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Comptoniaster michaelisi nom. nov. (Asteroidea, Goniasteridae): Revision of a starfish species from the lower Upper Cretaceous of central Europe previously described as *Pentagonaster semilunatus* and *Asterias schulzii*

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ABSTRACT

The goniasterid starfish *Comptoniaster michaelisi* nom. nov., previously known under the names of *Asterias schulzii* or *Stellaster schulzei*, is re-examined in terms of nomenclature and taxonomic significance. The species was described and illustrated by Schulze in 1760 as *Pentagonaster semilunatus*, a name that referred to an extant species and did not conform to the rules of binomial nomenclature. The species-group name *schulzii* is invalid, so that the replacement name *michaelisi* is suggested. This early Late Cretaceous species can now be accommodated in the genus *Comptoniaster*. A lectotype for the species is designated (i.e., Schulze's figured specimen), reillustrated and described in detail herein. Additional data provided include other occurrences of the species in middle Turonian to middle Coniacian strata in the Saxonian, North Sudetic and Intrasudetic Cretaceous subbasins (Germany, Poland and Czech Republic). Eighteen moulds of well-preserved, articulated specimens were available for this study, and 14 of them are illustrated. The skeletal morphology of the species is reconstructed and single elements are described, characterising *C. michaelisi* as a medium-sized asteroid with an outer radius of up to 90 mm, 45–50 paired supero- and inferomarginals and an arm-to-disc ratio of 2.2–2.5. Striking morphological affinities with *C. comptoni* from the upper Albian–lower Cenomanian indicate that species as a possible ancestor of *C. michaelisi*. The species lived on shallow-marine, medium- to coarse-grained sandy sea floors. Taphonomic pathways suggest that both death and rapid burial of these asteroids were most likely induced by tempestite deposition.

1. Introduction

Asteroids rank amongst the diverse and ecologically important members of marine ecosystems in all present-day oceans, encompassing nearly 1900 species, in approximately 370 genera and 36 families (Mah and Blake, 2012). They occur at all depths, from the intertidal to the abyssal (approximately 6000 m) and in all temperature zones, but are most diverse in tropical regions of the Atlantic and Indo-Pacific oceans (Hyman, 1955; Clark and Rowe, 1971; Blake, 1983, 1990; Clark and Downey, 1992). All extant starfish have been considered to be members of the post-Palaeozoic Asteroidea (crown-group *sensu* Blake, 1987, 2000; Neoasteroidea *sensu* Gale, 1987), first occurring in the middle Triassic (Blake and Hagdorn, 2003). Since their first appearance in Ordovician strata (Blake, 2007; Blake and Rozhnov, 2007), certain asteroids (stem-group *sensu* Blake, 1987; Palaeoasteroidea *sensu* Gale, 1987; out-group *sensu* Gale, 2011) show both similar and intermediate morphologies with the crown-group, and it is these similarities that have been treated differently by authors (see e.g., Blake, 1987; Gale, 1987; Blake and Hagdorn, 2003).

The classification of the Asteroidea has had a history of controversy since the nineteenth century, having been purely morphology based and relying on comparison of mostly dissociated ossicles in extinct taxa with complete extant starfish (see discussions in Gale, 1987; Blake and Portell, 2009). More or less complete asteroids are unusual finds, even in otherwise fossiliferous strata, because the skeleton is composed of numerous individual ossicles

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connected by soft tissues that decay rapidly after death. Many studies and reconstructions have relied solely on such ossicles (e.g., Spencer, 1913; Wright and Wright, 1940; Rasmussen, 1950). Occasionally, assemblages of abundant ossicles of one or more species are observed but, in general, asteroids are relatively rare fossils and well-preserved specimens are exceptional. Some examples of the latter have been known from the thick-bedded sandstones (i.e., 'Quader sandstones') in the Saxonian Cretaceous Basin (SCB) since the beginning of the eighteenth century (see Niebuhr, 2017). These have recently been documented in detail (Niebuhr and Seibertz, 2016).

From the Upper Cretaceous (lower Cenomanian–middle Coniacian) of the SCB, twelve asteroid species, in ten genera, are on record to date (Niebuhr and Seibertz, 2016). Seven of these (Table 1) are known only from isolated calcitic ossicles from the marly-calcareous facies in the northwestern part of the SCB, between Meißen and Dresden. Moulds of near-completely preserved starfishes from quartzose Quader sandstones are definitely the most beautiful fossils of the SCB, and comprise five taxa (Table 1). However, all of these are rare finds, with the exception of *Comptoniaster michaelisi* nom. nov., of which more than 18 individuals are now known. The aim of the present paper is to revise this taxon, previously described and figured as *Pentagonaster semilunatus* by Schulze (1760) and *Asterias schulzii* Cotta by Roemer (1840, 1841), and to provide a better picture of skeletal morphologies and mode of life of *C. michaelisi* nom. nov.

2. Geological setting and stratigraphy

The Mid-European Island is one of the main palaeogeographical features of the Cretaceous in central Europe, consisting of the western Rhenish and eastern Bohemian massifs (Rhenobohemia) as emergent areas (Fig. 1A). Striking roughly WNW–ESE, this island separates the temperate Boreal shelf sea in the north from the Tethyan warm-water settings in the south (compare Ziegler, 1990; Janetschke et al., 2015). The Saxonian (SCB), Bohemian (BCB), North Sudetic (NSCB) and Intrasudetic (ISCB) Cretaceous basins were closely connected marginal subbasins of the wide central European carbonate-dominated shelf sea. In all four subbasins marine sedimentation commenced during the Cenomanian. The oldest Cretaceous marine deposits are proximal red conglomerates of early to middle Cenomanian age (Meißen Formation) that are confined to the Meißen area, northwest of Dresden (Niebuhr et al., 2007). During this time interval, the land areas of the future West- and East-Sudetic islands (see Fig. 1A) were still connected with the large Mid-European Island in the southwest (compare Voigt, 2009). The Variscan basement structures of the Mid-European Island dominated the palaeogeography during the middle to late Cenomanian. A major relative sea level rise in the lower *Metoicoceras geslinianum* Zone (mid–late Cenomanian) led to inundation of many small palaeohighs and the establishment of fully marine conditions in all four subbasins (Fig. 1A). Successively, rising sea level resulted in narrow marine straits at the interface of Boreal and Tethyan domains between the Mid-European and West-Sudetic islands (SCB and northwestern BCB), as well as East- and West-Sudetic islands (NSCB and ISCB). The maximum flooding of the SCB is indicated by the Strehlen and Weinböhla limestones (mid–upper Turonian), the carbonate-richest sediment of the Elbtal Group (see Wilmsen and Niebuhr, 2014). Since the middle Turonian, inversion tectonics governed the depositional regime. The major clastic source area for the quartzose Quader sandstones of the SCB (Saxonian Switzerland) and northwestern part of the BCB (Bohemian Switzerland) was the West-Sudetic Island. The composition of both sandstones and clasts reveal that sedimentary rocks of Permotriassic–Cretaceous age were eroded (Voigt, 2009). The 'Heuschergebirge' of the ISCB is composed of erosional material from the East-Sudetic Island in the northeast, while the southeastern part of the BCB was filled up from the Bohemian Massif in the southwest (for a summary of palaeogeographical and stratigraphical data, see Uličný et al., 2008; Voigt, 2009; Janetschke and Wilmsen, 2014; Wilmsen and Niebuhr, 2014; Janetschke et al., 2015). Today, the northeastern margins of the SCB and the BCB, as well as the NSCB, ISCB and the Opole Cretaceous Basin (Fig. 1B), are characterised by faults; only the southwestern margins of SCB and BCB show the onlap pattern of the Upper Cretaceous transgressions.

Table 1
Late Cretaceous (early Cenomanian–middle Coniacian) asteroids from the Saxonian Cretaceous Basin in stratigraphic order (Niebuhr and Seibertz, 2016) preserved either as isolated ossicles in marly-calcareous facies (*) or as moulds of more or less complete articulated specimens in Quader sandstones.

Lophidiaster scupini (Andert, 1934)
Turonian–Coniacian boundary interval
**Chomataster coombii* (Forbes, 1848)
mid-upper Turonian
Nymphaster albensis (Geinitz, 1872)
middle Turonian–lower Coniacian
Comptoniaster michaelisi nom. nov.
middle Turonian–middle Coniacian
Calliderma lindneri Niebuhr and Seibertz, 2016
basal middle Turonian
**Manfredaster praebulbiferus* Niebuhr and Seibertz, 2016
upper upper Cenomanian–basal Coniacian
**Crateraster quinqueloba* (Goldfuss, 1829)
upper upper Cenomanian–mid-upper Turonian
**Metopaster parkinsoni* (Forbes, 1848)
upper upper Cenomanian–mid-upper Turonian
**Metopaster thoracifer* (Geinitz, 1871)
upper upper Cenomanian
**Hadranderaster simplex* (Geinitz, 1871)
upper upper Cenomanian
**Geinitzaster decoratus* (Geinitz, 1871)
upper upper Cenomanian
Calliderma ottoi (Geinitz, 1871)
lower upper Cenomanian

3. Localities and material

Regional occurrences of *Comptoniaster michaelisi* nom. nov. in the four subbasins are shown in Fig. 1B, indicated by stars. It is obvious from the fossil material that these asteroids are especially found in shallow-marine, quartzose Quader sandstones of the SCB, NSCB and ISCB. The reason why *C. michaelisi* nom. nov. was not yet found in Quader sandstones of Bohemian Switzerland in the northwestern part of the BCB and the southeastern part of the BCB is not known. Apart from a single specimen (MB.E.5313, in a fine-grained sandstone), all specimens (15 in number) known to date are moulds in weakly silicified, medium- to coarse-grained sandstones.

Most of the specimens stem from the SCB (for detailed stratigraphy see Niebuhr et al., 2007; Wilmsen and Niebuhr, 2014); all are historical finds, recovered in the eighteenth and nineteenth centuries during large-scale quarrying of freestones for buildings in the old town of Dresden and elsewhere. The oldest quarries are located near Pirna (locality 1 in Fig. 1B) where the Pirnaer Oberquader of the upper Postelwitz Formation was exploited, of early late Turonian age. The Pirnaer Oberquader, and the time-equivalent Sandstone c which crops out in southeastern direction in Wehlen, Rathen and the Saxonian Switzerland, are weakly silicified, poorly sorted, medium- to coarse-grained quartzose sandstones, white and yellowish variegated, with large, isolated detritic quartz grains