A remarkable example of a Late Jurassic shallow-water ophiuroid assemblage from the Swiss Jura Mountains

Ben Thuy · Daniel Marty · Gaël Comment

Abstract Although much effort has been put into attempts to unravel the Mesozoic ophiuroid fossil record, surprisingly little attention has been paid to the geological history of family-level compositions of brittle star assemblages. Here, we describe new ophiuroid material from the Late Oxfordian Bure Member as exposed in a construction site along the federal Highway A16 (Transjurane Highway) near Boncourt–Queue au Loup (Swiss Jura Mountains). The remains are exceptionally well preserved and partially articulated, enabling detailed morphological observations at a level comparable to Recent material. Three species are identified; they are here shown to display unequivocal affinities with extant ophiuroid lineages. The assemblage comprises a new ophiacanthid genus and species, *Juracantha hottingeri*, which is closely related to extant *Ophientrema*, an ophiolepidid close to extant *Ophiozonella* described here as a new genus and species, *Eozonella bergeri*, and a species previously described as *Ophiacantha? francojurassica*, which is here reassigned to the extant ophionereidid genus *Ophiodoris*. The assemblage was found in association with *Nanogyra* oyster buildups encrusted by serpulids and associated with partially-articulated crinoids, deposited in a shallow subtidal setting. Its family level composition is highly unusual with respect to modern equivalents, and instead is reminiscent of modern bathyal assemblages.

Keywords Oxfordian · Carbonate platform · Echinodermata · Ophiuroidea · Palaeoecology

Abbreviation
MJSN   Musée jurassien des sciences naturelles, Porrentruy (Canton Jura, Switzerland)

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B. Thuy (✉)
Section Paléontologie, Musée National d'histoire Naturelle du Luxembourg, rue Münster 24, 2160 Luxembourg, Luxembourg
e-mail: nebyuht@yahoo.com

D. Marty · G. Comment
Paléontologie A16, Section d'archéologie et paléontologie, Office de la culture, Hôtel des Halles, CP 64, 2900 Porrentruy 2, Switzerland

1 Introduction

Modern ophiuroids (brittle stars) are distributed globally at all depth ranges. Yet, in most oceans, there is a clear difference in higher taxonomic composition between shelf and deep-water communities. In fact, shallow-marine (<200 m) communities are commonly dominated by representatives of the families Ophiotrichidae, Ophiocomidae, Ophiodermatidae, Amphiuridae and Ophionereididae, whereas other families including the Ophiacanthidae, Ophiolepididae and Ophiuridae occur mainly in deep-water settings (Tyler, 1980; Stöhr et al., 2012). Comparatively little is known about the geological history of these depth-related patterns in the composition of ophiuroid communities, which is surprising considering the progress made during recent decades in unravelling the ophiuroid fossil record (e.g. Rasmussen, 1972; Hess, 1962, 1964, 1965, 1966, 1975a, b; Kutscher & Hary, 1991; Kutscher, 1996; Kutscher & Jagt, 2000; Kutscher & Villier, 2003; Thuy, 2005; Hess & Meyer, 2008; Thuy, 2011; Ishida et al., 2011; Thuy & Schulz, 2012; Thuy & Meyer, 2012). Many extinct

ophiuroid taxa have been described on the basis of diagnostic dissociated ossicles, in particular the spine-bearing lateral arm plates (e.g. Hess, 1975a and references therein; Kutscher & Jagt, 2000; Kutscher & Villier, 2003; Thuy, 2005). In addition, numerous fully-articulated ophiuroid fossils have been recorded, in spite of their general paucity owing to rapid post-mortem disarticulation of the ophiuroid skeleton (Kerr & Twitchett, 2004).

Thus far, hardly any study of ophiuroid palaeontology has gone beyond the level of mere taxonomic description. One major factor hampering meaningful comparisons between fossil and modern ophiuroid community compositions involve the uncertainties in the higher taxonomic placement of dissociated lateral arm plates. Only very recently, a systematic survey of lateral arm plate morphology in modern ophiuroids has highlighted a number of characters that are potentially diagnostic at the generic and higher taxonomic levels (Thuy & Stöhr, 2011). Articulated ophiuroid fossils generally enable a more conclusive taxonomic assignment since they potentially expose the set of external skeletal characters that is commonly used to describe modern ophiuroids (Stöhr et al., 2012). A remarkable example of such are locally abundant lots of articulated specimens of Ophiomusium gagnebini (Thurmann, 1851) in the Middle Oxfordian Schofgraben (Weissenstein) Lagerstätte of the Swiss Jura Mountains (Meyer, 1984). Although placement of these finds in extant Ophiomusium is most probably untenable (Kutscher & Jagt, 2000), affinities with that genus and the closely related Ophiosphalma are strong enough to permit a conclusive, albeit so far neglected, comparison of ancient and modern depth distributions in these taxa. Remarkably, extant Ophiomusium and Ophiosphalma are found exclusively in deep-water settings, implying that many Late Jurassic epicontinental shallow-marine environments were predominated by representatives of modern deep-sea lineages.

Here, we present new ophiuroid remains including articulated and semi-articulated arm and disc fragments, and dissociated ossicles. This material was discovered in the course of palaeontological excavations carried out by the *Paléontologie A16*, a project in charge of safeguarding the palaeontological heritage along the future course of the Transjurane (A16) highway in the Canton Jura, NW Switzerland (Hug et al., 2003; Ayer et al., 2006). The specimens described here are outstanding because they (1) are exceptionally well preserved and entirely free of matrix, allowing for detailed morphological observations at a level comparable to Recent material, (2) have unequivocal affinities with modern ophiuroid lineages, and thus (3) provide unprecedented insights into the composition of a Late Jurassic shallow-marine ophiuroid community. Another remarkable aspect of the new material is the absence of *Ophiomusium*-like forms, which are very frequent in the Early Oxfordian of sites located in the Northern Swiss and French Jura Mountains not far from the study locality (e.g. Hess, 1960), implying that the present assemblage documents a different and previously unknown type of Late Jurassic shallow-water fauna. The aim of this study is to assess taxonomically the new assemblage, compare it with modern equivalents in terms of composition, and discuss the implications of differences in depth distribution of the ophiuroid lineages found.

2 Geographical and geological setting

2.1 Geographical and geological setting

All material studied is from a palaeontological excavation site named Boncourt–Queue au Loup (abbreviation: BON–QLP), located about 2 km west of the village of Boncourt in the Ajoie district of the Canton Jura, northwest Switzerland (Fig. 1a). The site actually represents the most northwesterly tip (French: "Queue au Loup" = wolf's tail) of Switzerland, and is currently completely covered by the construction of Swiss Federal Highway A16 (Transjurane Highway), more precisely the customs platform ("*plate-forme douanière*") between Switzerland and adjacent France (Fig. 1b).

The Ajoie is located at the eastern end of the Rhine-Bresse transfer zone (Giamboni et al., 2004) between the Folded Jura Mountains to the south and east and the Upper Rhine Graben and Vosges Mountains to the north. The site Boncourt–Queue au Loup is within the Tabular Jura Mountains, which consist of slabs of subhorizontally layered Mesozoic strata, separated by narrow dislocation belts (Trümpy, 1980; Jordan et al., 2008).

2.2 Stratigraphical setting

At Boncourt–Queue au Loup, the Hauptmumienbank Member and the overlying Bure Member of the Late Oxfordian Vellerat Formation both cropped out. The boundary between these members corresponds approximately to the sequence boundary OX7 and the top of the Bure Member marks the boundary between the Vellerat Formation and the overlying Courgenay Formation (Gygi, 2000a, b, 2012). All samples studied are from the Bure Member, which according to Gygi (1995, 2000a, b) is of Late Oxfordian (Bimammatum ammonite Zone) age (Fig. 2).

2.3 Palaeogeographical and palaeoenvironmental setting

During the Late Jurassic, the domain of today's Jura Mountains was located along the northern margin of the
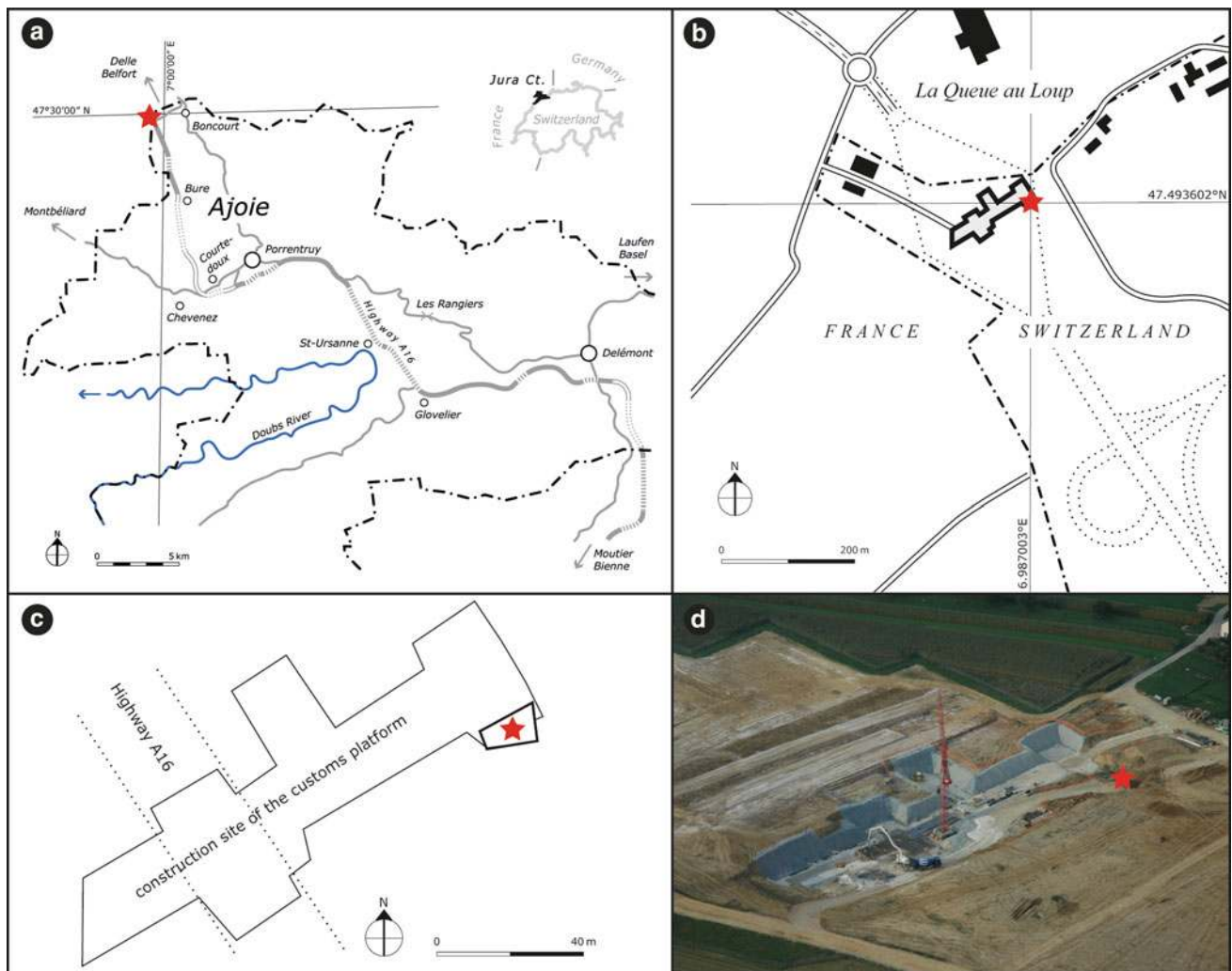
Fig. 1 Geographical setting. **a** Location of the Boncourt—Queue au Loup site within the Ajoie district and the Canton Jura, NW Switzerland. **b** Close-up of the Queue au Loup site and Highway A16 (*dotted line*). The area surrounded by the thick black line is the construction site of the customs platform ("*plate-forme douanière*") between Switzerland and adjacent France. **c** Detail of the construction area of the customs platform. The area of the emergency excavation (excavation area 10) is also shown in Fig. 3a. **d** Aerial photograph of the construction site after the emergency excavation had been terminated

oceanic Ligurian Tethys (e.g., Gygi, 1990; Thierry, 2000; Stampfli & Borel, 2002), as a large and structurally complex, epicontinental carbonate platform (Hug, 2003; Colombié & Strasser, 2005). Platform morphology was created by differential subsidence of tectonic blocks and by varying sediment accumulation (e.g., Pittet, 1996; Allenbach, 2001; Hug, 2003; Wetzel et al., 2003).

The Jura carbonate platform was situated at a palaeolatitude of around 30°N (Dercourt et al., 1994; Thierry, 2000), at the threshold between the Paris Basin to the northwest and the Tethys Ocean to the south and, thus, influenced by both the Tethyan and Boreal realms (Ziegler, 1988; Meyer & Schmidt-Kaler, 1989; Dercourt et al., 1994; Jank et al., 2006).

Based on samples from the Swiss Jura carbonate platform, Plunkett (1997) calculated 26–27 °C for Middle Oxfordian ocean surface temperatures. In the Late Oxfordian the climate was warm (subtropical), and abundant rainfall in the hinterland allowed vegetation growth and continental run-off of siliciclastics into the study area (Gygi, 1986; Pittet, 1996). Increased nutrient input periodically led to eutrophication and to coral reef crises (Dupraz and Strasser, 1999). By the end of the latest Oxfordian to earliest Kimmeridgian, the climate became more arid (Hallam, 1985; Moore et al., 1992; Weissert & Mohr, 1996), as indicated by predominant limestones, evaporite pseudomorphs and little siliciclastic input (Colombié, 2002; Hug, 2003).

In the study area, from the Middle Oxfordian onwards, a widespread shallow-marine platform developed as evidenced by carbonate deposits of the St. Ursanne Formation and the Vorbourg Member at the base of the Vellerat Formation (Ziegler 1956, 1962; Gygi, 2000a).
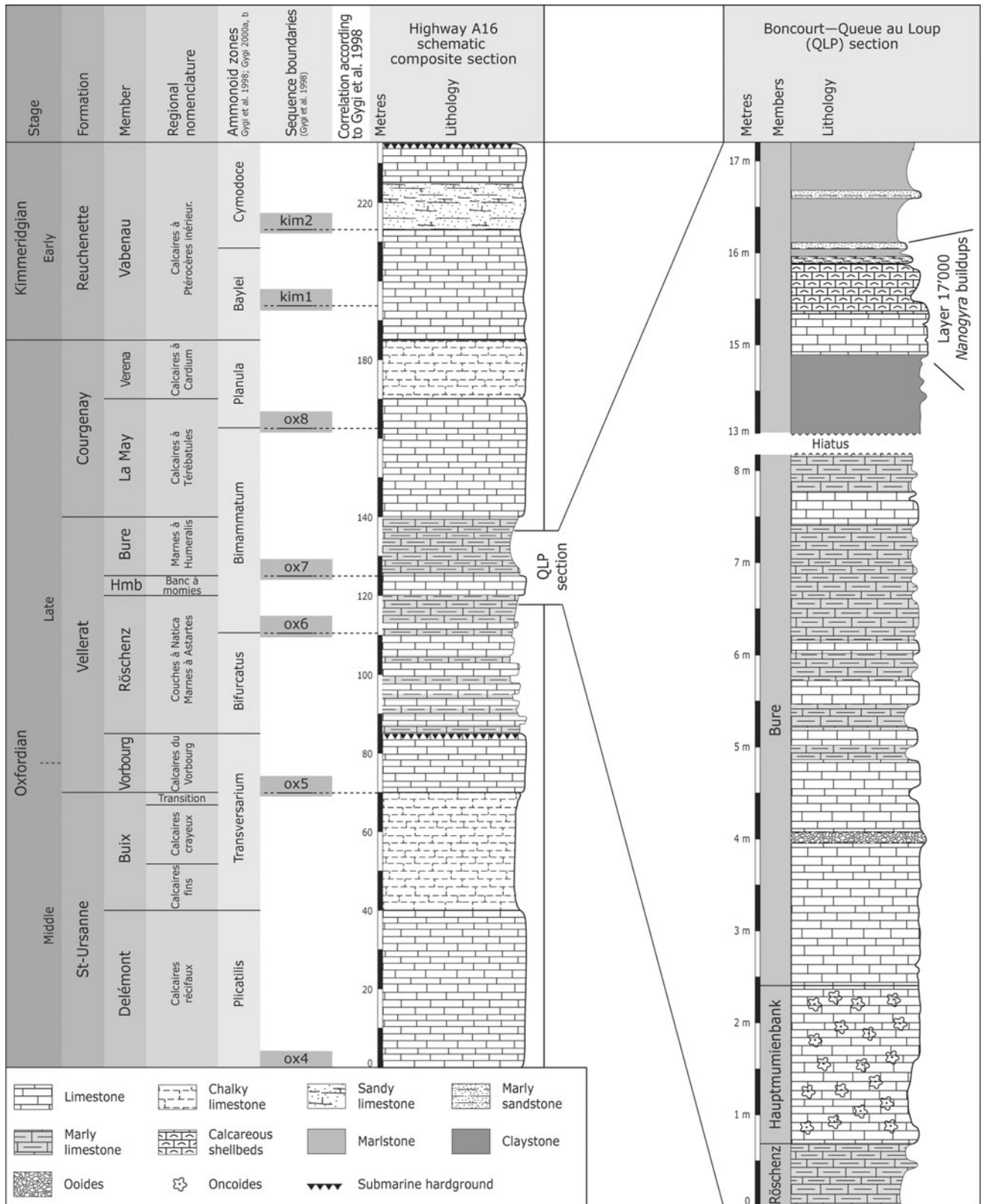
Fig. 2 Stratigraphical setting showing the location of the Boncourt—Queue au Loup (QLP) section within the Late Jurassic schematic composite section of Highway A16 (NW Switzerland). Note that no ammonites were found in the QLP section, and that the correlation of the sequence boundaries is based on Gygi et al. (1998). Ammonoid zones are after Gygi et al. (1998) and Gygi (2000a, b). Hmb is the Hauptmumienbank Member

In the overlying Röschenz Member, enhanced siliciclastic input suggests a return of more humid conditions (Védrine et al., 2007), and the carbonate platform diminished in size (Gygi, 2000a, b). In the middle part of the Röschenz Member, at the sequence boundary OX6, the first widespread emersion of the carbonate platform occurs. This is evidenced by calcareous biolaminites with prism cracks, wavy lamination, birdseyes, fenestrae and mud pebbles, attributed to an intertidal algal marsh environment (Gygi, 1992). These microbial biolaminites occur at several localities in the Jura Mountains of the cantons Jura, Bern and Baselland (e.g., at Crémines, Grandval, Saulcy, Sornetan, Corban, Liesberg; see Gygi, 1992, figs. 5–13), and they have also been documented by the *Paléontologie A16* in excavations at Boncourt and Bure (Marty et al., 2003; Billon-Bruyat et al., 2006). Laterally, near Vermes (Canton Jura), these biolaminites may also grade into a black pebble conglomerate with nerineid gastropods (e.g., near Vermes, Canton Jura; Gygi and Persoz, 1986, fig. 5). Terrestrial influence in the Röschenz Member is further documented by numerous plant remains from sites near Court and Péry-Reuchenette, both Canton Bern (Allenbach and Van Konijnenburg-van Cittert, 1997; Van Konijnenburg-van Cittert and Meyer, 1996; Gee et al., 2003), charophytes and limnic ostracods from sites near Courchavon, Canton Jura (Ziegler, 1962) and Bure, Canton Jura (unpublished material of the *Paléontologie A16*), and pterosaur remains (unpublished material of the collection *Fondation Paléontologique Jurasienne*) from the Péry-Reuchenette quarry (both Canton Bern). Notably, sites at Boncourt, Bure and Courchavon are located in close proximity to the ophiuroid locality described here.

In the overlying calcareous Hauptmumienbank Member, kaolinite is abundant but detrital quartz occurs only in small quantities (Gygi and Persoz, 1986). This may point to a northward shift of the siliciclastic source area and/or to diminishing rainfall in the hinterland (Védrine et al., 2007). Védrine et al. (2007) described four different types of oncoids from the Hauptmumienbank Member and interpreted the palaeoenvironment to have been a protected lagoon to fully marine lagoon. The presence of oncoids indicates a photic setting with frequent wave action, and accordingly a shallow-marine environment (Gasche, 1956; Dahanayake, 1983; Peryt, 1983).

The base of the overlying marly Bure Member (about 10 m thick) may be transitional and represent a paraconformity (Gygi, 2000a, b). The Bure Member is present mainly in the Canton Jura and in adjacent France; further south, it grades into the Oolithe rousse Member (Gygi, 2000b). The Bure Member was originally named "Humeralis Schichten" (Ziegler, 1956); it was defined by Gygi (2000a) based on an exploration well (BUR 2) from Highway A16. Possibly for this reason, the description of

this unit by Gygi (2000a, b) is rather limited in scope. However, based on observations made on drill cores from Highway A16 near Bresseaucourt, Canton Jura, in outcrops on the military training ground of Bure (Marty et al., 2003), and at Boncourt—Queue au Loup, it can be added that *Nanogyra* oyster buildups encrusted by serpulids and associated with partially-articulated crinoids (*Apiocrinites*, *Millericrinus*) are a typical and common faunal element of this member, as well as brachiopods (*Zeilleria humeralis*, *Z. corallina*). The latter may also occur as thin ribbons (Liniger, 1970).

On top of the Bure Member follows the La May Member of the Courgenay Formation, which is characterised by a succession of well-bedded and massive micritic limestones with peloids, oncoids, and small bio- and lithoclasts (Gygi, 2000a), laid down in a shallow-marine lagoonal palaeoenvironment.

3 Materials and methods

The BON–QLP site was discovered during construction of the customs platform of highway A16 and was excavated by the *Paléontologie A16* between August and October 2005 (Fig. 3). During this excavation, a large oyster reef, encrusted with crinoids, was discovered and recovered in no fewer than 62 blocks with a total weight of nearly 50 tons (Billon-Bruyat et al., 2006). Additionally, various marly layers and claystones below, in between, and above the reef were exhaustively sampled for microfossil screen-washing. In order to locate the recovered blocks and samples, nine sections were logged around the site. Thereby the number 17′000 is used as layer number for all the material from the oyster buildups as well as for the associated marly layers and claystones (Fig. 2). These clay- and marlstone samples were subjected to a standard screen-washing procedure and picked for microfossils. Besides the ophiuroid assemblage described below, these samples have also yielded numerous other microrests including remains of crinoids, asteroids, holothuroids, echinoids, gastropods, ostracods, foraminifers, and fish teeth and scales.

The material studied comprises several hundreds of dissociated ossicles and articulated arm fragments, and a number of articulated, yet mostly fragmentary discs. The articulated remains commonly have all plates preserved in place, in some cases even including arm spines and tentacle scales, and mouth papillae and teeth in the discs. Preservation of the skeletal calcite is generally very good, although some plates show signs of corrosion and/or slightly coarser recrystallisation. Most ossicles suffer from various degrees of syntaxial calcite overgrowth, as evidenced by micrometric impressions of small rhombic crystals on the plate surfaces. Nevertheless, the overall

Fig. 3 a Emergency excavation in 2005. The thick, nodular bed in the middle corresponds to layer 17'000 which is laterally highly variable and comprises the *Nanogyra* oyster buildups, storm shellbeds, and intercalated marls and claystones, the latter having yielded the ophiuroid remains. **b** Storm shellbeds from the very top of layer 17'000. Note concave-up *Nanogyra* shells on top of the upper shell bed and erosional features at its base. Besides *Nanogyra*, the shell bed also contains abundant remains of other bivalves, serpulids and crinoids. Sample QLP005-164, sub-layer 17000I located at the top of layer 17'000, scale bar is 5 cm

preservation of the specimens is outstandingly good, in particular considering that all specimens are completely free of matrix and observable from both ventral and dorsal sides, thus allowing to observe an exceptional number of morphological details.

Specimens selected were mounted on aluminium stubs and gold-coated for scanning electron microscopy. Morphological terminology follows Thuy and Stöhr (2011) for the lateral arm plates and Stöhr et al. (2012) for the general skeleton. Higher-level classification is adopted from Smith et al. (1995) and, where applicable, Martynov (2010).

All material studied has been deposited in the collections of the *Paléontologie A16* (PAL A16) of the Musée jurassien des Sciences naturelles (MJSN, Natural History Museum of the Canton Jura) in Porrentruy, Canton Jura, Switzerland.

4 Systematic palaeontology

Order Ophiurida MÜLLER and TROSCHEL, 1840

Family Ophiacanthidae LJUNGMAN, 1867
Genus *Juracantha* nov.

Type, and only known, species. *Juracantha hottingeri* sp. nov.

Etymology. A combination of "Jura", referring to the type locality of the new taxon in the Swiss Jura Mountains (Canton Jura), and "acantha", the name of a nymph from Greek mythology whose name literally translates into "thorny". Gender feminine.

Diagnosis: Ophiacanthid brittle star with lateral arm plates of neighbouring arm segments separated by large gaps; up to ten arm spines, at least the dorsal ones of which large, flattened, composed of coarsely reticulate stereom and with serrate edges; two leaf-like tentacle scales in proximal arm segments.

Juracantha hottingeri sp. nov. (Figs. 4, 5a–g)

Types. QLP005-809 (holotype); QLP005-810, QLP005-811, QLP005-812 and QLP005-813 (paratypes).

Additional material. QLP005-649 (18 arm fragments), QLP005-720 (5 arm fragments).

Diagnosis. As for genus.

Occurrence. Bure Member, Late Oxfordian; Boncourt–Queue au Loup, Swiss Jura Mountains.

Etymology. In honour of Professor Dr Lukas Hottinger (1933–2011), renowned foraminifera micropalaeontologist and longtime professor of geology and palaeontology at the University of Basel, Switzerland (Caus and Langer 2012).

Description of holotype. QLP005-810 is a large proximal arm fragment composed of four segments. Arm segments tall and narrow, nearly circular in section. Lateral arm plates (LAPs) robust, at least three times taller than wide, strongly arched; well-developed constriction resulting in concave dorsal edge and strongly elevated distal portion of LAPs; proximal edge of LAPs evenly concave, no spurs discernible; no vertical striation or conspicuous granulation on outer surface. Small ventral portion of LAPs protruding, pointed. Ten very large spine articulations on strongly elevated ridge, ear-shaped and with well-developed sigmoidal fold; strong dorsalward increase in size of spine articulations and of gaps separating them; no alternation in position of spine articulations between neighbouring segments. Tentacle notch very well developed and conspicuous, directly below ventralmost spine articulation. Inner side of LAPs not observable. LAPs of neighbouring segments not in contact, separated by a void nearly as wide
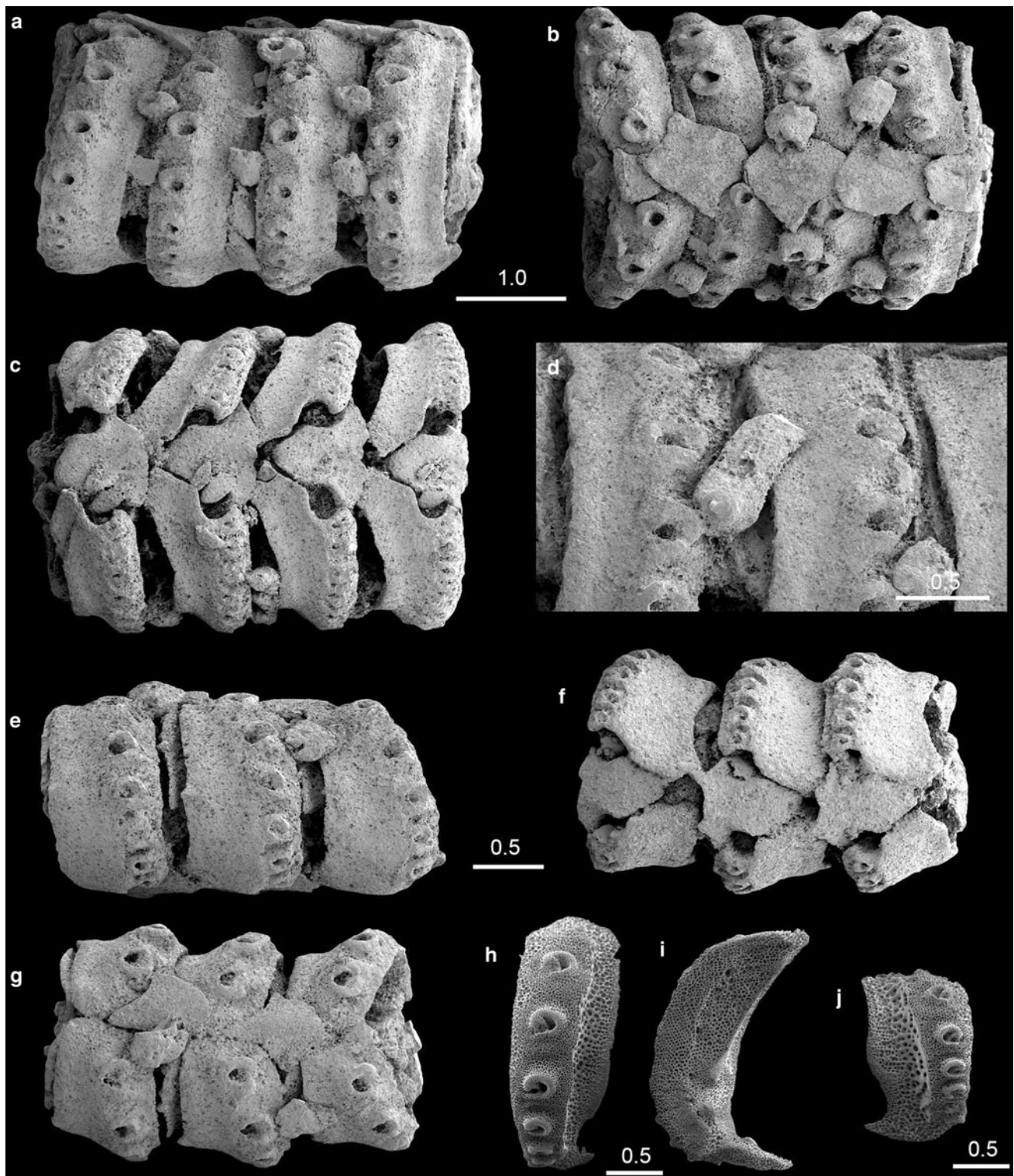
Fig. 4 *Juracantha hottingeri* gen. et sp. nov. from the Late Oxfordian Bure Member of the Boncourt—Queue au Loup site. **a–d** QLP005-809 (holotype), proximal arm segments in lateral (**a**), dorsal (**b**) and ventral (**c**) views, and detail of lateral view exposing an arm spine fragment (**d**). **e–g** QLP005-810 (paratype), median arm segments in lateral (**e**), ventro-lateral (**f**) and dorsal (**g**) views. **h–j** *Ophientrema scolopendrina* (Lyman, 1883), Recent, off Tanabe, Kii Peninsula, Japan, 975–1,112 m, proximal lateral arm plate in external (**h**) and internal (**i**) views, and median lateral arm plate in external view (**j**). All *scale bar* specifications are in mm. Note that *scale bars* in Fig. 3a–c and e–g, respectively, are drawn to *scale*, but that this is not the case for the *scale bars* in h–j
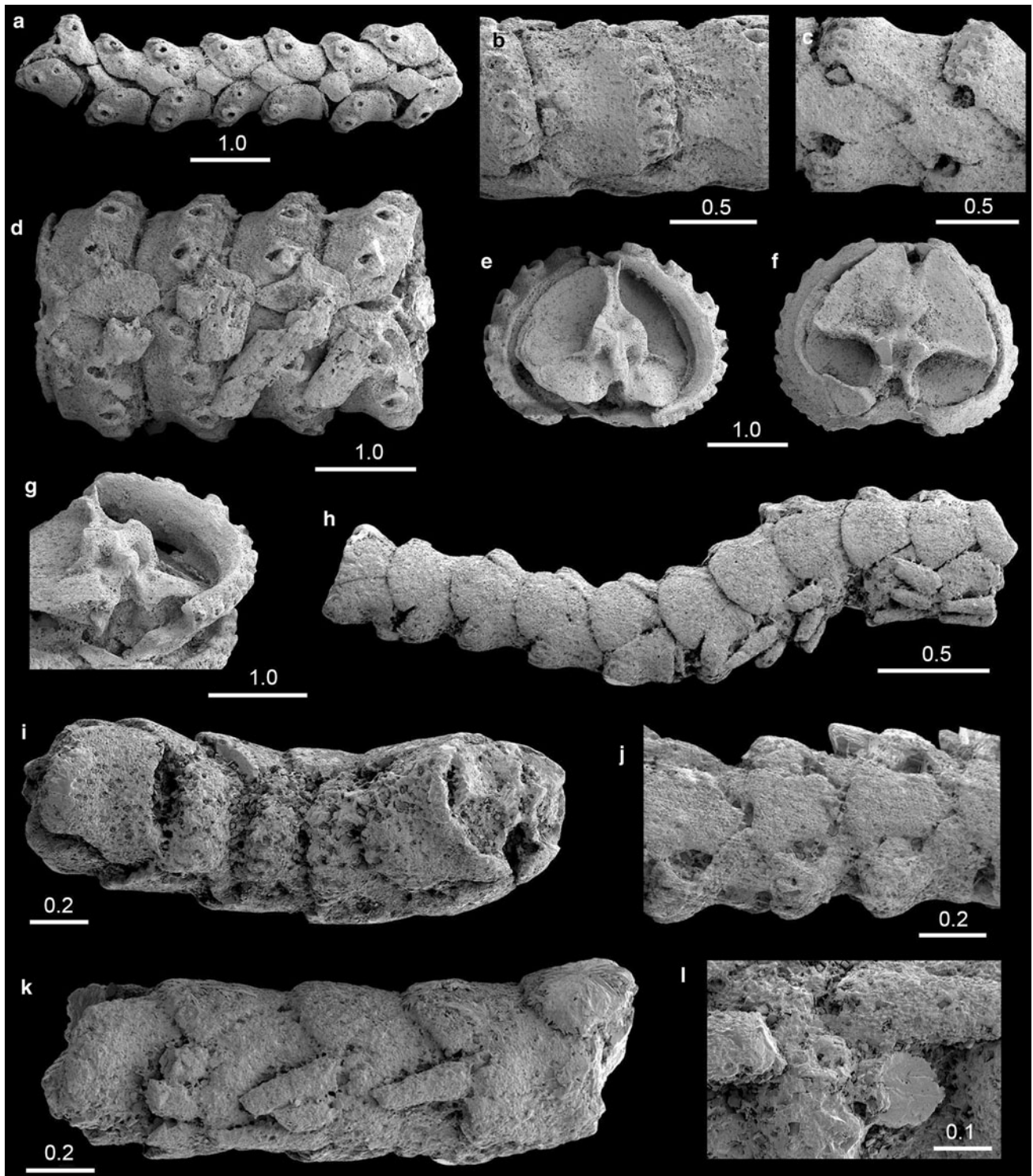
Fig. 5 **a–g** *Juracantha hottingeri* gen. et sp. nov. from the Late Oxfordian Bure Member of the Boncourt—Queue au Loup site. **a–c** QLP005-811 (paratype), distal arm segments in dorsal view (**a**) and with details of lateral (**b**) and ventral (**c**) views; **d** QLP005-812 (paratype), proximal arm segments in dorsal view, exposing arm spine fragments. **e–g** QLP005-813 (paratype), proximal arm segment in distal (**e**), proximal (**f**) and ventro-distal (**g**) views. **h–l** *Ophiodoris francojurassicus* (Hess, 1975b) from the Late Oxfordian Bure Member of the Boncourt—Queue au Loup site. **h** QLP005-814, median to distal arm segments in dorsal view. **i** QLP005-815, proximal arm segments in lateral view. **j** QLP005-816, median arm segments in ventral view. **k** QLP005-817, median arm segments in lateral view. **l** QLP005-818, detail of median arm segments in lateral view, exposing spine articulation. All *scale bar* specifications are in mm

as one-third of LAP width. Stumps of spines preserved in place on some of spine articulations, suggesting large, hollow and flattened spines composed of coarse stereom and with serrate edges.

Ventral arm plates large, widest distally, with acute proximal angle, strongly concave lateral edges and convex distal edge with a central notch; ventral arm plates very narrowly meeting and separating LAPs. Tentacle openings relatively small, covered by two leaf-like, near-equal sized tentacle scales.

Dorsal arm plates large, approximately as long as wide, nearly bell shaped, with rounded proximal tip, slightly concave lateral edges and right distal angle; dorsal arm plates of neighbouring segments overlapping, covering dorsal tips of LAPs.

Paratype supplements. QLP005-810 is a median arm fragment consisting of three segments. LAPs approximately twice taller than wide; proximal edge of LAPs with single, moderately well-developed, prominent and pointed, protruding spur. Six spine articulations per LAP. Dorsal arm plates slightly longer than wide, with acutely pointed proximal tip, concave lateral edges and broad, rounded distal tip. LAPs meeting dorsally but partly covered by dorsal arm plates. Single leaf-like tentacle scale.

QLP005-811 is a distal arm fragment composed of seven segments. LAPs nearly as wide as tall; proximal edge with single well-developed, prominent and protruding spur. Five spine articulations per LAP. Dorsal arm plates clearly longer than wide, separated by LAPs. Single tentacle scale.

QLP005-812 is a proximal to median arm fragment of four segments. Overall morphology in agreement with holotype. Arm spine fragments slightly more complete, documenting very large, flattened arm spines composed of coarsely reticulate stereom and irregularly serrate edges, slowly tapering at least near their base and therefore presumably very long.

QLP005-813 is a proximal arm fragment consisting of two vertebrae and three LAPs in place. Overall morphology in agreement with holotype. Unparalleled LAP exposing part of the inner side, displaying slender, prominent vertical ridge apparently truncated abruptly in the middle of the inner side and thus limited to the ventral portion of the LAP; vertical row of small perforations in part in well-defined shallow furrow over entire observable height of inner side of LAP.

Remarks. Large, freestanding, ear-shaped spine articulations with a well-developed sigmoidal fold, together with a vertical row of perforations on the inner side of the LAPs are a combination that unequivocally places these specimens in the extant family Ophiacanthidae (Thuy and Stöhr, 2011). This group is one of the most speciose amongst modern ophiuroids, counting more than 300 species (Stöhr et al., 2012). Yet, there is only a single extant ophiacanthid genus, *Ophientrema* Verrill, 1899, which displays the conspicuous gaps between LAPs of neighbouring arm segments as observed in the material described above. A closer comparison of LAP morphology between the type species, *Ophientrema scolopendrica* (Lyman, 1883), and the fossil specimens reveals striking similarities concerning overall shape of the LAPs, the lack of a conspicuous ornamentation on the outer surface, the dorsalward increase in size of spine articulations and gaps separating them, and the vertical row of small perforations on the inner side of the LAPs.

Here again, the fossil LAPs differ from both known extant species of *Ophientrema* in having a higher number of spine articulations, more clearly defined tentacle openings, two leaf-like tentacle scales in proximal segments, and flattened, coarsely reticulate and serrate rather than cylindrical and smooth arm spines. In addition, the Jurassic form described here has differently shaped dorsal and ventral arm plates. In the light of these differences, especially considering that both extant species of *Ophientrema* form a homogeneous lot sharing highly similar morphologies, the new genus *Juracantha* is introduced here to accommodate the fossil form in question. The highly distinctive general arm morphology shared by *Ophientrema* and the new Jurassic genus make a close phylogenetic relationship most likely, and it can be hypothesised that both are part of the same lineage within the Ophiacanthidae.

On the species level, only very few fossil ophiacanthids have so far been described which are comparable to the new Jurassic taxon. Among the numerous Late Jurassic species known exclusively from dissociated LAPs, *Ophiogaleus constrictus* (Hess, 1965) is by far the closest. In that species, however, LAPs are much more fragile, the row of spine articulations protrudes strongly ventrally, and spine articulations are evenly spaced and of equal size. The LAPs described as "Ophiacanthid B" from the Barremian of France (Thuy & Kroh, 2011) are closely similar to those of the new Jurassic taxon. Although the Barremian specimens have fewer spine articulations and granules on their outer surface, which commonly merge into a faint vertical striation, similarities with the new Jurassic form are such that they probably belong to the same genus. Other than this form (still unnamed), however, no currently known Mesozoic ophiacanthid species is compatible with the specimens described here. We therefore erect a new species to accommodate it.

Genus *Ophiodoris* Lütken, 1859

Type species Ophiodoris malignus (Koehler, 1904), by original designation.

Ophiodoris francojurassicus (Hess, 1975b) (Fig. 5h–l)

Material. QLP005-676 (7 arm fragments), QLP005-814 to -818 (5 arm fragments), QLP005-830 (18 arm fragments).

Description. Arm fragments relatively small, horizontally oval in section; LAPs of proximal arm segments slightly taller than wide, evenly bent and with large, protruding

ventral portion; no constriction, small and vertically elongate granules on outer surface, resulting in very faint, irregular vertical striation; proximal edge of LAPs without spurs; up to five spine articulations in proximal LAPs, relatively large, horseshoe-shaped with proximal part consisting of several knobs, freestanding on bulging distal portion of LAP and nearly equal in size; very large arm spines preserved on some segments, slightly flattened, finely granulated, rapidly tapering and pointed, equalling the length of one segment. Proximal ventral arm plates nearly as long as wide, bell-shaped, with pointed proximal edge, strongly concave lateral edges and gently convex distal edge, separating LAPs at least in proximal to median LAPs. Tentacle openings relatively large, covered by a single leaf-like to opercular scale. Dorsal arm plates very large, nearly as long as wide, fan-shaped, broadly overlapping in all observable segments; no accessory dorsal arm plates discernible. LAPs of median to distal arm segments as long as high or slightly longer. Three (distal LAPs) to four (median LAPs) spine articulations on bulging distal portion of LAPs.

Remarks. These arm fragments display a unique combination of relatively large tentacle openings and large, horseshoe-shaped spine articulations with a proximal row of knobs or ridges, which unequivocally places them in the extant family Ophionereididae. The relatively short and tumid arm spines and the single, near-opercular tentacle scale agree well with the ophionereidid affinities of the Jurassic specimens. The absence of accessory dorsal arm plates suggests assignment to the extant genus *Ophiodoris*, but this assignment must be considered tentative and is likely to change as soon as the disc morphology of the fossil species becomes known. Nevertheless, these specimens clearly belong to the modern ophionereidid lineage, which is significant as they represent the first unequivocal fossil record of the group. The presence of the Ophionereididae in the Late Jurassic corroborates the stratigraphic range of the group as predicted by Smith et al. (1995). A rigorous application of the observations by Martynov (2010) concerning spine articulation morphology strongly suggests that a number of previously described species, for instance *Ophiocoma*? *senonensis* (Valette, 1915) from the latest Cretaceous of northwest Europe (Jagt, 2000; Kutscher & Jagt, 2000), are, in fact, ophionereidids, rather than ophiocomids.

The LAPs of the arm fragments described here are reminiscent of those described as *Ophiacantha*? *francojurassica* Hess, 1975b. While the original description and the accompanying drawings reveal little on details of spine articulations, the SEM pictures clearly demonstrate the highly characteristic spine articulations displaying a proximal row of knobs or short parallel ridges (Hess, 1975b). Since no significant differences between *O.*?

francojurassica and the specimens described herein can be found, they are considered to be conspecific, and *O.*? *francojurassica* is transferred to the genus *Ophiodoris*.

Family Ophiolepididae L JUNGMAN, 1867

Genus *Eozonella* nov.

Type species Eozonella bergeri sp. nov.

Other species included. Ophiopetra? *bathonica* Hess, 1964; *Ophiopetra*? *oertlii* Hess, 1965.

Etymology. Combination of "Eos", Greek for dawn, and "zonella", Greek for little belt, referring to the assumed basal position of the new taxon within the lineage of extant *Ophiozonella*. Gender feminine.
Diagnosis. Ophiolepidid with uniform dorsal disc plates lacking granules; single, pointed apical oral papilla differing in shape from dorsally following teeth; between-plate tentacle openings on all arm segments, covered by two tentacle scales at least in proximal and median arm segments; up to five, non-erect arm spines.

Eozonella bergeri sp. nov. (Figs. 6, 7)

Types. QLP005-819 (holotype); QLP005-820 and QLP005-821 (paratypes).

Additional material. QLP005-626 (13 dissociated lateral arm plates), QLP005-631 (198 dissociated vertebrae), QLP005-653 (645 arm fragments), QLP005-656 (16 disc fragments), QLP005-659 (107 dissociated vertebrae), QLP005-677 (43 dissociated lateral arm plates), QLP005-685 (14 disc fragments), QLP005-692 (455 arm fragments), QLP005-706 (33 dissociated ventral arm plates), QLP005-822 (arm fragment), QLP005-823 (arm fragment), QLP005-824 (arm fragment), QLP005-825 (arm fragment), QLP005-826 (dissociated lateral arm plate), QLP005-827 (dissociated lateral arm plate), QLP005-828 (dissociated vertebra), QLP005-829 (dissociated vertebra).

Diagnosis. As for genus.

Occurrence. Bure Member, Late Oxfordian; Boncourt–Queue au Loup, Swiss Jura Mountains.
Etymology. In honour of Professor Jean-Pierre Berger (1956–2012), distinguished specialist in the stratigraphy and palaeogeography of the continental Cenozoic in Europe and professor of palaeontology at the University of Fribourg, Switzerland.

Description of holotype. QLP005-819 is a complete disc (disc diameter: 5.3 mm) exposing both dorsal and ventral sides and with all arms broken at or near their base. Disc originally circular in outline, covered dorsally by small rounded and imbricate plates, the largest of which is the
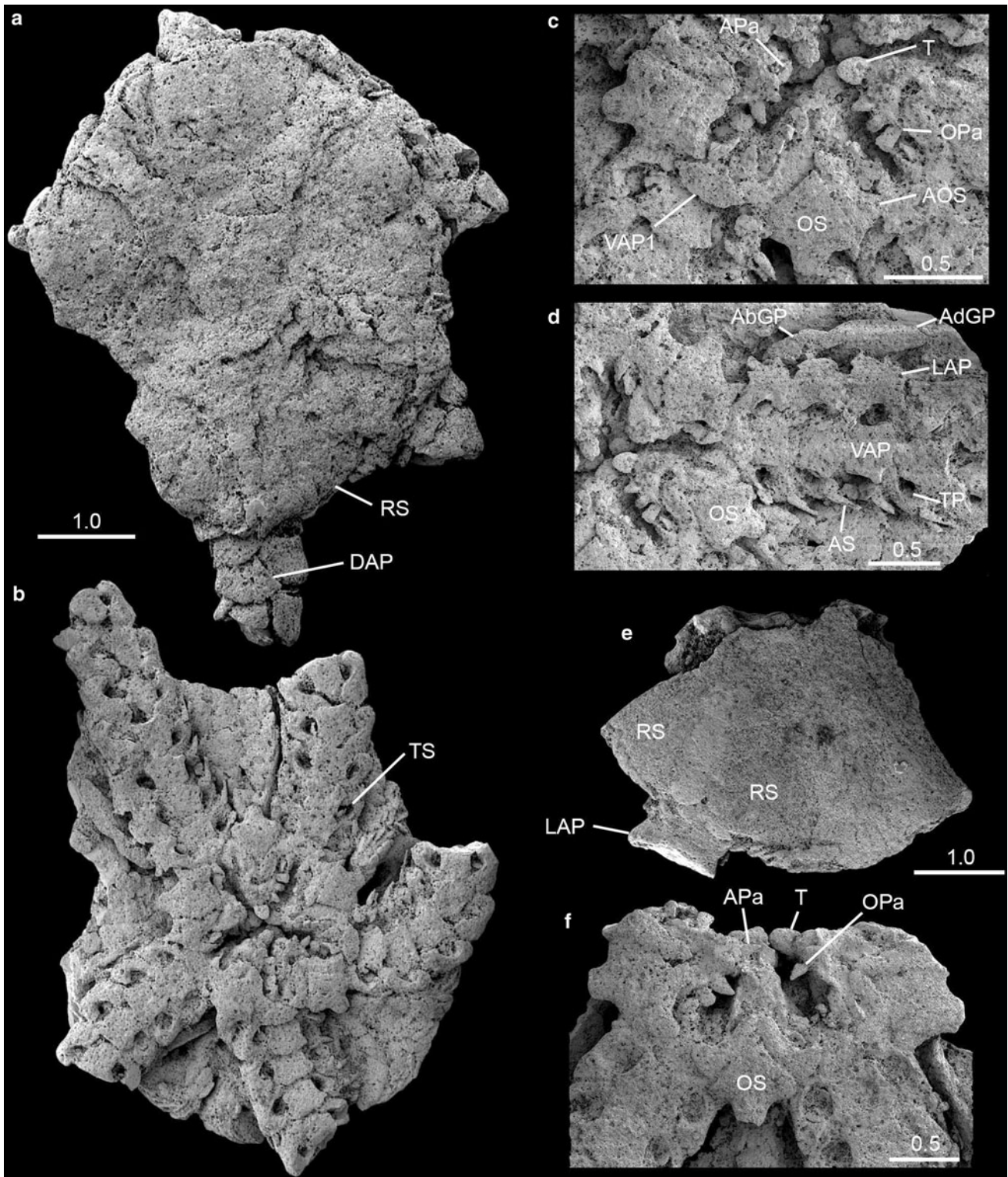
Fig. 6 *Eozonella bergeri* gen. et sp. nov. from the Late Oxfordian Bure Member of the Boncourt—Queue au Loup site. **a–d** QLP005-819 (holotype), articulated disc in dorsal (**a**) and ventral (**b**) views, and with details of mouth plating (**c**) and proximal arm segments (**d**) **e–f** QLP005-820 (paratype), articulated disc fragment in dorsal (**e**) and ventral (**f**) views. All *scale bar* specifications are in mm.

AbGP abradial genital plate, *AdGP* adradial genital plate, *AOS* adoral shield, *APa* apical papilla, *AS* arm spine, *DAP* dorsal arm plate, *LAP* lateral arm plate, *OPa* oral papilla, *OS* oral shield, *RS* radial shield, *T* tooth, *TP* tentacle pore, *TS* tentacle scale, *VAP* ventral arm plate, *VAP1* first ventral arm plate
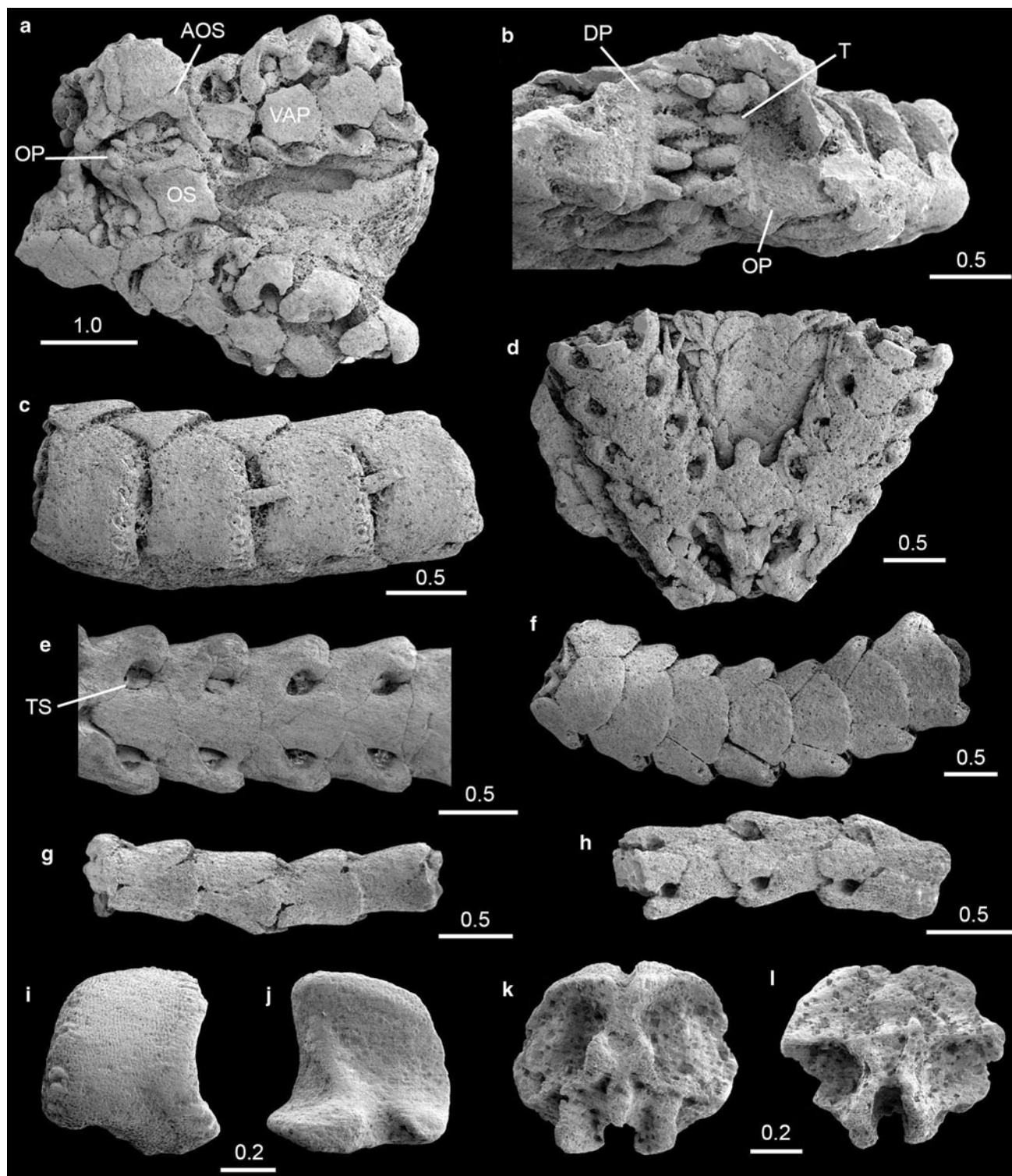
Fig. 7 *Eozonella bergeri* gen. et sp. nov. from the Boncourt—Queue au Loup site. **a–b** QLP005-821 (paratype), articulated disc fragment in ventral view (**a**) and in lateral view (**b**) exposing parts of the internal skeleton. **c** QLP005-822, proximal arm segments in lateral view. **d** QLP005-823, articulated disc fragment in ventral view. **e** QLP005-824, proximal arm segments in ventral view. **f** QLP005-825, proximal arm segments in dorsal view. **g** QLP005-826, distal arm segments in dorsal view. **h** distal arm segments in ventral view. **i** QLP005-826, median lateral arm plate in external view. **j** QLP005-827, median lateral arm plate in internal view. **k** QLP005-828, median vertebra in distal view. **l** QLP005-829, median vertebra in proximal view. All *scale bar* specifications are in mm. *AOS* adoral shield, *DP* dental plate, *OP* oral plate, *OS* oral shield, *T* tooth, *TS* tentacle scale, *VAP* ventral arm plate

circular central primary plate; details of plate patterns not discernible due to insufficient preservation; radial shields large, almond-shaped, almost equalling half the disc radius, separated by a single, narrow row of small plates; no disc appendages discernible. Ventral interradii completely covered by small, rounded plates. Oral shields conspicuously arrow-shaped, with right to acutely pointed proximal tip and much narrower rounded, tongue-like distal tip; adoral shields relatively small, narrow, meeting in front of the oral shield, not separating oral shield from ventral arm plates; jaws nearly as long as broad; five oral papillae, the two proximalmost of which conical, pointed, sitting on oral plate; following two papillae sitting on adoral shield and leaf-like, blunt, the distal one twice as large as the proximal one; distalmost papilla pointed, slightly curved, sitting on border between the adoral shield and the first ventral arm plate. Single small, apical papilla, less than half the size of successive (dorsalwards) teeth; single row of very large, blunt, tongue-shaped teeth. Both genital plates well developed, adradial one large and broad, abradial one smaller but similarly shaped.

All preserved arm portions with large tentacle pores, covered by two circular to leaf-like tentacle scales; first ventral arm plate twice as wide as long, pentagonal, with obtuse proximal angle; subsequent ventral arm plates irregularly pentagonal, nearly as wide as long, lateral edges concave, distal and proximal edges slightly convex to pointed with shallow central notch; ventral arm plates broadly separating lateral arm plates (LAPs) on all observable arm segments. Dorsal arm plates large, almost twice as wide as long, fan-shaped, broadly overlapping between neighbouring arm segments. LAPs robust, no constriction, no conspicuous ornamentation discernible on the outer surface; ventral portion encompassing tentacle opening strongly protruding; five small spine articulations sunken into distal edge of LAP; arm spines on segments incorporated into the disc almost half the length of an arm segment; arm spines on freestanding arm segments shorter, non erect.

Paratype supplements. QLP005-820 is a fragment of an articulated disc (reconstructed diameter: 6.0 mm) preserving two arm bases and the corresponding jaws. Overall morphology well in agreement with that of holotype. Oral papillae better preserved than in holotype. Second distalmost papilla nearly twice larger than proximal oral papillae. Apical papilla well preserved, small, conical, pointed, conspicuously smaller than following teeth, similar in shape and size to proximalmost oral papillae.

QLP005-821 is a fragment of an articulated disc (reconstructed diameter: 7.9 mm) preserving two arm bases and the corresponding jaws. Three tips of oral plate pairs with corresponding dental plates and teeth visible. Teeth in single rows, slightly increasing in size dorsalwards.

Isolated ossicles and arm fragments: Proximal arm fragments with five small spine articulations sunken into distal edge of LAP, dorsalmost spine articulation separated from others by a slightly larger gap. Arm spines shorter than half an arm segment. Median arm segments with two tentacle scales. Distal arm segments elongate, with dorsal and ventral arm plates longer than wide, separated by LAPs; tentacle scales in distal arm segments not discernible. Isolated LAPs robust, with strongly protruding ventral portion and without constriction; outer surface with fine granules, occasionally merging into very faint, irregular vertical striae; single prominent and slightly protruding, moderately well-defined spur on ventral portion of proximal LAP edge; tentacle notch large and conspicuous; inner surface of LAPs with single well-defined, oblique, prominent ridge, ventrally merging into thickened ventral edge of LAP, and dorsally broadening into tongue-like tip; diffuse and slightly prominent spur on ventro-distal edge of inner surface, corresponding to spur on proximal edge of outer surface. Vertebrae with typical zygospondylous articulation, relatively small ventral and large, wing-like dorsal muscular fossae.

Remarks. These specimens show marked similarities to the extant ophiolepidid *Ophiozonella*. Even details of LAP morphology, including arm spine articulations, suggest strong affinities with that genus. The almost 30 currently accepted extant species of this genus form a rather polymorphic group, including strongly paedomorphic forms, a species with disc granules (a highly atypical feature amongst ophiolepidids), and a recently described six-armed species (Stöhr, 2012), which strongly suggests that the concept of *Ophiozonella* as currently understood is in need of a thorough revision. The Jurassic specimens differ from most species of *Ophiozonella*, in particular the type species, *O. longispina* (H.L. Clark, 1908), in the higher number of arm spines and in the single, pointed apical papilla, which conspicuously differs from successive (dorsalwards) teeth. Therefore, in order not to expand the concept of *Ophiozonella* further and beyond meaningful limits, we propose the new genus *Eozonella* for the Jurassic specimens. *Ophiozonoida* H.L. Clark, 1915, an extant genus very close to *Ophiozonella*, shares the apical papillae with *Eozonella* but differs in having erect arm spines, a single tentacle scale throughout and small scales intermingled with larger plates on the dorsal disc. The extinct genera *Aplocoma* d'Orbigny, 1852 and *Ophiopetra* Enay and Hess, 1962 display disc granulation, smaller teeth, and, in case of the latter, erect arm spines, and thus clearly differ from *Eozonella*. Even though the Jurassic specimens are here suggested to represent a new genus, similarities with extant *Ophiozonella* are so marked that a close phylogenetic relationship appears unquestionable. *Eozonella* is most probably an early representative of the modern

Ophiozonella group, and further research, including a more detailed study of related fossil forms as well as a critical revision of extant species, is likely to reveal the *Ophiozonella* group as a stratigraphically long-ranging lineage which shares a highly similar basic morphology.

The LAPs of *Eozonella* are reminiscent of a type of LAPs commonly referred to as *Ophiopetra*? *oertlii* Hess, 1965. This species was originally described from the early Oxfordian of France. Subsequent finds from the Late Oxfordian (Hess, 1975b) and even from the Early Jurassic (e.g., Kutscher, 1996) were assigned to the same species, extending its concept beyond stratigraphically and morphologically meaningful limits. In fact, a closer examination of the LAPs assigned to *O.*? *oertlii* reveals that they represent several distinguishable LAP types rather than a single highly variable one. Admittedly, the differences between the types involve rather inconspicuous details, but this is in perfect agreement with the recent observation (Thuy & Stöhr, 2011) that closely related ophiuroid species share highly similar LAP morphologies, occasionally distinguishable by small details only, if at all. Against this background, the LAPs of the specimens described herein differ from the type specimens of *O.*? *oertlii* in having five, rather than three to (rarely) four, spine articulations. It thus seems warranted to propose a new species for the slightly younger material described herein. Nevertheless, similarities are so strong that *O.*? *oertlii* is transferred to the new genus *Eozonella*. The LAPs from the Late Oxfordian of Switzerland assigned to *O.*? *oertlii* (see Hess, 1975a, b) share the higher number of arm spine articulations with the specimens described here and thus probably belong to the same species. *Ophiopetra bathonica* Hess, 1964 from the Bathonian of Great Britain has much greater affinities with *Eozonella bergeri* than with *Ophiopetra lithographica* Enay and Hess, 1962, and is therefore transferred to the former, albeit tentatively, considering that the teeth and apical papillae are insufficiently preserved in the sole articulated disc known (Hess, 1964).

5 Discussion

5.1 Palaeoenvironment

The present brittle star assemblage was found in close association with *Nanogyra* oyster buildups, overgrown by serpulids and associated with partially-articulated crinoids. These buildups have a diameter of tens of centimetres up to several metres and predominantly consist of a rigid irregular framework composed of left valves of the oyster *Nanogyra*, whereby each individual was attached to another one. Very similar buildups occur in early Kimmeridgian deposits of northern Germany and are

interpreted as oyster patch reefs that supposedly grew at enhanced rates during periods of lowered sedimentation (Delecat et al., 2001). The growth was favoured by a high reproduction rate, since *Nanogyra* is interpreted to have been euryhaline to brachyhaline opportunists (r-strategists) (Hallam, 1976; Fürsich and Oschmann, 1986a). For northwest Switzerland, an initial water depth of approximately 60 m prior to the development of the Jura carbonate platform in the Middle Oxfordian has been assumed (Gygi, 2000a, b, 2012). From the Middle Oxfordian onwards, water depth gradually decreased, even though it was subjected to variations due to eustatic sea level changes, but also due to regional, small-scale tectonic subsidence (due to block faulting) (e.g., Pittet, 1996; Allenbach, 2001; Hug, 2003; Wetzel et al., 2003). The latter may also have been the case during the deposition of the Bure Member at the site studied, because the *Nanogyra* oyster buildups and associated crinoids, and the ophiuorids described here, were buried very rapidly by high-energy storm beds (tempestites). In the outcrop studied, in between and on top of the *Nanogyra* oyster buildups, the storm deposits are the *Nanogyra* shellbeds and tempestitic calcarenites, the latter with low-angle cross-stratification (possibly hummocky cross-stratification), erosional features at the base, loosely to densely-packed serpulid and crinoid remains and *Nanogyra* shells in preferred convex-up orientation, and normal grading (fining-upwards) (Fig. 3b). These are intercalated with terrigenous mudstones and marls, which have yielded the ophiuroid material described here. Similar *Nanogyra* shellbeds are typically interpreted as (rather proximal) storm shell beds (Fürsich and Oschmann, 1986b). Therefore, it is very likely that the Bure Member was deposited below fair-weather wave base and above storm-weather wave base in a shallow-marine, potentially protected, carbonate platform setting. Consequently, the maximum water depth certainly will not have exceeded several tens of metres.

5.2 Ophiuorid palaeoecology

Modern equivalents of the above-described habitat (i.e., shallow subtidal with mixed soft and hard substrates) are commonly predominated by members of the families Ophiactidae and Ophiuridae at high latitudes (e.g., Clark, 1911; Manjón-Cabeza and Ramos, 2003), by amphiurids, ophiotrichids and ophiurids at mid-latitudes (e.g., Mortensen, 1977; Boos and Franke, 2006) and by the Ophiocomidae, Ophionereididae, Ophiotrichidae and Ophiodermatidae in the tropics (e.g., Hendler et al., 1995; Stöhr, 2012).

The Late Jurassic assemblage described here comprises only three species, which is a low diversity for a normal marine subtidal ophiuroid fauna. However, future sampling efforts may be expected to increase the diversity to a level

comparable to other Late Jurassic assemblages (e.g. Hess, 1975b). The main point at this stage, however, is that the three species recorded can be considered to have been the dominant components of the fauna, since their presence in a time-averaged sample (which most micropalaeontological samples are) is not random but related to their abundance in the living fauna, assuming comparable preservation potential (Brett and Baird, 1986).

The Ophiolepididae–Ophiacanthidae–Ophionereididae assemblage described here thus has a highly unusual composition in comparison to modern faunas. In fact, the Ophiolepididae and in particular the Ophiacanthidae are known to be among the dominant components of bathyal and abyssal communities (Tyler, 1980; Thuy et al., 2012a, b) rather than subtidal ones.

Even more intriguing is a comparison on a lower taxonomic level. The new ophiacanthid described here clearly represents a basal member of the *Ophientrema* lineage. The two currently known extant species of this group occur at middle to lower bathyal depths (927–1,525 m) (Lyman, 1883; Clark, 1911; Matsumoto, 1915; Koehler, 1922). Extant *Ophiolebes*, the sister group of the *Ophientrema* lineage according to the phylogeny of Thuy et al. (2012a), occurs at depths greater than 100 m, with the exception of *Ophiolebes sagamiensis* Irimura, 1982, which is known from a single specimen from 60 m depth. Modern *Ophiozonella* and closely related forms, to which the new Jurassic genus *Eozonella* unquestionably belongs, have a wide bathymetric distribution, ranging from deep subtidal to abyssal (e.g., Clark, 1915; Vadon, 1990). Occasional shallower subtidal occurrences are known but are generally very rare (e.g., Stöhr, 2011), implying that the *Ophiozonella* lineage can be considered to be a predominantly deep-water group. *Ophiodoris* is an exception in the family Ophionereididae since, in present-day oceans, it occurs at bathyal depths (Koehler, 1904), in contrast to its typically shallow subtidal relatives (e.g., Hendler et al., 1995; Stöhr, 2012).

The Jurassic, shallow subtidal assemblage described herein is thus dominated by two extant deep-sea groups and a deep representative of an otherwise shallow-water group. This is not only unambiguous evidence that Jurassic shallow-water communities significantly differed from the modern ones in terms of composition, it also clearly documents the predominance of extant deep-sea ophiuroid groups in Mesozoic shallow-water marine settings. As a consequence, the ophiacanthid and ophiolepidid/ophiurid lineages documented in the present study must have undergone substantial shifts in bathymetric distribution since the Late Jurassic. This is perfectly in line with the trends observed in other groups such as stalked crinoids and hexactinellid sponges, which were much more abundant and widely distributed in shallow-marine habitats during the Mesozoic than they are in modern seas, and thus

underpins the pitfalls of using present-day bathymetric ranges for palaeodepth reconstructions (e.g., Thuy and Meyer, 2012). Further research is necessary in order to test whether these shifts in depth distribution document a migration of the groups into deep-water habitats, or rather a reduction of an initially wide bathymetric distribution to greater depths.

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