PALÆO VERTEBRATA

Two new scyliorhinid shark species (Elasmobranchii, Carcharhiniformes, Scyliorhinidae), from the Sülstorf Beds (Chattian, Late Oligocene) of the southeastern North Sea Basin, northern Germany

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Abstract: Based on isolated teeth two new scyliorhinid shark species, *Scyliorhinus biformis* nov. sp. and *Scyliorhinus suelstorfensis* nov. sp., are described from the Sülstorf Beds, early to middle Chattian, of Mecklenburg, north-eastern Germany. They form part of a speciose assemblage of nectobenthic sharks and batoids which populated the warm-temperate to subtropical upper shelf sea of the south-eastern North Sea Basin.

Keywords: *Scyliorhinus*, Scyliorhinidae, Elasmobranchii, Chattian, North Sea Basin.

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INTRODUCTION

Elasmobranch assemblages of the Chattian in the boreal province are comparably less well studied than those of the Rupelian and Neogene. This is mainly due to the limited access to Chattian deposits which have very localized occurrences and were only temporarily exposed in the northern peripheral zones of the Mesozoic low mountain ranges of Lower Saxony (Doberg, Astrup), and Hesse (Ahnetal, Glimmerode, Niederkaufungen), and in the lowlands of northern and north-eastern Germany, e.g. Söllingen, Johannistal/Heiligenhafen, Malliß, and near Sternberg and Schwerin (e.g. Kohnen, 1995a; Müller, 1996; Von Bülow & Müller, 2004; Gürs, 2005; Haye *et al.*, 2008). In the Netherlands, north-eastern Belgium and the adjacent Lower Rhine Embayment Chattian deposits (Voort Formation, Veldhoven Member, and Grafenberg Formation) commonly occur in the deeper underground (e.g. Laga *et al.*, 2001; Hiss, 2013). Sediment samples of these formations recovered from shafts driven for coal mining or from cored wells are rarely large enough to collect suitable numbers of teeth.

Elasmobranch teeth in Chattian shallow marine or coastal sediments are often polished and worn due to transport by wave or current action (e.g. Gille *et al.*, 2010). As teeth may be also partly reworked from older deposits, e.g. the Rupelian (Reinecke *et al.*, 2005: 31, 35), taphonomic conditions do not render a definite temporal correlation for some species. These problems are insignificant in the early to middle Chattian Sülstorf Beds of south-western Mecklenburg, northeastern Germany, which have produced a diverse parautochthonous assemblage of well-preserved elasmobranch teeth (Winkler, 1875; Freess, 1991; Reinecke *et al.*, 2005). Continued bulk sampling by the author since 2005 has particularly increased the number of small-toothed batoid and shark species. Based on this material two new scyliorhinid taxa are described here.

GEOLOGICAL SETTING

In western Mecklenburg, north-eastern Germany, the Chattian stage is represented by siliciclastic sediments, 15-120 m thick, deposited in moderately deep to shallow marine environments of the south-eastern North Sea Basin (Von Bülow & Müller, 2004; Standke *et al.*, 2005). The succession comprises the early Chattian basal Plate Beds (0-20 m), the early to middle Chattian Sülstorf Beds (ca. 80 m), and the late Chattian Rogahn Beds (ca. 30 m thick; Von Bülow, 2000). Whereas the Plate Beds consist of fossil-poor, silty clays and silts, continuing the basin-type sedimentation of the underlying Rupel Clay, the Sülstorf Beds (= "Sülstorfer Schichten", Lotsch, 1981) are a sequence of calcareous silts containing glauconite and white mica, that are coarsening upwards into well sorted fine sands. Compact calcite-cemented sandstones represent discontinuous layers in the unconsolidated deposits. The Sülstorf Beds enclose centimetre to decimetre thick layers with densely packed mollusc shells and - occasionally - elongate to spherical sand-/siltstone intraclasts. These layers that commonly show normal graded bedding and have sharp, erosional contacts to the basis, are interpreted as proximal tempestites (Suhr & Braasch, 1991). Thin-walled shells, fragile elasmobranch teeth and even delicate skeletal remains of teleosts are well preserved, which attests to single rapid events of sedimentation from suspension flows below the storm wave basis. Environmental demands of mollusc and ostracod associations suggest water depths of 25-75 m, indicating the upper sublittoral (Janssen, 1986; Endler & Herrig, 1995; Moths *et al.*, 1998). The common occurrence of thermophilic molluscs (e.g. *Athleta, Typhis, Ancilla, Lyria, Cancellaria, Conomitra, Conus, Hastula*) points to a warm climate. Relatively high bottom-water temperatures during the lower Chattian are inferred also from benthic foraminiferal assemblages occurring in the south-western regions of the North Sea Basin (Kohnen, 1995b; De Man & Van Simaeys, 2004).

Except for core drillings, the Sülstorf Beds are almost exclusively accessible as glaciofluvial pebbles and cobbles (commonly 3-15 cm, rarely more than 25 cm in diameter; Schulz, 1972) which may be locally abundant where the Paleogene deposits in the shallow underground were eroded by ice advances of the Weichselian glacial, e.g. in the region southwest of Sternberg and east of Schwerin (Schulz, 1972: text-fig. 5). All pebbles and cobbles collected for this study come from a single locality, the sandpit of "Thomas Beton" in Kobrow, near Sternberg (Fig. 1).

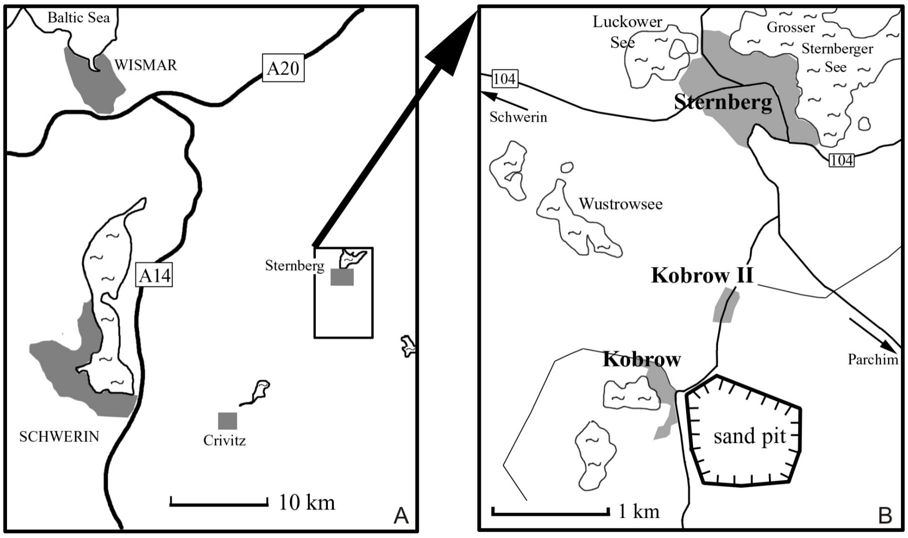

Figure 1. A. topographic sketch map of western Mecklenburg, north-eastern Germany, with larger towns and motorways A20 and A14 indicated, showing the location of the study area near Sternberg. **B.** location of the sandpit at Kobrow, south of Sternberg, from where glaciofluvial pebbles and cobbles of the Sülstorf Beds are derived.

MATERIAL AND METHODS

Several hundred kilograms of calcite-cemented, mollusc-rich sandstone samples were disintegrated in dilute formic acid. Samples of tempestites containing coarse, densely packed mollusc shells and endoclasts are preferentially treated, as they contain most fish remains. The fine sand fraction in the acid-insoluble residue was removed with a 0.5 mm mesh sieve and the remaining small volume dried and split into >3 mm, 1-3 mm, and 0.5-1 mm fractions. Fish remains were directly picked from the first two fractions. In the 0.5-1 mm fraction, yielding the largest amount of residue, fish remains were further concentrated with an isodynamic magnetic separator variably adjusting the track slope and electric current to remove paramagnetic (mainly iron oxyhydroxides) and diamagnetic mineral grains (mainly quartz and some calcite remaining after acid treatment).

Teeth shown in Figures 2 and 3 are imaged with a Zeiss 1530 Gemini scanning electron microscope. Larger teeth in Figure 4 are photographed with a Euromex Novex RZB-SF trinocular equipped with a 5 megapixel USB camera. 15-30 images sequentially taken at different levels of focus are combined into a single photo with the Euromex Image Focus Stacking Software. The illustrated material is deposited in the Palaeontological Collection of the Senckenberg Research Institute and Natural History Museum (SMF), Frankfurt, Germany.

SYSTEMATIC PALAEONTOLOGY

Order CARCHARHINIFORMES Compagno, 1973
Family SCYLIORHINIDAE Gill, 1862
Subfamily SCYLIORHININAE Gill, 1862
Genus *Scyliorhinus* Blainville, 1816

Scyliorhinus biformis nov. sp.
(Figs. 2 and 3)
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v 2005 - *Scyliorhinus* aff. c*oupatezi* Herman, 1975 - Reinecke *et al.*, p. 48.

v 2005 - *Bythaelurus steurbauti* Hovestadt & Hovestadt-Euler, 1995 - Reinecke *et al.*, p. 50, plate 31, fig. 5.

v 2008 - *Scyliorhinus* sp. - Haye *et al.*, p. 67, plate 10, fig. 6.

v 2008 - *Scyliorhinus* sp. - Reinecke *et al.*, p. 14, plate 2, figs 14-15.

- 2013 - *Scyliorhinus* sp. - Reinecke, p. 497, table 1.

Derivation of name. reminiscent of the differently shaped crown morphology and ornamentation referable to gynandric heterodonty.

Holotype. Senckenberg Research Institute and Natural History Museum, SMF P 9804 (fig. 2C).

Paratypes.

1 SMF P 9805 (Fig. 2B)

2 SMF P 9806 (Fig. 2G)

3 SMF P 9807 (Fig. 3A).

Locus typicus. sandpit of "Thomas Beton" in Kobrow, near Sternberg, Mecklenburg, Germany.

Stratum typicum. Sülstorf Beds: calcite-cemented, fine-grained sandstones with cm- to dm-thick mollusc-rich layers locally containing endoclasts; occurring as glaciofluvial drift (vernacular name: "Sternberger Gestein", see Von Bülow, 2000).

Age. early to middle Chattian, Late Oligocene; benthic foraminiferal *Palmula oblonga* Zone (Müller, 2000).

Material. 35 teeth including fragments.

Measurements (mm):

female morph	height	width
SMF P 9804 holotype	1.4	1.1
SMF P 9805 paratype 1	1.3	1.0
SMF P 9808	1.4	1.1
SMF P 9809	1.4	1.3
SMF P 9810	1.0	1.1
not illustrated	1.3	0.9
not illustrated	1.4	1.0
not illustrated	1.1	1.1
not illustrated	1.2	0.95

male morph	height	width
SMF P 9806 paratype 2	1.8	1.4
SMF P 9807 paratype 3	1.6	1.2
SMF P 9811	1.4	1.1
SMF P 9813	1.5	1.3
SMF P 9814	1.8	1.4
not illustrated	1.7	1.3
not illustrated	1.4	1.1
not illustrated	1.5	1.1
not illustrated	0.94	1.0

Description

Bulk processing of the Sülstorf Beds produced two sets of teeth manifesting differences in crown morphology at similar dimensions. One morph displays strong cusplets and a pronounced labial ornamentation, whereas the other shows weaker or missing cusplets and an indistinct ornamentation. These differences are ascribed to gynandric heterodonty in a single species (see discussion).

Teeth of the female morph have an upright to noticeably inclined principal cusp which is slender and not high. The cusp has a conical shape. Its mesial and distal cutting edges extend from the apex to the basal notch and continue to the lateral margins of the cusplets. There exists one pair of sharp cusplets in anterior teeth having a narrow crown basis (Figs 2A, B), and - more rarely - a second (outer), much lower pair occurring in basally broader teeth that probably derive from more lateral jaw positions (Figs 2C, E). In some specimens the outer cusplet occurs on the mesial heel only (Fig. 2D). While both crown faces are transversally convex, the lingual face is much more convex than the labial one. The apico-basally convex labial crown basis markedly overhangs the root. The lower third to half of the labial crown face is covered with sharp longitudinal ridges which are partly anastomosing. On the lingual crown face (including the cusplets) the ridges are more flexuous, less sharp and reach higher up to the apex than on the labial face. The root is not high, basally broader than the crown, and shows a salient lingual protuberance. The lobes are well separated and elongate in lateral files and have semicircular, well-rounded terminations. The basal face of the root is rather flat and lacks a nutrient groove. Two larger foramina open on the lingual side of the protuberance and in the labial axial region of the basal face (e.g. Figs 2A1 and 2A2). The lingual root faces on either sides of the protuberance are deepened and bear 3-4 larger foramina. Some smaller foramina are scattered on the root faces.

Teeth of the male morph have very similar characters in cusp and root morphology as teeth of the female morph, but dif-

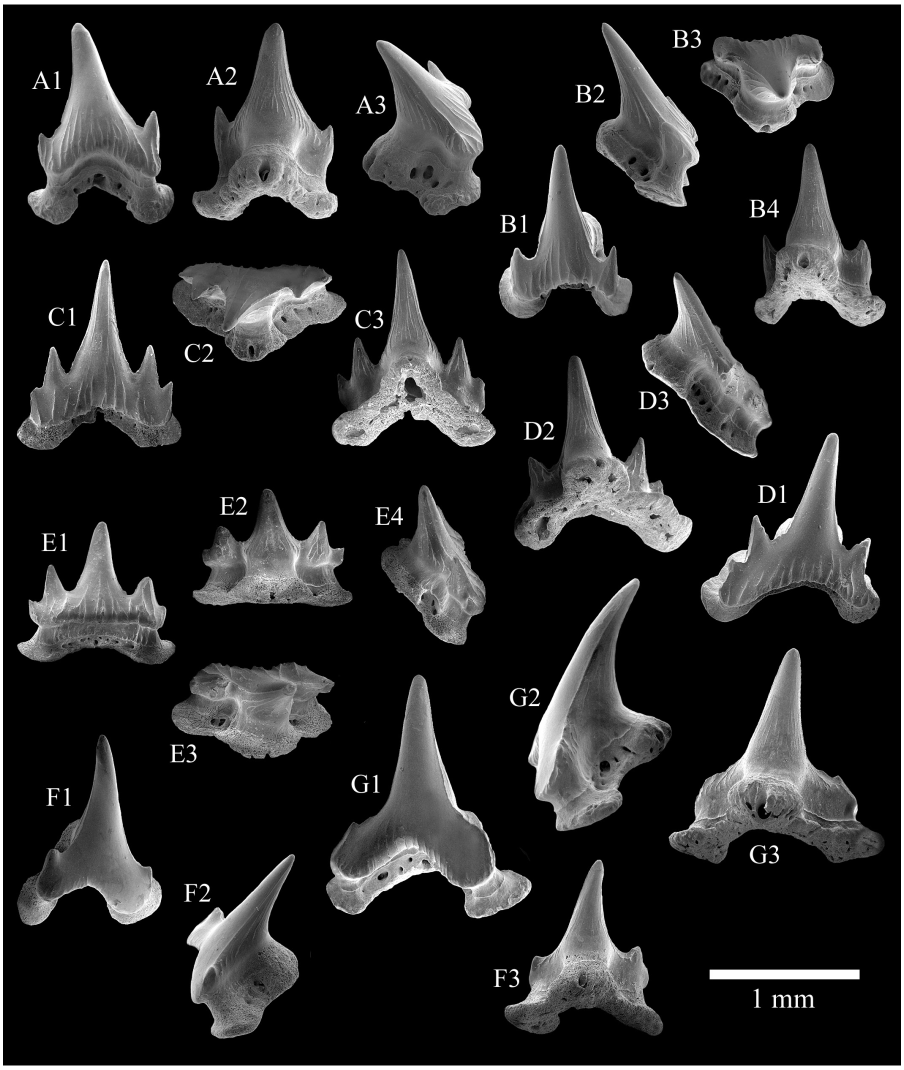

Figure 2. *Scyliorhinus biformis* nov. sp. Sülstorf Beds, Chattian, sandpit "Thomas Beton", Kobrow, Mecklenburg-Vorpommern, Germany. **A.** anterior tooth, H = 1.4 mm, W = 1.1 mm, A1 labial view, A2 lingual view, A3 distal view, SMF P 9808. **B.** anterior tooth, H = 1.3 mm, W = 1.0 mm, B1 labial view, B2 profile view, B3 occlusal view, B4 lingual view, SMF P 9805, paratype 1. **C.** anterolateral tooth, H = 1.4 mm, W = 1.1 mm, C1 labial view, C2 occlusal view, C3 lingual view, SMF P 9804, holotype. **D.** anterolateral tooth, H = 1.4 mm, W = 1.3 mm, D1 labial view, D2 lingual view, D3 mesial view, SMF P 9809. **E.** lateroposterior tooth, H = 1.0 mm, W = 1.1 mm, E1 labial view, E2 lingual view, E3 occlusal view, E4 profile view, SMF P 9810. **F.** anterolateral tooth, H = 1.4 mm, W = 1.1 mm, F1 labial view, F2 profile view, F3 lingual view, SMF P 9811. **G.** anterolateral tooth, H = 1.8 mm, W = 1.4 mm, G1 labial view, G2 profile view, G3 lingual view, SMF P 9806, paratype 2.

fer from these by the presence of much weaker ridges (being absent in some specimens) on the lowermost part of the labial crown face. The ornamentation of the lingual crown face is comparable to that of the female morph. The height of the cusplets in the male morph is quite variable. Some teeth lack cusplets on the mesial or distal heel (Fig. 2G), others have low, blunt cusplets on either sides (Fig. 2F) or display sharp cusplets which are as high as those observed in the female morph (Figs 3A, 3B). These differences are apparently not related to gradient monognathic heterodonty.

Two specimens of the female morph were chosen and defined as holotype and first paratype (Figs 2C, 2B), and two specimens of the male morph as second and third paratypes (Fig. 2G and Fig. 3A).

Differential diagnosis

We compared the teeth of S. *biformis* with all illustrated species, based on isolated teeth or on skeletons with preserved dentition, that Cappetta (2006) referred to *Scyliorhinus* sensu stricto, or have been further described since 2006 (Underwood & Ward, 2008; Guinot *et al.*, 2013). Comparison is occasionally hampered by poor quality or small size of illustrations, and more often by the small sample size used in many descriptions, which results in poor information on gradient monognathic, dignathic and/or sexual heterodonty. A few Late Cretaceous species, previously assigned to *Scyliorhinus* (Cappetta, 2006), and now transferred to other genera (Underwood & Ward, 2008; Cappetta, 2012), e.g. *Pseudoscyliorhinus schwarzhansi* Müller & Diedrich, 1991; *Crassescyliorhinus germanicus* (Herman, 1982); and *Prohaploblepharus riegrafi* (Müller, 1989), need not to be considered here, as their dental characters appear to be significantly different from those of *Scyliorhinus* sensu stricto. Closer similarity is only observed between *S. biformis* and the following fossil taxa: *Scyliorhinus arlingtonensis* Cappetta & Case, 1999 from the Cenomanian of Texas, *Scyliorhinus brumavirulensis* Underwood & Ward, 2008 from the Santonian/Campanian of southern England, *Scyliorhinus sulcidens* Noubhani & Cappetta, 1997 from the Thanetian of Morocco, and *Scyliorhinus woodwardi* Cappetta, 1976 from the Ypresian of SE England.

S. arlingtonensis differs from *S. biformis* in the lesser overhang of the labial crown basis, and the presence of longer and more regular ridges on the labial crown face of lateral teeth. Lateral teeth of *S. arlingtonensis* apparently also lack a second pair of cusplets. Teeth of *S. brumavirulensis* can be distinguished from *S. biformis* by their lower, basally broader principal cusp, stouter primary cusplets, less arched basal labial crown margin and root lobes, and by labial ridges reaching apically higher in some anterolateral teeth than in *S. biformis*. Differing from *S. biformis,* the teeth of *S. sulcidens* have only one pair of cusplets in lateral files, exhibit less elongate root lobes and show a pronounced V-shaped axial indentation of the labial crown basis.

A large sample of *S. woodwardi* teeth from the type locality (Burnham-on-Crouch, Essex, England, coll. Reinecke) shows similar dimensions and a similarly wide variation in labial crown ornamentation and cusplet shape as observed in *S. biformis*. Lateroposterior teeth of *S. woodwardi* usually have two pairs of cusplets (or two cusplets mesially and one distally), whereas anterior and lateral teeth either lack cusplets or have very low ones or a moderately high pair. The main distinctive character separating *S. woodwardi* from *S. biformis* is the basally wider and lower principal cusp in anterior teeth of *S. woodwardi.*

Scyliorhinus suelstorfensis nov. sp.

(Fig. 4)

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Derivation of name. after the municipality Sülstorf, near Schwerin, Mecklenburg-Vorpommern which is name-giving for the Chattian Sülstorf Beds.

Holotype. Senckenberg Research Institute and Natural History Museum, SMF P 9815 (Fig. 4B).

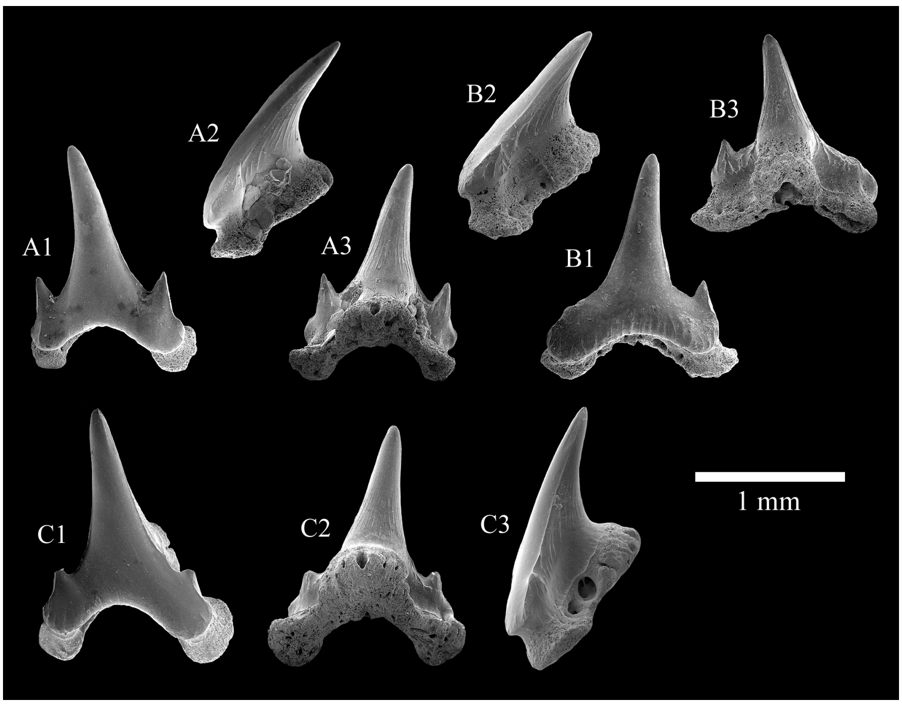

Figure 3. *Scyliorhinus biformis* nov. sp. Sülstorf Beds, Chattian, sandpit “Thomas Beton”, Kobrow, Mecklenburg-Vorpommern, Germany. **A.** anterolateral tooth, H = 1.6 mm, W = 1.2 mm, A1 labial view, A2 mesial view, A3 lingual view, SMF P 9807, paratype 3. **B.** anterolateral tooth, H = 1.5 mm, W = 1.3 mm, B1 labial view, B2 distal view, B3 lingual view, SMF P 9813. **C.** anterolateral tooth, H = 1.8 mm, W = 1.4 mm, C1 labial view, C2 lingual view, C3 mesial view, SMF P 9814.

Paratypes.
1 SMF P 9816 (Fig. 4A)
2 SMF P 9817 (Fig. 4C).
Locus typicus. same as for *Scyliorhinus biformis* nov. sp.
Stratum typicum. same as for *Scyliorhinus biformis* nov. sp.
Age. same as for *Scyliorhinus biformis* nov. sp.
Material. 3 teeth.

Measurements (mm):

	height	width
SMF P 9815 holotype	3.8	3.1
SMF P 9816 paratype 1	3.3	2.7
SMF P 9817 paratype 2	3.0	3.0

Description

The available teeth include two specimens derived from anterior files and one from a lateral file. The holotype (Fig. 4B), an anterior tooth, has a high, upright crown with an acute triangular, conical cusp and one pair of low cusplets. The cusp has similarly convex labial and lingual faces, separated by indistinct, straight cutting edges that extend from the apex to the basis of the cusp. The axially deepened and laterally protruding labial crown basis markedly overhangs the labial root face. The basal labial crown face is ornamented with strong, curved or straight ridges which in apical direction diminish at the height of the cusplets. The lower part of the lingual crown face is covered with very faint ridges. These are more strongly developed on the lingual side of the cusplets.

The root has well separated lobes which are laterally and labially much expanded and well rounded. The lingual protuberance is very distinct. The labial root face is much lower than the margino-lingual root faces. These are strongly deepened and concave below the cusplets and bear 1 or 2 large foramina near the edge with the basal root face. The slightly corroded basal face is rather flat. It is divided by a shallow nutrient groove with two larger foramina in non-central positions. Additional small foramina are scattered on the labial and lingual root faces.

The paratype 1 (Fig. 4A) is morphologically similar to the holotype. The cusp is more slender and its lingual curvature more pronounced. This specimen may therefore come from a more anterior position than the holotype. The paratype 2 (Fig. 4C) represents a lateral file, because the cusp is lower - at similar tooth width as the anterior teeth - and noticeably inclined distally, and the cusplets are sharper and clearly separated from the cusp. The well preserved root shows several foramina near the basis of the labial root face, not seen in the corroded roots of the anterior teeth. All other characteristics, in particular the shape of root lobes and the crown ornamentation, are very similar to those of the anterior teeth.

Differential diagnosis

Only one species of the genus *Scyliorhinus* with average tooth dimensions similar to those of *S. suelstorfensis* nov. sp. is hitherto known from Oligocene and Neogene deposits

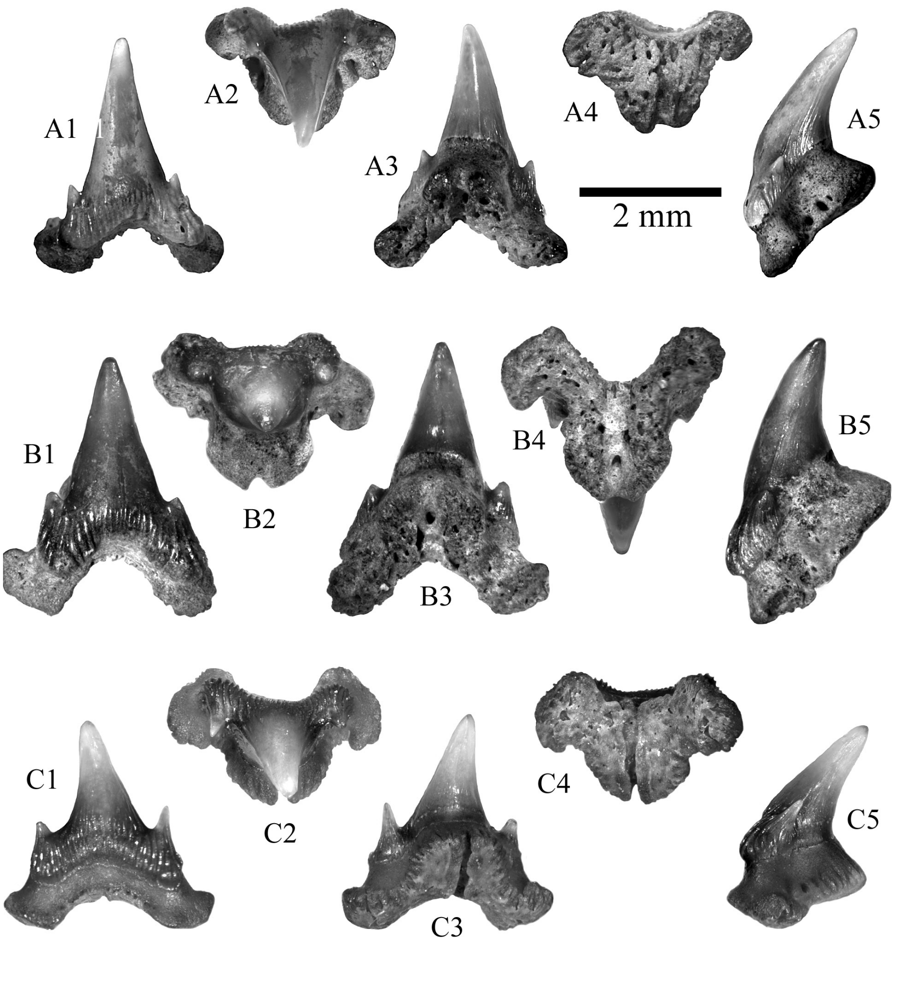

Figure 4. *Scyliorhinus suelstorfensis* nov. sp. Sülstorf Beds, Chattian, sandpit “Thomas Beton”, Kobrow, Mecklenburg-Vorpommern, Germany. **A.** anterolateral tooth, H = 3.3 mm, W = 2.7 mm, A1 labial view, A2 occlusal view, A3 lingual view, A4 basal view, A5 profile view, SMF P 9816, paratype 1. **B.** anterolateral tooth, H = 3.8 mm, W = 3.1 mm, B1 labial view, B2 occlusal view, B3 lingual view, B4 basal view, B5 profile view, SMF P 9815, holotype. **C.** lateral tooth, H = 3.0 mm, W = 3.0 mm, C1 labial view, C2 occlusal view, C3 lingual view, C4 basal view, C5 mesial view, SMF P 9817, paratype 2.

of the North Atlantic region including the North Sea Basin: *Scyliorhinus coupatezi* Herman, 1975, occurring in the early Pliocene Kattendijk Formation of northern Belgium (Herman, 1975: 23 and plate 2, fig. 4a-d; refigured by Hovestadt & Hovestadt-Euler, 1995: plate 10), differs from *S. suelstorfensis* by the partial lack of cusplets, the wider principal cusp and weaker ornamentation of the basal labial crown face in anterior teeth, and by the wider crown basis and presence of 2-3 pairs of cusplets in lateral teeth. In the Chattian and Aquitanian of the North Sea Basin, the larger scyliorhinids *Pachyscyllium braaschi* Reinecke *et al.,* 2005 and *Pachyscyllium* aff. *distans* (Probst, 1879) occur which are easily distinguishable from *S. suelstorfensis*. The cusplets in anterior and lateral teeth of *P. braaschi* and *P.* aff. *distans* (Reinecke *et al.*, 2005: plates 32-34) are wider, often less cuspidate, in *P.* aff. *distans* also proportionally higher, and more laterally and basally placed than in *S. suelstorfensis.* Dissimilar to *S. suelstorfensis*, the crown faces in teeth of *P. braaschi* are almost smooth, whereas the labial and lingual crown ornamentation in *P.* aff. *distans* may be similar to *S. suelstorfensis*. Finally, the root lobes in *S. suelstorfensis* are significantly wider than the crown basis and have a more lobate shape than teeth of *P. braaschi* and *P.* aff. *distans*.

DISCUSSION

The dental characters of the new taxa *biformis* and *suelstorfensis* are concordant with those of the genus *Scyliorhinus* Blainville, 1816, as given by Halter (1995: 74) and Cappetta (2012: 271) for the type species *Scyliorhinus canicula* (Linné, 1758). These are the variable height and number of cusplets due to gradient and sexual heterodonty, the details of labial and lingual crown ornamentation, the strong labial crown overhang, the anaulacorhize, hemiaulacorhize or rarely holaulacorhize root vascularization and the bulky lingual protuberance of the root. Our tooth material of *Scyliorhinus biformis* nov. sp. and *S. suelstorfensis* nov. sp. does not support evidence for dignathic heterodonty. This may be due to the minor number of teeth collected, but more probably the teeth do not impose a bias towards homodonty, because dignathic heterodonty is commonly poorly developed in recent scyliorhinids (Herman *et al.*, 1990; Halter, 1995; Soldo *et al.*, 2000). The degree of ontogenetic heterodonty in the two species is unknown, because teeth being much smaller than the bulk of the material were not found in the 0.5-1.0 mm fraction. For *S. suelstorfensis,* the material basis is rather low, but the few specimens acceptably define gradient-monognathic heterodonty and have concordant dental characteristics that allow a clear distinction from previously described scyliorhinid species.

Authors stated the marked presence of gynandric heterodonty in the Recent smallspotted catshark *Scyliorhinus canicula* (Herman *et al.,* 1990; Ellis & Shackley, 1995; Cappetta, 2012: 272) and several other scyliorhinids (Compagno, 1988: 34), but also noted its absence in dentitions of the Recent nursehound *Scyliorhinus stellaris* (Linné, 1758) (Soldo *et al.*, 2000). In *S. canicula,* the teeth of females tend to have high, sharp cusplets and distinctive labial ridges that may cover nearly the whole labial crown face. Teeth of male individuals are characterized by fewer, weaker and shorter ridges restricted to the lowermost region of the labial crown face, by more strongly arched roots, and by lower cusplets that may be missing in anterior teeth (Herman *et al.*, 1990: plates 32-33; Cappetta, 2012: fig. 252). These differences are also reflected in the dental morphologies observed in *S. biformis*. I therefore suggest that the two morphs derive from female and male individuals. A conservative approach would likely define two different species, but the co-occurrence of two similarly abundant taxa with dentitions of similar size and degree of specialization, likely occupying the same ecological niche, seems implausible.

Miocene representatives of the genus *Scyliorhinus* with closer relationship to *S. suelstorfensis* nov. sp. occur in the Miste Bed, early Langhian, at Winterswijk-Miste, The Netherlands (Bor *et al.*, 2012: *Scyliorhinus* sp.). *Scyliorhinus* sp. has one pair of low, conical cusplets in anterolateral teeth, but two mesial cusplets and one distal cusplet in lateroposterior teeth (Bor *et al.*, 2012: plate 24). Different from *S. suelstorfensis* nov. sp., the longitudinal ridges of the labial crown face are weaker and the mesial and distal margins of the cusp in anterolateral teeth of *Scyliorhinus* sp. are sensibly concave in labial view, rather than straight in *S. suelstorfensis.* Other dental characteristics of the two taxa are so similar, that *Scyliorhinus* sp. can be regarded as descendent of S. *suelstorfensis*.

From the Kerniel Sands Member, early Rupelian, of north-eastern Belgium, Baut & Génault (1999: 29 and text-fig. 14) described a few teeth, 3-4 mm high, as *Scyliorhinus* sp., which also have characteristics similar to *S. suelstorfensis*. One anterior tooth with corroded root lobes and a triangular cusp lacking cusplets illustrated by Baut & Génault (op. cit., text-fig. 14) is similar to the holotype of *S. suelstorfensis* with respect to crown shape and ornamentation. Another specimen (not illustrated) is reported to have a single pair of cusplets. On basis of the description and illustration I can not decide, if *Scyliorhinus* sp. from the Kerniel Sands is conspecific with *S. suelstorfensis*.

Another, still unnamed species is reported from the Alzey Formation, Rupelian, of the Mainz Basin as *Scyliorhinus* ex gr. *stellaris* (Linné, 1758) (Von der Hocht, 1978, 1986) or *Scyliorhinus* aff. *coupatezi* Herman, 1975 (Reinecke *et al.*, 2001). It is different from *S. suelstorfensis* and *S. biformis* by a distally more inclined cusp, 1-3 pairs of sharp cusplets, the presence of longer and more flexuous ridges on the labial crown face, and a wider crown basis in lateral teeth (Reinecke *et al.*, 2001: plate 40; Schindler *et al.*, 2009: fig. 9e).

In the Paleogene of the North Sea Basin and North Atlantic region, several scyliorhinid taxa were recognized and assigned to the genera *Apristurus, Casieria*, *Foumtizia*, *Megascyliorhinus, Microscyliorhinus, Pachyscyllium, Platyrhizoscyllium, Porodermoides, Premontreia,* and *Scyliorhinus* (e.g. Noubhani & Cappetta, 1997; Cappetta, 1976; Cappetta & Ward, 1977; Adnet, 2006; Cappetta, 2012), but none of these are comparable with *S. suelstorfensis* or *S. biformis.*

Presently, *S. biformis* nov. sp. and *S. suelstorfensis* nov. sp. are only known from the southern North Sea Basin. In addition to the Sülstorf Beds (early/middle Chattian) *S. biformis* is rarely observed in the Chattian Silt (latest Chattian) at Johannistal, Schleswig-Holstein (Haye *et al.*, 2008, as *Scyliorhinus* sp.), in the Vierlande Finesands, regional Vierlandian stage (Aquitanian to early Burdigalian) cored in a well at Kaköhl, north-eastern Schleswig-Holstein; Reinecke *et al.*, 2008) and in sandstones of the same age occurring as boulders in glaciofluvial sand and gravel deposits of eastern Schleswig-Holstein (Reinecke *et al.*, 2008; Reinecke, 2013: as *Scyliorhinus* sp.). *S. biformis* seems to be also present in the Kakert Beds, regional Vierlandian stage (Aquitanian) of the Lower Rhine Embayment (Reinecke *et al.*, 2008: as *Scyliorhinus* sp.), but is definitely absent from deposits of the regional Hemmoor stage (middle to late Burdigalian and early Langhian) of the southern North Sea

Basin (Reinecke *et al.*, 2011; Bor *et al.*, 2012), which yield a scyliorhinid assemblage with *Scyliorhinus joleaudi* Cappetta, 1970, *Scyliorhinus* sp. sensu Bor *et al.* 2012, *Pachyscyllium dachiardii* (Lawley, 1876), and *Pachyscyllium distans* (Probst, 1879). Opposed to Cappetta (2012: 267) who designates *P. distans* as junior synonym of *Pachyscyllium dachiardii,* I consider *P. distans* as discrete species (Reinecke *et al.*, 2011: 53).

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