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A Jurassic relict of the Triassic stem euryalid brittle star *Aspiduriella* (Echinodermata, Ophiuroidea)

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Abstract

During recent years, the study of extinct brittle stars has gained significant momentum thanks to advances in our understanding of the group's skeletal morphology. On the basis of these novel insights and the discovery of new, exceptionally preserved material from the middle Hettangian of Belgium, we here re-describe the enigmatic brittle star *Mesophiomusium kianiae*. We show that it represents a new genus, *Persoonaster* **gen. nov.**, which shares a number of striking similarities with the Triassic genus *Aspiduriella*, forming a paedomorphic lineage at the stem of the extant Euryalida for which we here introduce the new family Aspidurielliidae. The *Aspiduriella* lineage was among the most common and widey disributed in the Triassic, and unexpectedly survived into the Lower Jurassic as evidenced by recognition of the new genus *Persoonaster*.

Key words: Ophiuroids, Euryalida, microfossils, Hettangian, Belgium

Introduction

Ophiuroids, also called brittle stars, are the slender-armed cousins of starfish and have been an important component of marine benthos since the Ordovician (Stöhr *et al.* 2012). Their fossil record is comparatively rich for an animal group with a multi-element skeleton that is prone to rapid *post-mortem* disintegration. Finds of fully articulated ophiuroid skeletons have been reported from all major intervals of post-Cambrian Earth history. Yet, when examined more closely, the seemingly rich ophiuroid fossil record turns out to be strongly biased towards a few common taxa that predominantly occur in depositional settings that were inducive to intact preservation of multi-element organisms, while the bulk of ophiuroid palaeobiodiversity remains hidden in the microfossil record of the fully dissociated ossicles (Thuy & Stöhr 2011; Thuy 2013).

One of these common ophiuroid taxa is the Triassic genus *Aspiduriella* Bolette, 1998, representatives of which often occur as mass accumulations and often so abundant to the point of reaching rock-forming accumulations (Hagdorn & Reich 2023). This genus also includes the first fossil ophiuroid ever described, *Aspiduriella scutellata* (Blumenbach, 1804), making it one of the most iconic extinct brittle stars. However, it took more than 200 years following the original description to unravel the systematic position of *A. scutellata* and reveal the taxon's stem euryalid affinities (Thuy & Stöhr 2018). The key to these new insights lies in recent advances in our understanding of skeletal micromorphologies and in systematic analyses of dissociated ossicles. With this knowledge in hand, the ophiuroid fossil record can be unlocked well beyond the few common taxa known from intact fossils.

Here, we present new finds of the enigmatic ophiuroid species *Mesophiomusium kianiae* Thuy, 2005, originally described from the Hettangian of Belgium and Luxembourg (Fig. 1). Thanks to the serendipetous discovery of an articulated skeleton in a micropalaeontological sample and the above-mentioned novel insights into ophiuroid

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morphology, we here are able to demonstrate that the species belongs to a new genus which shares close ties with the iconic Triassic stem euryalid *Aspiduriella*, suggesting that the *Aspiduriella*-lineage survived into the Jurassic.

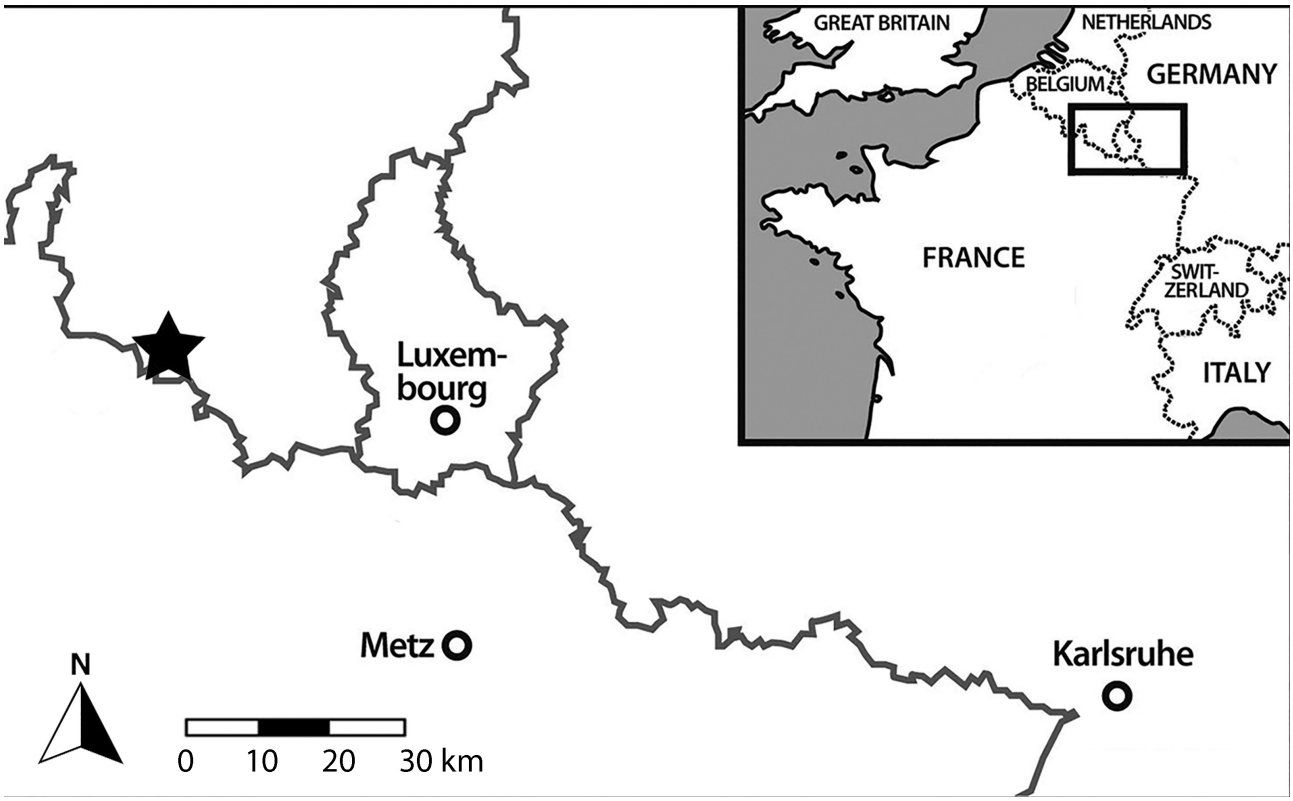

FIGURE 1. Location of the Fontentoille site (indicated by a star) that yielded the specimens of *Persoonaster* n. gen. *kianiae* (Thuy, 2005) described in the present paper.

Material and methods

The material described in the present paper comprises an articulated, fully exposed skeleton, and a series of dissociated lateral arm plates. All specimens were handpicked from sieving residues of bulk sediment samples. These were taken from bed C of Delsate *et al.* (2002) in the so-called Marnes de Jamoigne, dated as middle Hettangian *Alsatites liasicus* ammonite Zone and exposed in a disused clay pit near Fontenoille (province of Luxembourg, south-east Belgium).

Selected specimens were cleaned in an ultrasonic bath, mounted on aluminium stubs and gold-coated for scanning electron microscopy. All figured specimens are deposited in the collection of the National Museum of Natural History, acronym MNHNL. We adopt the classification by O'Hara *et al.* (2017, 2018) and use the terminology proposed by Stöhr *et al.* (2012), Thuy & Stöhr (2011, 2016) and Hendler (2018).

Results

Systematic palaeontology

Ophiuroidea Gray, 1840

Subclass Myophiuroida Matsumoto, 1915

Infraclass Metophiurida Matsumoto, 1913

Superorder Euryophiurida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Order Euryalida Lamarck, 1816

Family Aspiduriellidae nov.

Genera included: *Aspiduriella* Bolette, 1998 and *Persoonaster* **gen. nov.**

Diagnosis: Stem euryalids with a round to rounded pentagonal disc covered by conspicuously large, very thick radial shields forming a continuous or at least near-continuous ring encompassing granule-covered primary plates; adoral shields meeting over their entire length; second oral tentacle pores entering mouth slit via shallow embayment; teeth and oral papillae small; arms short and rapidly tapering; lateral arm plates tumid, devoid of outer surface ornamentation except for poorly defined spurs and/or a central depression on proximal edge; spine articulations very small to moderately large, with muscle opening bordered by poorly defined, arched ridge proximally, and by thick lip-shaped vertical ridge distally; distal articulation face of vertebrae with tiny zygosphene between two large, parallel zygocondyles.

Genus *Persoonaster* nov.

Type and only known species: *Mesophiomusium kianiae* Thuy, 2005, by present designation.

Diagnosis: Small aspiduriellid with very large, thick adoral shields; oral shields absent or inconspicuous; lateral arm plates of rounded rectangular outline, with a flat to slightly concave outer surface; very large dorsal and ventral contact surfaces with the opposite lateral arm plate and very small vertebral space; spine articulations very small; large, ventralwards pointing tentacle notch.

Etymology: Genus named after Dominique, Fabienne and Julius Persoone, for producing chocolates that helped sweeten moments of frustration during the present study.

***Persoonaster kianiae* (Thuy, 2005)**
Figs 2–3

Description of articulated skeleton: MNHNL OPH045(Fig. 2) is a fully articulated skeleton exposing both dorsal and ventral sides and preserving proximal to median portions of fours arms, one of which broken after discovery; disc round, 1.6 mm in diameter, dorsal side with rounded-trapezoidal radial shields forming a closed circle accounting for half the disc radius and enclosing a poorly preserved set of rounded pentagonal primary plates; ventral side of disc with very large, conspicuous, bulging adoral shields meeting over their entire length; no oral shields discernible; only inconspicuous proximal tips of oral plates exposed; three to four relatively large, block-shaped oral papillae; single, short, rounded-triangular ventralmost tooth, slightly smaller than oral papillae; second oral tentacle pores entering mouth slit via shallow embayment between adoral shield and small, pentagonal first ventral arm plate.

Arms very short, rapidly tapering, longest preserved arm (broken after discovery) slightly shorter than disc diameter, composed of six segments; lateral arm plates thick, stout and strongly bulging, meeting dorsally and ventrally in all segments including those incorporated into the disc; proximal lateral arm plates higher than long, distal ones as high as long; at least three tiny, conical arm spines at the distal edge of the lateral arm plates, equalling one quarter of an arm segment in length; dorsal arm plates very small, fan-shaped; ventral arm plates small, mushroom-shaped with a pointed proximal tip, concave lateral edges and an expanded distal portion showing a convex distal edge; tentacle pores relatively large, developed as between-plate openings in all observable segments, covered by a row of tiny scales attached to a low, slender ridge along the tentacle notch on the lateral arm plates, and two to three larger, block-shaped tentacle scales; vertebrae unknown.

Description of dissociated lateral arm plates (MNHNL OPH046–OPH049): lateral arm plates (Fig. 3) thick, stout, of characteristic rounded rectangular outline and with bulging edges; proximal lateral arm plates slightly higher than long, distal ones as high as long; dorsal, ventral and distal edges evenly convex, proximal edge evenly concave, lined by a very poorly defined band of slightly more coarsely meshed stereom, devoid of spurs; outer

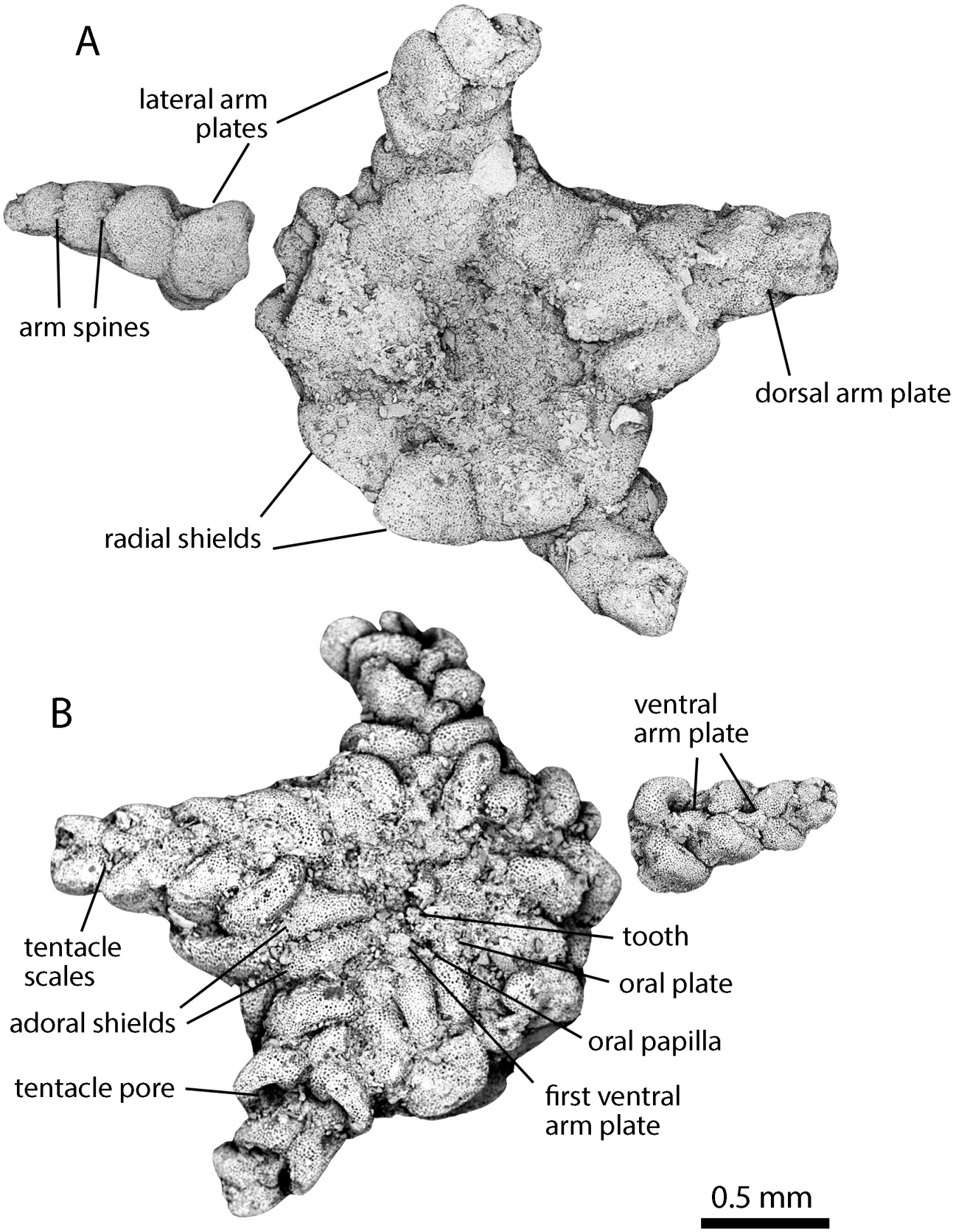

FIGURE 2. Articulated skeleton (MNHNL OPH045) of *Persoonaster* n. gen. *kianiae* (Thuy, 2005) from the Hettangian, Lower Jurassic, of Fontentoille, Belgium, exposing the dorsal (A) and ventral (B) sides.

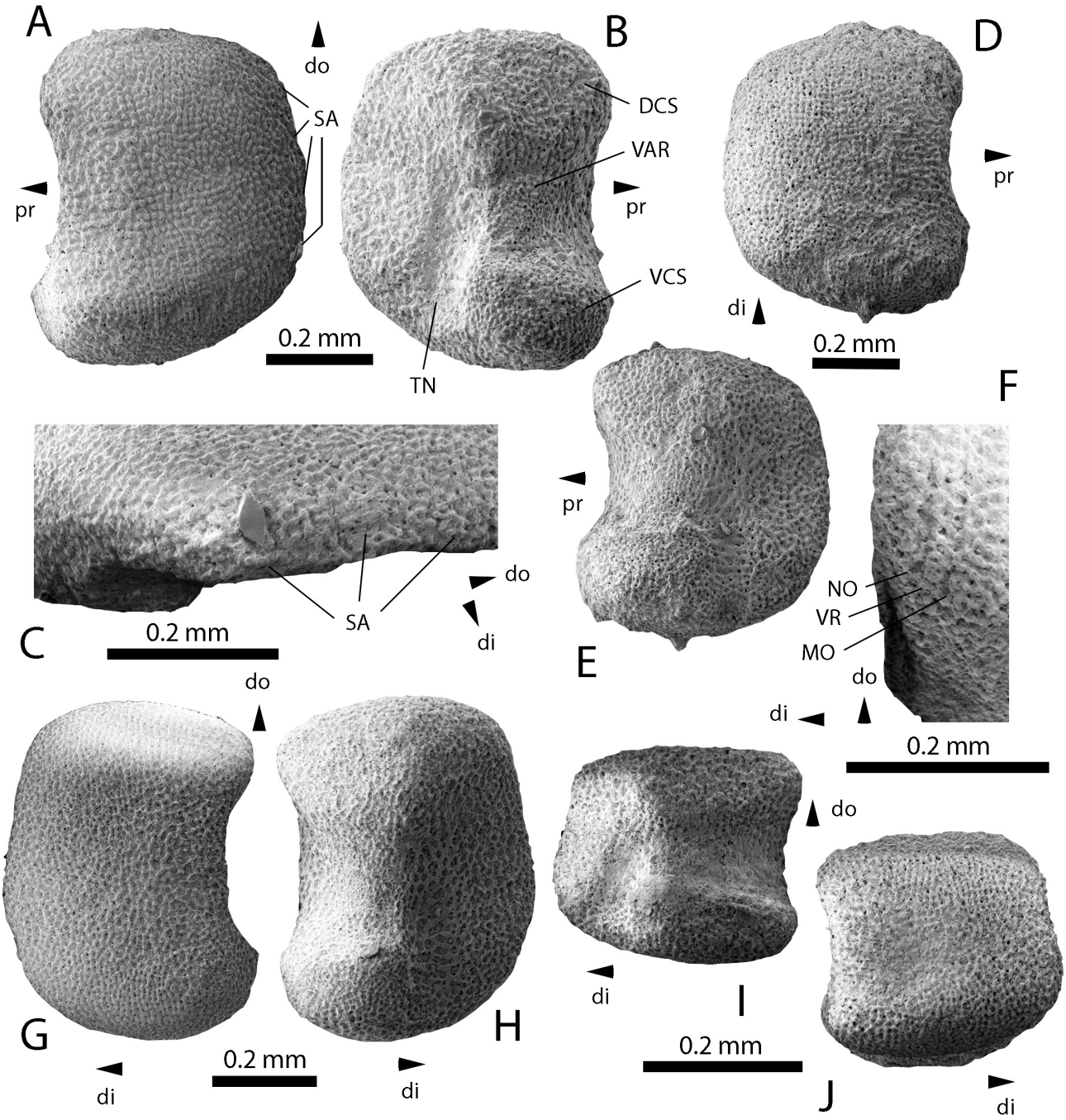

FIGURE 3. Dissociated lateral arm plates of *Persoonaster* n. gen. *kianiae* (Thuy, 2005) from the Hettangian, Lower Jurassic, of Fontentoille, Belgium. A–C: MNHNL OPH046, proximal lateral arm plate in external (A) and internal (B) views, and with details of spine articulations (C); D–F: MNHNL OPH047, median lateral arm plate in external (D) and internal (E) views, and with details of spine articulations (F); G–H: MNHNL OPH048, proximalmost lateral arm plate in external (G) and internal (H) views; I–J: MNHNL OPH049, distal lateral arm plate in internal (I) and external (J) views. *Abbreviations*: DCS: dorsal contact surface; di: distal; do: dorsal; MO: muscle opening; NO: nerve opening; pr: proximal; SA: spine articulation; TN: tentacle notch; VAR: vertebral articular ridge; VCS: ventral contact surface; VR: vertical ridge.

surface stereom moderately coarsely meshed but without tubercles or other elements of ornamentation, large but poorly defined depression in the centre of the outer surface at the proximal edge, resulting in bulging dorsal and ventral plate portions; distal edge with two (distal lateral arm plates) to four (proximal lateral arm plates) small, inconspicuous spine articulations inserted in the outer surface stereom and composed of a slit- to comma-shaped muscle opening bordered by very poorly defined, arched and rugose ridge proximally, and by a slender to moderately

thick, well-defined, lip-shaped vertical ridge distally; spine articulations of equal size and equidistant. Inner side of lateral arm plates with conspicuously large dorsal and ventral contact surfaces with the opposite lateral arm plate; vertebral space small and with a small, poorly defined, rounded triangular vertebral articular ridge composed of slightly more finely meshed stereom, distally bordered by a large, ventrally pointing tentacle notch.

Discussion

The material described in the present paper is unambiguously assignable to the species *Mesophiomusium kianiae* Thuy, 2005, originally described on the basis of dissociated lateral arm plates from the Hettangian of Belgium and Luxembourg, and sheds a new light on the taxonomic affinities of this enigmatic species. The new set of specimens includes an articulated skeleton that shows striking similarities to the Triassic genus *Aspiduriella*, especially regarding the short, tumid arms and the (near-) closed ring of large radial shields. These features alone are not decisive in assessing taxonomic relationships, irrespective of how conspicuous they are, given that they occur in various largely unrelated extant taxa such as the ophiopyrgid *Amphiophiura bullata* (Thomson, 1877) and the ophiolepidid *Ophioteichus multispinum* Clark, 1938. However, in combination with the adoral shields meeting over their entire length, the second oral tentacle pores entering the mouth slit via a shallow embayment, and the characteristic spine articulation morphology, the above-mentioned similarities provide strong evidence for close taxonomic ties. Compared to its Triassic relatives, the Jurassic taxon has inconspicuous oral shields (if at all) and rounded rectangular lateral arm plates with very large dorsal and ventral contact surfaces with the opposite lateral arm plate, and very small spine articulations. These differences would expand the concept of *Aspiduriella* beyond meaningful limits, which is why we erect a new genus, *Persoonaster*, to accommodate the Jurassic species.

In spite of its small size, the articulated skeleton described in the present paper is not a juvenile. In fact, the height-length ratio of the proximal lateral arm plates, the stereom structure on the outer surface of the arm plates, and the size similarity with the largest dissociated lateral arm plates described for *Persoonaster kianiae* both in the new material and the type lot all suggest that the individual is mature (Thuy & Stöhr 2011). The juvenile traits expressed in some of the skeletal characters is here interpreted as paedomorphosis, as outlined below.

Given the striking morphological similarities between *Aspiduriella* and *Persoonaster* n. gen., we assume close phylogenetic ties between the two genera. They most probably form a lineage at the stem of the order Euryalida (Thuy & Stöhr 2018) that had originated by the Middle Triassic and persisted at least into the Lower Jurassic. We introduce a new family, Aspidurielliidae, to reflect this hypothesis. The currently known species of *Aspiduriella* seem to show a paedomorphic gradient, with *A. streichani* (Kutscher, 1987) being the least and *A. similis* (Eck, 1865) the most strongly paedomorphic when considering typical paedomorphosis indicators such as disc plating, arm length, size of dorsal arm plates, and height-length ratio of arm segments (Stöhr & Martynov 2016). On this gradient, *Persoonaster* n. gen. seems closest to the strongly paedomorphic *A. similis*. The Early to Middle Jurassic stem euryalid *Melusinaster* Thuy & Stöhr, 2018, in contrast, is closest to the least paedomorphic *Aspiduriella streichani* (Thuy & Stöhr 2018) and shares a number of synapomorphies with the crown Euryalida, especially where vertebral articulation, lateral arm plate shape and spine articulation morphology are concerned. We therefore assume that the lineage leading to *Melusinaster* and the crown euryalids diverged early during the Middle Triassic from within the Aspidurielliidae n. fam.

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