MIDDLE EOCENE SHARK COPROLITES FROM SHALLOW MARINE AND DELTAIC COASTS OF THE PRE-NORTH SEA BASIN IN CENTRAL EUROPE

CAJUS G. DIEDRICH[1] AND HORST FELKER[2]

[1] PaleoLogic, Research Institute, Nansenstrasse 8, D-33790 Halle/Westphalia, Germany;
[2] Bersenbrücker Strasse 12, D-49577 Ankum, Germany

Abstract—Middle Eocene (Paleogene, Cenozoic) transgressive marine conglomerates of two German localities in the southern Pre-North Sea basin of Central Europe contain a large number of more then 19 different large- to medium-sized shark taxa (teeth size > 4 mm). Only 0.05% of the vertebrate remains are shark coprolites (n = 556), which can be classified in five main types, most having a heteropolar-spirally-coiled morphology. These are classified into five different main shape types. Possibly the largest forms (Type A), in part containing medium-sized fish bones and vertebrae, belong to megatooth and white shark ancestors (*Otodus*, *Carcharocles*, *Procarcharodon*), whereas the most abundant, medium-sized variable forms (Type B) might have been produced by laminid sharks (*Isurus*, *Jaeckelotodus*, *Xiphodolamia*, *Brachycarcharias*, *Hypotodus*, *Sylvestrilamia*), but the very abundant sand shark ancestor *Striatolamia* is expected as their main producer. Type C is rare and a thin-elongated form with zigzag-heteropolar external structure (producers: ?rays/small-sized carchariniform sharks such as *Galeocerdo*, *Pachygaleus*). The smaller, including the smallest (only 3 mm) oval-round pellets, and also the unclearly heteropolar Type D oval- to round-shaped pellets have only poorly developed surface coil structures, and are preliminarily referred to sharks or rays. Rare, irregularly-formed excrement can be referred preliminarily to a crocodile producer, which supports the deltaic distal position of the Dalum site, and more shallow marine position of the Osteroden locality. At the latter, larger shark coprolites (Type A) are much more abundant, indicating more shallow marine environments, whereas at Dalum a mixture of shallow marine and deltaic palaeoenvironments were present during the Middle Eocene of the southern Pre-North Sea Basin of Central Europe.

INTRODUCTION

Modern shark excrement is well-known based on their shape resulting from a special intestine shape in sharks and rays (Fiedler, 1991), which is also demonstrated by modern faeces experiments (McAllister, 1985). From the Mesozoic and Cenozoic fossil record, only very few publications reported and analyzed or partly classified shark excrement (Buckland, 1829; Broughton, et al., 1977; Jain, 1983; McAllister, 1985; Hunt et al., 1994; Northwood, 2005; Månsby, 2009; King, 2011; Erikkson et al., 2011). Those works did not attribute fossil shark coprolites to their exact shark producer--genera or even species. A modern analysis comparing modern shark coprolites to fossil ones is lacking and will be the only solution to the better identification of fossil excrement, which will be based on their shapes. A few different-shaped fossil Tertiary shark coprolites have been described from the marine Danian (Paleogene) deposits of Denmark (Milàn, 2011). Late Eocene material was preliminarily published with more then 1000 excrement specimens found in the marine central Gulf Coast deposits of North America, but those have not yet been presented in detail (King, 2011).

Here, a large number (556 coprolites) of undescribed Early to Middle Eocene (Paleogene) shark faeces from the two marine sites Dalum and Osteroden in northwestern Germany from the Pre-North Sea Basin (Fig. 1; Diedrich, 2012) is presented with a morphological study to classify those into morphological types, and with an attempt to attribute them to sharks at the ordinal level. The different-shaped coprolites are used in a statistical analysis for palaeoenvironmental and palaeoecological interpretations of sharks. The qualitative and quantitative statistics of different coprolite types is compared to the preliminarily studied shark tooth material of 6946 identified teeth of 19 taxa (Diedrich, 2012).

GEOLOGY AND SEDIMENTOLOGY

The Tertiary sediments of the two sites Dalum and Osteroden in the called Ankumer Mountains of northwestern Germany were deformed and compressed as a result of Middle Pleistocene glacial tectonics, which caused the Eocene sediments (marine Fürstenau Formation which is exposed over a thickness of about 22 meters) at the Dalum and Osteroden sites to be strongly folded (Diedrich, 2012; Fig. 1). The shark-fossil-bearing marine siliciclastic series consist of slightly glauconitic marine sands, with thinly-bedded sandstone layers which are overlain by 1 to 2 meters of thick gray-green clays with lenses of glauconitic sand (possibly still Early Eocene). The top of the clays has been eroded and covered by the shark-tooth and coprolite-rich conglomerate bed, which is up to 40 cm thick at Osteroden and 80 cm thick at Dalum (Diedrich, 2012). These vertebrate-rich conglomerates are of basal Lutetian (basal Middle Eocene) age and are decalcified at Dalum but are slightly calcareous at Osteroden, where they contain calcareous shells of marine invertebrates (Diedrich, 2012). The conglomerates above the middle Middle Eocene marine glauconitic sands (NP 15 Zone) are composed of at least seven parasequence sets which are highly bioturbated by crustaceans (mainly *Ophiomorpha* burrows), and their potential crustacean producers are also found within phosphorite nodules in the gravels (Diedrich, 2012).

MATERIAL AND METHODS

In May 2011, a four-day field program using heavy-machinery was completed at the Dalum and Osteroden marine vertebrate sites (Fig. 1), where a total amount of 180 cubic meters of conglomeratic material was excavated from the Dalum site for sieving. Only 250 buckets (10 liters each) were sieved (i.e., only 0.1 % of the recovered material). In total, 14,437 fossils were recovered and studied, of which 95% are shark teeth and only 0.05% are coprolites (n = 42). About half of the 13,683 shark teeth recovered were identified (Diedrich, 2012). Additionally, larger amounts of 514 coprolites from Dalum and fewer specimens from Osteoden (coll. H. Felker, n = 514: 26 specimens from Osteroden, and 488 specimens from Dalum) were included. All the material described and illustrated here is housed in the Shark Center, Bippen (SCB) in the UNESCO Geopark Terra-Vita.

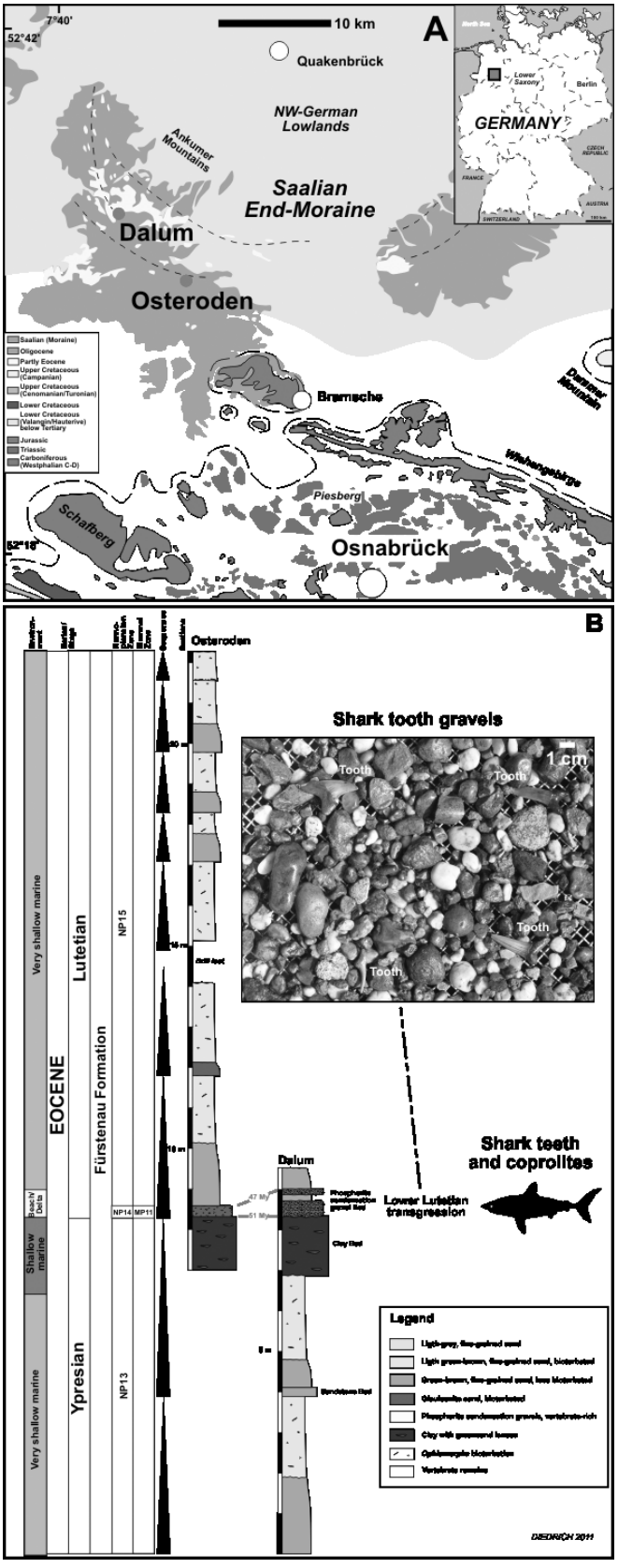

FIGURE 1. **A**, Ankumer Mountains and Tertiary deposits with the two shark localities Dalum and Osteroden in NW-Germany, and **B**, Lutetian (Middle Eocene) vertebrate and shark-tooth-rich localities Dalum and Osteroden, Germany, and other shark localities in the Eocene Pre-North Sea Basin of Central Europe (modified from Diedrich, 2012).

PALEONTOLOGY

The heteropolar-spirally-coiled form of shark coprolite and excrement is the result of the spiral-stomach, such as is demonstrated here for a modern nurse shark valvular intestine (Fig. 2A). The terminology of the fossil coprolites is shown in Fig. 2B. The shape of the excrement can vary, especially in the number of added coils (Fig. 2C), but it can also be the result of the different-shaped valvular intestines of different taxa (King, 2011). Therefore, only large samples of pellets must be used to distinguish growth forms and forms of different taxa. Spiral coprolites tend to have moderately distinct to well-defined twisting patterns externally, which are used here to distinguish at least some main forms with narrow and wide spirals. Major external features of the scroll coprolites were the moderately incised to deeply incised, very distinctive folds and grooves. The key differences in the spiral and scroll coprolites are the twisting features versus fold and groove features and the orientation of these structures (width versus length, after King, 2011). In total, 556 heteropolar-spirally-coiled shark coprolites of different sizes between 5 mm and 10 cm are separated here based on those characteristics into five main forms following the descriptions based only on external morphological features (Figs. 3-6):

Type A (Figs. 3.1-3.9): Those more rare forms are up to 70 mm in length and can reach a maximum width of 50 mm. The coils are not more then three, clearly-developed ones in complete specimens (Figs. 3.3b, 3.4b), which are wide. Proximally the spiral folds and groves are less clearly developed (Figs. 3.3a, 3.4a); instead, distally the coiling is "snail-like" and wide (Figs. 3.3c, 3.4c). In cross section in the middle of the excrement these coprolites are nearly round, if not compressed. In some cases, medium-sized fish bones and vertebrae are inclusions of the last prey taken (Figs. 3.5-3.6).

Type B (Figs. 4.1-4.27): The most abundant coprolite types, which have 4-20 short-distance coils, are highly variable in their width and length, which is certainly also a result of coprolite growth (Fig. 2C). This type can be subdivided into four preliminary subtypes. 1. The first is the largest and reaches up to 40 mm in length and 30 mm in width and has less coils, up to 7 (Fig. 4.1-4.7). 2. A second most abundant type is slimmer and elongated, medium-sized (about 25 mm in width, length variable depending on the coil amounts, but maximum is 40 mm in length). The coil amounts also depend on the growth stage of the excrement, but do not exceed 12 (Figs. 2C, 4.13). 3. A third medium-sized subtype is slim and more elongated (Figs. 4.16-4.18), and reaches 16 mm in width and 45 mm in length. 4. Another quite different subtype is "small cone shaped" (Figs. 4.19. 4.24, 4.26). Those measure only 20 mm in length and 15 mm in width. Those short forms have more distinct and sculptured coil layers – whereas also the proximal area is differently developed, which makes the proximal and distal side identification problematic. A clear proximal last coil with sinuous folds is absent, such as in all other subtypes of Type B.

Type C (Fig. 5. 1): A rare form is elongated and only 5 mm in width and has an indeterminate maximum length. The coils are not spindle-like - they cross each other at about 45° angles.

Type D (Figs. 5.2-5.7): The second most abundant types are small, round-oval to high-oval shaped feces that reach maximum sizes of 20 mm in length and 8 mm in width. The surfaces lack clear, distinct coils, but surface ornamentation is quite similar to type E.

Type E (Fig. 5.8): A last and most tiny round-oval form is only 3 mm in length and width. These also those have some spiral-like folding as in the above mentioned type D.

DISCUSSION

Phosphatic vertebrate coprolites are described and figured from the Early Lutetian (Middle Eocene) freshwater lake site Messel (Wuttke, 1988), which were identified as irregular crocodile and amphipolar-shaped fish excrement. There are two main types figured, whereas here a single incomplete large coprolite of Dalum (Fig. 5.9) must be referred prelimi-

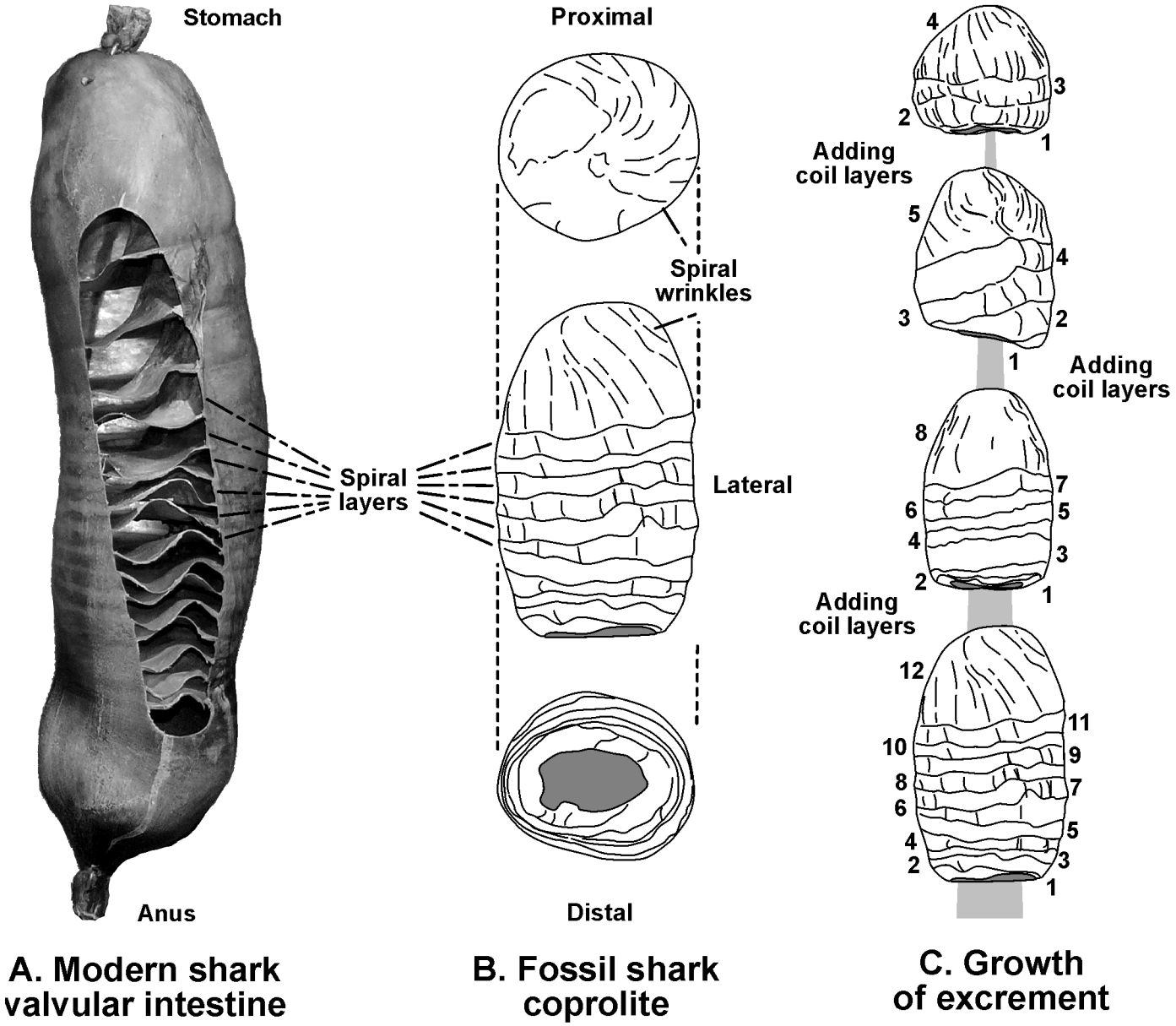

FIGURE 2. **A**, The spiral valve of a nurse shark (*Ginglymostoma cirratum*, photo source: Aquazoo Löbbecke Düsseldorf). **B**, Fossil coprolite from the Lutetian (Middle Eocene) locality Dalum, Germany, and coprolite terminology. **C**, Growth stages of fossil coprolites from the Lutetian (Middle Eocene) locality Dalum, Germany.

narily as an irregular shaped large form to freshwater crocodiles, which are also represented by a few teeth and osteoderm plate fragments from Dalum Delta (Diedrich, 2012), whereas also other rare mammal tooth remains (Franzen and Mörs, 2007) were washed into this delta. Also the oldest seal remains were found on those Pre-Northsea coasts as marine mammals (Diedrich, 2011).

All other coprolitic material (99.9%) from the Dalum and Osteroden shallow marine sites can be referred to sharks with their typical heteropolar, spindle-like forms following the descriptions of fossil Mesozoic shark coprolites (cf. Buckland, 1929; McAllister, 1985; Milàn, 2011; King, 2011). Spiral coprolites in general have long been identified as feces produced by primitive fish (Hunt et al., 1994; Northwood, 2005). The spiralling is a result of the fecal matter passing a spiral intestinal valve (Fig. 2), which has been seen in both extant taxa and fossil specimens (Williams, 1972; Jain, 1983). Demonstrated in experiments with extant taxa, sharks or rays have more complex intestinal valves (Parker, 1885) that both produce heteropolar feces. Instead, bony fishes produce differently-shaped, amphipolar feces (McAllister, 1985; Wuttke, 1988; Fiedler, 1991; Hunt et al., 1994; Northwood, 2005).

The Dalum coprolites can be used to distinguish at least five different shape types, A to E, and are all more (Type A-C) or less (Type D-E) heteropolar, spindle-like forms, which are provisionally attributed here to their shark producers, but only on the order level at the moment (Fig. 6D). The largest forms (Type A) correlate to the largest carcharodontoform sharks, megatooth and white shark ancestors (*Otodus*, *Carcharocles*, *Procarcharodon*), which are well known from Dalum (Diedrich, 2012). The most abundant medium-sized forms (Type B) seem to have been produced by different medium-sized lamnid sharks such as are found at Dalum (*Isurus*, *Jaeckelotodus*, *Xiphodolamia*, *Brachycarcharias*, *Hypotodus*, *Sylvestrilamia*; Diedrich, 2012). The high abundance of this Type B coprolite correlates well to the high amounts of teeth of the sand shark ancestor *Striatolamia* (Diedrich, 2012; Fig. 6B). Therefore, the Type B subtype 2 as the most abundant coprolite in the Dalum material is expected to be the product of this shark species.

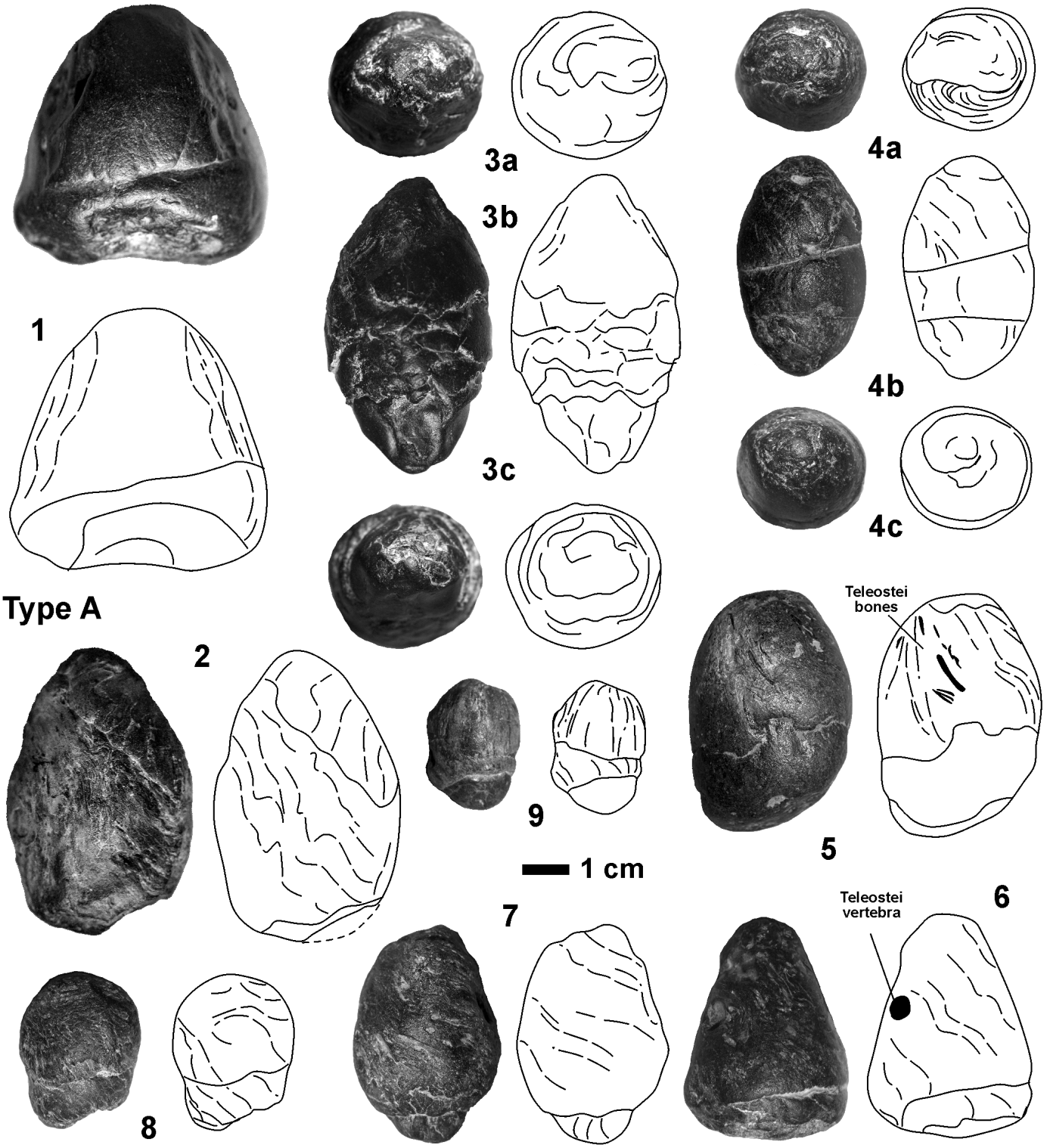

FIGURE 3. Large heteropolar, spirally-coiled coprolite types with 3-4 wide-distance coils (Type A) partly with fish remains from the Lutetian (Middle Eocene) localities Dalum and Osteroden, Germany. **1**, Largest specimen ever found from Osteroden (SCB no. Ost-SelKopr-3), lateral. **2**, Second largest specimen from Osteroden (SCB no. Ost-SelKopr-2), lateral. **3**, Large specimen from Osteroden (SCB no. Ost-SelKopr-1), **a**, proximal, **b**, lateral, **c**, distal. **4**, Medium–sized specimen from Osteroden (SCB no. Ost-SelKopr-5), **a**, proximal, **b**, lateral, **c**, distal. **5**, Medium–sized specimen with fish bones from Dalum (SCB no. Dal-SelKopr-1), lateral. **6**, Large specimen with fish vertebra from Osteroden (SCB no. Ost-SelKopr-4), lateral. **7**, Medium–sized specimen from Osteroden (SCB no. Ost-SelKopr-6), lateral. **8**, Medium–sized specimen from Osteroden (SCB no. Ost-SelKopr-9), lateral. **9**, Small–sized specimen from Osteroden (SCB no. Ost-SelKopr-7), lateral.

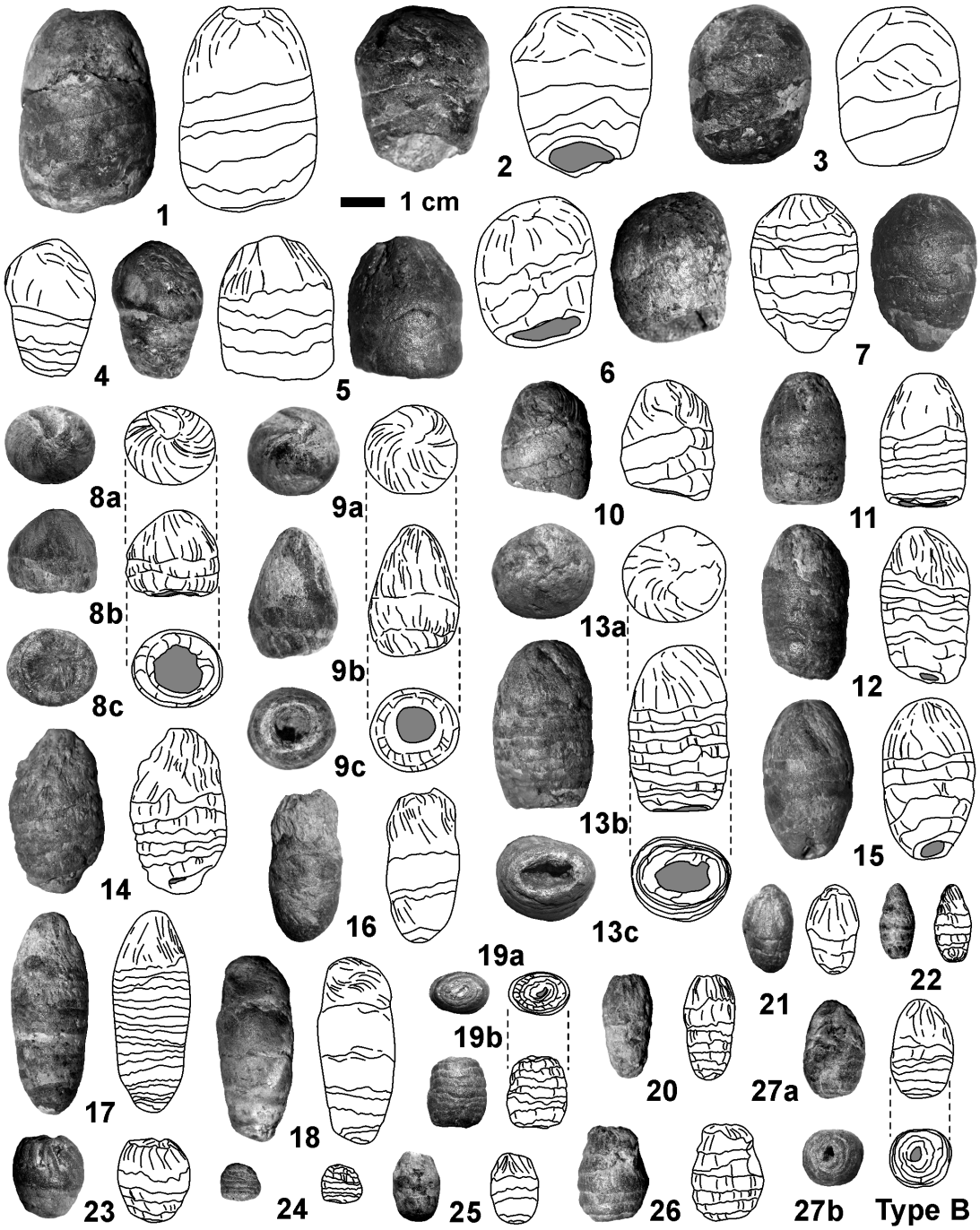

FIGURE 4. Medium-sized heteropolar, spirally-coiled coprolite types with 5-20 wide-distance coils (Type B) from the Lutetian (Middle Eocene) localities Dalum and Osteroden, Germany. **1**, Large specimen from Dalum (SCB no. Dal-SelKopr-22), lateral. **2**, Large specimen from Osteroden (SCB no. Ost-SelKopr-7), lateral. **3**, Large specimen from Osteroden (SCB no. Ost-SelKopr-8), lateral. **4**, Large specimen from Osteroden (SCB no. Ost-SelKopr-19), lateral. **5**, Large specimen from Dalum (SCB no. Dal-SelKopr-2), lateral. **6**, Large specimen from Dalum (SCB no. Dal-SelKopr-9), lateral. **7**, Large specimen from Osteroden (SCB no. Ost-SelKopr-20), lateral. **8**, Elongated specimen from Dalum (SCB no. Dal Sel-891), lateral. **9**, Elongated specimen from Dalum (SCB no. Dal Sel-890), lateral. **10**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-9), lateral. **11**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-8), lateral. **12**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-5), lateral. **13**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-4), lateral. **14**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-7), lateral. **15**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-3), lateral. **16**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-120), lateral. **17**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-147), lateral. **18**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-138), lateral. **19**, Small type from Dalum (SCB no. Dal-SelKopr-128), lateral. **20**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-129), lateral. **21**, Small type from Dalum (SCB no. Dal-SelKopr-137), lateral. **22**, Elongated specimen from Dalum (SCB no. Dal-SelKopr-119), lateral. **23**, Small type from Dalum (SCB no. Dal-SelKopr-19), lateral. **24**, Small type from Dalum (SCB no. Dal-SelKopr-21), lateral. **25**, Small type from Dalum (SCB no. Dal-SelKopr-118), lateral. **26**, Small type from Dalum (SCB no. Dal-SelKopr-107), lateral. **27**, Small type from Dalum (SCB no. Dal-SelKopr-126), lateral.

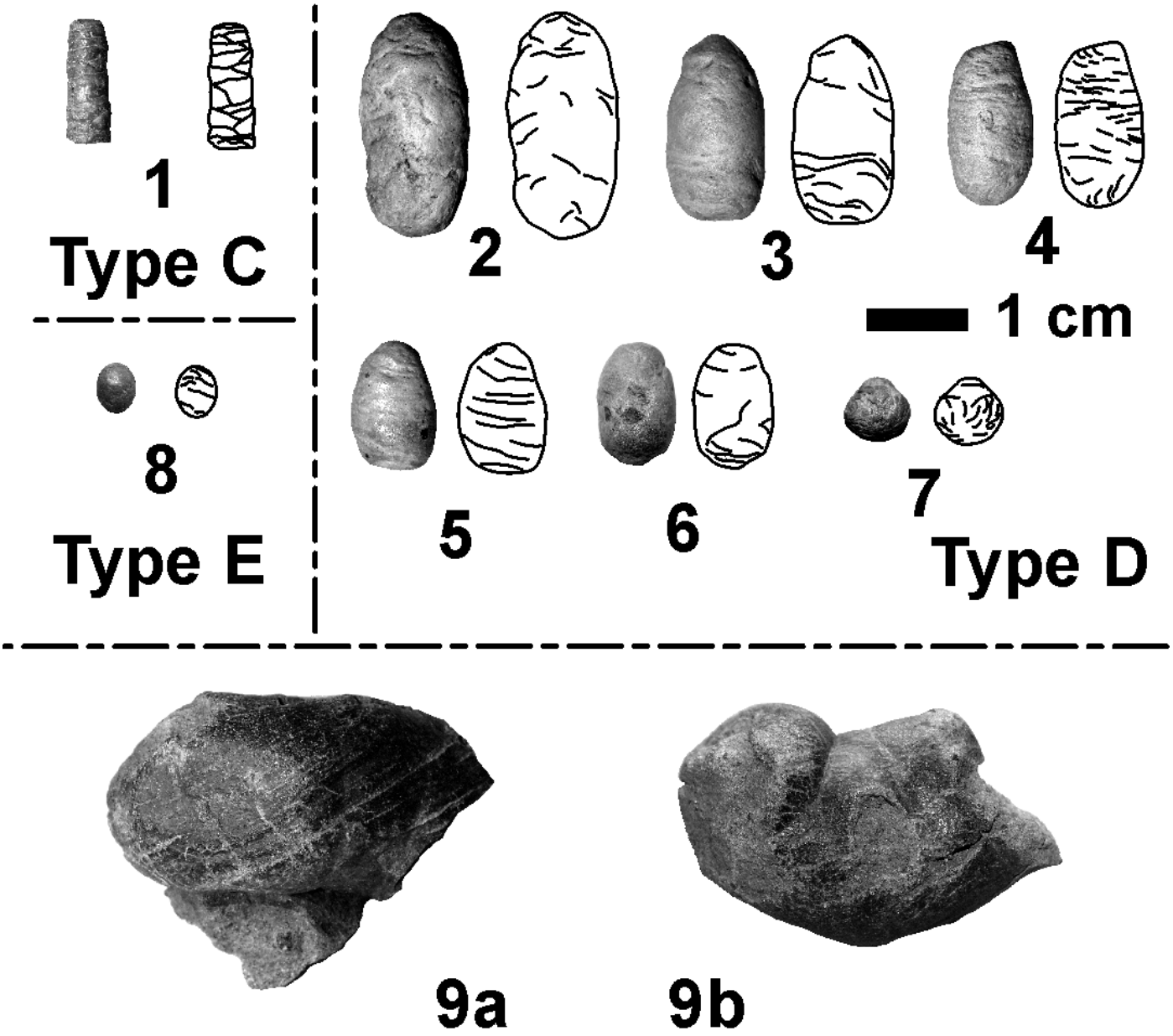

FIGURE 5. Small-sized shark/ray and large reptile coprolite types (Types C-F) from the Lutetian (Middle Eocene) localities Dalum and Osteroden, Germany. **1**, Type C. Elongated zigzag coiled specimen from Dalum (SCB no. Dal-SelKopr-176), lateral. Type D. **2**, High-oval specimen from Dalum (SCB no. Dal-SelKopr-180), lateral. **3**, High-oval specimen from Dalum (SCB no. Dal-SelKopr-179), lateral. **4**, High-oval specimen from Dalum (SCB no. Dal-SelKopr-177), lateral. **5**, Oval specimen from Dalum (SCB no. Dal-SelKopr-184), lateral. **6**, Oval specimen from Dalum (SCB no. Dal-Sel-898), lateral. **7**, Round specimen from Dalum (SCB no. Dal-SelKopr-185), lateral. **8**, Small oval specimen from Dalum (SCB no. Dal-SelKopr-188), lateral. **9**, Fragment of a ?crocodile excrement from Dalum (SCB no. Dal-SelKopr-190), a. lateral, b. side view.

Type C is much more rare, and the thin-elongated form with zigzag-heteropolar external structure is difficult yet to asssign, but may be from rays or small-sized carchariniform sharks such as *Galeocerdo*, or *Pachygaleus*, known in the Dalum fish fauna (Diedrich, 2012). The Type D has no clear heteropolar pellets. Therefore, these smaller, oval- to round-shaped forms are only preliminarily referred to sharks or rays, such as the smallest, 3 mm oval-round pellets (Type E). The latter types D-E cannot be fully excluded from teleostean fish, as was suggested by Erikkson et al. (2011).

The comparison of the few coprolites from Osteroden and the large amount from Dalum is problematic, but obviously in Dalum, where much more material was obtained, the largest forms (Type A) are quite rare, and instead they are 50% of the excrement at Osteroden (Fig. 6B). This might be useful for palaeoenvironmental reconstruction, because Dalum was in a distal deltaic situation, whereas Osteroden seems to be nearly shallow marine (Diedrich, 2011; Fig. 6C), which is underlined by the coprolite type statistics. The higher abundance of large shark excrement (= large shark predators) would also coincide (Fig. 6D), because those larger megatooth (*Carcharodon*) and white shark (*Procarcharodon*) ancestors were cosmopolitan open marine sharks (Van den Eeckhaut and De Schutter, 2009). These statistics of coprolites have to be tested against the tooth record, which has been analyzed for Dalum (Fig. 6B), but not yet for the Osteroden site.

However, the Middle Eocene shark excrements do show a quite large number of variable forms, which might relate to at least 19 shark taxa, and several ray species (Fig. 6D). Further material, comparisons to

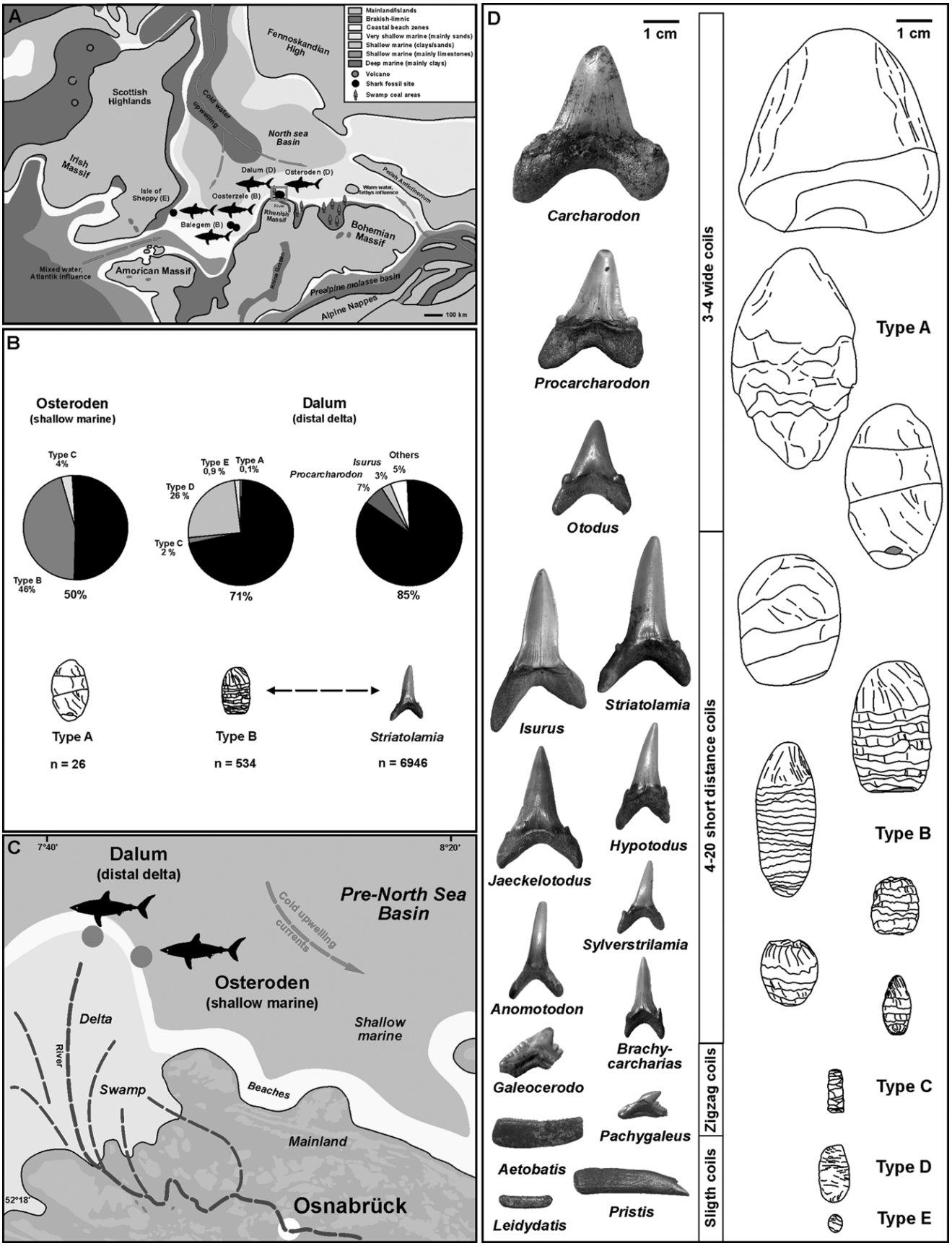

FIGURE 6. **A**, Palaeogeography and shark sites in Central European Pre-North Sea Basin (after Diedrich, 2011). **B**, Correlation between shark species and coprolite abundance, and coprolite type assemblage differences at the two sites Dalum and Osteroden, **C**, Palaeoenvironmental differences at Dalum and Osteroden, **D**, Shark species and main coprolite shape types.

modern shark excrement and possibly geochemical analyses might allow in the future a better attribution of shark coprolites to the exact producer.

CONCLUSION

Five different, morphologically-distinct coprolite types (Type A-E) from the marine and deltaic influenced Middle Eocene Pre-North Sea basin coastal gravels of Dalum and Osteroden (Germany) can be definitely referred to sharks, and possibly some forms to rays or even bony fish, and in only one case to crocodiles. The typical shark feces are heteropolar, spirally-coiled phosphatic excrement, which often contain teleost fish remains. The different-shaped forms, which also depend in their forms on the individual sizes and growth stage of the excrement, can be correlated approximately to sharks on the ordinal level at least. The greater abundance of large shark coprolites (Type A) indicates more "open shallow marine" conditions at the Osteroden site; their rareness and the presence of likely crocodile excrement at Dalum support the distal delta position of this site, both close to each other in the Pre-North Sea Basin of Central Europe.

ACKNOWLEDGMENTS

The project was sponsored by the private company "PaleoLogic" and by the "Geo and Naturpark TERRA.Vita" (H. Escher), the Landkreis, Osnabrück. The Kuhlhoff education center leaders Mr. A. Bruns and Mr. W. Hollermann, and the mayor of Bippen, Mr. H. Tolsdorf we thank for installing the field sieving laboratory and for support.

REFERENCES

Broughton, P.L., Simpson, F. and Whitaker, S.H., 1977, Late Cretaceous coprolites from southern Saskatchewan: comments on excretion, plasticity and ichnological nomenclature: Bulletin of Canadian Petroleum Geology, v. 25, p. 1097–1099.

Buckland, W., 1829, On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations: Geological Society of London Transactions, Series 2, v. 3, 223–236.

Diedrich, C., 2011, The world's oldest fossil seal record: Natural Sciences, v. 3, p. 914-920.

Diedrich, C., 2012, Early Eocene (Lutetian) coastal shark-rich deltaic conglomerate palaeoenvironments of NW-Germany – the marine Fürstenau Fm biodiversity of the southern European Northsea Basin: International Journal of Oceanography, v. 2012, doi:10.1155/2012/565326, 22 p.

Erikkson, M.E., Lindgreen, J., Chin, K. and Mânsby, U., 2011, Coprolite morphotypes from the Upper Cretaceous of Sweden: Novel views on an ancient ecosystem and implications for coprolite taphonomy: Lethaia, v. 44, p. 455-468.

Fiedler, K., 1991, Lehrbuch der Speziellen Zoologie, Band II, Teil 2: Fisch. Gustav Fischer Verlag Jena.

Franzen, J.L. and Mörs, T., 2007, Das nördlichste Vorkommen paläogener Säugetiere in Europa: Paläontologische Zeitschrift, v. 81, p. 447-456.

Hunt, A.P., Chin, K. and Lockley, M. G., 1994, The palaeobiology of vertebrate coprolites; *in* Donovan, S.K., ed., The Palaeobiology of Trace Fossils: Chichester John Wiley, p. 221-240.

King, L., 2011, Further studies on Late Eocene shark coprolites from the Yazoo Clay in northern Lousiana: Geological Society of America, Abstracts with Programs, v. 43, p. 7.

Jain, S.L., 1983, Spirally coiled coprolites from the Upper Triassic Maleri Formation, India: Palaeontology, v. 26, p. 813-829.

Månsby, U., 2009, Late Cretaceous coprolites from the Kristianstad Basin, southern Sweden: Unpublished thesis, Lunds University, Sweden, p. 19.

McAllister, J.A., 1985, Reevaluation of spiral coprolites: University of Kansas, Paleontological Contributions, v. 144, p. 1-12.

Milàn, J., 2011, Coprolites from the Danian limestone (Lower Paleocene) of Faxe quarry, Denmark: New Mexico Museum of Natural History and Science, Bulletin 51, p. 215-226.

Northwood, C., 2005, Early Triassic coprolites from Australia and their palaeobiological significance: Palaeontology, v. 48, p. 49-68.

Parker, T.J., 1885, On the intestine spiral valve in the genus *Raja*: Transactions of the Zoological Society London, v. 11, p. 49-61.

Rayner, D, Mitchel, T., Rayner, M. and Clouter, F., 2009. London Clay fossils of Kent and Essex: Kent, Caxton and Holmesdale Press, Medway Fossil and Mineral Society, 228 p.

Van den Eeckhaut, G. and De Schutter, P., 2009. The elasmobranch fauna of the Lede Sand Formation at Osterzele (Lutetian, Middle Eocene of Belgium): Palaeofocus, v. 1, p. 1-57.

Williams, M.E., 1972, The origin of spiral coprolites: University of Kansas Paleontological Contributions, v. 59, p. 1–19.

Wuttke, M., 1988, Erhaltung, Lösung Umbau – zum Verhalten biogener Stoffe bei der Fossilisation; in. Schaal, S. and Ziegler, W., eds., Messel – ein Schaufenster in die Geschichte der Erde und des Lebens: Frankfurt am Mein, Waldemar Kramer,, p. 265-275.