

A new brittle star (Ophiuroidea: Ophiodermatina) from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA).

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A new brittle star (Ophiuroidea: Ophiodermatina) from the Early Triassic 1 of Idaho (USA) 2 3 Ben Thuy¹, Gilles Escarguel² and the Paris Biota team 4 5 6 ¹Natural History Museum Luxembourg, 25, rue Münster, 2160 Luxembourg-city, 7 Luxembourg; bthuy@mnhn.lu 8 ²Université Claude Bernard Lyon 1, Laboratoire d'Ecologie des Hydrosystèmes Naturels et 9 Anthropisés, CNRS, F-69622 Villeurbanne, France 10 Key words 11 Ophiuroids, evolutionary history, modern clades, morphology, Shoshonura bravardi 12 13 14 Abstract 15 16 17 Our knowledge of the morphology of Early Triassic ophiuroids is very limited, in spite of the relatively high number of described species. This hampers attempts to use morphology-based 18 phylogenetic analyses in order to explore the early diversification of modern ophiuroid clades 19 between the latest Paleozoic and early Mesozoic. Here, a new ophiuroid from the Early 20 Triassic of southern Idaho (USA) is described and assigned to the new taxon Shoshonura 21 brayardi gen. et sp. nov. It is part of an exceptional Early Triassic faunal assemblage recently 22 described as the Paris Biota. Based on the arm morphology, the shape of the arm spines and 23 the arm spine articulations, Shoshonura brayardi gen. et sp. nov. is considered a basal 24 25 member of the suborder Ophiodermatina.

1. Introduction

| 29 | The Late Permian to Early Triassic interval was a time of global-scale environmental |
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| 30 | perturbations, including the most devastating mass extinction to ever occur on Earth (e.g. |
| 31 | Sepkoski 1981; Erwin 1993). At the same time, however, it is considered a pivotal time in the |
| 32 | early evolution of many modern marine invertebrate groups, in particular setting the kick-off |
| 33 | for crown-group cladogenesis in echinoderms (e.g. Twitchett & Oji 2005). |
| 34 | With respect to the late Permian to Early Triassic fossil record, ophiuroids are certainly the |
| 35 | most prolific group. Chen and McNamara (2006) record as many as 14 ophiuroid species for |
| 36 | the boundary interval, which by far outnumbers the coeval fossil record of the other four |
| 37 | echinoderm classes (Twitchett & Oji 2005; Villier et al. in press). Regrettably, the majority of |
| 38 | the late Permian to Early Triassic ophiuroid occurrences are poorly known. Although |
| 39 | commonly named to species level, most records are based on insufficiently preserved |
| 40 | specimens and/or superficial descriptions (e.g. Detre & Mihaly 1987; Chen et al. 2004; Chen |
| 41 | & McNamara 2006). So far, the only Early Triassic ophiuroid species for which a reasonably |
| 42 | exhaustive description is available is Praeaplocoma hessi Broglio Loriga and Bert-Cavicchi, |
| 43 | 1972 from the Italian Dolomites. Yet, even P. hessi remains poorly known with respect to its |
| 44 | higher systematic affinities and its position within ophiuroid evolutionary history. |
| 45 | The latest studies of ophiuroid phylogeny and evolution converge to a mid-Permian origin for |
| 46 | the crown group Ophiuroidea followed by a relatively quick radiation of the major extant |
| 47 | groups (O'Hara et al. 2014; Thuy & Stöhr 2016). Against this background, the poor state of |
| 48 | knowledge of Triassic ophiuroids is particularly unfortunate as it hampers a better |
| 49 | understanding of the crucial early cladogenesis of the group. |

The present study describes a remarkable new ophiuroid from the Early Triassic of 50 southestearn Idaho, USA, previously highlighted as part of the so-called Paris Biota, a highly 51 diversified fossil assemblage documenting an unexpectedly rapid post-Permian recovery of 52 complex marine ecosystems (Brayard et al. 2017). The new ophiuroid allows for the 53 elucidation of at least a small part of the insufficiently known Triassic ophiuroid fossil 54 record. 55 56 2. Geological context 57 58

The described specimens were collected from the Early Triassic outcrops near the city of Paris, southeastern Idaho, USA, that exposes thin-bedded mudstones of the Lower Shale unit within the Lower Triassic Thaynes Group. The strata yielding the ophiuroid specimens were dated to the early Spathian based on ammonoid and conodont evidence. The depositional setting is interpreted as a distal upper offshore environment on a flat platform above stormwave base, originally in a near equatorial position on the western margin of Pangea. For details of the geological setting of the ophiuroids, see Brayard et al. (2017).

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67 **3. Material and Methods**

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The described specimens are housed in the collections of the Université de Bourgogne, Dijon,
France (acronym UBGD). Part of the paratype specimen was detached from the slab,
mounted on an aluminium stub and gold-coated for scanning electron microscopy using a
Jeol Neoscope JMC-5000. Terminology follows Stöhr et al. (2012), Thuy and Stöhr (2011)
and Thuy and Stöhr (2016), and higher systematic classification follows O'Hara et al. (in
press).

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| 76 | 4. Systematic paleontology (B. Thuy) |
| 77 | |
| 78 | Class OPHIUROIDEA Gray, 1840 |
| 79 | Subclass MYOPHIUROIDEA Matsumoto, 1913 |
| 80 | Infraclass METOPHIURIDA Matsumoto, 1913 |
| 81 | Superorder OPHINTEGRIDA O'Hara et al., in press |
| 82 | Order OPHIACANTHIDA O'Hara et al., in press |
| 83 | Suborder OPHIODERMATINA Ljungman, 1867 |
| 84 | |
| 85 | Genus Shoshonura nov. gen. |
| 86 | |
| 87 | Derivation of the name: Name formed to honour the Shoshoni Native American tribe who |
| 88 | originally inhabited the southeastern part of Idaho where the fossil ophiuroid was discovered. |
| 89 | |
| 90 | Type species: Shoshonura brayardi sp. nov., monotypic. |
| 91 | |
| 92 | Species included: only the type species. |
| 93 | |
| 94 | Occurrence: Paris Canyon, Bear Lake County, Idaho. |
| 95 | |
| 96 | Diagnosis: as for species. |
| 97 | |
| 98 | Shoshonura brayardi nov. sp. |
| 99 | Figs. 1-4 |

| 101 | Derivation of the name: Species named in honour of Arnaud Brayard (Dijon, France) who |
|-----|--|
| 102 | drew my attention to the new ophiuroid described herein, and who skillfully coordinated the |
| 103 | compilation of evidence from various taxonomic groups, including the ophiuroids, to unravel |
| 104 | the big picture behind the extraordinary Paris Biota. |
| 105 | |
| 106 | Type material: Holotype UBGD 305651 (Fig. X-Y); A single paratype: UBGD 305652 (Fig. |
| 107 | X-Y); |
| 108 | |
| 109 | |
| 110 | Type locality and horizon: Paris Canyon, west of the city of Paris, Bear Lake County, |
| 111 | Idaho, United-States of America; Early Triassic, earliest Spathian (after Brayard et al., 2017). |
| 112 | |
| 113 | Occurrence: only known as yet from the type locality. |
| 114 | |
| 115 | Diagnosis: Large ophiuroid with disc interradii covered by minute spherical granules; two |
| 116 | genital slits per interradius, no genital papillae; single apical oral papilla; ventral midline of |
| 117 | arms depressed, forming a shallow radial furrow; proximal ventral arm plates with deeply |
| 118 | concave lateral edges bordered by an elevated ridge; tentacle pores rapidly decreasing in size |
| 119 | from proximal to median segments and reduced to within-plate perforations in distal |
| 120 | segments; lateral arm plates thick, with finely meshed stereom devoid of conspicuous |
| 121 | ornamentation on outer surface; at least five spine articulations sunken in depressions of |
| 122 | distal lateral arm plate portion in proximal arm segments; spine articulations composed of |
| 123 | proximally merged dorsal and ventral lobes forming an oblique horse-shoe-shaped ridge |

encompassing small muscle and nerve openings; arm spines thick, conical, as long as half anarm segment.

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Description: Large, articulated specimen exposing the ventral side (Fig. 1), disc diameter of 127 14 mm; disc round, interradial areas convex and with small, rounded scales covered by 128 minute spherical granules (Fig. 2A-B). Two genital slits per interradius, approximately 129 130 equaling one third of the disc radius in length, no papillae or modified granules discernible on edge of genital slit. One abradial genital plate visible in ventral view (Fig. 2C), long, sabre-131 132 like with widened distal portion and straight to slightly convex adradio-distal edge, no groves or perforations discernible. 133 Oral shields small (Fig. 2A-B), equaling one sixth of the disc radius in length, with nearly 134 right, rounded proximal angle and slightly narrower rounded, square-like distal portion. 135 Adoral shields (Fig. 2A-B) with a pointed proximal tip and a wider distal portion, densely 136 covered by granules extending on the edges of the oral shields. Jaws (Fig. 2A-B) slender and 137 elongate, covered by granules, bearing a single conical apical oral papillae; at least four 138 lateral oral papillae, the proximal ones conical and slightly larger than apical oral papillae, 139 and the median ones elongate with oblique distal tip and two to three times larger than apical 140 oral papillae; distalmost lateral oral papillae not unambiguously discernible. Second oral 141 tentacle openings and first and second ventral arm plates concealed by matrix. 142 143 Five arms completely preserved from the base to the tip, evenly tapering, composed of up to 53 segments each. Ventral midline of arms (Fig. 2D) slightly sunken and concealed by matrix 144 in most proximal to median segments; ventral arm plates separating lateral arm plates in arm 145 segments covered by disc and in the proximalmost quarter of the remaining arm segments; 146 proximal ventral arm plates widest distally (Fig. 2D), with slightly convex distal edge, deeply 147 concave lateral edges bordered by an elevated ridge, and obtuse proximal angle; median 148

ventral arm plates devoid of ridge bordering lateral edges. Ventral arm plates rapidly 149 decreasing in size from proximal to median arm segments, reduced to minute, round plates in 150 distal segments. Tentacle openings within disc and in proximalmost free arm segments very 151 large, covered by at least three small, rounded, elongate tentacle scales (Fig. 2D) on tentacle 152 notch of lateral arm plate and at least one slightly smaller, round tentacle scale at lateral edge 153 of ventral arm plate; tentacle pores reduced to small between-plate openings (Fig. 3D) in 154 155 median arm segments, and to within-plate perforations in distal segments. Lateral arm plates thick (Fig. 3A), with ventro-distal tip prominent with respect to the ventral 156 157 arm surface; proximal edge lined by shallow dorso-ventral groove, presence of spurs unknown; outer surface of lateral arm plates with finely-meshed stereom devoid of 158 conspicuous ornamentation; distal portion of lateral arm plates bulging; spine articulations 159 (Fig. 3B) sunken in depressions of distal lateral arm plate portion, evenly spaced, at least five 160 in proximal segments and four in median ones; spine articulations composed of slender, 161 evenly arched and proximally merged dorsal and ventral lobes forming an oblique horse-162 shoe-shaped ridge encompassing small muscle and nerve openings; arm spines approximately 163 equal-sized, conspicuously thick, conical, pointed, as long as half an arm segment. Proximal 164 lateral arm plates with deeply concave tentacle notch lined by a shallow groove (Fig. 2D); 165 tentacle notch rapidly decreasing in size from proximal to median arm segments, and 166 replaced by within-plate perforation in distal arm segments. 167

168

Paratype supplements: UBGD 305652 is an articulated arm portion (Fig. 4A) associated with external molds of two further arms, all preserving median to distalmost segments, situated on the edge of the slab with the holotype specimen. The physically preserved articulated arm portion exposing the ventral side and showing a median to distal arm morphology similar to that seen in holotype specimen. Scanning electron microscopy of

median arm segments corroborating the absence of conspicuous outer stereom ornamentation
on the outer surface of the lateral arm plates and the arm spines. Arm spine articulations (Fig.
4B) forming an oblique horse-shoe-shaped ridge composed of slender, evenly arched dorsal
and ventral lobes proximally merged by a lower, less sharply defined ridge, encompassing
small muscle and nerve openings. Single, large, leaf-shaped tentacle scale.

179

180 **5. Discussion**

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182 The specimens described herein add to the rather long list of ophiuroid occurrences known from the Early Triassic (e.g. Chen & McNamara 2006; Twitchett et al. 2005). The new 183 material stands out, however, when it comes to body size; with a disc diameter of 14 mm, the 184 holotype specimen by far exceeds all other currently known Lower Triassic ophiuroids 185 (Twitchett et al. 2005). With respect to skeletal morphology, exhaustive comparison with 186 previously described species is hampered by the superficial state of knowledge of most Early 187 Triassic ophiuroids (e.g. Chen & McNamara 2006). Nevertheless, judging from the amount 188 of information available, none of the currently known species shows a radial depression on 189 the ventral side of the arms combined with swollen lateral arm plates bearing conspicuously 190 thick, short arm spines. The specimens at hand are thus described as the new genus and 191 species Shoshonura brayardi nov. gen. et nov. sp. 192

The higher systematic position of *Shoshonura brayardi* nov. gen. et nov. sp. was briefly outlined in the supplementary materials of Brayard et al. (2017). The most compelling evidence of systematic value is provided by the arm spine morphology, unequivocally placing *Shoshonura* nov. gen. in the order Ophiacanthida. Unfortunately, the holotype and only known complete specimen of *Shoshonura* nov. gen. does not expose the dorsal side, making many characters of diagnostic relevance for the position within the Ophiacanthida

inaccessible, at least for the time being. Novel non-destructive techniques, in particular 199 micro-computed tomography, might provide insights into these hidden structures. 200 In spite of these limitations, the morphological evidence available effectively excludes the 201 living members of the suborder Ophiacanthina, especially on account of the short, non-erect 202 arm spines, the thick, non-constricted lateral arm plates and the spine articulations sunken 203 into shallow depressions of the distal lateral arm plate edge. These same characters, in 204 205 contrast, strongly favour assignment to the suborder Ophiodermatina. However, because crucial features of the dorsal disc skeleton are unknown, the family-level position of 206 207 Shoshonura is left open for the time being. The radial furrow along the ventral midline of the arms and the tentacle openings developed as within-plate perforations in distal arm segments 208 seem to represent plesiomorphic character states (Thuy et al. 2015), suggesting a basal 209 position of Shoshonura nov. gen. within the Ophiodermatina. These character states are 210 211 unknown from any living member of the Ophiodermatina, and instead favour assignment to a new, extinct family. 212

The existing knowledge of the late Paleozoic and early Mesozoic fossil record of the
ophiuroids is too sparse to assess the phylogeny of the early diversification of modern
ophiuroid clades. Many more studies, particularly on Early Triassic ophiuroids, are necessary
to assess this crucial interval of the ophiuroid evolutionary history. Future works should
specifically aim at an exhaustive analysis of the skeletal features in order to allow for an
inclusion in morphology-based phylogenetic estimates.

219

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| 225 | This work is a | contribution to | the AND | project AFTED | (AND 12 ISO | 6 0001 01 |) and was |
|-----|----------------|-----------------|---------|---------------|-------------|-----------|-----------|
| 225 | This work is a | contribution to | the ANK | project AFIEK | (ANK-13-JSU | 0-0001-01 |) and was |

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300 Figure captions





302 Figure 1: Shoshonura brayardi nov. gen. et nov. sp., articulated ophiuroid in ventral view,

303 UBGD 30565 (holotype); Lower Shale unit, Thaynes Group, earliest Spathian, Early Triassic;

- 304 Paris Canyon, Bear Lake County, Idaho, USA. Scale bar equals 1 cm.
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- 306



Figure 2: *Shoshonura brayardi* nov. gen. et nov. sp., details of ophiuroid shown in figure 1,
UBGD 30565 (holotype); Lower Shale unit, Thaynes Group, earliest Spathian, Early Triassic;
Paris Canyon, Bear Lake County, Idaho, USA. A: detail of mouth plating; B: interpretative
drawing of detail shown in A; C: detail of basal arm segments with disc margin; D: detail of
basal arm segments. Abbreviations: AbGP: abradial genital plate; AOP: apical oral papilla;
AOS: adoral shield; AS: arm spine; G: granule; LAP: lateral arm plate; LOP: lateral oral
papilla; OS: oral shield; TS: tentacle scale; VAP: ventral arm plate. Scale bars equal 1 mm.



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Figure. 3. *Shoshonura brayardi* Thuy nov. gen. et nov. sp., UBGD 30565 (holotype): details

- of the ophiuroid specimen shown in Fig. 1; Lower Shale unit, Thaynes Group, early
- 319 Spathian, Early Triassic; Paris Canyon, Bear Lake county, Idaho, USA. A. Detail of basal
- arm segments. B. 980 🛛 980-pixel area from a 1024 🖾 1024-pixel false color RGB
- 321 composite of the mouth area and basal arm segments. Image was spatially registered and each
- 322 color corresponds to the following illumination/detection spectral ranges:
- 323 blue: 435 nm/435 nm, 70 nm FWHM; green: 385 nm/650 nm, 60 nm FWHM; red: 365
- 324 nm/650 nm, 60 nm FWHM. Image intensity levels in each channel were adjusted using a
- 325 Gaussian stretch (ENVI software, EXELIS). Abbreviations: AS: arm spine; LAP: lateral arm
- plate; OS: oral shield; TS: tentacle scale; VAP: ventral arm plate. Scale bars: 1 mm.



Figure 4: *Shoshonura brayardi* nov. gen. et nov. sp., details of ophiuroid shown in figure 1,
UBGD 30565 (holotype); Lower Shale unit, Thaynes Group, early Spathian, Early Triassic;
Paris Canyon, Bear Lake county, Idaho, USA. A: proximal arm segments in lateral view; B:
proximal arm segments in lateral view; C: median arm segments in ventral view; D: distal
arm segments in ventral view. Abbreviations: ASA: arm spine articulations; TO: tentacle
opening. Scale bars equal 1 mm.





Figure 5: *Shoshonura brayardi* nov. gen. et nov. sp., ophiuroid arm fragment, UBGD 30566
(paratype); Lower Shale unit, Thaynes Group, earliest Spathian, Early Triassic; Paris Canyon,
Bear Lake County, Idaho, USA. A: arm fragment in ventral view; B: detail of A showing arm
spine articulation in latero-ventral view. Abbreviations: AS: arm spine; DL: dorsal lobe;
LAP: lateral arm plate; VAP: ventral arm plate; VL: ventral lobe. Scale bars: 500 µm (A),
200 µm (B).