low to moderately high cusp, never displaced or inclined distally; and well developed heels. Apex of cusp well rounded, showing a smoothly convex outline in labial/lingual view; transverse crest often indistinct, slightly displaced lingually; cutting edges absent on crown heels.

Oligoraja pristina sp. nov.

(Figs. 9 and 10)

v 2005 *Raja* sp. 2 - Reinecke *et al.*, p. 67, pl. 57, fig. 6.

Derivation of name. after the Latin word “*pristinus/-a*” = former, early.

Holotype. Senckenberg Research Institute and Natural History Museum, SMF P 9849 (Fig. 9A).

Paratypes.

1. SMF P 9850, Fig. 9B
2. SMF P 9851, Fig. 9C
3. SMF P 9852, Fig. 9D
4. SMF P 9853, Fig. 9E
5. SMF P 9854, Fig. 9F
6. SMF P 9855, Fig. 10A
7. SMF P 9856, Fig. 10B
8. SMF P 9857, Fig. 10C
9. SMF P 9858, Fig. 10D
10. SMF P 9859, Fig. 10E

Material. 190 teeth.

Measurements (mm):

	<u>height</u>	<u>width*</u>	<u>length*</u>
SMF P 9849 holotype	0.9	1.0	1.1
SMF P 9850 paratype 1	1.0	1.0	1.0
SMF P 9851 paratype 2	1.1	1.2	1.1

	<u>height</u>	<u>width*</u>	<u>length*</u>
SMF P 9852 paratype 3	0.8	1.0	0.8
SMF P 9853 paratype 4	0.8	0.8	0.7
SMF P 9854 paratype 5	0.7	0.7	0.8
SMF P 9855 paratype 6	0.9	1.3	1.1
SMF P 9856 paratype 7	1.0	1.2	1.1
SMF P 9857 paratype 8	0.8	1.3	1.0
SMF P 9858 paratype 9	0.9	1.3	0.9
SMF P 9859 paratype 10	1.0	1.2	1.3

higher-crowned anterior/male teeth (n = 12)

height: 0.7 – 1.2 mm (average 1.0 mm)

width*: 0.7 – 1.2 mm (average 0.9 mm)

length*: 0.7 – 1.1 mm (average 0.9 mm)

lower-crowned lateral male/female teeth (n = 24)

height: 0.7 – 1.1 mm (average 0.9 mm)

width*: 0.8 – 1.4 mm (average 1.1 mm)

length*: 0.7 – 1.3 mm (average 1.0 mm)

* mesio-distal (width) and labio-lingual (length) diameter of the crown basis.

Description

This batoid species has the smallest teeth extracted from the Sülstorf Beds, as their maximum diameter is always less than 1.4 mm. Our material can be divided into two different morphological groups. About two dozen specimens, displaying minor dimensional variation, show a cuspidate crown, set on a stocky, low root (Figs. 9A-D). The bulk of the material has lower crowns that are almost equidimensional (Fig. 10) and shows a continuous, though minor variation of height-to-width and width-to-length ratios which may be indicative of gradient heterodonty. A few smaller specimens with apically rounded, rather low cusps are intermediate between the two morphs (Figs. 9E-F). While the cuspidate, higher-crowned teeth likely represent anterior jaw positions of male individuals, the lower-crowned teeth are possibly from lateral files of male dentitions and from female dentitions. The smallest, cuspidate specimens, measuring less than 1 mm in maximum diameter (Figs. 9E-F), may be considered as anterior teeth of juvenile/subadult males.

The cuspidate teeth have a symmetrical crown with a strong, lingually inclined cusp, which merges into a laterally expanded, elliptical crown basis with lobate outline in occlusal view (see Figs. 9A5, 9B5, 9C5, 9D5). Weak cutting edges, displaced to the lingual part of the cusp, extend from the apex to half of the cusp length. A labial cutting edge (labial keel) is not present. In profile view, the labial outline of the cusp is straight (Fig. 9B4), or smoothly convex (Figs. 9C4, 9D3) or slightly kinked (Fig. 9A4). The crown tip is sometimes shortened by wear (Figs. 9B4, 5). The lingual visor has a smoothly convex outline. In the holotype, the labial visor forms a prominent bulge which markedly overhangs the root (Figs. 9A2, 4, 5). The labial bulge is less prominent in other, probably more laterally placed teeth (Figs. 9B5, 9C5, 9D5). The holaulacorhize root is always lower than the crown and branches into wide root lobes which in basal

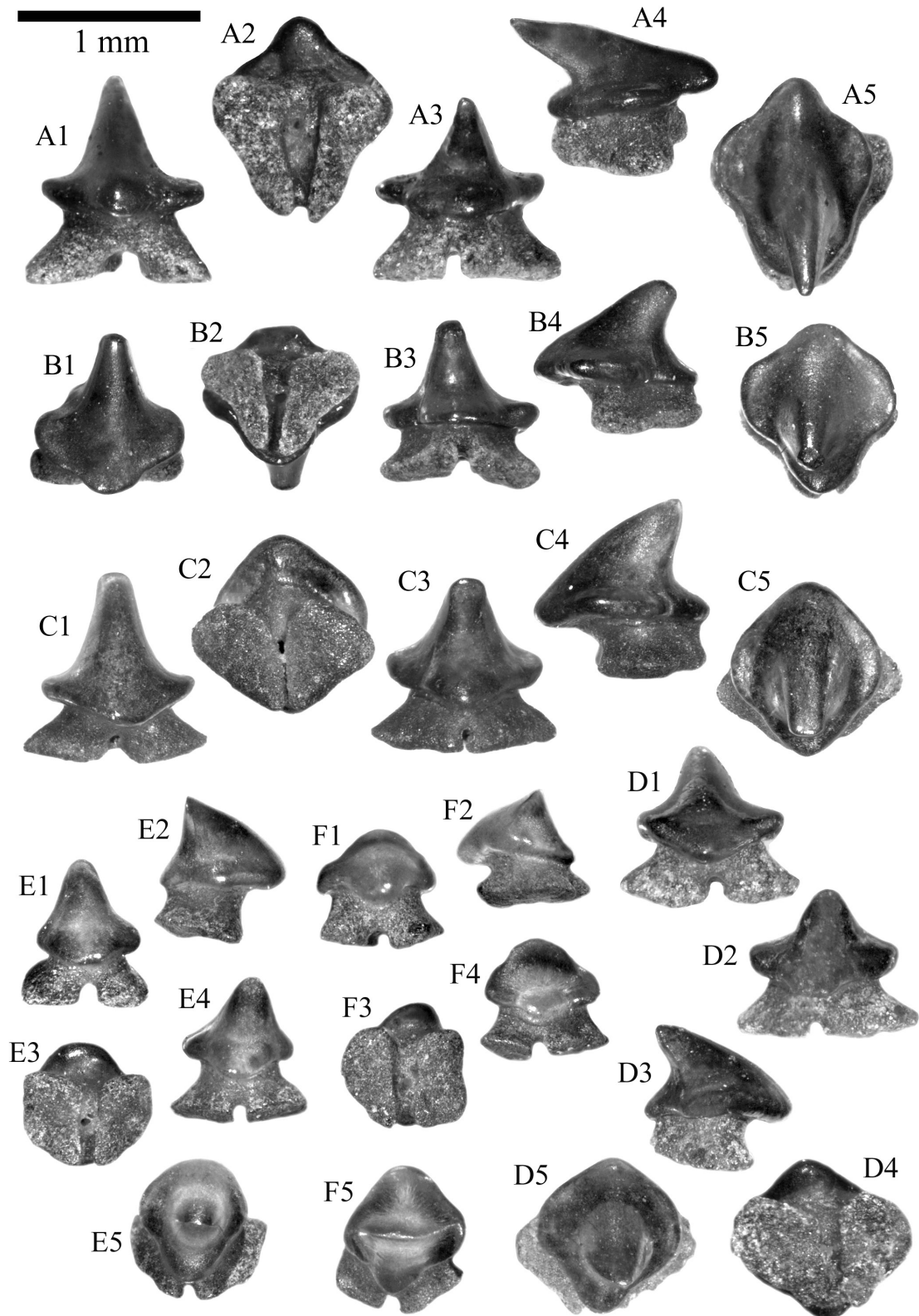


Figure 9. *Oligoraja pristina* gen. et sp. nov., Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. **A**, anterior tooth of a male, H = 0.9 mm, W = 1.0 mm, L = 1.1 mm, A1 labial view, A2 basal view, A3 lingual view, A4 profile view, A5 occlusal view, SMF P 9849, holotype. **B**, anterior tooth of a male, H = 0.98 mm, W = 0.96 mm, L = 1.04 mm, B1 labial view, B2 basal view, B3 lingual view, B4 profile view, B5 occlusal view, SMF P 9850, paratype 1. **C**, anterior tooth of a male, H = 1.11 mm, W = 1.16 mm, L = 1.12 mm, C1 labial view, C2 basal view, C3 lingual view, C4 profile view, C5 occlusal view, SMF P 9851, paratype 2. **D**, anterior tooth of a male, H = 0.8 mm, W = 1.0 mm, L = 0.8 mm, D1 labial view, D2 lingual view, D3 profile view, D4 basal view, D5 occlusal view, SMF P 9852, paratype 3. **E**, anterior tooth of ? juvenile male, H = 0.8 mm, W = 0.8 mm, L = 0.7 mm, E1 labial view, E2 profile view, E3 basal view, E4 lingual view, E5 occlusal view, SMF P 9853, paratype 4. **F**, anterior tooth of ? juvenile male, H = 0.7 mm, W = 0.7 mm, L = 0.8 mm, F1 labial view, F2 profile view, F3 basal view, F4 lingual view, F5 occlusal view, SMF P 9854, paratype 5.

direction diverge more laterally than lingually (e.g. Figs. 9A3, 4). One or two small foramina open into the wedge-shaped nutrient groove. Marginolingual foramina are not present.

The submillimetric teeth with cuspidate to globular crown morphology (Figs. 9E, F) have a variably strong labial bulge, a rounded crown apex in labial/lingual view, and a transverse crest with short mesial and distal cutting edges.

Lower-crowned teeth (Figs. 10A-E) have a lateral-symmetrical crown with a transverse crest that is slightly shifted in

lingual direction. In labial/lingual view the transverse crest forms a well rounded cusp which merges into oblique to sub-horizontal heels. In occlusal view, the crown basis shows a lobate outline which is similar to that of cuspidate teeth (see above). The lobate shape is enhanced in teeth with the labial visor forming a distinct bulge (Figs. 10A4, 10C4, 10E4) and the lingual visor a moderate uvula (Figs. 10B4, 10C4). The crown faces are always smooth. The axial regions of the labial and lingual crown face are convex, whereas the lateral regions are flat to slightly concave. Cutting edges are missing in several

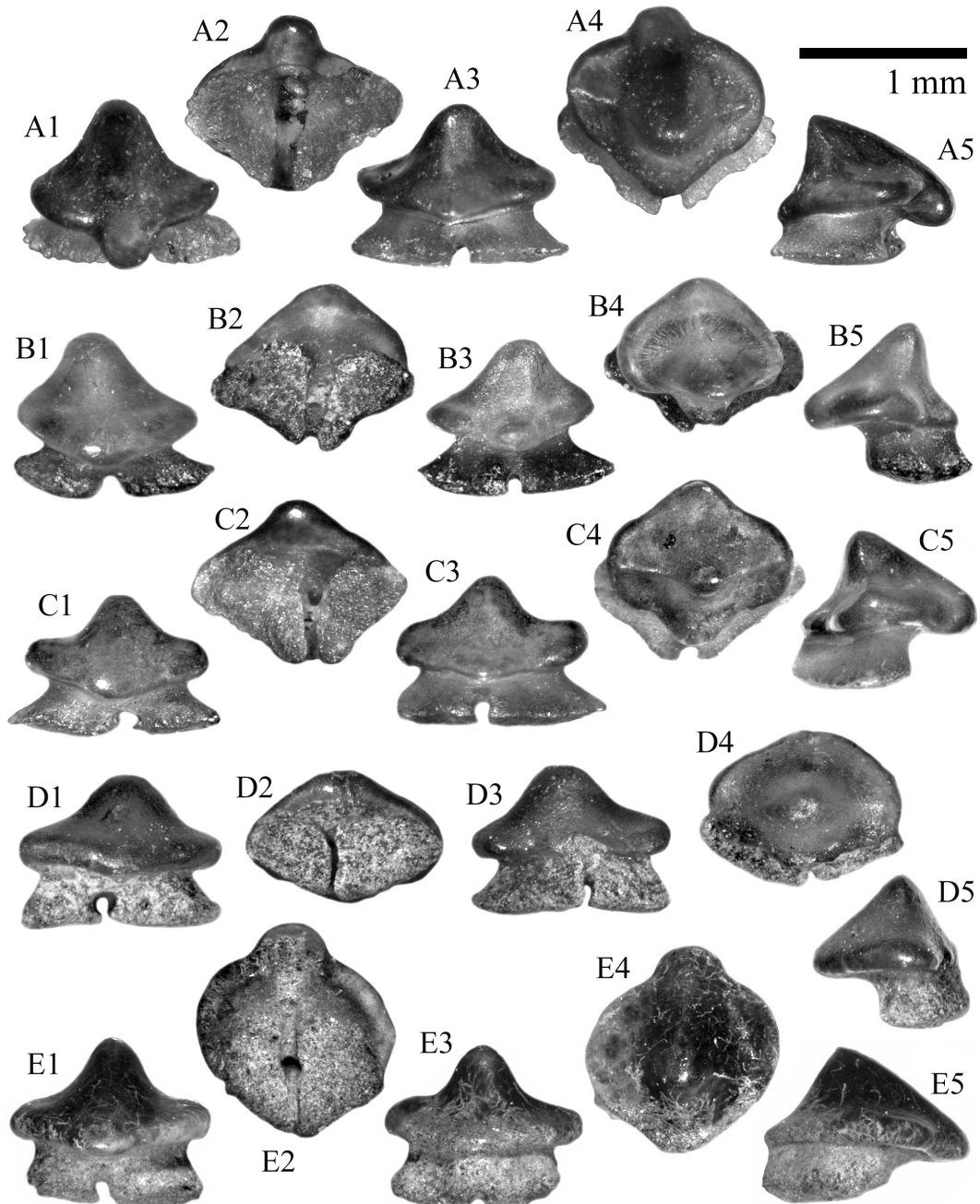


Figure 10. *Oligoraja pristina* gen. et sp. nov., lateral teeth, Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. **A**, lateral tooth, H = 0.9 mm, W = 1.3 mm, L = 1.1 mm, A1 labial view, A2 basal view, A3 lingual view, A4 occlusal view, A5 profile view, SMF P 9855, paratype 6. **B**, lateral tooth, H = 1.0 mm, W = 1.2 mm, L = 1.1 mm, B1 labial view, B2 basal view, B3 lingual view, B4 occlusal view, B5 profile view, SMF P 9856, paratype 7. **C**, lateral tooth, H = 0.8 mm, W = 1.3 mm, L = 1.0 mm, C1 labial view, C2 basal view, C3 lingual view, C4 occlusal view, C5 profile view, SMF P 9857, paratype 8. **D**, lateral tooth, H = 0.9 mm, W = 1.3 mm, L = 0.9 mm, D1 labial view, D2 basal view, D3 lingual view, D4 occlusal view, D5 profile view, SMF P 9858, paratype 9. **E**, lateral tooth, H = 1.0 mm, W = 1.2 mm, L = 1.3 mm, E1 labial view, E2 basal view, E3 lingual view, E4 occlusal view, E5 profile view, SMF P 9859, paratype 10.

teeth (Figs. 10D, 10E). If short, faint cutting edges are present in the apical region, they do not extend to the lateral heels. In profile view, the outline of the labial crown face is straight to convex, and the outline of the lingual face is variably concave (Figs. 10A5, 10C5, 10D5).

Discussion

Herman *et al.* (1994, 1995, 1996) extensively documented the dental morphology of extant rajoid genera and species in the families Arynchobatidae Fowler, 1934; Rajidae Blainville, 1816; and Anacanthobatidae Von Bonde & Swart, 1924. Their iconography covers all genera listed by Compagno (2005), except for some species representing undescribed genus-group taxa nominally retained in *Raja* (Compagno, 2005: 537). At least one (and up to three) species in each genus were characterized by representative teeth from different jaw positions in adult male and/or female dentitions. If available, Herman *et al.* (1994, 1995, 1996) preferably documented the type species.

Comparing the dental character complex of *Oligoraja* gen. nov. we find no resemblance with anyone of the illustrated extant species/genera. Among them the monotypic genus *Rostroraja* (including the white skate *Rostroraja alba* (Lacépède, 1803)) and several species of the genus *Leucoraja* Malm, 1877 (e.g. *Leucoraja naevus* (Müller & Henle, 1841); *Leucoraja circularis* (Couch, 1838); *Leucoraja fullonica* (Linné, 1758), coll. Reinecke) have anterolateral teeth which may develop an apron. Most other dental characteristics of these taxa, however, are different from those of *Oligoraja* gen. nov. For example, teeth of adult individuals of *Rostroraja alba* and *Leucoraja* spp. have high, sometimes very slender cusps in anterior to lateral files. Mesial and distal cutting edges are weak or well developed and may reach, in contrast to *Oligoraja* gen. nov., the lateral, basal crown extensions (e.g. in *Rostroraja alba*, *Leucoraja naevus*). Teeth with a well-rounded crown apex, typical of *Oligoraja pristina* gen. et sp. nov., are apparently not observed in *Rostroraja* and *Leucoraja*. Hence, it is reasonable to define a new genus and species for the present batoid teeth.

Oligoraja pristina gen. et sp. nov. is so far unknown from contemporaneous Chattian deposits in the southern NSB (e.g. Grafenberg Formation, Doberg Formation, Kassel Formation, Söllingen Formation), probably because their batoid assemblages have not been thoroughly investigated, except for the Grafenberg Formation (Von der Hocht, pers. communication 2014).

Differential diagnosis

Oligoraja pristina gen. nov. sp. nov. differs from all rajoid taxa hitherto described from Rupelian and Chattian deposits in the NSB and North Atlantic region by combinations of at least two dental characters. Anterior teeth of *O. pristina* gen. et sp. nov. have much lower, more stocky and upright cusps than anterolateral male teeth of *Atlantoraja ceciliae* (Steurbaut & Herman, 1978) new comb. (Fig. 3A). Low-crowned, lateral teeth of *O. pristina* gen. et sp. nov. develop symmetrical, rather smooth, convex crowns with a well-rounded apex and smooth heels, that are easily distinguishable from the sharp transverse crests with pointed, distally inclined cusp, commonly observed in female

teeth of *A. ceciliae*. Teeth of *O. pristina* gen. et sp. nov. are not only much smaller than those of *Dipturus casieri* (Steurbaut & Herman, 1978) new comb., but also lack sharp cutting edges and a sharp transverse crest. Low-crowned specimens of *O. pristina* gen. et sp. nov. have distinct crown heels and a cambered central cusp, which is different from the globular and commonly much flatter crowns of “*Raja*” *holsatica* Reinecke *et al.*, 2008. Anterior teeth of *O. pristina* gen. et sp. nov. differ from anterolateral teeth of *Raja thiedei* sp. nov. and *Raja mccollumi* Cicimurri & Knight, 2009 by a lower and basally wider cusp, a lobate crown basis, and presence of an apron.

A small number of rajoid species, based on isolated teeth, has been described from Paleocene and Eocene deposits (listed in the differential diagnosis of *Raja thiedei* sp. nov.), but none of these are morphologically similar with *O. pristina* gen. et sp. nov. The dimensionally much larger anterior teeth of the Miocene batoids *Rostroraja* aff. *olisiponensis* (Jonet, 1968) (late Burdigalian to Langhian of the NSB; Bor *et al.*, 2012: pls 39-40, text-fig. 14) and *Rostroraja olisiponensis* (Jonet, 1968) superficially resemble the high-crowned specimens of *Oligoraja pristina* gen. et sp. nov., but their lateral teeth differ from corresponding teeth of *O. pristina* gen. et sp. nov. by a broader crown with larger, flatter labial face and pointed apex and by the presence of distinct mesial and distal cutting edges on the heels (see Bor *et al.*, 2012: pl. 40, figs. 5-6, pl. 41, figs. 1-3).

Order TORPEDINIFORMES De Buen, 1926

Family TORPEDINIDAE Bonaparte, 1838

Genus *Torpedo* Houttuyn, 1764

Torpedo chattica sp. nov.

(Fig. 11)

v 2005 *Torpedo* sp. - Reinecke *et al.*, p. 68, pl. 50, figs. 4-5.

Derivation of name. named after the Chattian stage, Late Oligocene.

Holotype. Senckenberg Research Institute and Natural History Museum, SMF P 9866, Fig. 11G.

Paratypes.

1. SMF P 9860, Fig. 11A.
2. SMF P 9861, Fig. 11B.
3. SMF P 9862, Fig. 11C.
4. SMF P 9864, Fig. 11E.

Material. 9 teeth.

Measurements (mm):

	<u>height</u>	<u>width</u>
SMF P 9866 holotype	1.3	1.8
SMF P 9860 paratype 1	1.1	1.3
SMF P 9861 paratype 2	1.0	1.6
SMF P 9862 paratype 3	1.0	1.5
SMF P 9864 paratype 4	0.7	1.2

	<u>height</u>	<u>width</u>
SMF P 9863	1.0	1.7
SMF P 9865	0.9	1.4

Description

Nine torpedinid teeth, including the two specimens previously illustrated (Reinecke *et al.*, 2005), were recovered from the Sülstorf Beds. These form a morphologically homogeneous sample which can be distinguished from all fossil and extant species for which dental characters have been illustrated. The teeth show slight differences in the width-to-length ratio of the crown basis, the cusp height and inclination of the cusp. These can be interpreted as due to a slight gradient monognathic heterodonty.

One specimen (Fig. 11A) displays a noticeable crown asymmetry and rather high height-to-width ratio (1.1/1.3). It is tentatively referred to an anterior jaw position. Other specimens have a mesio-distally more elongate crown basis and are likely derived from anterolateral files (Figs. 11B-D, 11F-G), while the smallest and labio-lingually thinnest tooth, equipped with a low, hooked cusp (Fig. 11E), may represent a lateroposterior tooth.

In occlusal or basal view, the crown basis of most teeth is nearly twice as wide (mesio-distally) as long (labio-lingually), and has a broadly rectangular outline with well rounded lateroanterior and lateroposterior edges. The labial visor is straight or slightly flexuous in basal view (e.g. Figs. 11B5, 11C5, 11D4). In labial view, it shows a basally convex outline (Figs. 11B1, 11C1, 11D1, 11F1) or - more rarely - an almost straight outline (Figs. 11A1, 11E1). In profile view, the labial visor forms a narrow, convex bulge (apron) which markedly overhangs the root-crown junction. The axial region of the lingual crown basis shows a pronounced depression (in occlusal view), which divides the lingual crown basis into wide mesial and distal lobes and is placed just above the nutrient groove of the root. In two teeth the axial depression is more irregular in outline, resulting in differently large mesial and distal lobes of the lingual crown basis (Figs. 11D2, D4 and 11F2, F5).

The crown basis bears a moderately high, narrow cusp which is erect or distally inclined in labial view. Mesial and distal cutting edges extend from the apex (or the upper thirds of the cusp) onto the anterior region of the crown basis, but disappear before reaching the lateral crown edges. In labial view, the lateral cutting edges appear as a short, subhorizontal ridges which on one or either sides terminate in a low, broad cusplet or hump. The labial crown face is rather flat (in profile view), whereas the lingual crown face is convex at the cusp and flat to slightly concave at the basal crown lobes.

The holaulacorhize root is much lower than the crown and markedly displaced in lingual direction with respect to the vertical crown axis (e.g. Figs. 11A3, 11B3). The thin root lobes are curved in lingual direction and separated by a wide nutrient groove. One large foramen occurs in the nutrient groove.

The holotype (Fig. 11G) combines the typical dental characters described above, whereas the paratypes (Figs. 11A-C, E) are chosen to represent the range of morphological variation.

Differential diagnosis

In addition to the ca. 22 known extant species of the genus *Torpedo* (Compagno, 2005; Nelson, 2006; Froese & Pauly, 2014) a small number of fossil species has been described thus far (Cappetta, 2006, 2012). These are *Torpedo acarinata* Adnet, 2006 (middle Lutetian, Angoumé, Aquitaine Basin, SW France), *Torpedo pessanti* Adnet, 2006 (upper Ypresian/Lutetian, Saint Géours d'Auribat, Aquitaine Basin, SW France), *Torpedo dormaalensis* Smith, 1999 (Thanetian/Ypresian transition, Dormaal, Belgium), and *Torpedo egertoni* De Zigno, 1876 (Ypresian, Monte Bolca, Verona, Italy). The description of the latter species is based on an articulated specimen and lacks illustrations of the teeth.

T. chattica sp. nov. differs from the holotype of *T. acarinata* (Adnet, 2006: pl. 40, fig. 1) - among other characters - by the smaller labial and proportionally larger lingual crown face, the longer mesial and noticeable distal cutting edge, and the rectangular outline of the crown basis. Teeth of *T. chattica* sp. nov. can be distinguished from those of *T. pessanti* (Adnet, 2006: pl. 40, figs. 3-4) by the much lower cusp, by well rounded corners of the lateroanterior crown edges, by the commonly deeper axial depression at the lingual crown basis, and by the presence of low, broad cusplets at the marginal cutting edges. *Torpedo chattica* sp. nov. is comparable with the holotype of *T. dormaalensis* (Smith, 1999: pl. 1, fig. 6a-e), probably a lateral tooth, by its cusp height and outline of the crown basis as well as by the presence of mesial and distal cutting edges, but shows a much stronger curvature of the labial visor (in profile view) and higher, subhorizontal heels.

Cappetta (1988) and Herman *et al.* (2002) figured representative teeth of five extant species, i.e. *Torpedo torpedo* (Linné, 1758), *T. marmorata* Risso, 1810, *T. nobiliana* Bonaparte, 1835, *T. californica* Ayres, 1855, and *T. sinuspersici* Olfers, 1831. Teeth of *T. chattica* sp. nov. differ from those of *T. sinuspersici*, *T. californica*, and *T. nobiliana* by a lower cusp height and straighter shape of the labial visor (all three species), presence of lateral cutting edges (apparently not present in *T. californica*), a more angular outline of the lateroanterior corners of the crown basis (*T. californica*); and by smoothly declining lateral cutting edges (*T. nobiliana*). Occasionally, anterolateral teeth of *T. nobiliana* have - similar as in *T. chattica* sp. nov. - raised lateral heels with low, broad cusplets (Herman *et al.*, 2002: pls. 21-22). *T. chattica* sp. nov. is morphologically closer only to *T. torpedo* and *T. marmorata*, but in both species the cusp appears to be higher and the labial visor is commonly axially deepened in occlusal or basal views, which is not observed in teeth of *T. chattica* sp. nov. We are aware that due to an unknown extent of dental variability in some of the above species and the limited material basis of extant species available for this study some of our inferences may weaken.

Discussion

In addition to the above fossil species some isolated teeth of *Torpedo*, denoted in open nomenclature, are reported and illustrated from Middle/Late Eocene deposits of Egypt (Underwood *et al.*, 2011), from the Upper Marine Molasse, Burdigalian, of Switzerland (Bolliger *et al.*, 1995) and south-western Germany (Bracher, 2005), and from Zanclean

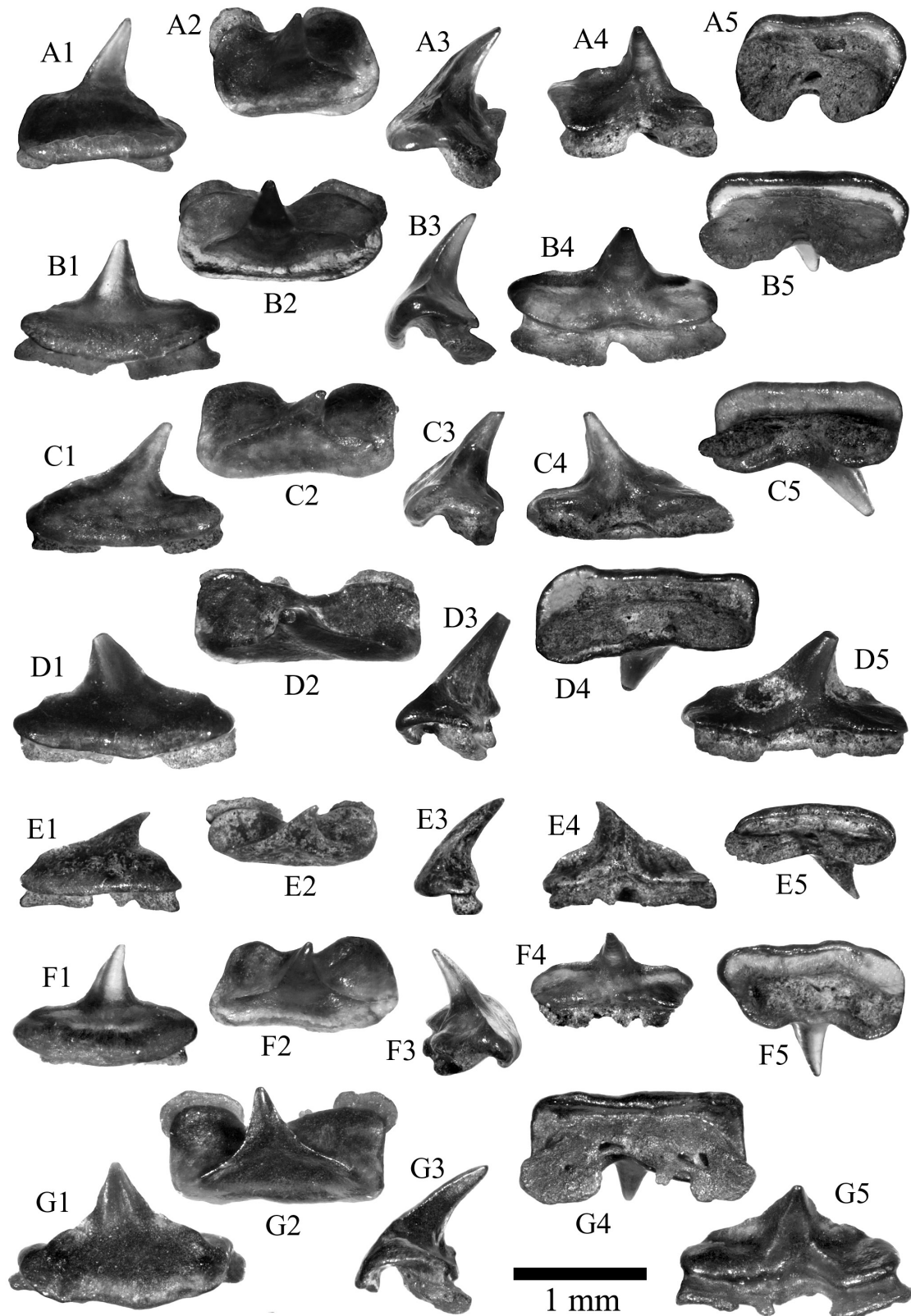


Figure 11. *Torpedo chattica* sp. nov., Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. **A.** anterior tooth, H = 1.1 mm, W = 1.3 mm, L = 0.9 mm, A1 labial view, A2 occlusal view, A3 profile view, A4 lingual view, A5 basal view, SMF P 9860, paratype 1. **B.** anterolateral tooth, H = 1.0 mm, W = 1.6 mm, L = 0.8 mm, B1 labial view, B2 occlusal view, B3 profile view, B4 lingual view, B5 basal view, SMF P 9861, paratype 2. **C.** anterolateral tooth, H = 1.0 mm, W = 1.5 mm, L = 0.8 mm, C1 labial view, C2 occlusal view, C3 profile view, C4 lingual view, C5 basal view, SMF P 9862, paratype 3. **D.** anterolateral tooth, H = 1.0 mm, W = 1.7 mm, L = 0.8 mm, D1 labial view, D2 occlusal view, D3 profile view, D4 basal view, D5 lingual view, SMF P 9863. **E.** lateroposterior tooth, H = 0.7 mm, W = 1.2 mm, L = 0.5 mm, E1 labial view, E2 occlusal view, E3 profile view, E4 lingual view, E5 basal view, SMF P 9864, paratype 4. **F.** anterolateral tooth, H = 0.9 mm, W = 1.4 mm, L = 0.8 mm, F1 labial view, F2 occlusal view, F3 profile view, F4 lingual view, F5 basal view, SMF P 9865. **G.** anterolateral tooth, H = 1.3 mm, W = 1.8 mm, L = 0.9 mm, G1 labial view, G2 occlusal view, G3 profile view, G4 basal view, G5 lingual view, SMF P 9866, holotype.

deposits at Puget-sur-Argens, SE France (Cappetta & Nolf, 1991). Although the variation of dental characters is commonly not obvious for these specimens, it appears that they are all morphologically different from *Torpedo chattica* sp. nov.

Torpedo chattica sp. nov. is the first torpedo ray reported from Oligocene deposits. It demonstrates the rare, but continuous presence of the genus *Torpedo* from the latest Paleocene/early Eocene (*T. dormaalensis*) and early/middle Eocene (*Torpedo acarinata*, *Torpedo pessanti*) to the Miocene and Pliocene (*Torpedo* sp., see above), especially in the Atlantic Ocean, Paratethys, Mediterranean, and NSB.

Present-day torpedo or electric rays (genera *Torpedo*, *Narcine*) occur in tropical to temperate waters on continental shelves. They are bottom dwellers and/or favour a benthopelagic habit. Some species may be present down to depths of more than 1000 m, but most, like *Torpedo chattica* sp. nov., live in shallow-marine environments on soft to coarse grounds (e.g. Stehmann & Bürkel, 1984; Miller & Loates, 1997; McEachran & De Carvalho, 2002; Heemstra & Heemstra, 2004; Kells & Carpenter, 2011).

Order MYLIOBATIFORMES Compagno, 1973

Family DASYATIDAE Jordan, 1888

Genus *Dasyatis* Rafinesque, 1810

***Dasyatis* cf. *rugosa* (Probst, 1877)**

(Fig. 12)

v* 1877 *Raja rugosa* n. sp., Probst, p. 76, pl. 1, figs. 5-7, ? 8, ? 9.

v 2005 *Dasyatis* (sensu lato) sp. - Reinecke *et al.*, p. 71, pl. 51.

v 2008 *Dasyatis rugosa* (Probst, 1877) - Reinecke *et al.*, p. 23, pl. 7, figs. 1-5, text-figs. 5c-d.

v 2008 *Dasyatis rugosa* (Probst, 1877) - Haye *et al.*, p. 78, pls 11-12.

Material. 37 teeth.

Measurements:

female morph (n = 16)

height: 1.8 – 3.0 mm (average 2.2 mm)

width*: 2.5 – 3.3 mm (average 2.9 mm)

length*: 2.0 – 3.2 mm (average 2.5 mm)

male morph (n = 8)

height: 1.7 – 2.8 mm (average 2.5 mm)

width*: 1.6 – 3.1 mm (average 2.7 mm)

length*: 1.7 – 2.8 mm (average 2.4 mm)

* mesio-distal (width) and labio-lingual (length) diameter of the crown basis.

Description

The tooth sample collected from the Sülstorf Beds comprises teeth of the male and female morphs which both show gradient monognathic heterodonty. In teeth of the female morph, the transverse crest divides the crown into similar-sized labial and

lingual faces. In occlusal view the transverse crest is distinctly arched in lingual direction. In profile view it is variably high and inconspicuous (Figs. 12C4, 12D3) or slightly bulging (Fig. 11F4). In some teeth the apical crown region is flattened by wear (Figs. 12B2, 12A2). If unworn, the top of the transverse crest bears coarse ridges and notches which extend to the apical region of the lingual crown face. The lower region of the labial crown face is convex in apico-basal and mesio-distal directions, whereas the apical region shows a transverse shallow depression. The labial crown face is ornamented with numerous pits of irregular shape and depth, while the concave lingual face is always smooth. The labial visor has a rounded, convex outline in occlusal/basal view. The lingual visor is commonly smoothly convex. A weak axial depression of the lingual visor is observed in a few low-crowned teeth probably derived from lateral files (Figs. 12E2, 12F1). The lateral edges of the crown basis meet the labial visor with an angle of 90-120 degrees. The basal labial face of the crown forms a moderately broad, convex rim which is always smooth (e.g. Figs. 12A3, 12C3, 12F3). The lingually displaced root is lower than the crown. It has narrow root lobes which are lingually directed (in profile view) and are slightly wider than the crown-root junction (in basal view). If unworn, their basal faces are almost flat (e.g. Figs. 12C3, 12E3, 12F3). The lobes are separated by a deep nutrient groove with one or two foramina occurring in central position.

A single, well preserved specimen of the male morph, illustrated in Fig. 12G, shows a high, triangular, apically worn cusp, almost straight lateral crown edges, and a strongly ornamented labial crown face with a narrow, deep axial depression.

Discussion

The present teeth add to the small number of morphologically similar teeth, that were reported in a previous study (Reinecke *et al.*, 2005: 71) as *Dasyatis* (sensu lato) sp., namely a single specimen from the Sülstorf Beds and ca. a dozen teeth (male and female morphs) from late Chattian deposits of the southern North Sea shelf (Ratzeburg Formation at Groß-Pampau, Schleswig-Holstein, and glauconitic calcarenites at Astrup, Lower Saxony). Morphologically indistinguishable teeth from the late Chattian Silts at Johannistal, northern Germany, and the Ratzeburg Formation were assigned by Haye *et al.* (2008: pls 11-12) to *Dasyatis rugosa* (Probst, 1877). Actually, all these teeth are closely comparable with the middle Burdigalian (Ottangian) type specimens of *D. rugosa* (compare with Probst, 1877: pl. 1, figs. 5-7 for the female morph; refigured by Reinecke *et al.*, 2011: text-fig. 36) with respect to tooth size and morphological details of the crown, e.g. shape and ornamentation of the labial depression, transverse crest, and labial visor, width and convexity of the basal labial crown face. Compared with Early to Middle Miocene teeth of *D. rugosa* (Probst, 1877; Reinecke *et al.*, 2011: pls 94-95; Bor *et al.*, 2012: pl. 47) the ornamentation of the labial crown face in the Chattian *rugosa*-type teeth tends to be coarser (more irregular wrinkles and deeper pits), but these differences are minor and do not justify the definition of a distinct species for the Chattian specimens.

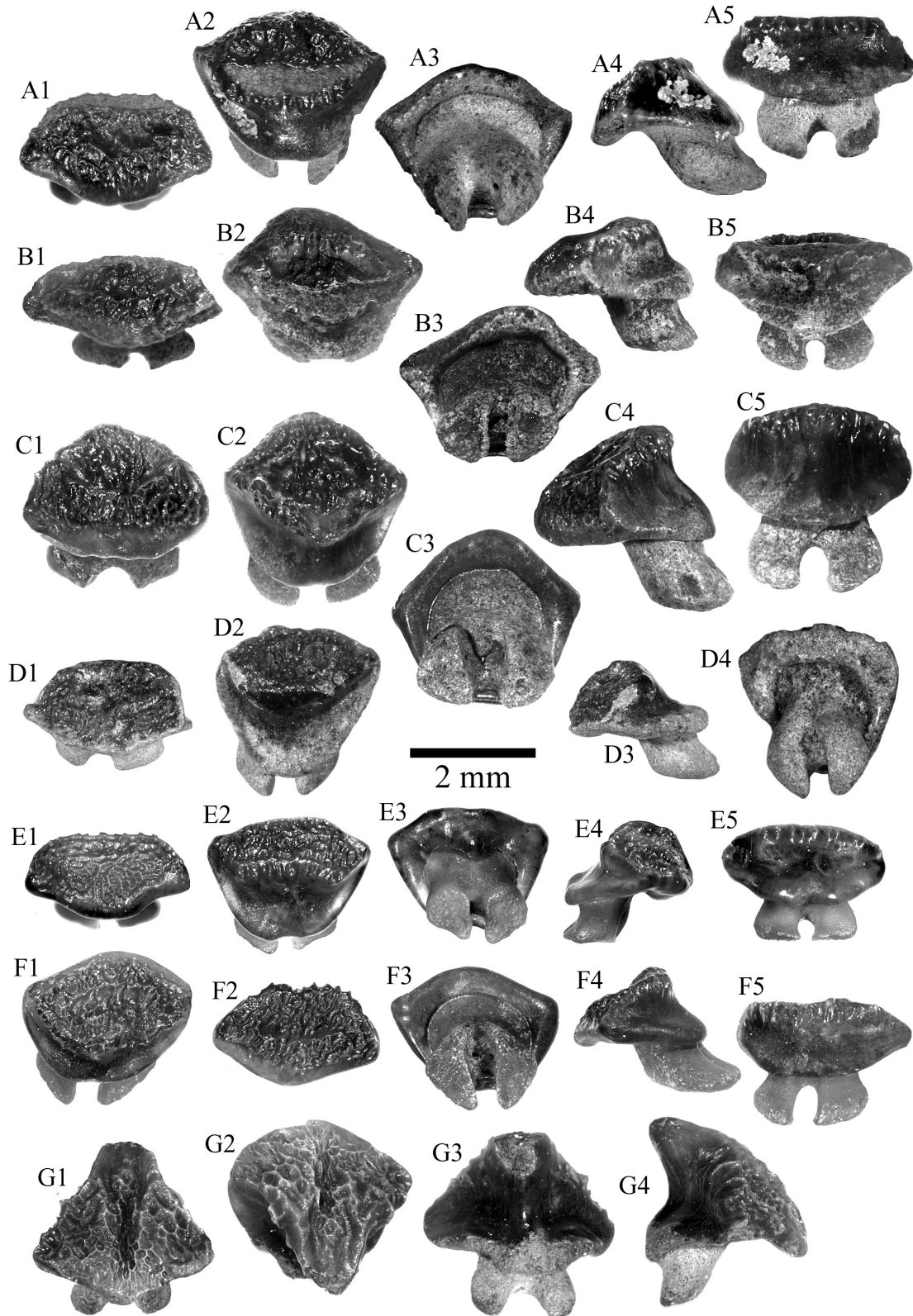


Figure 12. *Dasyatis cf. rugosa* (Probst, 1877), Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. **A**, anterolateral tooth, female morph, H = 2.3 mm, W = 3.1 mm, L = 2.5 mm, A1 labial view, A2 oblique occlusal view, A3 basal view, A4 profile view, A5 lingual view, SMF P 9867. **B**, anterolateral tooth, female morph, H = 1.9 mm, W = 3.2 mm, L = 2.4 mm, B1 labial view, B2 occlusal view, B3 basal view, B4 profile view, B5 lingual view, SMF P 9868. **C**, anterolateral tooth, female morph, H = 3.0 mm, W = 3.0 mm, L = 2.9 mm, C1 labial view, C2 occlusal view, C3 basal view, C4 profile view, C5 lingual view, SMF P 9869. **D**, anterolateral tooth, female morph, H = 2.0 mm, W = 2.6 mm, L = 2.4 mm, D1 labial view, D2 occlusal view, D3 profile view, D4 basal view, SMF P 9870. **E**, anterolateral tooth, female morph, H = 2.0 mm, W = 2.6 mm, L = 2.0 mm, E1 labial view, E2 occlusal view, E3 basal view, E4 profile view, E5 lingual view, SMF P 9871. **F**, anterolateral tooth, female morph, H = 2.1 mm, W = 2.7 mm, L = 2.1 mm, F1 occlusal view, F2 labial view, F3 basal view, F4 profile view, F5 lingual view, SMF P 9872. **G**, anterolateral tooth, male morph, H = 2.8 mm, W = 2.9 mm, L = 2.5 mm, G1 labial view, G2 occlusal view, G3 lingual view, G4 profile view, SMF P 9873.

In the NSB, *Dasyatis* cf. *rugosa* is apparently lacking in early to late Rupelian deposits, e.g. Borgloon Formation, Boom Clay Formation, and Rupel Formation, which yield very few, small and often indeterminable dasyatid teeth (Hovestadt & Hovestadt-Euler, 1995: pl. 2, fig. 2; Bor, 1980: pl. 2; Reinecke, unpubl. data). *Dasyatis* cf. *rugosa* first appears in the early Chattian, where it is still quite rare. Also in late Chattian deposits (Chattian Silt and Ratzeburg Formations of northern Germany; Reinecke *et al.*, 2005; Haye *et al.*, 2008) and Aquitanian to early Burdigalian sandy deposits (Vierlande Finesand and Kakert Formation; Reinecke *et al.*, 2008) teeth of *D. cf. rugosa* are quite uncommon. *Dasyatis rugosa* was reported by Cicimurri & Knight (2009: fig. 8C) from the Chattian Chandler Bridge Formation of South Carolina, USA. The illustrated female tooth has a weaker labial ornamentation than our specimens and a transverse depression at the labial crown basis, but may still belong to *D. rugosa*.

Family GYMNURIDAE Fowler, 1934

Genus *Gymnura* Kuhl in Van Hasselt, 1823

Gymnura cf. *altavela* (Linné, 1758)

(Figs. 13B-D)

* 1758 *Raja altavela*, Linné, p. 232.

v 2005 *Gymnura* sp. - Reinecke *et al.*, p. 72, pl. 47, fig. 3.

? 2008 *Gymnura* sp. - Reinecke *et al.*, p. 26, pl. 7, figs. 6-7.

v 2013 *Gymnura* sp. - Reinecke, p. 497, table 1.

Material. 5 teeth.

Measurements (mm):

height: 1.3 1.0+ 1.2 1.3 0.8

width: 0.84 1.0 0.8 0.85 1.0

Remarks

This genus was previously known by a single, incomplete tooth only (Reinecke *et al.*, 2005: pl. 47, fig. 3). The five teeth, now available, form a morphologically consistent group displaying minor variations in crown shape that can be explained by gradient monognathic heterodonty. Comparison of our specimens with the composite dentition of the extant *Gymnura altavela* (Linné, 1758) illustrated by Herman *et al.* (1998: pl. 28-30) suggests a close correspondence in most details of crown and root morphology. In particular our specimen, shown in Fig. 13B, which has a rather narrow crown with a strongly deepened, labial face, may represent an anterior tooth file, whereas the specimen in Fig. 13C with the broader crown and shallower labial crown face is likely from a lateral file. A fourth (Fig. 13D) and fifth specimen (not figured) have, differing from the other specimens, a single, low cusplet on the crown margin.

The genus *Gymnura* presently includes 14 living species (Froese & Pauly, 2014), but in few of them the dental morphology is reasonably well known. Teeth of *Gymnura micrura* (Bloch & Schneider, 1801) and *Gymnura marmorata* (Cooper, 1864) have much narrower and delicate cusps and their basal lateral

crown extensions diverge more laterally (Cappetta, 1984: pl. 1, figs. 9-10) than in teeth of *G. altavela* and our specimens of *G. cf. altavela*. Teeth of *G. marmorata* have low mesial and distal cusplets which are occasionally present also in *G. altavela* and *G. cf. altavela*.

Few fossil species of *Gymnura* based on isolated teeth are hitherto described (Cappetta, 2006), and teeth referable to this genus are mostly reported in open nomenclature. Outside the NSB two occurrences of *Gymnura* teeth are known from Oligocene deposits. Varone (2012) and Cicimurri & Knight (2009: fig. 6h) described and illustrated single, millimetric teeth from bioclastic, calcareous sands of Chattian age at Saint-Paul-lès-Dax, Aquitaine Basin, SW France, and from the Chandler Bridge Formation of South Carolina, USA, respectively, which both are morphologically close to *G. altavela* and *G. cf. altavela* and could be conspecific with our specimens. *Gymnura hovestadi* Herman, 1984, occurring in the Berg Member of the Bilzen Formation, early Rupelian, at Vliermaal, Belgium, differs from the Chattian *G. cf. altavela* by a lower cusp, labio-lingually thicker and more lingually curved root lobes (seen in profile view), a more sigmoid curvature of the lateral crown extensions, and probably by a less deepened, labial crown face (Herman, 1984: pl. 2, fig. 1-2).

Gymnura sp.

(Fig. 13A)

Material. 1 tooth.

Measurements (mm):

height: 1.3

width: 1.2

Description

The specimen has a moderately high, laterally expanded crown and a much lower root with well separated, rounded root lobes. The crown faces are smooth. In labial view, the crown has a roughly triangular, almost symmetrical shape with concave lateral crown margins which pass into the narrow, upright apex. The triangular labial face is plain in the apical part of the crown, but develops in the basal region a narrow, U-shaped depression that separates broad, lateral expansions. In occlusal and lateral view (Figs. 13A1, A4), these crown expansions have smooth, well rounded terminations. The lateroposterior crown faces join at a distinct lingual ridge extending from the apex to the crown basis. They are concave near the lingual ridge, but almost plain in the anterior region near the “winged” lateral expansions.

The height of the root is about one third of the tooth height. It is lingually much displaced with respect to the gravity centre of the crown and its lingual surface is almost continuous with the lingual ridge of the crown (Fig. 13A4). The nutrient groove divides the short lobes and has a single foramen. Marginolinguinal foramina are not present.

Discussion

The single specimen of *Gymnura* sp. can be easily distinguished from *G. altavela* and *G. cf. altavela* by the much

thicker and well rounded lateral crown expansions which are less salient in profile view (compare Fig. 13A4 with Figs. 13B5 and 13C5), as well as by the mesio-distally narrower and apico-basally shorter depression of the labial crown face. Whereas the mesial and distal crown edges are almost straight in teeth of *G. altavela* and *G. cf. altavela*, they have a distinctly concave

and rather flexuous shape in *Gymnura* sp.

Teeth of *Gymnura hovestadti* Herman, 1984, occurring in the Berg Member of the Bilzen Formation, early Rupelian, of eastern Belgium have thinner and more salient lateral crown expansions, a transversally wider labial crown depression and a mesio-distally thicker root than *Gymnura* sp. (compare with

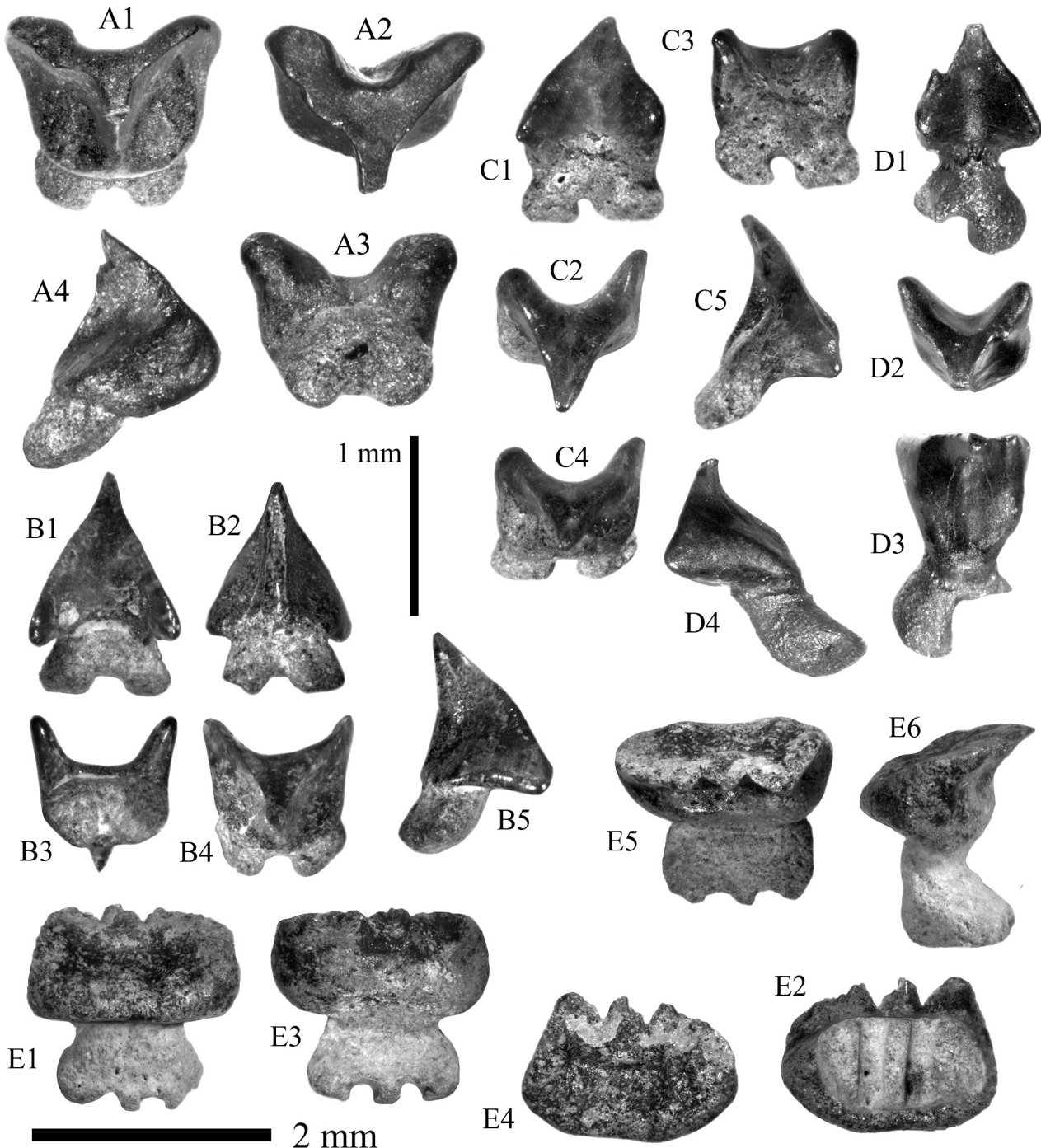


Figure 13. **A**, *Gymnura* sp., Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany; anterolateral tooth, H = 1.3 mm, W = 1.2 mm, A1 oblique lingual view, A2 occlusal view, A3 basal view, A4 profile view, SMF P 9874. **B-D**, *Gymnura cf. altavela* (Linné, 1758), Sülstorf Beds, Chattian, Kobrow, MVP. **B**, anterolateral tooth, H = 1.3 mm, W = 0.8 mm, B1 labial view, B2 lingual view, B3 basal view, B4 occlusal view, B5 profile view, SMF P 9875. **C**, anterolateral tooth, H = 1.2 mm, W = 0.8 mm, C1 labial view, C2 occlusal view, C3 basal view, C4 oblique lingual view, C5 profile view, SMF P 9876. **D**, anterolateral tooth, H = 1.3 mm, W = 0.8 mm, D1 labial view, D2 occlusal view, D3 lingual view, D4 profile view, SMF P 9877. **E**, *Mobula* sp., Sülstorf Beds, Chattian, Kobrow, MVP; anterolateral tooth, H = 1.6 mm, W = 1.8 mm, E1 labial view, E2 basal view, E3 lingual view, E4 occlusal view, E5 oblique occlusal view, E6 profile view, SMF P 9878.

Herman, 1984: pl. 2, figs. 1-2). Teeth of *Gymnura grootaerti* Herman, 1984, occurring in Ypresian deposits of Belgium, can be easily distinguished from *Gymnura* sp. by their much smaller size; the slightly convex to flat labial crown face; the narrow, salient basal crown expansions; and the rather low, laterally expanding root lobes (see Herman, 1984: pl. 1, figs. 1-3).

The anterior and lateral teeth of *Gymnura delpiti* Cappetta, 1984 (Thanetian of the Ouled Abdoun Basin, Morocco) resemble the specimen of *Gymnura* sp. from the Sülstorf Beds with respect to the broad, well rounded terminations of the lateral crown expansions, but different from it have a more elongate and mesio-distally broader crown apex and a bulging lateral crown basis broadly overhanging the root lobes (Cappetta, 1984: pl. 1, figs. 1-7).

Family MYLIOBATIDAE Bonaparte, 1835

Genus *Myliobatis* Cuvier, 1816

Myliobatis sp.

(Figs. 14 and 15)

. 1996 *Myliobatis* cf. *oligocaena* Leriche, 1910 - Müller, p. 40, pl. 1, figs. 4-5.

v 2005 *Myliobatis* sp. - Reinecke *et al.*, p. 73, pl. 45, 46, and pl. 47, figs. 1-2.

. 2010 *Myliobatis* sp. - Gille *et al.*, p. 25, fig. 25.

. 2010 *Rhinoptera* sp. - Gille *et al.*, p. 25, fig. 26.

Material. 267 teeth.

Measurements:

medial teeth (n = 34)

height: 1.2 – 9.5 mm (average 3.1 mm)

width: 2.4 – 30.7 mm (average 12.6 mm)

length: 1.7 – 9.0 mm (average 3.9 mm)

lateral teeth (n = 68)

height: 0.9 – 7.3 mm (average 3.2 mm)

width: 1.7 – 7.5 mm (average 3.9 mm)

length: 1.6 – 9.1 mm (average 4.9 mm)

posterior teeth (n = 22)

height: 1.7 – 3.3 mm (average 2.6 mm)

width: 2.2 – 4.3 mm (average 3.1 mm)

length: 4.0 – 9.9 mm (average 6.2 mm)

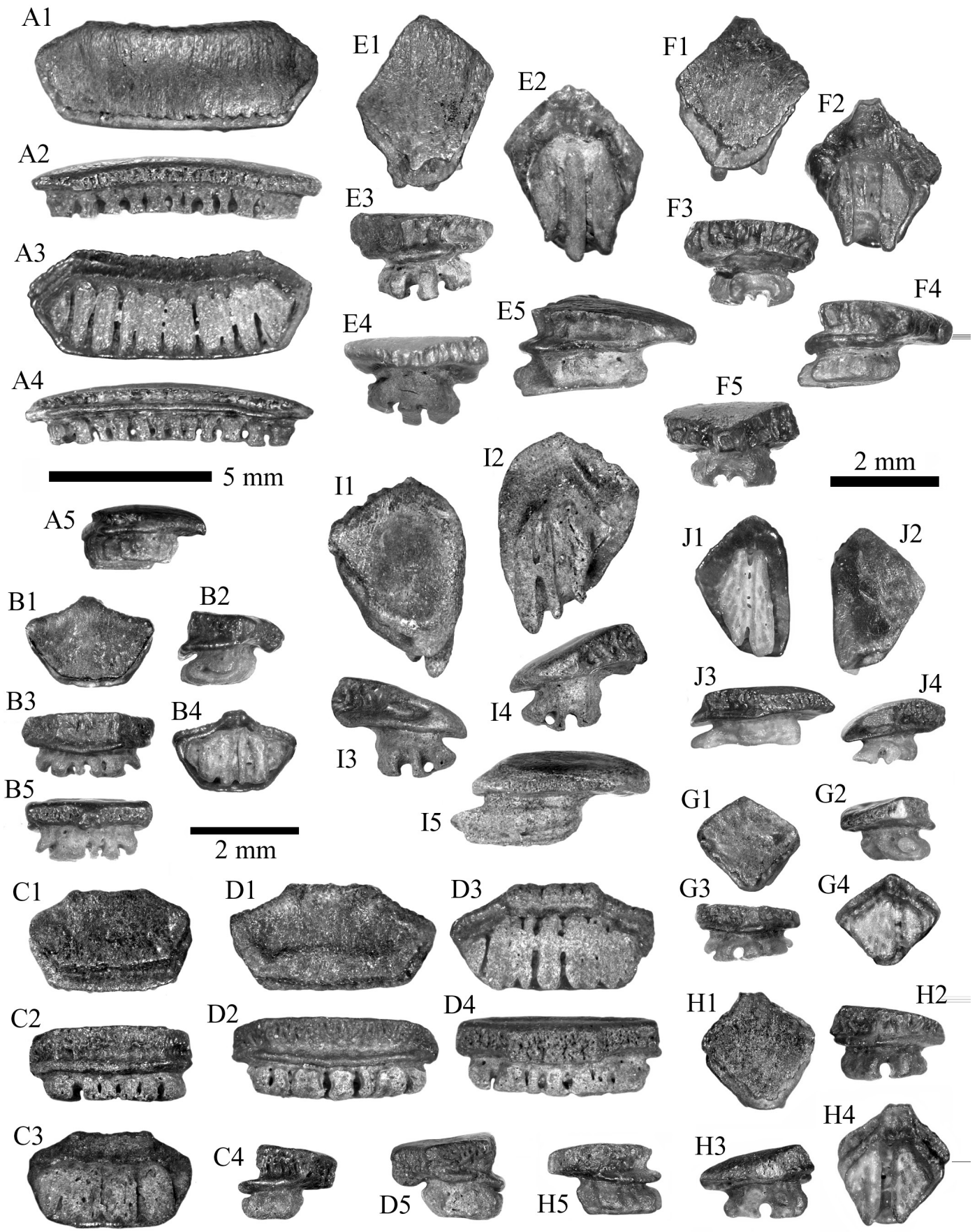
height = height of crown + root measured axially, width = mesio-distal diameter of the crown basis, length = labio-lingual diameter of the axial crown basis.

Description

Isolated myliobatid teeth are rather common in the Sülstorf Beds. Complete or partially preserved tooth plates were not found. The teeth reveal a significant range of morphological variation which can be referred to disjunct heterodonty between medial, lateral and posterior files. There is also noticeable variation observed in medial and lateral teeth which is related with tooth size and can be interpreted as due to ontogenetic heterodonty (see below). The tooth and tooth plate terminology is adopted from Hovestadt & Hovestadt-Euler (2013: text-fig. 2). The width (mesio-distal diameter), height (apico-basal diameter in the mid of a tooth), and length (labio-lingual diameter at the axial crown base) was measured in several teeth to develop the quantitative relationships discussed below. Medial teeth range from 2.4 to 31 mm in width. Larger medial teeth (> 15 mm wide) available in an earlier study are adequately illustrated (Reinecke *et al.*, 2005: pl. 45, figs. 1-4; pl. 46, figs. 1, 2, 4), whereas several small-sized medials (2-15 mm wide, Figs. 14B-D) were not recovered until extensive bulk-sampling yielded the material for this study.

In occlusal view, larger medials have a roughly hexagonal, mesio-distally elongate outline with a width-to-length ratio ranging from 3.1 to 4.9 (mean = 3.8; n = 14). The labial and lingual crown margins are either straight or slightly curved. The crown height is quite variable because of abrasion due to grinding of hard-shelled prey, and accordingly the occlusal face of most specimens is covered with scratches. Medial teeth with relatively high, less abraded crowns tend to be highest in the axial region and are tapering distally. The labial and lingual crown faces show a rough surface made up of irregular wrinkles and pits (“locking ornamentation” of Hovestadt & Hovestadt-Euler, 2013: 13). The lingual crown base is marked by a transverse ridge which in profile view forms a protruding shelf and constitutes the basal support for the labial basal crown edge of the successive medial tooth in the dental plate.

Figure 14. *Myliobatis* sp., subadult and juvenile teeth, Sülstorf Beds, Chattian, Kobrow, Mecklenburg-Vorpommern, Germany. The 5 mm scale bar refers to Figs. A, E, F, and I, the lower right 2 mm scale bar to Fig. K, and the lower left to Figs. B-D and G-H. **A**, medial tooth of a subadult individual, H = 1.3 mm, W = 6.5 mm, L = 2.5 mm, A1 occlusal view, A2 labial view, A3 basal view, A4 lingual view, A5 profile view, SMF P 9879. **B**, medial tooth of a juvenile individual, H = 1.2 mm, W = 2.4 mm, L = 1.7 mm, B1 occlusal view, B2 profile view, B3 lingual view, B4 basal view, B5 labial view, SMF P 9880. **C**, medial tooth of a juvenile individual, H = 1.4 mm, W = 3.0 mm, L = 1.6 mm, C1 occlusal view, C2 lingual view, C3 basal view, C4 profile view, SMF P 9881. **D**, medial tooth of a juvenile individual, H = 1.5 mm, W = 3.8 mm, L = 1.9 mm, D1 occlusal view, D2 lingual view, D3 basal view, D4 labial view, D5 profile view, SMF P 9882. **E**, lateral tooth, H = 1.8 mm, W = 3.1 mm, L = 3.8 mm, E1 occlusal view, E2 basal view, E3 lingual view, E4 labial view, E5 profile view, SMF P 9883. **F**, lateral tooth, H = 2.0 mm, W = 3.1 mm, L = 3.4 mm, F1 occlusal view, F2 basal view, F3 lingual view, F4 profile view, F5 labial view, SMF P 9884. **G**, lateral tooth of a juvenile individual, H = 1.1 mm, W = 1.9 mm, L = 1.8 mm, G1 occlusal view, G2 profile view, G3 lingual view, G4 basal view, SMF P 9885. **H**, lateral tooth of a juvenile individual, H = 1.4 mm, W = 2.1 mm, L = 2.1 mm, H1 occlusal view, H2 lingual view, H3 labial view, H4 basal view, H5 profile view, SMF P 9886. **I**, posterior tooth of a subadult individual, H = 2.0 mm, W = 3.2 mm, L = 4.5 mm, I1 occlusal view, I2 basal view, I3 lingual view, I4 labial view, I5 profile view, SMF P 9887. **J**, posterior tooth of a juvenile individual, H = 1.0 mm, W = 1.7 mm, L = 2.6 mm, J1 basal view, J2 occlusal view, J3 profile view, J4 labial view, SMF P 9888.



Small medial teeth (Figs. 14B-D) differ by several features from larger medials (Fig. 14A). While the hexagonal outline is retained, the teeth are narrowing mesio-distally, i.e. the width-to-length ratio ranges from 1.4 to 3.4 (mean = 2.6; $n = 21$). With decreasing tooth size the length of the labial crown margin shortens more strongly than that of the lingual margin (compare Fig 14A1 with 14D1 and 14C1; accordingly the labial distal edges often becomes relatively wider than the lingual distal edges. This trend is most apparent in the smallest medial tooth (Fig. 14B1) where the length of the labial crown margin is less than 25% of the lingual margin. The labial and lingual crown ornamentation and the lingual transverse ridge of the crown is similarly developed as in larger medial teeth.

In larger medials, the lobes and nutrient grooves of the polyaulacorhize root are rather straight, well separated, and evenly spaced (Reinecke *et al.*, 2005: pl. 45, fig. 3e; pl. 46, fig. 4e). The number of lobes in 15-31 mm wide medial teeth varies from 14 to 32. In 2-15 mm wide medial teeth, the number of root lobes decreases (6-16) and the lamellae of lobes and nutrient grooves are variably wide. In 2-8 mm wide teeth two or more lobes are fused at their basal plane and cover the interjacent grooves (Figs. 14A3, 14C3, 14D3).

Changes in morphology and root development with tooth size are recognizable also in lateral teeth. Although variable in details of the crown and root morphology (width-to-length ratio, width of the basal lingual crown ridge, crown ornamentation), most larger specimens (3-7 mm wide) display a distorted hexagonal to lozenge-shaped outline (i.e. they are labio-lingually longer than mesio-distally wide) and possess 3-5 root lobes (Fig. 14E; Reinecke *et al.*, 2005: pl. 45, fig. 5; pl. 46, fig. 3). Smaller specimens, 1.7-3 mm wide, have 2 or 3 root lobes and their outline in occlusal view often adopts a more rectangular shape (Figs. 14G, 14H; Reinecke *et al.*, 2005: pl. 47, fig. 1).

Posterior teeth are located at dental plate margins and have a three-sided outline with angular crown margins on the mesial side and a straight to convex margin on the distal side. There are commonly three root lobes in larger and two lobes in smaller specimens (Figs. 14I, 14J). Again, the basal face of adjacent root lobes is often fused in smallest specimens (Fig. 14J1). Specimens smaller than 4 mm in length and 2.2 mm in width have not been found.

Discussion

In the Palaeogene and Neogene fossil record, isolated teeth of myliobatid batoids are often difficult to distinguish and identify at genus level because variations in dental morphology are extensive and unique criteria are lacking. Hovestadt & Hovestadt-Euler (2013) characterized the dental plates and individual teeth of extant myliobatids and emphasized the intergeneric differences between *Myliobatis* Cuvier, 1816, *Aetomylaeus* Garman, 1908, *Pteromylaeus* Garman, 1913, and *Aetobatus* Blainville, 1816, as a basis for the more reliable identification of fossil taxa. On the basis of various morphological characters White (2014) puts *Pteromylaeus* in synonymy with *Aetomylaeus*. Also molecular evidence (mtDNA) strongly suggests that *Pteromylaeus* is nested within *Aetomylaeus* (Aschliman, 2014).

Based on Hovestadt & Hovestadt-Euler's study and the generic definitions of Cappetta (2012) the myliobatid dental assemblage of the Sülstorf Beds can be fully assigned to the genus *Myliobatis*. Medial teeth or tooth fragments characterized by chevron shape or variably strong axial curvature, as observed in adult lower teeth of *Aetobatus* spp. and *Aetomylaeus bovinus* (Geoffroy Saint Hilaire, 1817), respectively, and/or by width-to-length ratios greater than 5-6, typical of adult medial teeth in extant species of *Aetobatus* and *Aetomylaeus*, are not present in the Sülstorf Beds. Medial teeth of juvenile individuals of *Aetomylaeus* spp. have slightly curved crown margins, width-to-length ratios less than 5, and crown-root features that are closely comparable with medials of *Myliobatis* (Hovestadt & Hovestadt-Euler, 2013: 21 and pl. 17, fig. 1a-e). Also lateral teeth of juvenile *Aetomylaeus* (Herman *et al.*, 2000: pls 27-28) are similar to those of *Myliobatis* and may be difficult to separate from *Myliobatis* spp. The occurrence of juvenile *Aetomylaeus* teeth, however, among our myliobatid teeth seems unlikely, because subadult or adult *Aetomylaeus* teeth have never been found in the Sülstorf Beds.

Hovestadt & Hovestadt-Euler (2013) emphasized the lack of ontogenetic heterodonty in *Myliobatis* and *Aetobatus*, although they observed strong ontogenetic heterodonty in different species of *Aetomylaeus* (*A. maculatus* (Gray, 1834), *A. milvus* (Müller & Henle, 1841), *A. vespertilo* (Bleeker, 1852)), but not in *Aetomylaeus bovinus* (Geoffroy Saint Hilaire, 1817). Juvenile individuals of *Aetomylaeus* spp. have one medial tooth file, and two lateral and one posterior files on either sides in upper and lower tooth plates (Herman *et al.*, 2000: textplate 7). During ontogenetic tooth replacement the medial file considerably broadens with resulting increase of the width-to-length

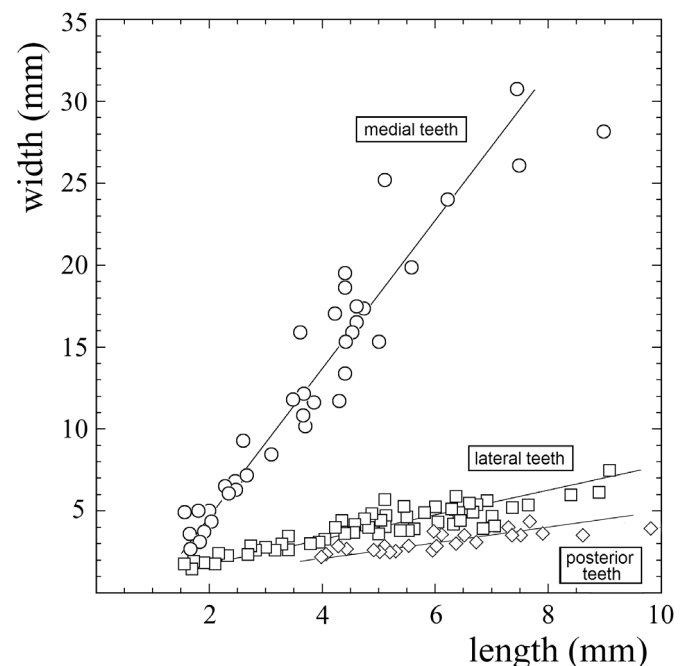


Figure 15. Bivariate plot showing the width (mesio-distal diameter) versus length (labio-lingual diameter) of medial, lateral, and posterior teeth of *Myliobatis* sp. from the Sülstorf Beds. Linear slopes are fitted to data points of each tooth file.

ratio and the lateral/posterior files become reduced and finally lost (Hovestadt & Hovestadt-Euler, 2013: table 4).

Notwithstanding the findings of Hovestadt & Hovestadt-Euler (2013) for *Myliobatis*, there are conclusive arguments for ontogenetic heterodonty also in *Myliobatis*. If length and width data of all complete medial, lateral, and posterior teeth are displayed in a bivariate plot (Fig. 15), each group follows a different linear trend. Measurements of tooth height are not shown because the occlusal crown face is variably abraded and lowered by feeding during a tooth's replacement cycle. Fig. 15 indicates that during ontogenetic growth the medial teeth (slope = 4.5) develop more strongly in mesio-distal (width) than labio-lingual direction (length), whereas growth of lateral (slope = 0.75) and posterior teeth (slope = 0.48) in subsequent replacement cycles prefers the labio-lingual direction. This pattern resembles ontogenetic heterodonty in *Aetomylaeus* spp. where medial teeth are much more elongate in adults than in juveniles/subadults and laterals and posteriors become lost in adults (see above). Fig. 15 also indicates that earliest ontogenetic stages of *Myliobatis* have an almost homodont dentition (in terms of tooth dimensions).

The scatter band is significantly larger in medial than in lateral and posterior teeth (Fig. 15). This can be explained by the systematically greater width of upper than lower medials in jaws of extant *Myliobatis* species (Hovestadt & Hovestadt-Euler, 2013), which may be relevant in fossil *Myliobatis* dentitions too. The intraspecific variation of width-to-length ratios, noticed in medial teeth of some extant species like *Myliobatis aquila* (Linné, 1758) and *Myliobatis californica* Gill, 1865 (Hovestadt & Hovestadt-Euler, 2013: 9-14), may also contribute to dimensional scatter in Fig. 15. The particular growth trends of the medial, lateral and posterior files could be a distinctive characteristic of *Myliobatis*. In dental plates of extant *Rhinoptera* species the dimensional differences between mesial and lateral tooth files are more gradual (e.g. Bigelow & Schroeder, 1953: figs. 108-109; Herman *et al.*, 2000: textpl. 10, pl. 31; Cappetta, 2012: fig. 446; and own collection) and their width-to-length bivariate plots will provide slopes different from those in Fig. 15.

Isolated teeth of *Myliobatis* sp. with dental characteristics very similar to our specimens are known from the Kassel Formation, early Chattian, of northern Hesse, Germany (Weiler, 1943; Müller, 1996: as *Myliobatis* cf. *oligocaena* Leriche, 1910; Gille *et al.*, 2010: *Rhinoptera* sp. for a 4 mm wide juvenile medial tooth; and *Myliobatis* sp. for larger teeth), and from the Doberg Formation (Weiler, 1957; Reinecke *et al.*, 2005: as *Myliobatis* sp.). The Chattian *Myliobatis* teeth could be conspecific with *Myliobatis aquila* var. *oligocaena* Leriche, 1910 from the Boom Clay Formation, Rupelian, of Belgium, but a detailed revision and documentation of myliobatid taxa in Rupelian deposits of the NSB and Mainz embayment beyond the generic characterisations by Hovestadt & Hovestadt-Euler (2013) is needed.

Family MOBULIDAE Gill, 1893

Genus *Mobula* Rafinesque, 1810

Mobula sp.

(Fig. 13E)

Material. 1 tooth.

Measurements (mm):

height: 1.6

width: 1.8

length*: 0.9

* labio-lingual diameter at crown basis.

Description

The tooth has a crown wider than high with almost rectangular outline and rounded basal margins in labial or lingual view (Figs. 13E1, 2). The crown is strongly inclined in lingual direction and tapers apically to the sharp edge of the lingual visor developing three uneven cusplets. The surface is slightly corroded, but ornamentation is not apparent. The labial face is apico-basally convex (Fig. 13E6) and transversally almost plane except for a few shallow depressions occurring in the mid of the crown face. The lingual face is slightly concave only beneath the lingual visor. In occlusal view, the labial visor is slightly angular (Fig. 13E4). In profile view, the labial crown basis markedly overhangs the root, which is lingually displaced relative to the crown (Fig. 13E6).

The polyaulacorhizid root is somewhat lower and mesio-distally and labio-lingually narrower than the crown (Figs. 13E1, 2). The short stem of the root widens both lingually and laterally in basal direction (Figs. 13E1, 6). Small foramina occur in the grooves and on the labial root face.

Discussion

The present tooth belongs to the group of mobulids with comb-like teeth, which includes the six extant species *M. thurstoni*, *M. eregoodootenke*, *M. kuhlii*, *M. munkiana*, *M. rochebrunei*, and *M. hypostoma* (Adnet *et al.*, 2012), and the valid fossil species *Mobula loupianensis* Cappetta, 1970, *Mobula pectinata* Cappetta, 1970, and *Mobula melanyae* (Case, 1980).

The crown and root morphology of our specimen appears to be close to that of *Mobula thurstoni* (Lloyd, 1908) from which it mainly distinguishes by the lack of labial crown ornamentation (Adnet *et al.*, 2012: fig. 3T-M^c). Similar teeth from the Ottangian, middle Burdigalian, of Walbersweiler, southern Germany (Pfeil in Barthelt *et al.*, 1991: pl. 4, fig. 15) and the Langhian of Winterswijk-Miste (Bor *et al.*, 2012: pl. 52, figs. 2-3) displaying a weak or missing labial ornamentation were referred to as *Mobula* sp.

Devil rays (genus *Mobula*) became infrequently known by isolated teeth from Chattian deposits in the Northern Atlantic region including the NSB. Cicimurri & Knight (2009) reported on a morphologically heterogeneous sample of *Mobula* teeth from the Chandler Bridge Formation in South Carolina, USA, which they affiliate to *Mobula* cf. *M. loupianensis* Cappetta, 1970 (but see Adnet *et al.*, 2012: 139, for a dissent). None of the specimens illustrated by Cicimurri & Knight (2009: fig.

9a-f) corresponds to the specimen from the Sülstorf Beds. Dissimilar to that, teeth of *Mobula melanyae* (Case, 1980) from the middle-late Oligocene River Bend Formation in North Carolina show a strong ornamentation with irregular folds and grooves (in adult holotype) or few vertical folds on the labial crown face (in subadult paratype). Teeth of *Mobula* sp. from the Old Church Formation, late Chattian to Early Miocene, of Virginia (Müller, 1999; cautiously assigned to *Mobula pectinata* by Adnet *et al.*, 2012: 139) differ from the Sülstorf specimen by their much stronger labial folds and very pronounced cusplets. Mobulid teeth rarely occur also in the early to late Chattian Grafenberg Formation of the Lower Rhine embayment (Von der Hocht, personal communication, 2013). One well preserved specimen recovered from a boring at Willich, western Germany (regional stage Chattian B, early to middle Chattian) could be conspecific with the specimen from the Sülstorf Beds. A similar mobulid tooth with narrow, bicuspidate crown and almost flat, poorly ornamented labial crown face is known from the middle-late Chattian Thalberg Beds of southern Germany (Reinecke *et al.*, 2014). Due to the

rareness of mobulid teeth in Chattian deposits and the unknown variation and significance of their dental characters in the context of ontogenetic and sexual heterodonty, the present specimen can not be identified at species level.

DISCUSSION

Continued bulk-sampling and enrichment of small sized fish remains by means of combined acid treatment, sieving and magnetic separation from fossil-rich tempestites of the early-middle Chattian Sülstorf Beds has considerably increased the dental material of cartilaginous fishes since a previous study (Reinecke *et al.*, 2005). In this material the batoid teeth (ca. 13000 specimens) largely outnumber the sharks teeth (ca. 6300) and chimaeroid dental plates (2). Some very rare batoid species are first identified (*Sympterygia* sp., *Mobula* sp., *Gymnura* sp.). Other previously uncommon, poorly known taxa are now characterized more precisely (*Gymnura* cf. *altavela*) or described as new species (*Raja thiedei* sp. nov.;

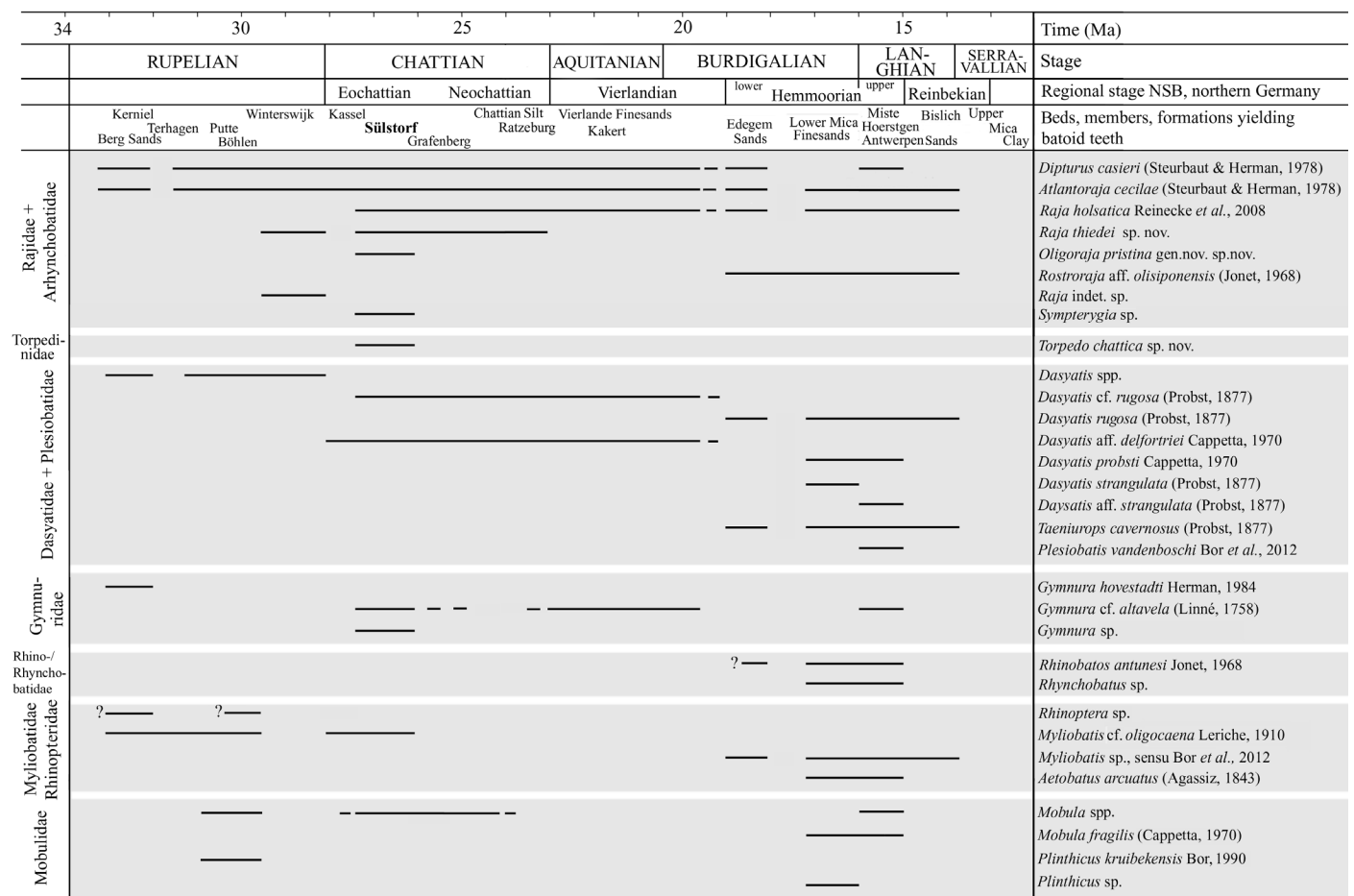


Figure 16. Stratigraphic distribution of batoid taxa in Rupelian to early Middle Miocene deposits of the NSB. Data for the Rupelian are from Leriche (1910), Van den Bosch (1971), Van den Bosch *et al.* (1975), Sturbaut & Herman (1978), Müller (1983), Herman (1984), Bor (1990), Hovestadt & Hovestadt-Euler (1995), Baut & Genault (1999), and Moths (2001), supplemented with data notified by Taco Bor, Sliedrecht (Kerniel Member, Berg Member) and Leo Dufrain, Beerse (Winterswijk Member). Data for the Chattian are from Weiler (1943), Von der Hocht (1986, and pers. comm., 2014), Müller (1996), Reinecke *et al.* (2005), Haye *et al.* (2008), Gille *et al.* (2010), and this study; for the Vierlandian from Reinecke *et al.* (2008), and Reinecke (2013); for the early Hemmoorian (late Burdigalian) from Reinecke *et al.* (2011) and Leo Dufrain (Edegem Sands Member, pers. comm. 2007); for the late Hemmoorian and Reinbekian (Langhian) from Reinecke & Wienrich (2009), Bor *et al.* (2012), and Fritz von der Hocht (Hoerstgen Beds, pers. comm. 2008).

Oligoraja pristina gen. et sp. nov.; *Torpedo chattica* sp. nov.). Two very common species are reallocated to other genera, i.e. *Atlantoraja ceciliae* (Sturbaut & Herman, 1978) new comb. and *Dipturus casieri* (Sturbaut & Herman, 1978) new comb.

The batoid fauna of the Sülstorf Beds is the best documented and most diverse presently known from the Late Oligocene in the North Atlantic region. It comprises thirteen taxa with six species of skates (*Raja thiedei* sp. nov., *Atlantoraja ceciliae*, *Sympterygia* sp., *Dipturus casieri*, "*Raja*" *holsatica*, *Oligoraja pristina* gen. et sp. nov.), two species of butterfly rays (*Gymnura* cf. *altavela*, *Gymnura* sp.), two species of sting rays (*Dasyatis* cf. *rugosa*, *Dasyatis delfortriei*), and each one species of electric rays (*Torpedo chattica* sp. nov.), eagle rays (*Myliobatis* sp.) and devil rays (*Mobula* sp.). Except the Rhynchobatidae and Rhinopterae, all families of batoids, recorded in nearly contemporaneous Chattian deposits of the Northwest Atlantic (Chandler Bridge Formation of South Carolina, USA: ca. 12 species (Cicimurri & Knight, 2009); Old Church Formation, late Chattian to Early Miocene of Virginia, USA: ca. 8 species (Müller, 1999)), were also present in the NSB. At species level, however, there exists low correspondence in faunal composition between the different regions.

These interregional differences in faunal composition appear to be significant and systematic. The North American Chattian yields teeth of *Rhynchobatus*, *Rhinoptera*, and *Aetobatus* (Müller, 1999; Cicimurri & Knight, 2009) which have not been detected in the southern NSB, although the shallow-water habitats with mainly soft bottoms of the Chattian Kassel Formation, Sülstorf Beds, and Doberg Formation would have been suitable for these genera. Extant species of these genera largely prefer tropical to warm-temperate coastal waters, often associated with shallow bays, estuaries and lagoons (e.g. Compagno *et al.*, 1989; McEachran & De Carvalho, 2002; Last & Stevens, 2009; Ebert & Stehmann, 2013). Their absence from the boreal Chattian may thus indicate either climatic differences (i.e. relatively lower temperatures of coastal waters) or the inability of these batoids to re-enter the semi-closed, restricted marine setting of the NSB from the Northeast Atlantic realm after a longer period of reduced marine temperatures prevailing during the Rupelian.

Several studies of the last decades have reported on batoids in various lithostratigraphic units of the Oligocene and Early to Middle Miocene (see caption of Fig. 16). In addition, there is a pool of unpublished data and personal observations which complements the published data. Fig. 16 presents the present state of knowledge on the stratigraphic distribution of batoids in the NSB. Major efforts in bulk-sampling and physical enrichment necessary to recover significant numbers of batoid microteeth have been made in productive layers of the Boom and Rupel Clay Formations, Rupelian (e.g. septaria layers, or layers rich in molluscan plankton; Hovestadt & Hovestadt-Euler, 1995; Moths, 2000; Leo Dufraing, pers. communication, 2014). Batoid teeth were further extracted from mollusc-rich layers in siltites and glauconite-rich sands, and from shelly sandstones and unconsolidated fine sands of late Chattian, Aquitanian to middle Burdigalian age (Chattian Silt, Ratzeburg Formation, Vierlande Finesands, Kakert Beds, Edegem Sands Member; Haye *et al.*, 2008; Reinecke *et al.*, 2008; Leo Dufraing, pers. communication, 2014; Artur Piehl, pers. communication,

2007). Processed volumes of these beds are less than those of the Sülstorf Beds, which may partly explain the apparent lower diversity in the temporal range from late Chattian to middle Burdigalian (Fig. 16).

A few comments on the temporal distribution patterns would be necessary. They seem to be incomplete for the Torpedinidae, Dasyatidae, Gymnuridae, and Mobulidae in the Rupelian, and for the Torpedinidae, Dasyatidae, Gymnuridae, Myliobatidae, and Mobulidae in the late Chattian, Aquitanian, and early-middle Burdigalian. Some records of medial and lateral teeth of *Rhinoptera* sp. in the Chattian (Gille *et al.*, 2010) and early Rupelian (Baut & Génault, 1999; Müller, 1983) can be questioned on the background of intraspecific and ontogenetic dental variations of *Myliobatis* spp. discussed above. Hence, *Rhinoptera* appears to have been largely absent in the boreal realm. *Myliobatis* sp. (mostly referable to *Myliobatis* cf. *aquila* var. *oligocaena* Leriche, 1910) is present in the Rupelian and early to middle Chattian, but apparently absent from the late Chattian to early Burdigalian. With the establishment of stable marine connections between the southern NSB and the north-eastern Atlantic during the Mid-Miocene thermal optimum, a new species of *Myliobatis* (sensu Bor *et al.*, 2012) entered the NSB which is common in all formations of late Burdigalian to Langhian age.

Eagle rays of the genus *Aetobatus* did not settle the NSB during the Rupelian, Chattian and Aquitanian. They first appeared in the middle/late Burdigalian and vanished again during the Langhian (e.g. Reinecke *et al.*, 2011; Bor *et al.*, 2012). As with other thermophilic batoids (*Rhynchobatus*, *Rhinobatos*) their transient occurrence in the boreal NSB was triggered by the Mid-Miocene thermal optimum.

Teeth of the pelagic devil rays, Mobulidae, are very uncommon during the Oligocene and Miocene in the NSB. *Plinthicus kruibekensis* Bor, 1990 from the Boom Clay Formation of Belgium, and an unnamed, new species of *Mobula* from the Böhlen Formation, Saxony, Germany (Woydack, 1997: as *Plinthicus kruibekensis*) are the only representatives of the family presently known from the Rupelian. *Mobula* sp. is similarly rare in the early to middle Chattian. The genus is apparently missing from the late Chattian to the middle Burdigalian, but reappears with different species in the late Burdigalian and Langhian (LMFS Formation, Miste Bed, Antwerpen Sands Member, Hoerstgen Beds; Bor *et al.*, 2012; F. Von der Hocht, personal communication, 2010; T. Reinecke, unpublished data). The conspicuous occurrence of mobulids in the boreal realm during the relatively warmer periods of the Chattian and late Burdigalian to Langhian corresponds to the widespread occurrence of extant species of the Mobulidae in tropical and warm-temperate seas.

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Rupel Clay Formation (at Raesfeld, north-western Germany), and the Kerniel Sands (at Gellik, north-eastern Belgium) and Berg Sands (at Vliermaal, Belgium) of the Bilzen Formation, early Rupelian. Thomas Schindler, Fritz von der Hocht, and Kai Nungesser borrowed batoid teeth from their collections for comparisons. The several helpful comments and recommendations of Dirk Hovestadt, Taco Bor and an anonymous reviewer and the editorial support by Sylvain Adnet are gratefully acknowledged.

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Raja thiedeii: [lsid:zoobank.org:act:2B3918EE-F4E6-45B4-847D-DB38D916F1D8](https://zoobank.org/act:2B3918EE-F4E6-45B4-847D-DB38D916F1D8)

Oligoraja pristina: [lsid:zoobank.org:act:EE381B1C-EF86-46B9-A02C-BFE45FC34958](https://zoobank.org/act:EE381B1C-EF86-46B9-A02C-BFE45FC34958)

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