



urn:lsid:zoobank.org:pub:1682E191-10B1-4C71-87BC-31EF246963F1

## Late Triassic (Rhaetian) ophiuroids from Winterswijk, the Netherlands; with comments on the systematic position of *Aplocoma* (Echinodermata, Ophiolepididae)\*

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\*In: Kroh, A. & Reich, M. (Eds.) Echinoderm Research 2010: Proceedings of the Seventh European Conference on Echinoderms, Göttingen, Germany, 2–9 October 2010. *Zoosymposia*, 7, xii+316 pp.

### Abstract

An ophiuroid assemblage from Rhaetian dark shales in a subsrosion pipe (or sinkhole) penetrating middle Triassic (Muschelkalk) strata, and, outside the subsrosion pipe, discordantly overlying middle Triassic strata, east of Winterswijk, the Netherlands, is described, discussed and assessed taxonomically. The material consists of nearly intact and articulated as well as wholly disintegrated skeletons, almost all of which are pyritised, yet so well preserved that the diagnostic characters could be studied in detail. All specimens belong to *Aplocoma agassizi* (von Münster, 1839). Examination of the type material of *Ophiolepis damesii* Wright, 1874 (housed at the Roemer and Pelizäus Museum in Hildesheim, Germany, collection numbers NKP 7821 to NKP 7828) from Rhaetian strata at Hildesheim, Germany, comparable to those exposed at Winterswijk, has revealed that *O. damesii* is to be considered a *nomen dubium* due to the insufficient preservation of the type material. Based on the present lot, which documents the first Triassic echinoderms from the well-known Winterswijk quarry complex, we suggest that the genus *Aplocoma* is best reassigned to the family Ophiolepididae, in proximity to the extant *Ophiozonella*, and that the family Aplocomidae is to be suppressed. From a palaeoecological point of view, the Winterswijk assemblage illustrates preservation under the influence of storms in an otherwise very quiet environment; it is here interpreted as a monospecific assemblage amidst an oligospecific bivalve community in a near-coastal, shallow, muddy setting with fluctuating or low salinity levels and/or dysoxic bottom waters.

**Key words:** Ophiuroidea, brittle stars, palaeoecology, Rhaetian, taxonomy, the Netherlands

### Introduction

Ophiuroid systematics is based almost exclusively on external characters of the calcitic skeleton. One would therefore expect extinct brittle stars to be directly comparable with their modern relatives. However, the majority of studies of ophiuroid fossils have so far failed to integrate these taxa into the classification of extant brittle stars in a meaningful way. Instead, most fossil brittle star taxa were compared amongst each other, even though some were assigned to extant genera, mostly, if at all, with highly dubious justification (Hess 1965). This holds true in particular for the Triassic, which ranks amongst those time slices that show the greatest abundance of articulated brittle stars, yet con-

comitantly is characterised by the poorest understanding of their phylogenetic relationships (Hess 1965). A preliminary cladistic analysis of present-day brittle stars by Smith *et al.* (1995) suggested much of the early diversification of modern ophiuroid groups to have taken place during the Triassic and Early Jurassic, discrediting the separation of fossil and extant brittle star systematics as purely artificial. The importance of fossil taxa for our understanding of the evolution and diversification of modern ophiuroids is undeniably immense. All the more important is a thorough knowledge of the skeletal morphology of fossil forms and their affinities with modern relatives.

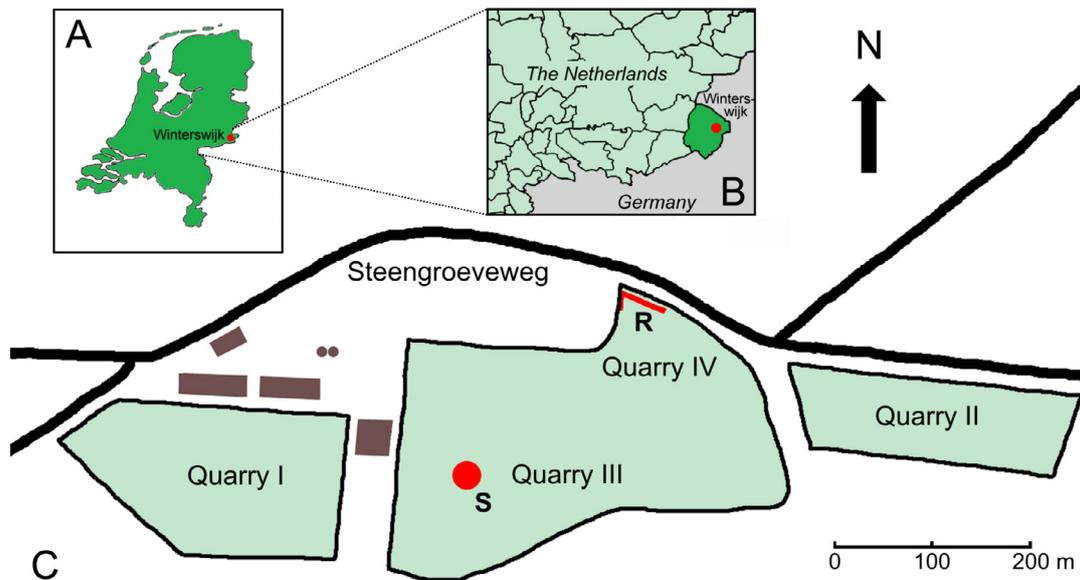
In 2006 and 2007, a series of articulated ophiuroids were discovered in Rhaetian sediments in the Winterswijk quarry complex, the eastern Netherlands (Fig. 1). Their preservation enabled a detailed assessment of the affinities with modern relatives. Here, we provide a detailed morphological description of the Winterswijk material, based upon which we attempt a taxonomic assignment and reinterpretation of the position within the modern groups of ophiuroids. In addition, we suggest a palaeoecological model for the Winterswijk brittle star assemblage and interpret it within the context of Rhaetian ophiuroid diversity.

### Geological and palaeontological context

The Winterswijk quarry complex consists of four pits, the fourth being an extension of the third (Fig. 1). Most strata exposed are of Middle Triassic (Anisian, Bithynian, ‘Muschelkalk’) age, and are assigned to the Vossenveld Formation which yields a predominantly marine fauna consisting of piscivorous and durophagous reptiles, various fishes, bivalves, gastropods, ammonites, arthropods and brachiopods, as well as land-derived plants and footprints of various vertebrate taxa (see *e.g.*, Oosterink 1986; Diedrich 2001; Oosterink *et al.* 2003; Klompmaker & Fraaije 2011). Upper Triassic (middle Rhaetian) dark shales were encountered at several isolated spots, for instance in a subsrosion pipe or sinkhole (a geological phenomenon that occurs due to dissolution of strata in the subsurface causing the overlying sediments to collapse) at Quarry III (see Oosterink *et al.* 2006; Klompmaker *et al.* 2010) and along the northern edge of Quarry IV (Fig. 1). Eight bivalve species as well as numerous palynomorphs have pinpointed the age of these shales (Herngreen *et al.* 2005; Klompmaker *et al.* 2010) as middle Rhaetian. Because of collapse of the subsrosion pipe, probably during the Eocene, the Rhaetian shales (2–4 m in overall thickness) were mixed with Hettangian clays (Klompmaker *et al.* 2010). The ~4 m of Rhaetian shales at Quarry IV discordantly overlie the Anisian strata, and, in turn, are discordantly overlain by Oligocene clays (Klompmaker *et al.* 2010). The clays in the subsrosion pipe were dated as middle to late Hettangian on ammonite evidence (Klompmaker & Van den Berkmortel 2007). Some lower Oligocene, Pleistocene and Holocene deposits, all barren of macrofossils, complement the sedimentary sequence at this quarry (Herngreen *et al.* 2005; Klompmaker *et al.* 2010). The brittle stars studied herein were collected from the middle Rhaetian shales in the subsrosion pipe and from Quarry IV; at the former, these shales have all been excavated now. The first ophiuroid was found in the subsrosion pipe in November 2006, and many additional finds followed.

### Material and methods

The material described herein was collected by splitting the dark shales from the subsrosion pipe and



**FIGURE 1.** A: Location of the Winterswijk quarry complex in the eastern Netherlands; B: Location of the quarry in the Winterswijk municipality close to the German-Dutch border; C: Overview of the quarry complex with the location of the subrosion pipe (S) in Quarry III containing some Rhaetian shales and the Rhaetian shales at Quarry IV (R) (from Klompmaker *et al.* 2010, modified).

from Quarry IV. Selected specimens were subsequently immersed in a 5% solution of hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), which removed clayey encrustations and detached the specimens from the surrounding matrix, making them available for examination from both ventral and dorsal sides. Isolated skeletal plates were extracted by disintegrating a slab preserving a near-completely disarticulated skeleton. The majority of specimens are pyritised to a significant extent, if not completely. Fortunately, pyritisation preserved the fine structures of the skeleton in most cases, allowing for a detailed assessment of hard-part morphology. In some specimens, the original skeleton is replaced by white, powdery gypsum, probably as a result of pyrite decay in the presence of skeletal calcite.

Selected specimens were mounted on aluminium stubs and gold-coated for SEM examination (LEO 1450 VP). Morphological terminology follows Stöhr (2005) for skeletal plates (ossicles) and Thuy & Stöhr (2012) for features of the lateral arm plates. Higher-level classification is adopted from Smith *et al.* (1995). All material described and illustrated herein is housed in the collections of the Naturalis Biodiversity Center (Leiden; NCB-RGM 344 003–344 037) and Freriks Museum, Winterswijk (FMW 0242–21364); additional specimens remain in several private collections, at least for the time being (H.W. Oosterink, W. Winkelhorst and B.J.H.M. van den Berkmortel).

### Systematic palaeontology

**Order Ophiurida Müller & Troschel, 1840**

**Suborder Ophiurina Müller & Troschel, 1840**

**Family Ophiolepididae Ljungman, 1867**

**Genus *Aplocoma* d'Orbigny, 1852**

Type species: *Acrourea agassizi* von Münster, 1839, by original designation.

## *Aplocoma agassizi* (von Münster, 1839)

Figures 2–3

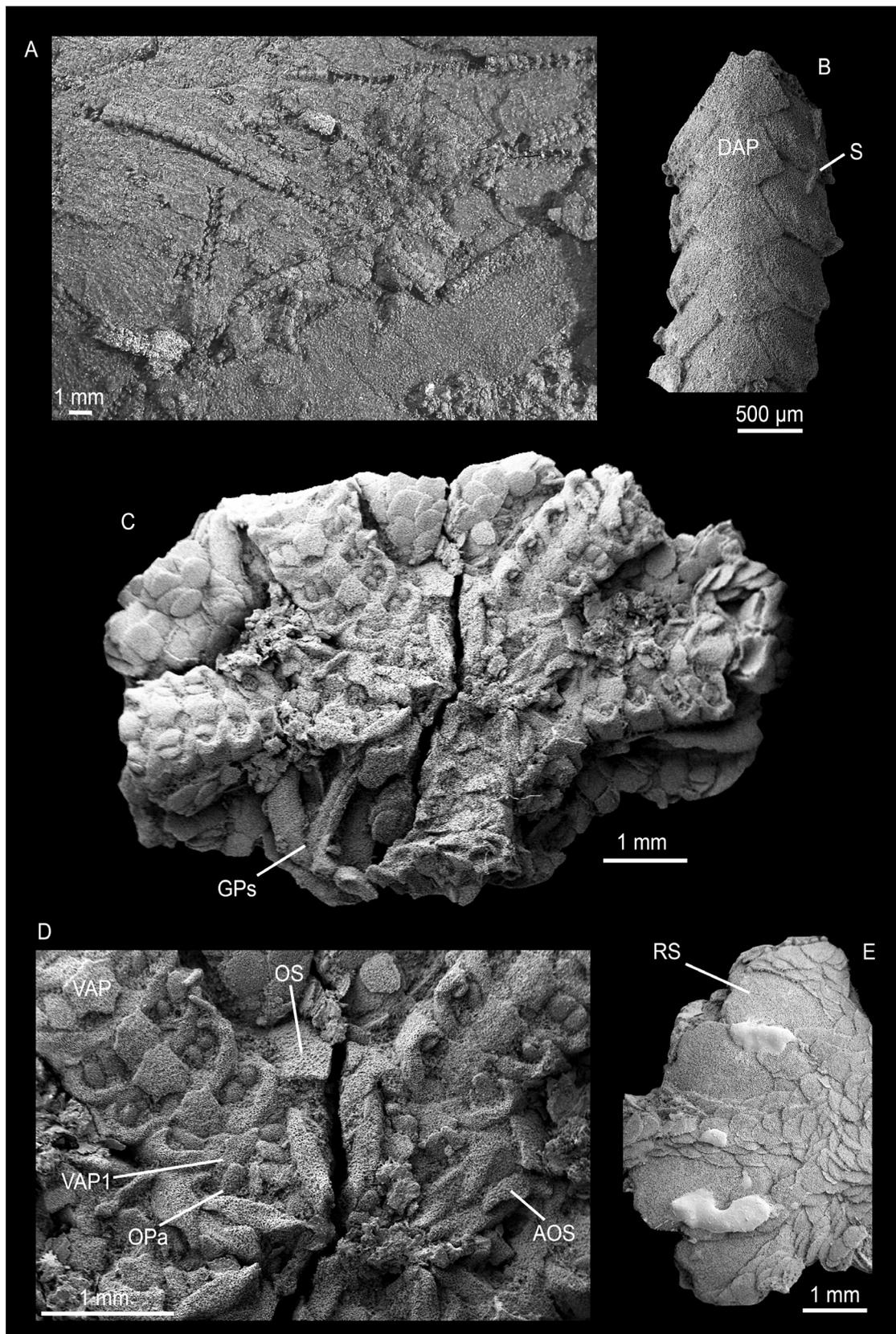
*Acrourea agassizi*—von Münster 1839: 99, Pl. 11, Fig. 2.

*Aplocoma agassizi* (von Münster, 1839)—Hess 1965: 157, 164–165, Pls. 13–15; Hess & Meyer 2008: 34.

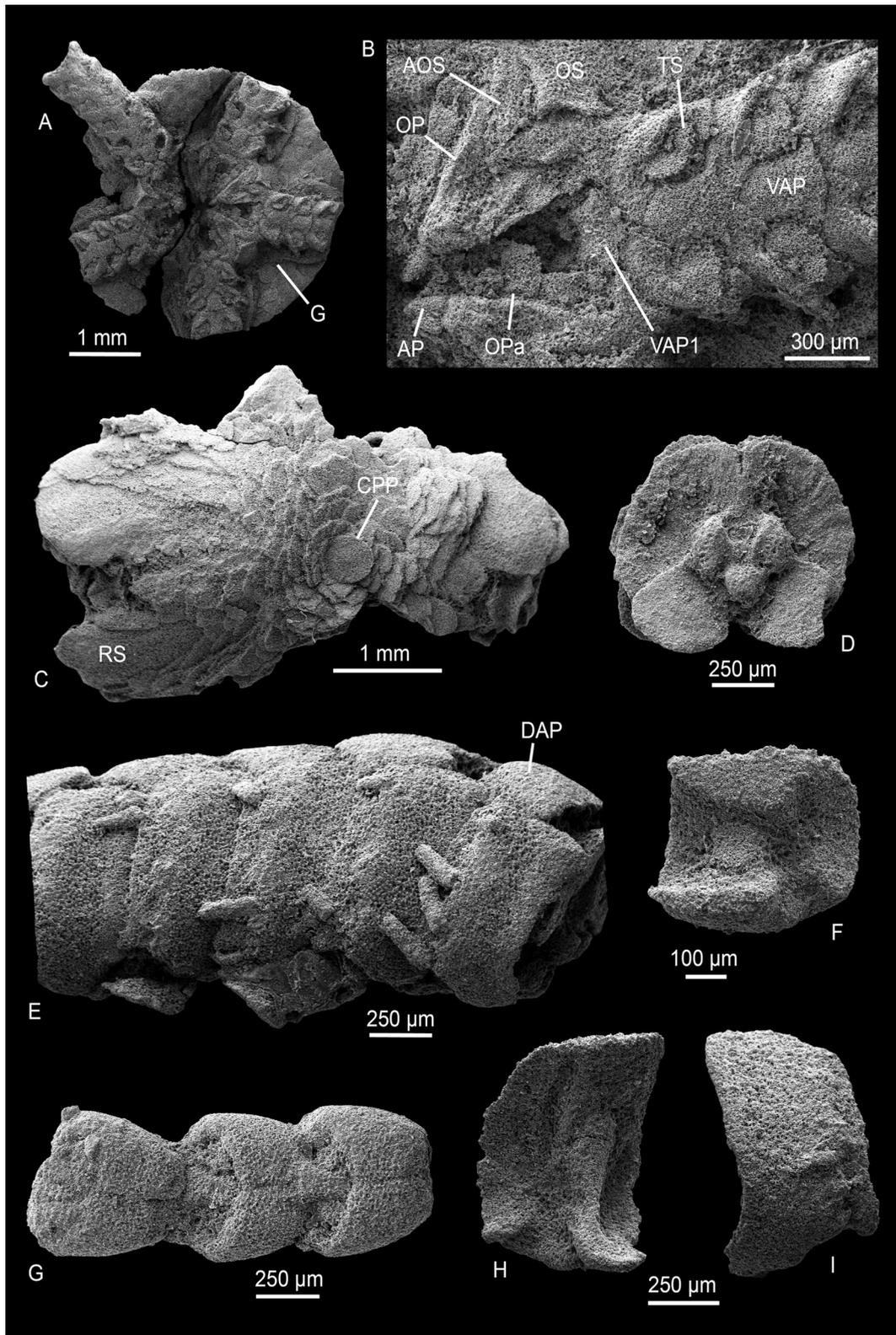
**Material.** At least 20 articulated discs and disc fragments, mostly with proximal arm portions preserved; at least 20 articulated arm fragments; one near-completely disarticulated skeleton.

**Diagnosis.** Disc covered with fine granulation on both sides; dorsal disc plates round, small and uniformly sized; radial shields moderately large; leaf-like oral papillae in continuous row with single, small, conical apical papilla; arms slender and moderately long; lateral arm plates without any conspicuous ornament or constriction; arm spines few, short and appressed; dorsal arm plates mostly contiguous.

**Description.** Disc circular, diameter ranging between 1.4 mm and 9.0 mm (5.0 mm on average); dorsal disc plating consisting of small, round imbricate scales; radial shields rounded triangular, equaling almost half the length of the disc radius, contiguous distally and partially covered by disc scales proximally. Ventral interradii covered by small, round scales similar to those of the dorsal disc plating. Small granules scattered on the dorsal and ventral interradii disc scales in a few specimens. Oral plates long and slender; adoral shields rather short, wing-like, broadly contiguous proximally; oral shields pentagonal to arrow-shaped, nearly as long as broad, with obtuse proximal angle and concave lateral edges. Second oral tentacle opening within the mouth slit, not superficial. Edge of jaw bordered by a continuous row of five to six blunt, leaf-like papillae; distalmost papilla positioned on the edge of the adoral shield; remaining papillae on oral plate, larger than papilla on adoral shield, except for the proximalmost one. Single, slender, conical apical papilla, smaller than oral papillae. Abradial genital plate elongate and bar-like, adradial one shorter, slightly broader and flat. First ventral arm plate nearly twice as broad as long, with obtuse distal angle; successive ventral arm plates nearly as long as broad or slightly elongate, with obtuse proximal and distal angles and strongly concave lateral edges; ventral arm plates separated by lateral arm plates over almost the entire length of the arm; tentacle pores developed over the entire length of the arm, covered by two blunt, leaf-like tentacle scales. Proximal lateral arm plates higher than wide, with pointed dorso-proximal edge and ventro-proximal protrusion; outer surface with fine tuberculation bordered proximally by a band of more finely meshed stereom, paralleling the proximal edge of the lateral arm plate; no spurs on the outer proximal and inner distal edges; four small, equal-sized spine articulations, sunken into slightly elevated ridge near the distal edge of the lateral arm plate; increase in distance between spine articulations in dorsal direction; arm spines conical, blunt, nearly as long as one arm segment in proximalmost portions of the arms, becoming increasingly shorter towards the tip of the arm; conspicuous, prominent ridge on the inner side of the proximal lateral arm plates, dorsal portion nearly straight, with rounded dorsal tip, ventral portion gently bent and confluent with ventro-proximal protrusion of lateral arm plate; dorsal portion of ridge distally paralleled by shallow, poorly defined furrow; distal lateral arm plates with ridge reduced to round, prominent, well-defined knob on the inner side; dorsal contact area with opposite lateral arm plate conspicuously large in distal lateral arm plates; tentacle notches large and well developed in all lateral arm plates; dorsal arm plates large, pentagonal with obtuse distal angle and straight lateral edges, broadly contiguous in proximal arm segments while separated by lateral arm plates in distal segments; vertebrae disc-like, with large, rounded, nearly vertical dorsal and ventral fossae and coarse, well-defined but not markedly protruding articulation pegs.



**FIGURE 2.** *Aplocoma agassizi* (von Münster, 1839) from the Rhaetian (A: subrosion pipe; B–E: Quarry IV) near Winterswijk, the Netherlands. A: three articulated specimens (all dorsal aspect), as found upon splitting the shales (FMW 0242–21364). B: proximal to median arm fragment in dorsal view, NCB-RGM 344 003, C: articulated disc in ventral view, slightly distorted, NCB-RGM 344 004. D: detail of C showing mouth plating. E: dorsal view of NCB-RGM 344 004 (see Fig. 2C, D). Abbreviations: AOS = adoral shield; DAP = dorsal arm plate; GPs = genital plates; OPa = oral papillae; OS = oral shield; RS = radial shield; S = spine; VAP1 = first ventral arm plate; VAP = ventral arm plate.



**FIGURE 3.** *Aplocoma agassizi* (von Münster, 1839) from the Rhaetian (subrosion pipe) near Winterswijk, the Netherlands. A: articulated disc with proximal arm portion preserved, ventral view, NCB-RGM 344 005. B: detail of A showing mouth plating. C: fragmentary articulated disc in dorsal view, NCB-RGM 344 006. D: proximal vertebra in distal view, NCB-RGM 344 007. E: proximal arm portion in lateral view, NCB-RGM 344 008. F: distal lateral arm plate, internal view, NCB-RGM 344 009. G: distal arm portion in ventral view, NCB-RGM 344 010. H: proximal lateral arm plate, internal view, NCB-RGM 344 011. I: proximal lateral arm plate, external view, NCB-RGM 344 012. Abbreviations: AOS = adoral shield; AP = apical papilla; CPP = central primary plate; DAP = dorsal arm plate; G = disc granules; OPa = oral papillae; OP = oral plate; OS = oral shield; RS = radial shield; TS = tentacle scale; VAP1 = first ventral arm plate; VAP = ventral arm plate.

**Discussion.** The short, appressed arm spines and the absence of any conspicuous ornament or constriction on the lateral arm plates, in combination with large, well-developed tentacle openings, moderately large radial shields, and a single small, conical apical papilla, place the present specimens in the genus *Aplocoma* as defined by Hess (1965) and Hess & Meyer (2008). The granulation of the disc, typically observed in *Aplocoma*, is barely visible in the material available, probably as a result of preparation and/or preservation. Scattered groups of small granules are, however, seen in some specimens, documenting the former presence of disc granulation. Within the genus *Aplocoma*, the uniformly leaf-like oral papillae, the broadly contiguous adoral shields, the concave lateral edges of the oral shield, the rather narrow ventral arm plates and the arm spines barely equalling the length of an arm segment allow the Winterswijk specimens to be assigned to *Aplocoma agassizi* (for comparisons with congeners see Hess & Meyer 2008), originally described from the upper Muschelkalk (Anisian) of Bayreuth, southern Germany, by von Münster (1839), and subsequently also recorded from the Rhaetian of Allgäu, southern Germany, and possibly from the upper Muschelkalk of Teruel, northeast Spain (Hess 1965). The studied specimens show little morphological variation other than related to the state of preservation.

From strata outcropping near Hildesheim (Germany), which are comparable both in age and facies to the Rhaetian dark shales of Winterswijk, Wright (1874) described several articulated ophiuroids as *Ophiolepis damesii*. The type material was long thought to be lost, thus precluding a revision of its nomenclatural status (Hess 1965). Recent investigations, however, have revealed its presence in the collections of the Roemer and Pelizaeus Museum at Hildesheim. The type material consists of seven slabs, each comprising several articulated specimens. The original description is insufficient to define the species properly, and Wright failed to designate a type. To make matters worse, the two individuals illustrated cannot be unequivocally identified as they potentially match several of the specimens on the slabs. Irrespective of these uncertainties, however, none of the specimens of the type lot is sufficiently well preserved to permit a detailed characterisation and clear distinction of *Ophiolepis damesii* from other species. The replacement of the original skeleton by coarsely crystallised pyrite, which explains the poor state of preservation of the type material in that particular case, prevent us from revealing diagnostic characters, including the oral papillae or the oral shields, by renewed preparation. The type material must thus be considered as specifically indeterminate, making *Ophiolepis damesii* a *nomen dubium*.

The material described by Wright (1880) and Horwood (1916), under the name of *Ophiolepis damesii*, and subsequent records of *Aplocoma damesii* by Swift & Martill (1999) from the Rhaetian of England, originates from strata which are broadly comparable to those formerly outcropping at Winterswijk and most probably were deposited in the course of the same transgressive event (Klomp-maker *et al.* 2010). Thus, it seems highly probable that the English material is conspecific with the Winterswijk ‘population’. Unfortunately, the figures of *Aplocoma damesii* by Wright (1880), Horwood (1916) and Swift & Martill (1999) are not detailed enough for an unequivocal identification, not to mention that the illustrations in Wright (1880) are reproductions of the Hildesheim type figures supplied by Wright (1874). A detailed reassessment of the English material is needed to resolve this issue.

The first attempt to integrate *Aplocoma* into the classification of present-day brittle stars was undertaken by Hess (1965), who found the genus incompatible with any modern family concept. A similar conclusion was drawn concerning the higher taxonomic position of *Ophiopetra lithographica* Enay & Hess, 1962, from the Upper Jurassic of France, which prompted Hess (1965) to erect a new family, the Aplocomidae, to accommodate the fossil genera *Aplocoma* and *Ophiopetra*. Smith *et al.* (1995)

included the Aplocomidae in their cladistic analysis of extant ophiuroids and considered it a putative plesiomorphic ancestral group to the chilophiurine/gnathophiurine clade. The reasons for doing so were stratigraphical, rather than morphological, in nature. Recently, the concept of the family Aplocomidae has been further refined and reinforced with the inclusion of additional fossil genera, and with a subdivision into two subfamilies, the Aplocominae and Ophiopetrinae (Hess & Meyer 2008).

Within the synoptic key compiled by Fell (1960), the Aplocomidae can, indeed, be justifiably distinguished from other currently accepted brittle star families. A critical re-evaluation of the distinctive characters of the Aplocomidae, however, reveals that the combination of a granulated disc, relatively short appressed or erect spines, a continuous row of oral papillae, second oral tentacle pores opening into the mouth slit and oral plates lacking lateral wings is by no means unique. In fact, the families Ophiolepididae and Ophiochitonidae both include representatives which display this set of characters (e.g., Matsumoto 1917). The almost dogmatic assumption that representatives of these two families lack disc granulation is a generalisation propagated by Fell (1960) in order to simplify his synoptic key. The ophiochitonid genus *Ophioplax*, for example, displays granulation on the ventral side of the disc, and the ophiolepidid *Ophiozonella granulifera* H.L. Clark, 1941 has both sides of the disc covered by granules, clearly analogous to the disc granulation observed in aplocomids. Thus, even if it applies to the majority of ophiochitonids and ophiolepidids, the absence of disc granulation clearly cannot be generalised. The inevitable consequence is that the family Aplocomidae is based on a set of characters which is far less distinctive than previously assumed, and therefore should be abandoned.

Hess & Meyer (2008) included five fossil genera in their revised family Aplocomidae, one of which has recently been shown to have affinities with the ophiurid subfamily Ophioleucinae (Thuy *et al.* 2011). Rather than reinterpreting all former aplocomid genera, which would be beyond the scope of the present note, we shall attempt to reassign the genus *Aplocoma* on the basis of the material described herein. We agree with Hess (1965) that similarities with the Ophiodermatidae are rather superficial, in view of fundamental differences in arm structure and arm spine arrangement. Possible affinities with the Ophiochitonidae, the Ophiolepididae and the Ophioleucinae, however, merit more detailed consideration. As shown by Martynov (2010), ophiochitonids have large, horseshoe-shaped spine articulations. Although the preservation of the Winterswijk specimens precludes a detailed description of spine articulation morphology, it does allow to discard the presence of the characteristic ophiochitonid horseshoe shape. Thus, assignment to the Ophiochitonidae would appear unlikely. Spine articulations in the Ophiolepididae and Ophioleucinae are generally less conspicuous (Martynov 2010). On the whole, ophioleucines have slowly tapering arms with very widely contiguous dorsal arm plates. For that reason, we consider assignment of *Aplocoma agassizi* to the Ophiolepididae more likely, although an attribution to the Ophioleucinae cannot be ruled out entirely. Within the Ophiolepididae, the presence of large tentacle pores throughout the arm, the unfragmented dorsal arm plates and the uniformly sized dorsal disc scales place *Aplocoma agassizi* closest to the extant genus *Ophiozonella*, which is known to include forms with disc granulation, as mentioned above.

### Palaeoecology and taphonomy

It is a well known fact that ophiuroid skeletons are prone to extremely rapid post-mortem disintegration (Kerr & Twitchett 2004), requiring quick and effective burial to be preserved intact. The material studied herein consists of both fully articulated skeletons, articulated yet fragmented skeletons

(mostly detached arms) and completely disintegrated skeletons, all assignable to the same species. It is therefore very likely that the animals lived at or very close to their place of burial. As in comparable occurrences in Germany (Wright 1874) and England (Swift & Martill 1999), the articulated ophiuroids from Winterswijk were not restricted to a single bed, suggesting a number of burial events to have taken place. Deposition of the shales at Winterswijk occurred in a near-coastal, assumedly very shallow, setting (Klompaker *et al.* 2010), making storms the most likely candidates for the effective burial of the articulated brittle star skeletons. The presence of a completely disarticulated single skeleton within a small slab suggests quiet conditions between storm events.

The oligospecific bivalve assemblage and the absence of other benthic groups such as corals, bryozoans and brachiopods (Klompaker *et al.* 2010) are indicative of either fluctuating or low salinity levels, dysoxic bottom waters or a combination of both. The presence of a single brittle star species rather than a diverse assemblage as commonly observed in soft-bottom habitats (*e.g.*, Hess 1966) corroborates the assumption of a stressed regime. Although the Late Triassic witnessed a significant extinction of marine benthos (Kiessling *et al.* 2007), we interpret the extremely low ophiuroid diversity in the Rhaetian of central Europe, as exemplified by the assemblage described herein, as a sampling artefact, strongly preferring strata that produce numerous articulated ophiuroids but deposited under stressed regimes, rather than as evidence of extinction. The diverse ophiuroid assemblage described from the Rhaetian of Iran on the basis of disarticulated skeletal plates (Kristan-Tollmann *et al.* 1979) corroborates this observation.

Rhaetian ophiuroid diversity is far from being well understood, even more so when relationships of fossil taxa with their modern relatives are considered. The present study is a first attempt to integrate a Triassic ophiuroid species into the classification of extant brittle stars drawing detailed morphological comparisons with close extant relatives.

## Acknowledgements

We thank Henk W. Oosterink (Winterswijk, the Netherlands), Bram J.H.M. van den Berkmortel (Gemert, the Netherlands) and Wout Winkelhorst (Aalten, the Netherlands) for providing some of the specimens studied, Hartmut Schulz (Tübingen, Germany) for valuable assistance with SEM imaging, Hans Hess (Basel, Switzerland) for fruitful discussions, Jürgen Vespermann (Hildesheim, Germany) for kindly providing access to the type material of *Ophiolepis damesii*, the ‘Working Group Muschelkalk’ and the exploiting ‘Ankerpoort Company’ for permission to access and study the Rhaetian sediments, and Hans Hess, two anonymous referees and the editors of this volume whose comments greatly improved an earlier version of this manuscript. Furthermore, we are grateful to Betsie Klompaker, Edo Klompaker and Lucy van der Heiden-Klompaker for their support.

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