

An almost complete specimen of the Late Cretaceous (Campanian) octocoral '*Isis*' *ramosa* Voigt (Gorgonacea) from the Lower Saxony Basin, northwest Germany

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Abstract

An almost completely preserved specimen of the octocoral '*Isis*' *ramosa* (Mitteil. Geol. Staatsinst. Hamburg 27 (1958) 5) (Gorgonacea) is described. The specimen was found in Campanian strata in the Lower Saxony Basin near Hannover (NW Germany), presumably in the *Pachydiscus stobaeilGaleola basiplanata* Zone of the regional northwest German zonation. It consists of a small, rigid, fan-shaped corallum that was formerly known only from a few poorly preserved fragments. This feature separates '*I.*' *ramosa* significantly from related extant Isididae that expose a corallum subdivided into calcified internodes and horny nodes. 'Isidid' species from deeper shelf settings with rigid branches and a presumed articulation only between root system and fan are interpreted as ancestral to extant gorgonaceans.

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Keywords: Octocorallia; Gorgonacea; Campanian; Late Cretaceous; Northwestern Germany

1. Introduction

Octocorals are marine, mostly fixosessile anthozoans that are poorly sclerotized. Their hard tissues consist of either isolated sclerites or compound horny and calcified axes. Some types have also developed skeletons that consist of fibrous or even massive calcite (Family Helioporidae; Löser, 1993), while others lack any preservable skeleton. Consequently, fossil octocoral specimens in most cases are preserved as separated sclerites or fragments of the partly calcified axes. Thus, descriptions of fossil octocoral taxa are generally restricted to the limited diagnostic features displayed by these fragments and sclerites (e.g., Deflandre-Rigaud, 1957; Voigt, 1958). This has resulted in the use of concurrent parataxonomies, that, for example, consider octocoral bases only (Malecki, 1982). Owing to the lack of a continuous fossil record of complete specimens, fossil octocorals have

only been examined systematically in a limited way (e.g., Ausich & Babcock, 1998). It is presumed that they strongly resemble an early level of the hypothetical 'gallertoid coral' (Grasshoff & Gudo, 1998) and, therefore, represent the most primitive evolutionary stages of extant corals.

The fossil record of octocorals can be traced back to the early Paleozoic (e.g., Lindström, 1978; Bengtson, 1981; Ausich & Babcock, 1998), but the first major burst in diversity is not recorded until strata as young as Cretaceous have been reached. A wide variety of isolated sclerites (e.g., Alexandrowicz, 1977; Herrig et al., 1996) and fragments of calcified internodes (e.g., Nielsen, 1918; Voigt, 1958; Floris, 1979, 1980) as well as the first representatives of massively calcified Helioporidae have been described (Morycowa, 1971; Löser, 1993) from Cretaceous successions.

Octocorals are common in Campanian successions near Hannover in the Lower Saxony Basin, northwest Germany, although their remains chiefly occur as separate bases and few other calcified fragments, as elsewhere in European Upper Cretaceous strata (e.g.,

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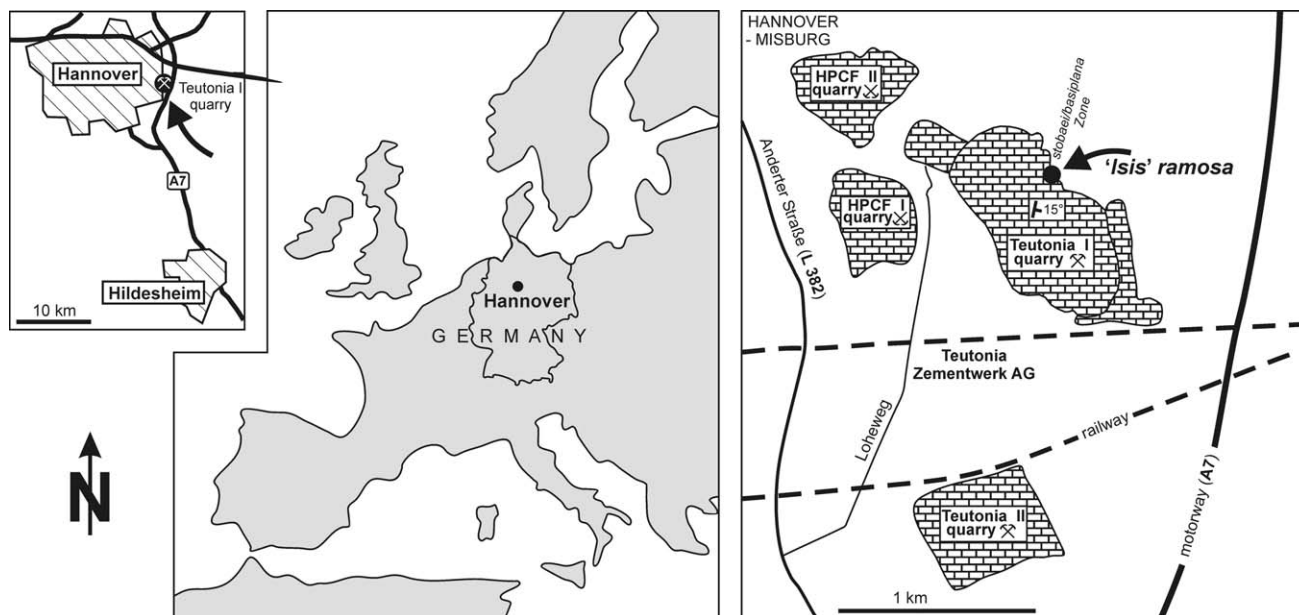


Fig. 1. Location of Teutonia I quarry, east of Hannover, Germany.

Maastrichtian of Rügen, northeast Germany: Nestler, 1982; Kutscher, 1998; Campanian of Hannover, northern Germany: König, 1991; Campanian near Cracow, Poland: Malecki, 1982). Applying the parataxonomy of Malecki (1982) that is based on octocoral bases from the Polish Campanian, König (1991) distinguished a wide variety of different taxa which in terms of diversity closely resemble the Polish material. Fragments other than bases were also identified, but were not correlated with the octocoral bases. In our study, we present the first completely preserved specimen of *'Isis' ramosa*, a species first described by Voigt (1958) based on fragmented calcified internodes. Unfortunately, our specimen lacks a base, so that a correlation with the respective 'base-parataxonomy' is not possible.

2. Geological setting

Late Cretaceous strata in southern Lower Saxony crop out in a variety of isolated secondary, marginal depressions of salt structures and intervening synclines (e.g., Ernst et al., 1997; Niebuhr et al., 1997; Niebuhr, 1999, and references therein). Our octocoral specimen comes from the Teutonia I quarry, which is located on the western flank of the Lehrte West syncline, 5 km east of Hannover (grid reference: TK 25 3635 Lehrte, r 3560300, h 5805300; Fig. 1). The Campanian strata exposed dip gently 20–12° ESE, decreasing from base to top of the succession, to the centre of the foredeep of Lehrte salt structure. A Lower to lower Upper Campanian succession about 260 m thick is exposed in the quarry. The section extends from the upper part of the *Echinocorys conical/Galeola papillosa* Zone to the

lower part of the *Belemnitella minor/Bostrychoceras polyplocum* Zone. The specimen was encountered in the northeast wall where lower Upper Campanian strata are exposed. These belong to the *Pachydiscus stobaeil Galeola basiplana* Zone of North German regional macrobiozonation. This zone corresponds to the lower part of the *Hoploscaphites (Trachyscaphites) spiniger* Zone of the *Scaphites* zonation (Ernst et al., 1997).

The specimen comes from an alternation of light coloured, fossiliferous marls and limestones. The marly limestone to limestone beds of varying (decimetre to metre-scale) thickness as are interbedded with thinner marls (Ernst et al., 1997). The rhythmicity of the succession is thought to reflect orbital forcing (Milankovich cycles). According to Niebuhr (1999) the conspicuous hierarchical cyclic pattern represents large-scale 400-ky eccentricity cycles (c. 28 m thick) and short-term 20 ky precession cycles (c. 1.5 m).

The faunal content is comparatively large and consists of siliceous sponges, echinoids, pycnodontid oysters, belemnites and rare corals and ammonites. The sediments were deposited on a temperate epeiric platform mostly below storm-wave base (80–100 m). The few indications of bottom-current activity (tempestites) are restricted to lowstand phases of the 400-ky cycles (Niebuhr 1999) when the depth of water might have been less than 80 m.

3. Systematic palaeontology

Current knowledge of Late Cretaceous and early Tertiary octocorals is rather unsatisfactory. Almost all fragmented remains have been referred to the extant

genus '*Isis*' (Family Isididae). This attribution has been based on the fragmentary fossil record of calcareous internodes of octocorals, and the assumption that the remaining axes consist of hard horny tissues comparable to those of recent Isididae (e.g., Voigt, 1958). The completely calcified axes of our material indicate either a different generic alignment or the necessity of a major revision of the evolutionary development of Cretaceous octocorals (Voigt, 1958; see below). On the other hand we strongly believe that the erection of new taxa based on only a single specimen is an unsound palaeontological procedure, and, consequently, defer reconsideration of octocoral phylogeny to a later study when more material has been found.

The specimen described here has been deposited in the collection of the Institut für Geologie und Paläontologie, University of Hannover, under catalogue no. GPH 2001 X-1.

Class: Anthozoa Ehrenberg, 1834
 Subclass: Octocorallia Haeckel, 1866
 Order: Gorgonacea Lamouroux, 1816
 Family: Isididae Lamouroux, 1816
 ?Genus *Isis* Linné, 1758

Type species. *Isis hippuris* Linné 1758, by subsequent designation of Milne Edwards & Haime, 1851.

'*Isis*' *ramosa* Voigt, 1958
 Figs 2A–E, 3

?1850? *Axogaster cretacea* var.?; Lonsdale 1850, pl. 18A, fig. 34.

1958 *Isis ramosa* Voigt, pp. 16, 17, pl. 12, figs 1–6.

1958 *Isis?* sp.; Voigt, pp. 17, 18, fig. 2.

2000 '*Isis*' *ramosa* Voigt; Helm 2000, figs 8–11.

Description. '*I.*' *ramosa* is characterized by having a comparatively simple flattened tree- to fan-shaped corallum about 5 cm in height and 7 cm in diameter. The main axis is circular to transversely oval in outline, with a maximum basal diameter of up to 0.3 cm. The surface of the axes is smooth to slightly rough. The branches are completely calcified and successively taper to their tips. In cross section the branches are concentrically laminated. Branching of the axes occurs at irregular intervals ranging from a few mm to cm. The branching angles vary between typical y-shaped dichotomous (70°) to acute (c. 15°). In a few cases the branches are bent backwards. The branches, estimated to be up to 100, are slightly bent to strongly arched, but in most cases are arranged in a planar fan. The basal area of the main axis shows a deep depression, which we interpret as a joint socket. Owing to sediment cover, the depth and shape of the basal depression cannot be seen (Fig. 2C).

Discussion. The specific identification of our specimen as '*I.*' *ramosa* seems to be settled although the original

description of Voigt (1958) differs considerably from ours. However, these differences are attributed to the very different preservation of the material and the interpretations based on Voigt's incomplete material. He described (Voigt, 1958, p. 16): 'Eine *Isis*, die sich durch sehr kleine und zarte glatte Internodien von 0.3–0.5 mm Dicke und 3–5 mm Länge auszeichnet' (translated from German: 'A (species of) *Isis* with very small, delicate, and smooth internodes that are 0.3–0.5 mm thick and 3–5 mm long'). These 'internodes', which he interpreted to be intercalated into mainly horny branches, are, in fact, only fragmented parts of the complete branches which display no horny 'nodes' at all. Additionally, differentiation between calcified internodes (representing the branching parts of the axes) and horny and unbranched nodes is not possible. Therefore, the 'articulation planes' at the ends of the 'internodes' of Voigt (1958) are random fracture planes with no anatomical function. The only characters that can be used for specific identification are the shape of the branches and their surface to which our specimen conforms. These features also allow the synonymization of '*I.*' *ramosa* with Voigt (1958) *Isis?* sp.

On the other hand, the generic assignment of this species, and possibly all fossil Cretaceous octocorals described on the basis of fragmented parts of the branches, needs to be reconsidered. The differentiation of the branches into horny nodes and calcified internodes, which is typical for extant representatives of the genus *Isis*, and for the Family Isididae as a whole, is not developed in our specimen. However, there are some extant and fossil genera (e.g., Cretaceous *Moltkia*; see Grasshoff & Zibrowius, 1983, p. 116) of the family Isididae that are characterized by a rigid axis and are, thus, similar to '*I.*' *ramosa*. *Moltkia* differs from our material by the secondary covering of the early-formed horny nodes with additional layers of calcite (Grasshoff & Zibrowius, 1983). This phenomenon of wrapping calcite crusts is lacking in our specimen and in Voigt's material.

Hence, attribution of '*I.*' *ramosa* to this family is not possible. The only articulation observed in our specimen is between the encrusted base and the rigid fan. The 'bauplan' resembles that of Ordovician *Nonnegorgonides zieglerei* (Lindström, 1978), a possible predecessor of modern Gorgonacea. Nevertheless, as noted above, we refrain from erecting a new taxon (and possibly a new family) based on a single specimen, preferring instead to describe the specimen under a generic name to which some phylogenetic affinities may exist.

4. Evolutionary ecology

The differences between the formation of the skeleton of Late Cretaceous '*I.*' *ramosa* and earlier forms such as

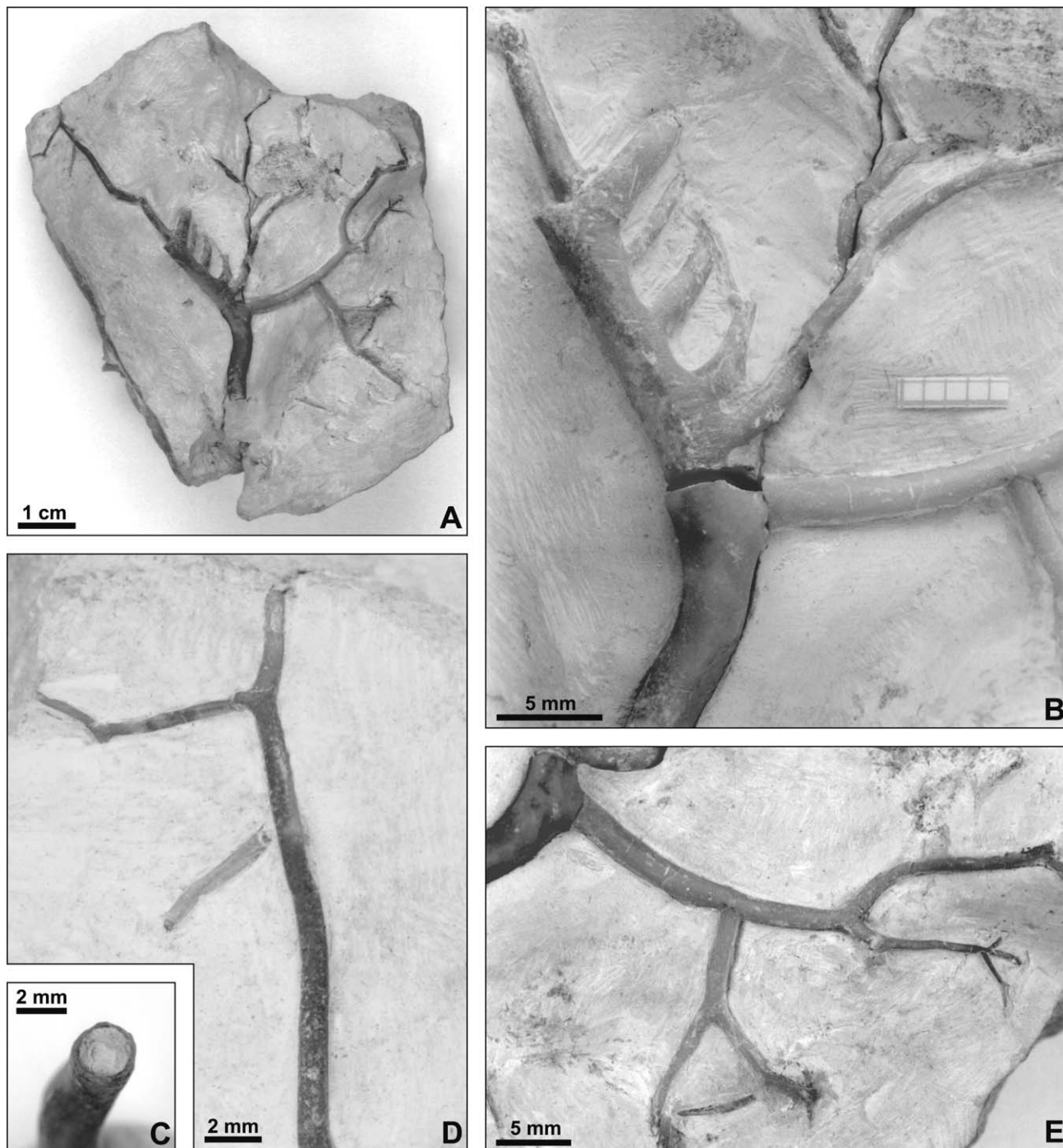


Fig. 2. *Isis ramosa*, Teutonia I quarry, east of Hannover, *stobaeilbasiplana* Zone, Campanian, Late Cretaceous. A, overview. B, detail of branching pattern and branching angles (acute and dichotomous) of the main axis; note slightly roughened surface of the axes. C, sediment-filled joint socket of rigid fan, base of main axis. D, E, details of distal branches both showing dichotomous (y-shaped) branching and branching at acute angles.

Nonnegorgonides zieglerei, and extant gorgonaceans has presumably resulted from different life strategies. The primitive early gorgonaceans with their rigid fans and only a single articulation between base and fan gave rise to the highly articulated modern forms with horny nodes and calcified internodes, and coincided with a change in habitat.

The rigid, fragile gorgonaceans in the Upper Cretaceous deposits of the Lower Saxony Basin settled on secondary hardgrounds (e.g., echinoids) in a temperate deep-water epeiric platform environment well below storm wave-base (80–100 m). Octocorals reflecting a similar habitat are known from the Danian of Denmark where they co-occurred with other corals

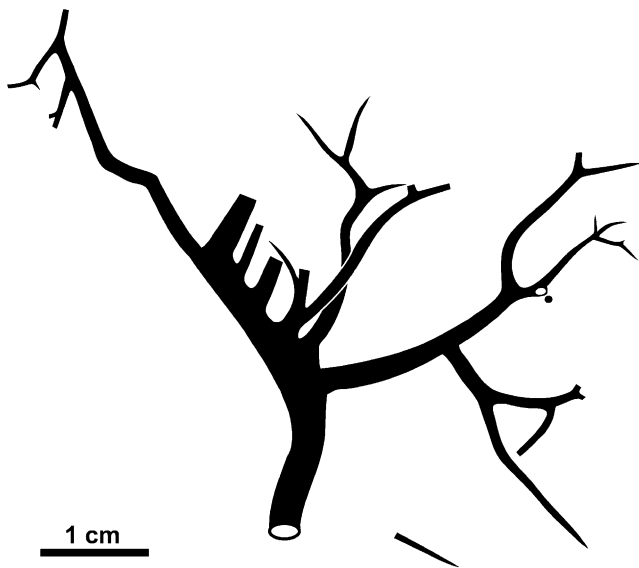


Fig. 3. Schematic drawing of the ‘*Isis*’ *ramosa* fan. Branches that are covered with sediment or broken off are drawn with stubby tips to indicate their difference from the tapering tips of those that are complete.

forming mounds under moderately deep-water conditions (Bernecker & Weidlich, 1990; Willumsen, 1995).

In contrast, some of the articulated Pliocene–Holocene species of, e.g., *Isis*, inhabited, and continue to inhabit, extremely shallow water attached to primary hardgrounds (e.g., Grasshoff, 1980). Under these conditions, water energy is the most selective ecological factor to which the gorgonaceans are well adapted by their fans, made flexible as a result of alternating horny and calcified nodes (Langer, 1989). Consequently, flexibility was an evolutionary advantage or prerequisite for dwelling under shallow-water conditions. On the other hand, extant deep-water gorgonaceans also form branches with alternating horny nodes and calcified internodes, but achieve rigidity by secondary calcareous encrusting of the horny parts of the axes (Grasshoff & Zibrowius, 1983), which is advantageous in passive filter-feeding from weak laminar water currents (Langer, 1989).

The stratigraphic interval at which this evolutionary step, the loss of completely calcified axes, happened has not yet been determined. Possibly during the Late Cretaceous both gorgonacean ‘bauplans’ coexisted, but presumably all ‘isidid’ species described from deeper shelf settings had rigid branches and must be interpreted as phylogenetic forerunners of extant gorgonaceans.

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