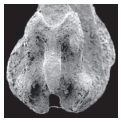
Ophiuroids (Echinodermata) from the Lower Cretaceous of Štramberk, Moravia (Czech Republic)

Richard Štorc & Jiří Žítt



Extremely rare skeletal remains of brittle stars, originating from Lower Cretaceous deposits in the Štramberk area are described and a preliminary discussion of depositional environments represented by these rocks is added. Several assemblages of dissociated ossicles from the Kopřivnice Formation (upper Valanginian; mostly from the Kotouč and Lower Blücher quarries) comprise only vertebrae. In contrast, an assemblage from the ?Hradiště Formation (Hauterivian and Barremian; Municipal quarry) has yielded taxonomically important lateral arm plates, which have enabled the present study of ophiuroid diversity. A total of five species have been found, including a single new taxon, *Ophiotitanos moravica* sp. nov. The remaining taxa are left in open nomenclature. Similar to what has been documented from the Cenomanian and Turonian of the Bohemian Cretaceous Basin, representatives of the genus *Ophiotitanos* predominate in the present assemblages. The presence of *Ophiotitanos*, euryalids, ophiomusaids and ophiacanthins is reminiscent of some ophiuroid faunas from the Upper Cretaceous of Europe. The assemblage from the Municipal quarry differs markedly from ophiuroid faunas of the Aptian of Cuchía (Spain) and Wizard Way (Texas), but is closely similar to the one from the Barremian of Serre de Bleyton (France). Problems surrounding echinoderm occurrences in the Kopřivnice and ?Hradiště Formations are discussed. • Key words: Brittle stars, Valanginian, Hauterivian, Barremian, taxonomy, Tethys, Moravia, Central Europe.

Štorc, R. & Žítt, J. 2024. Ophiuroids (Echinodermata) from the Lower Cretaceous of Štramberk, Moravia (Czech Republic). *Bulletin of Geosciences 99*(*3*), 255–269 (6 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received October 17, 2023; accepted in revised form August 23, 2024; published online October 13, 2024; issued October 13, 2024.

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Recently, considerable attention has been paid to the occurrence of ophiuroid remains in Cretaceous sedimentary rocks in the Czech Republic. A large number of species have been recorded from nearshore deposits (upper Cenomanian and lower Turonian), and hemipelagic strata in the Bohemian Cretaceous Basin (upper Turonian) have been shown to yield thousands of isolated brittle star ossicles (Štorc 1996, 1997, 2002, 2004a, b; Štorc & Žítt 2008). In stark contrast, our knowledge of Early Cretaceous ophiuroids in the Czech Republic has remained very limited due to the great paucity of material. Remeš (1902, pl. 20, figs 28, 29) was the first to document the existence of brittle stars in the Lower Cretaceous of Štramberk. Unfortunately, details of preservation and current repository of these specimens are unknown to us. From Remeš's drawings, it is clear that he had only two fragmentary vertebrae of the zygospondylous type available, but on account of poor preservation, these cannot be assigned to any taxon. This material probably came from the red limestones of Kopřivnice, most likely from the area of the Blücher quarries. Fortunately, old rock samples, tentative old rock washings and sets of Early Cretaceous biota from the Štramberk area, fossils collected and studied in the 1960s–1980s, have now yielded new ophiuroid ossicles. This unique material is described herein.

In the literature on Cretaceous ophiuroids, the emphasis is mostly on Late Cretaceous forms, whereas knowledge of Early Cretaceous forms is more limited, being often based solely on articulated individuals (*e.g.* König 1825, Alexander 1931, Taylor 1966, Hess 1970, Cornell *et al*. 1991, Martin-Medrano *et al*. 2009, Fernández *et al*. 2019). Only in recent years has our knowledge of their biodiversity been significantly increased by works based on the study of dissociated skeletal elements, especially from the Barremian and Aptian of Europe and North America (Thuy & Kroh 2011; Thuy *et al.* 2012, 2014; Thuy 2013).

Geological setting and localities

Structurally speaking, the Štramberk area belongs to the Silesian unit, which is one of important constituents of

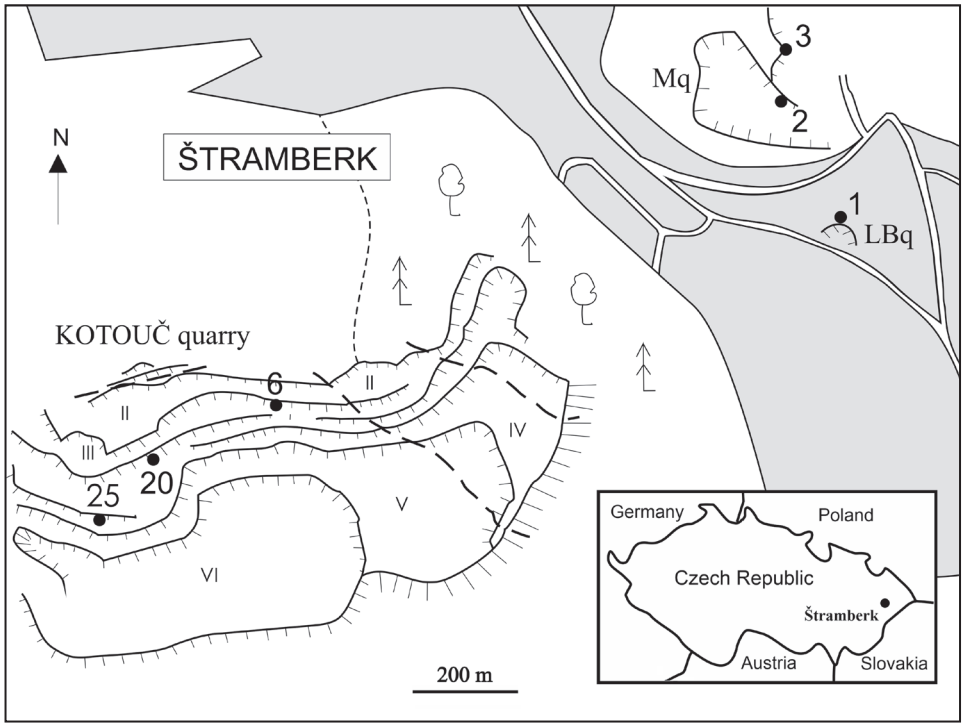


Figure 1. Map of Štramberk and its surroundings showing the Kotouč, Municipal (Mq) and Lower Blücher (LBq) quarries. Localities from which ophiuroid remains have been recovered in the Kopřivnice Formation are designated as numbers 1, 3, 6, 20 and 25. The ?Hradiště Formation at the Municipal quarry is represented by locality number 2. Numbers II–VI are the Kotouč quarry levels in the 1970s, as published by Houša (1976). His map provided precise data on the position of localities in the complex morphology at an actively worked quarry.

the geological structure of the Moravian–Silesian Beskydy mountains and the Beskydy uplands (Outer Western Carpathians; for a map see Svobodová *et al*. 2004, 2011; Vašíček *et al.* 2018). The Mesozoic history of the wider area is connected with the deposition of the Štramberk Limestone (Tithonian–Berriasian), as a part of a carbonate platform rimming the northern margin of the Tethys Ocean (see Houša 1976, Houša & Vašíček 2004, Vašíček *et al.* 2018, Kowal-Kasprzyk *et al*. 2021). However, quite soon after carbonate deposition ceased, a gradual Lower Cretaceous sedimentation of several clayey, slightly carbonaceous units started. However, the old carbonate ramp gradually disintegrated into blocks and coarse clastics and, together with the above-mentioned Lower Cretaceous units or their relics, these progressivelly moved (*e.g.* by submarine slides, turbidity currents) down the slopes of the basin. The complex scenario of not yet fully understood geological processes were finished during Cenozoic tectonic thrusting and formation of the Silesian Nappe. The present-day position of localities (mainly those at which the Kopřivnice Formation crops out) is related to these post-sedimentary processes. As a result, only limited portions of the original Lower Cretaceous rocks and faunal assemblages have been preserved in the Štramberk area. The fauna studied here has been recovered from three huge limestone bodies situated in the immediate vicinity of the town of Štramberk (Fig. 1). As far as ophiuroids are concerned, the most important levels are the Kopřivnice Formation (Kotouč, Municipal and Lower Blücher quarries) and the ?Hradiště Formation (= Plaňava Formation at the Municipal quarry, *sensu* Houša 1976; see Svobodová *et al*. 2011).

Strata assigned to the Kopřivnice Formation (upper Valanginian) occur either as fissure fillings intersecting Štramberk Limestone bodies at the Kotouč and Municipal quarries (*i.e.* at sites 3, 6, 20 and 25; originally described and labelled with the letter 'Š' by Houša 1976) or in the roughly coeval limestone body as exposed at the Lower Blücher quarry (*i.e.* the so-called Nesselsdorf Limestone; for all localities see Fig. 1). The ?Hradiště Formation at the Municipal quarry is formed mainly of locally deformed, grey to black, slightly sandy shales (Hauterivian and Barremian, according to Svobodová *et al*. 2011). Ophiuroid ossicles are very rare at all localities mentioned, while some other faunal elements (crinoids, echinoids, asteroids, brachiopods, worms, ichnofossils and others) are often extremely common (see Houša 1959, 1974; Nekvasilová 1974, 1980; Žítt 1983, 1986; Houša & Nekvasilová 1987; Mikuláš 1992).

Detailed geological and stratigraphical investigations of the Štramberk Limestone (lower Tithonian–Berriasian) and associated Lower Cretaceous rocks have been carried out mainly by Houša (*e.g.* 1961, 1964, 1976, 1990) and Eliáš (*e.g.* 1970, 1997). For additional data and views on stratigraphy and geology of the Štramberk area, reference is made to Menčík *et al*. (1983), Skupien & Vašíček (2002), Picha *et al.* (2006), Skupien & Smaržová (2011), Svobodová *et al.* (2011), Fraaije *et al*. (2013), Vašíček & Skupien (2013), Kočí *et al*. (2015) and Vašíček *et al.* (2018).

Material and methods

Strata assigned to the Kopřivnice Formation comprise soft calcareous claystones to clayey limestones, both well washable, while those referred to the ?Hradiště Formation consist of clayey, dark grey shales with a slight local admixture of sand and coarse clasts of sandstone. The ophiuroid material was recovered in part from older rock samples and sieving residues, as well as from sets of Early Cretaceous fossils from Štramberk collected and studied in the 1960s–1980s by V. Houša, J. Žítt and O. Nekvasilová (all Institute of Geology ASCR, Prague). The sediment samples and old washings were carefully washed or rewashed in water, sieved and individual brittlestar ossicles handpicked from residues. Finally, fossils were cleansed in an ultrasonic bath, mounted on aluminium stubs, gold coated and scanned by electron microscopy. On account of the fact that all lateral arm plates collected come from the ?Hradiště Formation at the Municipal quarry, this constitutes the most important assemblage in the present study. Unfortunately, the other assemblages do not include any lateral arm plates. With regard to the vertebrae recognised in this assemblage, these look either closely similar or are identical to vertebral ossicles recovered from the Kopřivnice Formation. In total, 303 ossicles have been collected from the Kopřivnice and ?Hradiště formations, namely 173 vertebrae, 123 lateral arm plates and four dorsal and ventral shields. Unfortunately, merely three disc plates have been identified; no arm fragments or other articulated remains are available.

The morphological terminologies used follow Spencer & Wright (1966), Štorc (1997, 2002, 2004a, b) and Kutscher & Jagt (2000).

Systematic palaeontology

Our higher-level classification of ophiuroids follows that proposed by O'Hara *et al.* (2017, 2018). All studied specimens are deposited in the collections of the National Museum (Prague), under catalogue numbers NM-O9255 to NM-O9275. Abbreviation: LAP – lateral arm plate.

Class Ophiuroidea Gray, 1840
Subclass Myophiuroidea Matsumoto, 1915
Infraclass Metophiurida Matsumoto, 1913
Superorder Euryophiurida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Euryalida Lamarck, 1816
Family Euryalidae Gray, 1840

Genus *Squamophis* Okanishi, O'Hara & Fujita, 2011

Type species. – *Asteroschema amamiense* Okanishi & Fujita, 2009, by original designation.

***Squamophis*? sp.**
Figure 2A–D

Material. – Twenty-one vertebrae in total. From the Municipal quarry (locality 2), ?Hradiště Formation, came 14 vertebrae, 4 of these (NM-O9268–O9271) are illustrated here. From the Kopřivnice Formation, the Lower Blücher quarry (locality 1) came 1 vertebra, and from Kotouč quarry (localities 20 and 25) – 5 and 1 vertebrae, respectively.

Description. – Vertebrae of streptospondylous type, height exceeding the distance between lateral sides of these ossicles (in proximal and distal view); dorso-proximal inclination of all vertical elements characteristic, best seen in distal vertebrae. Vertebrae with dorsal and lateral saddle-shaped depressions; outer surface mostly smooth, lateral and dorsal sides lacking sharply defined knobs, granules or other elements. Vertebrae with moderately deep dorsal furrows and conspicuously deep, but uncovered, ventral furrows. Proximal zygocondyles vertically hourglass shaped; distal zygocondyles large, horizontally hourglass shaped. View of both distal and proximal sides showing no development of wide vertebral wings; consequently, vertebrae appearing relatively narrow.

Discussion. – None of the lateral arm plates found at Štramberk can be assigned to these vertebrae, which makes taxonomic assessment very difficult. A large number of streptospondylous vertebrae have been found in the Lower Turonian of the Czech Republic (Štorc 1996, 1997, 2002), but these differ considerably from the present form. In addition, various taxa representing the order Euryalida recorded from the Mesozoic and Cenozoic (see *e.g.* Müller 1950; Rasmussen 1950, 1952, 1972; Maryańska & Popiel-Barczyk 1969; Jagt 1985, 1999, 2000a; Kutscher 1987, 2011; Kutscher & Jagt *in* Jagt 2000a; Kroh 2003, 2004; Kroh & Jagt 2004; Thuy 2015a; Thuy & Stöhr 2018) all have vertebrae that differ from the present material. However, the type of vertebra described from the upper Maastrichtian of South Carolina, USA (Thuy *et al*. 2018, fig. 5d), provides a good match with the present form. The overall vertebral shape, the morphology of the zygocondyles, the dorsal and ventral furrows, the structure of the muscular fossae proximally and distally are similar, as is the absence of laterally or dorsally located sharply defined knobs or granules. Thuy *et al*. (2018) pointed out similarities with the extant genus *Squamophis* (Euryalidae) on the basis of associated lateral arm plates and vertebrae in their material. For this reason, the Early Cretaceous form examined here is also tentatively referred to as *Squamophis*? sp. Its exact systematic position can only be resolved in case LAPs or parts of articulated specimens are discovered.

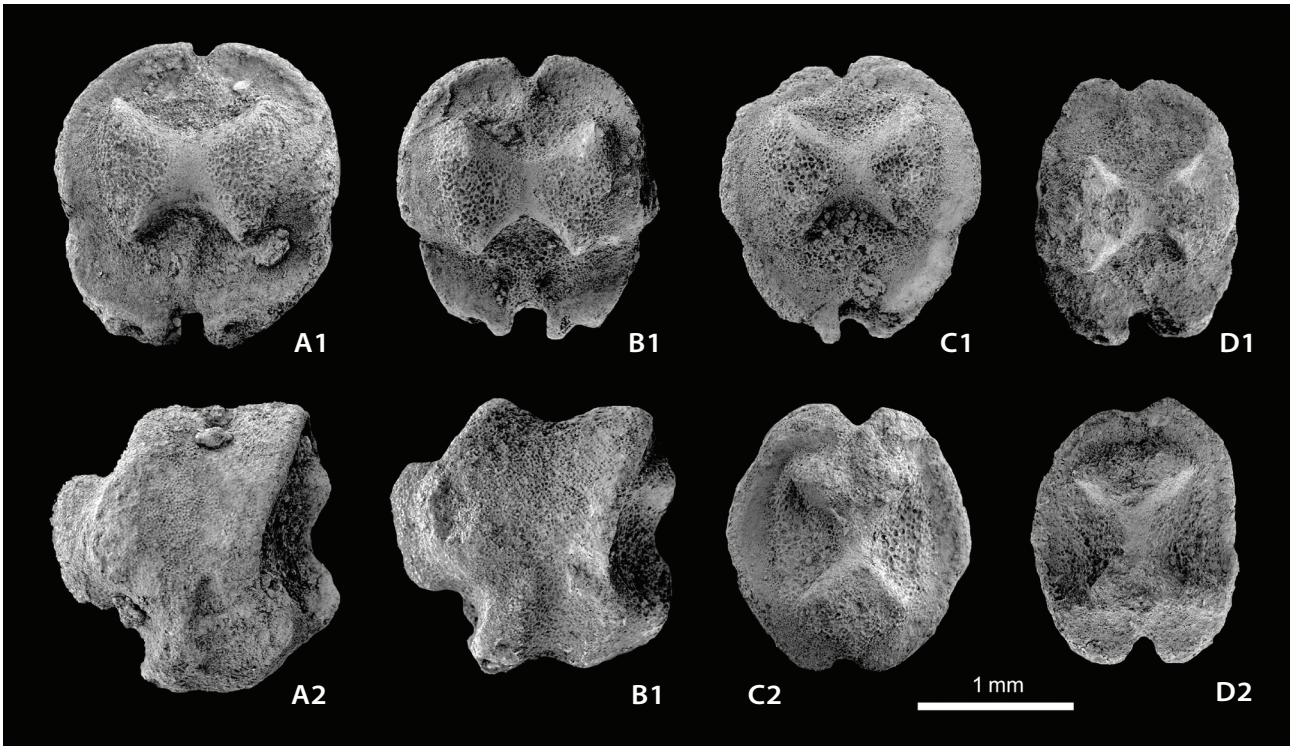


Figure 2. A–D – Streptospondylous vertebrae of *Squamophis*? sp., ventral side down. A – NM-O9268, proximal or median vertebra; A1 – distal view; A2 – lateral view. B – NM-O9269, proximal or median vertebra; B1 – distal view; B2 – lateral view. C – NM-O9270, median vertebra; C1 – distal view; C2 – proximal view. D – NM-O9271, distal vertebra; D1 – distal view; D2 – proximal view. All specimens are from locality No. 2, ?Hradiště Formation at the Municipal quarry.

Order Ophiurida Müller & Troschel, 1840 *sensu* O'Hara *et al.*, 2017
Suborder Ophiomusina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Family Ophiomusaidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Genus *Ophiomusa* Hertz, 1927

Type species. – *Ophiomusa lymani* (Wyville Thomson, 1873), by original designation.

***Ophiomusa* sp.**
Figure 5C, D

Material. – Six dissociated lateral arm plates from the Municipal quarry (locality 2), ?Hradiště Formation. Two of them are illustrated here (NM-O9255, NM-O9256).

Description. – Small, robust, elongated and very weakly constricted lateral arm plates, usually with near-rectangular shape in lateral view; outer proximal margin bearing at least two flattened articulation elements, corresponding to similar structures on inner distal margin. Dorsoventral depression between articulation margin and remainder of outer surface. Ornament very fine, either lacking (connected to state of preservation) or in form of microscopic dorsoventral striation, outer surface stereom therefore appearing relatively coarsely meshed. Ornament extending to distal margin and including small, barely visible spine articulations. Inner surface dominated by wall-like ridge, including flattened element for articulation with vertebra. Dorsal side more massive than ventral when seen from inner surface. Small tentacle pores noted in all specimens, close to wall-like ridge.

Discussion. – Only six lateral arm plates of this taxon have been encountered; all are rather poorly preserved. As a result, it is impossible now to define differences between proximal, median and distal LAPs, variations in the number of spine articulations or detailed characteristics of the articulatory spurs, outer surface ornament and other features. Similar LAPs have been described from Mesozoic strata in several countries and have almost always been assigned to the genus *Ophiomusa*. The fossil record of ophiomusines is indicative of widespread distribution across Europe during the Cretaceous (*e.g.* Rasmussen 1950, 1972; Maryańska & Popiel-Barczyk 1969; Jagt 1999, 2000a; Kutscher & Jagt *in* Jagt 2000a; Štorc 2002; Štorc & Žítt 2008; Thuy & Kroh 2011). Material from Štramberk is difficult to assign to any pre-

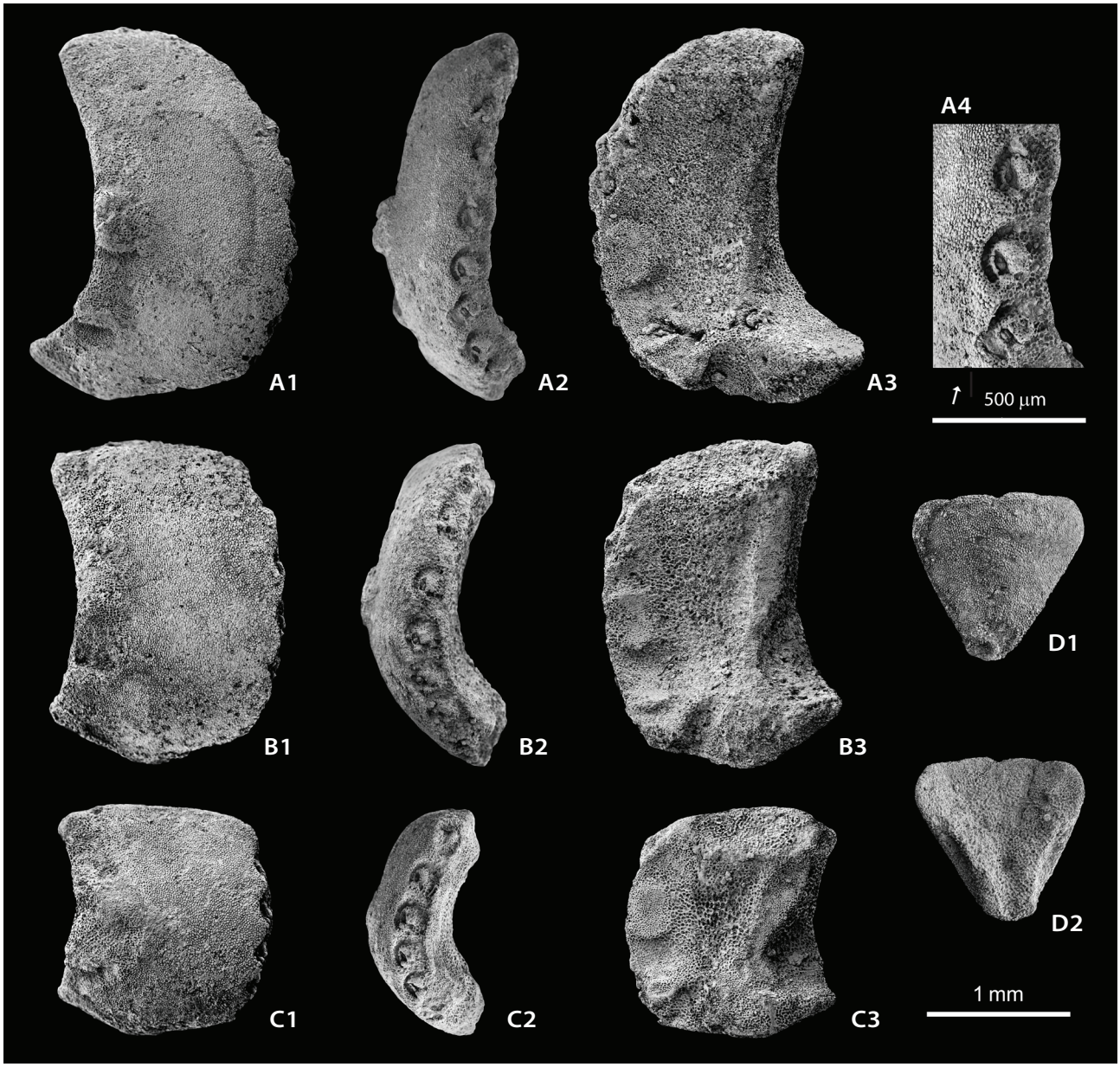


Figure 3. A–D – *Ophiotitanos moravica* sp. nov. A – NM-O9273, holotype, proximal lateral arm plate; A1 – outer view (distal to the right); A2 – distal view; A3 – inner view (distal to the left); A4 – detail of spine articulations. B – NM-O9274, paratype, proximal or median lateral arm plate; B1 – outer view (distal to the right); B2 – distal view; B3 – inner view (distal to the left). C – NM-O9275, paratype, median lateral arm plate; C1 – outer view (distal to the right); C2 – distal view; C3 – inner view (distal to the left). D – NM-O9272, dorsal shield (proximal side down); D1 – outer view; D2 – inner view. All specimens are from locality No. 2, ?Hradiště Formation at the Municipal quarry.

viously described taxon; in view of the small sample size, this form is best left in open nomenclature, at least for the time being.

Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Suborder Ophiodermatina Ljungman, 1867
Incertae familiae

Genus *Ophiotitanos* Spencer, 1907

Type species. – *Ophiotitanos tenuis* Spencer, 1907, by original designation.

***Ophiotitanos moravica* sp. nov.**
Figures 3A–D, 4

Types. – The holotype is NM-O9273 (Fig. 3A), paratypes are NM-O9274 (Fig. 3B) and NM-O9275 (Figs 3C, 4),

all deposited in the collections of the National Museum (Prague).

Type horizon and locality – Hauterivian–Barremian, ?Hradiště Formation at the Municipal quarry (locality No. 2).

Etymology. – In reference to the occurrence in Moravia.

Material. – A total of 99 dissociated lateral arm plates; several dorsal shields and probably also vertebrae.

Diagnosis. – Species of *Ophiotitanos* with relatively massive lateral arm plates; two large articulation spurs on outer proximal edge; extremely fine ornament on outer surface; two or three dorsalmost spine articulations separated by larger gaps than remaining ones.

Description. – Holotype: NM-O9273 is a dissociated proximal lateral arm plate, relatively massive and thick walled; higher than wide, with ventral part pointed and protruding proximally. Ornament extremely fine, outer plate surface appearing almost smooth (high magnification revealing microscopic granules or nodes). Proximal part of LAP serving connection with adjacent plate and carrying two large articulation spurs, dorsal one larger and more protruding than ventral. Dorsal spur oval to round (occasionally rectangular), ventral one with thinner, elongated shape. Distal edge of outer surface with almost sawtooth-wavy shape and row of eight spine articulations sunken into shallow notches behind. Articulations similar in size and nearly equidistant, except for two or three dorsalmost ones separated by slightly larger gaps than remaining ones. Inner side of LAP with distinctive oblique ridge for connection of vertebra; ventral end widening. Tentacle notch well developed. Distal part of inner side of LAP with two large, flattened spurs, corresponding the spurs on outer proximal edge; dorsal spur larger than ventral one.

Paratypes: NM-O9274 is a dissociated proximal to median LAP, higher than wide; ventral part pointed, but less protruding proximally than in the holotype; seven spine articulations. Other morphological characters of LAP generally well in agreement with that of holotype. NM-O9275 is a dissociated median LAP, nearly as high as wide; ventral part pointed, but less protruding proximally; six spine articulations. The ridge for connection of vertebra on the inner side of LAP is overall broader than in the holotype. Other morphological characters of LAP generally well in agreement with that of holotype and the aforementioned paratype.

Remarks. – Proximal LAPs higher than wide, median ones of near-equal hieght and width, distal plates slightly elongated. In proximal LAPs 7–9 spine articulations, median ones with 5–7 and distal ones 4–5. Proximal and median LAPs with well-developed tentacle notch, in the distal elongated plates tentacle pore rather than notch.

Discussion. – These lateral arm plates illustrate the highly characteristic combination of features typically found in the extinct genus *Ophiotitanos*. *Ophiotitanos magnus* Spencer, 1907 (Upper Cretaceous of England), *Ophiotitanos aschmannicor* Thuy, 2015 (Middle Jurassic of France; see Thuy 2015b) and *Ophiotitanos pilleri* Thuy & Kroh, 2011 (Barremian of France) all have LAPs of a rather different type. No dissociated LAPs were found in association with *Ophiotitanos smithi* Ewin & Thuy, 2017 (Middle Jurassic of England), making direct comparisons with the present material difficult. Nevertheless, LAPs on a nearly complete articulated individual have a different number and arrangement of spine articulations and larger gaps separating them (see Ewin & Thuy 2017). In contrast, the lateral arm plates of a widespread Late Cretaceous species *Ophiotitanos serrata* (Roemer, 1840) (see Štorc 1997, 2002; Štorc & Žítt 2008) are similar in overall shape and identical in size. The morphology and size of the spine articulations is very similar in both species. However, the LAPs of *O. moravica* sp. nov. generally have a thicker wall, are more robust overall, have a different shape of proximal articulation spurs and an almost smooth outer surface (ornament in *O. serrata* consists of a fine, close-set longitudinal striation). The LAPs of *Ophiotitanos*? sp. from the Aptian of Cuchía (Spain) also reveal certain similarities (Thuy *et al.* 2014). Even more closely similar are LAPs of *Ophioderma*? *spectabilis* Hess, 1966 from the Upper Jurassic of Raedersdorf (eastern France; see Hess 1966, 1975a, b). Overall shape, more massive structure and ornament of that form are close to *O. moravica* sp. nov., but the spurs on the outer proximal edge have a different shape. The greatest similarity in features of the lateral arm plates are seen in *Ophiotitanos* sp. from the Barremian of Serre de Bleyton (southern France; Thuy & Kroh 2011). Both taxa have more massive LAPs, a similar overall shape and ornament, a ridge for the connection with vertebrae, spurs on the outer and inner surface *etc*. The difference is that the LAPs from Serre de Bleyton, even the most proximal ones, have a large, oblique contact surface with the dorsal shield. In fact, *Ophiotitanos moravica* sp. nov. and *Ophiotitanos* sp. from Serre de Bleyton may be conspecific, but this can only be decided by a more detailed comparison of a larger number of proximal, median and distal lateral arm plates of both forms.

Other taxa, such as *Ophiarachna*? *liasica* Kutscher, 1996 (Lower–Middle Jurassic of Germany) and *Ophioderma*? *waliabadensis* Kristan-Tollmann, Tollmann & Hamedani, 1979 (Upper Triassic of Iran), have very different lateral arm plates.

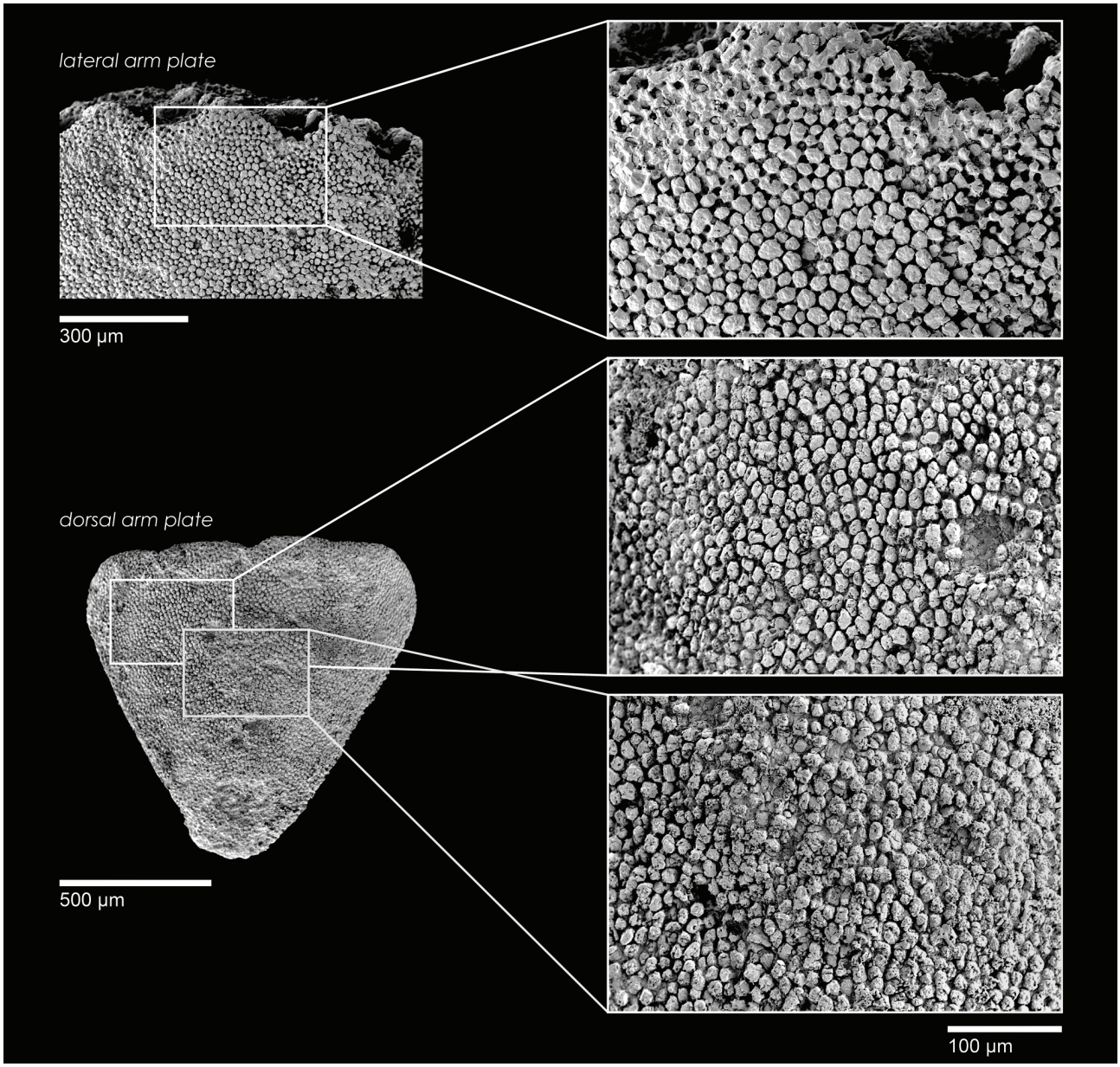


Figure 4. At high magnification, different skeletal elements of *Ophiotitanos moravica* sp. nov. show the same ornament of the outer surface, formed by microscopic granules/nodes of similar size (proximal side down). Lateral arm plate (NM-O9275; paratype) and dorsal shield (= dorsal arm plate; NM-O9272), both from locality No. 2, ?Hradiště Formation at the Municipal quarry.

As seen in Figure 4, high magnification has revealed an important taxonomic feature of *O. moravica* sp. nov. All lateral arm plates and associated dorsal shields have the same outer surface ornament; ventral shields have not yet been discovered.

Incertae familiae

Genus *Dermocoma* Hess, 1964

Type species. – Dermocoma wrighti Hess, 1964, by original designation.

***Dermocoma* sp.**
Figure 5A, B

Material. – Eleven dissociated lateral arm plates from the Municipal quarry, ?Hradiště Formation (locality 2). Two of them are illustrated here (NM-O9257, NM-O9258).

Description. – Lateral arm plates relatively thin, and overall more fragile. Median LAPs of near-equal height and width; distal ones elongated; complete proximal LAPs not yet recovered, only fragments to date. Orna-

ment consisting of fine vertical striation covering almost entire outer surface. Typically, proximal part of LAPs elevated relative to remainder of outer surface and carrying two spurs. Both articulation spurs low, indistinct and lacking clearly defined shape. Ventral portion of LAPs protruding ventro-proximalwards. Distal edge of outer surface with almost sawtooth-wavy shape and row of spine articulations sunken into shallow notches behind it. Distal LAPs have three or four, median ones five spine articulations; with gradual proximality number increases. Ventralmost articulation more protruding. Inner surface of LAPs with thin, oblique ridge, ventral end widening. Median and distal LAPs with tentacle notch. Distal part of inner side of LAPs with two flattened spurs.

Discussion. – This is the second representative of the suborder Ophiodermatina in this assemblage. As gleaned from the above description, the present form shares significant similarities with LAPs of the genus *Dermocoma* (see *e.g.* Hess 1964, 1975a; Thuy 2013). The greatest similarity with the ossicles from Štramberk is displayed by five lateral arm plates described and illustrated by Thuy (2013): the specimen in fig. 25.5 – *Dermocoma subtilirugosa* (Kristan-Tollmann & Gramann, 1992), Rhaetian of Austria; specimens in fig. 27.5 and 27.6 – *Dermocoma biformis* (Hess, 1975), Oxfordian of Switzerland; and specimens in fig 28.7 and 28.8 – *Dermocoma simonschneideri* Thuy, 2013, Kimmeridgian of Portugal. A more detailed comparison with *Dermocoma*? sp. indet. (Cenomanian) is difficult due to poor preservation of material from Algeria (Štorc & Benyoucef 2021).

Other taxa mentioned above, such as *Ophiotitanos moravica* sp. nov., *Ophioderma*? *waliabadensis*, *Ophiotitanos magnus*, *Ophiotitanos aschmannicor*, *Ophioderma*? *spectabilis*, *Ophiotitanos*? sp. (Cuchía) and *Ophiotitanos* sp. (Serre de Bleyton), have very different lateral arm plates. However, *Ophiarachna*? *liasica* shows some similarities, but its LAPs have different spine articulations, a different overall shape and, in part, a different ornament. The lateral arm plates of *Ophiotitanos pilleri* and *O. serrata* show the closest similarities to the present form. As far as ornament is concerned, it is similar to that in *O. serrata*, but in the LAPs of *O. pilleri* the dorsoventral stripes and grooves are broader and more pronounced. The elongated distal LAPs from Štramberk and of *O. serrata* from the Bohemian Cretaceous Basin, laid side by side, are practically identical – they have the same shape, size, ornament, spine articulations *etc*.; on the other hand, the median LAPs of both taxa are different. However, the present form differs from the above-mentioned representatives of the genus *Ophiotitanos* in having relatively thin and overall more fragile plates, proximal part of LAPs elevated to remainder of outer surface and carrying low and indistinct articulation spurs, bigger and more protruding spine articulations, and a different shape of ventral portion of LAPs.

Ossicles of *Dermocoma* sp. are rare and, moreover, no complete proximal LAP have been found, only median and distal specimens. At present it would be unwarranted to describe this taxon as a new species.

Suborder Ophiacanthina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Incertae familiae

Ophiacanthin gen. et sp. indet.
Figure 5E

Material. – A single fragmentary lateral arm plate (NM-O9259) from the Municipal quarry, ?Hradiště Formation (locality 2).

Description. – LAP (probably proximal or median) with dorsal and ventral part and thin lateral edges broken off. Part of outer surface covered by irregular striation composed of lamellae; distal part strongly elevated and with spine articulations freestanding in continuous vertical row. Articulations large, sharply bordered, nearly of equal size and ear shaped; only four preserved, original number unknown. Inner side of LAP is mostly flattened, only few features preserved due to fragmentary nature.

Discussion. – Features visible indicate that this is a taxon belonging to the suborder Ophiacanthina (see *e.g.* Štorc 1997, 2002; Thuy 2013). Representatives of the family Ophiacanthidae have some features in common with the present form. Unfortunately, based on this fragment alone, an assignment to a family-level clade within the Ophiacanthina is difficult. The Czech material is left in open nomenclature for the time being.

Ophiuroidea *incertae sedis*
Figure 6A–H

Remarks. – Dissociated vertebrae have been found in all samples from all localities studied, the largest number from sites No. 20 (Kotouč quarry) and No. 2 (Municipal quarry). Everywhere, the zygospondylous vertebral type predominates and some specimens might probably be assigned to members of the genus *Ophiotitanos* distinguished on LAPs, and very abundant in the assemblage from locality No. 2. In contrast, streptospondylous vertebrae, which are here referred to *Squamophis*? sp., are a minor element in all assemblages. Different types of zygospondylous vertebrae at all Štramberk sites

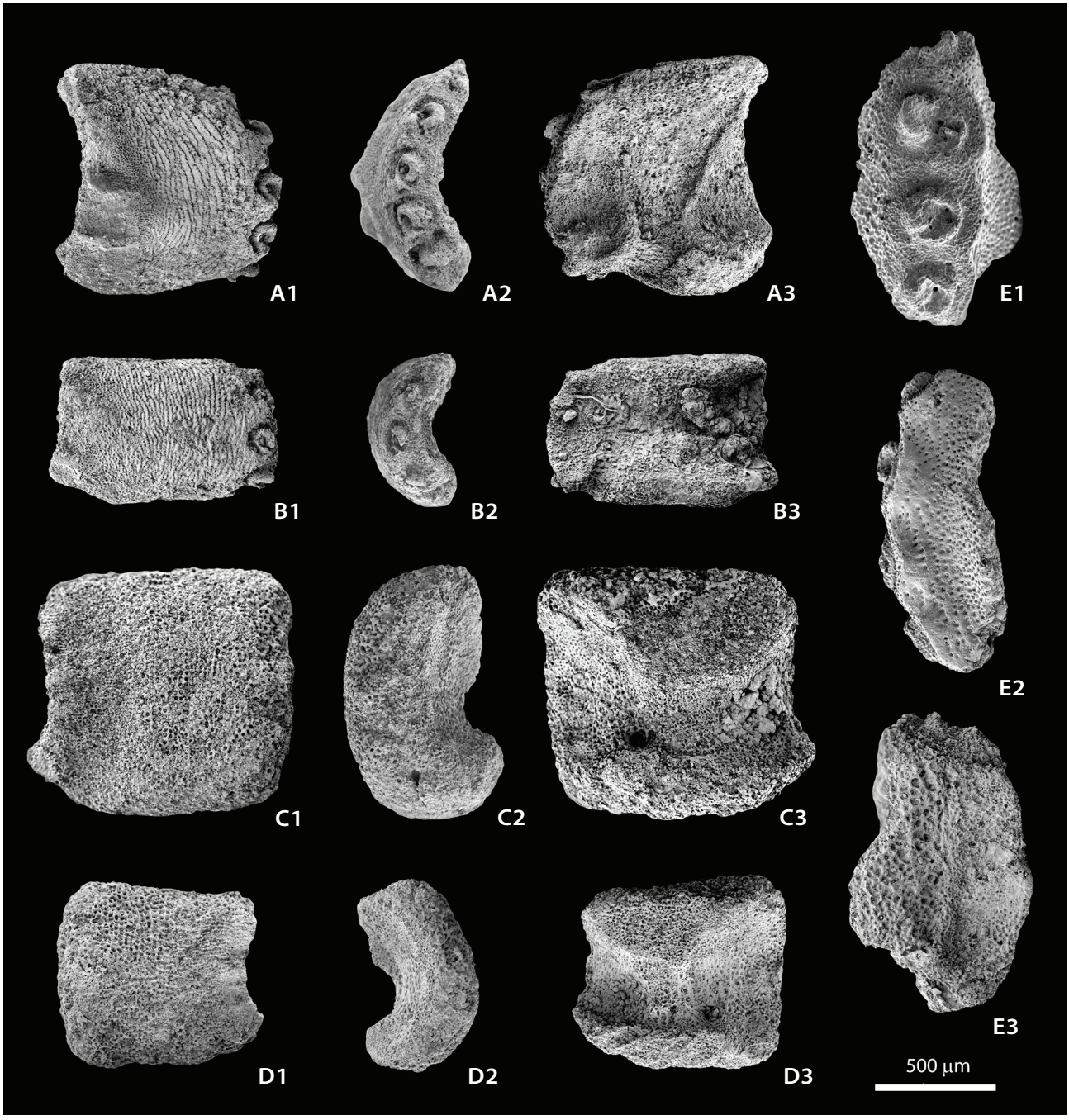
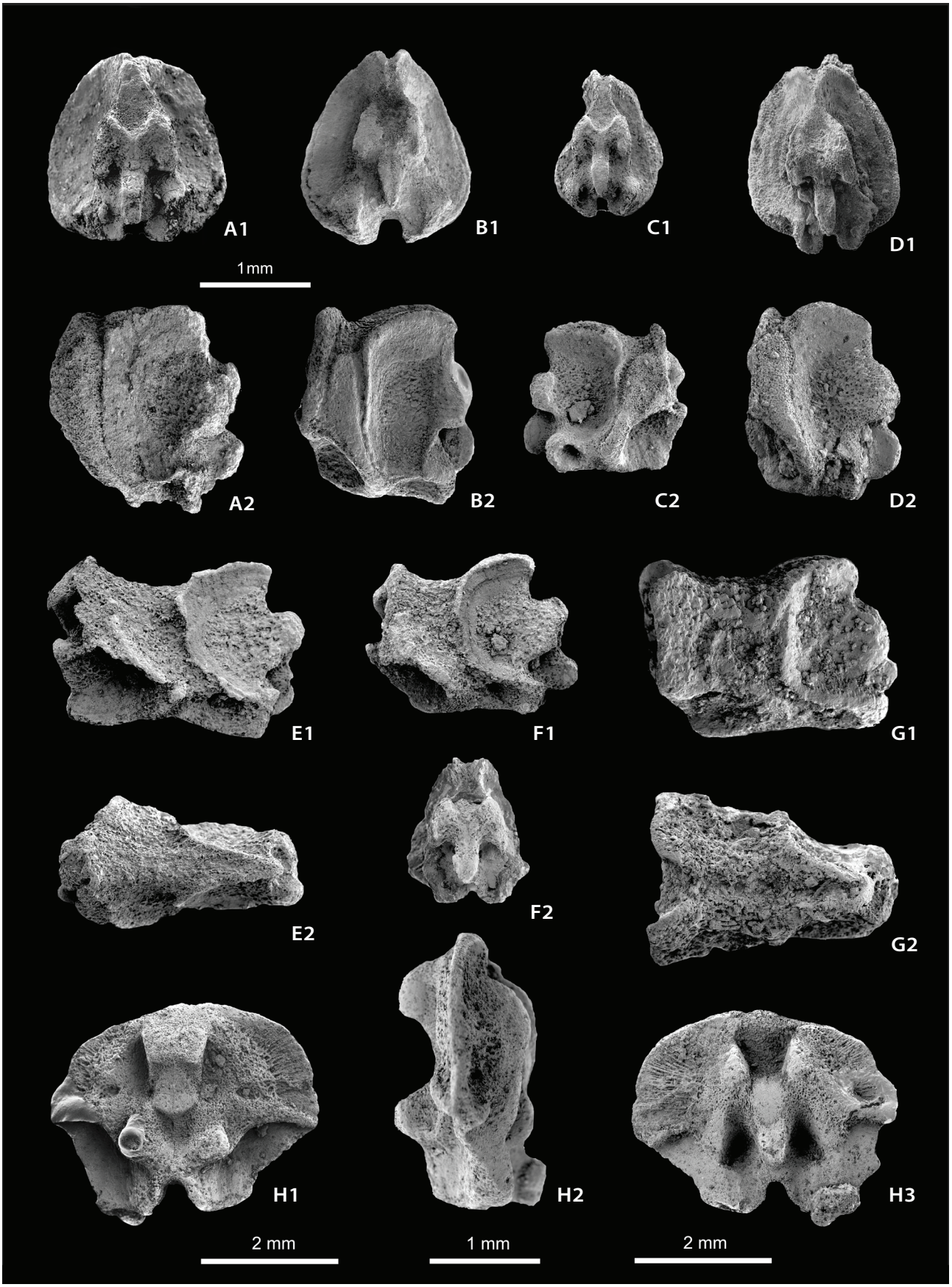


Figure 5. A, B – *Dermocoma* sp. A – NM-O9257, probably median lateral arm plate; A1 – outer view (distal to the right); A2 – distal view; A3 – inner view (distal to the left). B – NM-O9258, distal lateral arm plate; B1 – outer view (distal to the right); B2 – distal view; B3 – inner view (distal to the left). • C–D *Ophiomusa* sp. C – NM-O9255, proximal or median lateral arm plate; C1 – outer view (distal to the right); C2 – distal view; C3 – inner view (distal to the left). D – NM-O9256, median or distal lateral arm plate; D1 – outer view (distal to the left); D2 – distal view; D3 – inner view (distal to the right). • E – Ophiacanthina, fam. et gen. indet., NM-O9259, fragmentary lateral arm plate with broken off margins; E1 – outer view; E2 – oblique proximal view; E3 – inner view. All specimens are from the locality No. 2, ?Hradiště Formation at the Municipal quarry.

indicate the presence of several species of brittle star. Their systematic value is, however, relatively low (Hess 1962; Štorc 1996, 2002; Jagt 2000a) and any conclusions relative to ophiuroid taxonomy would be premature at this point.

Notes on sedimentary processes and palaeoecology

A special type of deposition, namely in fissures and depressions (Houša 1976), plus complex tectonics led to


A1
B1
C1
D1
1 mm
A2
B2
C2
D2
E1
F1
G1
E2
F2
G2
H1
H2
H3
2 mm
1 mm
2 mm

the total absence of a continuous Lower Cretaceous sedimentary succession in the Štramberk area. The precise recognition of mutual relationships between echinoderm assemblages at the various localities and their history is therefore considerably masked by these drawbacks.

From the start of studies, echinoderms and other faunal elements of the Kopřivnice Formation have been considered to be merely redeposited from immediately underlying Lower Cretaceous strata in the Štramberk area (*i.e.* Olivetská hora Formation *sensu* Houša 1976 or Čupek and Gloriet formations *sensu* Houša & Vašíček 2004). However, the echinoderms of these three formations are only poorly known, because of their deficiency in preserved source rocks (*in situ* rock relics, later formed litoclasts). Nevertheless, they seem to be similar to identical to those from Kopřivnice Formation. Thus, the problem of echinoderm redepositions into the Kopřivnice Formation remains open.

With some rare exceptions (echinoids; see Žítt 1986), all echinoderm skeletons in the taphocoenoses studied are completely disarticulated. The spectrum of ossicle types in each echinoderm assemblage is fairly wide and often indicates slight size and shape selection and sorting (more or less increased or reduced amount of small elements derived from, *e.g.* crinoid pinnules and cirri, asteroid discs, various small echinoderm spines *etc*.). In the Kopřivnice Formation, the individual echinoderm (including ophiuroid) localities may differ slightly from each other both in species and quality of preservation (mainly abrasion and fragmentation) of ossicles. Quality of preservation, especially of some fragile morphological structures (*e.g.* interradial processes of phyllocrinids) could be related to the *post-mortem* mobility of ossicles, both during redeposition to the Kopřivnice Formation or during a previous depositional phase. In every case, the taphocoenoses studied formed mostly under less agitated bottom conditions.

The deposits of the ?Hradiště Formation are of completely different type (see above), even though the ophiuroids show close links with those from the Kopřivnice Formation. The genus *Ophiotitanos* is probably related to the family Ophiodermatidae. It is interesting that modern ophiodermatids are mostly carnivores but their diet may also include plant material (Jagt 2000b). However, we cannot determine why *O. moravica* sp. nov. was so abundant at Štramberk (mainly in the ?Hradiště Formation) and what type of food it preferred. The occurrence of *Squamophis*? sp. in the Kopřivnice and ?Hradiště formations points to similar living conditions in the wider area, their survival for a long time (late Valanginian, Hauterivian and Barremian) or re-establishments of living conditions preferred by this form. Streptospondylous vertebrae allowed individuals of *Squamophis*? sp. (Euryalidae) to coil their arms and cling to some higher-level bottom objects in order to obtain food particles (Spencer & Wright 1966, Jagt 2000b). A similar feeding posture is common in many extant crinoids using filtration fans. The co-occurrence of euryalids with long-stemmed isocrinids in the ?Hradiště Formation is suggestive in this respect.

Conclusions

Based on a detailed study of > 300 dissociated skeletal elements, new data on Early Cretaceous ophiuroids have been obtained from several localities in the Štramberk area. Five species have been identified; one of these is new (*Ophiotitanos moravica* sp. nov.) and four are left in open nomenclature. This unique material has allowed the first description of Early Cretaceous ophiuroids from the Tethyan Realm of Central Europe.

The ossicles have been recovered from the Kopřivnice and ?Hradiště formations of late Valanginian and Hauterivian–Barremian age, respectively, and are unique for the Western Carpathians. Unfortunately, only vertebrae are known to date from most localities exposing the Kopřivnice Formation (Lower Blücher Quarry, Kotouč Quarry and Municipal Quarry No. 3). However, their different types indicate the possible presence of several, currently ophiuroid taxa. Some zygospondylous vertebrae probably belong to the genus *Ophiotitanos*, which predominates in the ?Hradiště Formation. Lateral arm plates of this genus are the commonest in an assemblage from locality No. 2 at the Municipal Quarry. It is noteworthy that *Ophiotitanos* is the most abundant genus even in the Cenomanian and Turonian of the Bohemian Cretaceous Basin. Streptospondylous vertebrae, which are here assigned to *Squamophis*? sp., form a minority in all assemblages, and their paucity is striking at Štramberk. None of the LAPs found at Štramberk can be assigned to this species.

Figure 6. A–H – different zygospondylous vertebrae, ventral side down (except in Figs E2 and G2). A – NM-O9264, proximal vertebra; A1 – distal view; A2 – lateral view. B – NM-O9260, proximal vertebra; B1 – distal view; B2 – lateral view. C – NM-O9267, probably median vertebra; C1 – distal view; C2 – lateral view. D – NM-O9261, proximal vertebra; D1 – distal view; D2 – lateral view. E – NM-O9266, distal vertebra; E1 – lateral view; E2 – dorsal view. F – NM-O9265, distal vertebra; F1 – lateral view; F2 – distal view. G – NM-O9262, distal vertebra; G1 – lateral view; G2 – dorsal view. H – NM-O9263, large proximal vertebra; H1 – proximal view; H2 – lateral view; H3 – distal view. Specimens in Figs A, C, D, E and F are from locality No. 2, ?Hradiště Formation at the Municipal quarry; all other specimens are from Kotouč quarry, Kopřivnice Formation (Figs B, G – locality No. 20, Fig. H – locality No. 25).

The ophiuroid assemblage from locality No. 2 (Municipal Quarry) consists of a rich collection of lateral arm plates and vertebrae, dominated by representatives of the genus *Ophiotitanos* and by euryalids, but also yields ophiomusines (*Ophiomusa* sp.), ophiodermatins (*Dermocoma* sp.) and ophiacanthins (Ophiacanthina, fam. et gen. indet.). This assemblage can be preliminarily considered to be related to some Late Cretaceous ophiuroid faunas of Europe (*e.g.* Štorc 1997, 2002; Jagt 1999, 2000a and references therein). With regard to ophiuroid faunas of Early Cretaceous age, the best-studied at this time are shallow-water assemblages from the lower Aptian of Cuchía (Cantabria, Spain), the uppermost Aptian of Wizard Way (Texas, USA) (see Thuy *et al.* 2014), the Barremian of Serre de Bleyton (southern France) (see Thuy & Kroh 2011) and a middle bathyal assemblage of latest Aptian to earliest Albian age at Blake Nose (Atlantic Ocean, off Florida; Thuy *et al.* 2012, Thuy 2013). The composition of species in assemblages from Cuchía and Wizard Way differs completely from that from the Municipal Quarry No. 2 assemblage at Štramberk. The sole similar taxon is *Ophiotitanos*? sp. from Cuchía. In contrast, the Serre de Bleyton fauna and the Municipal Quarry No. 2 assemblage are quite similar: both are dominated by the genus *Ophiotitanos* (more than 70 per cent at Serre de Bleyton) and both include ophiomusines and ophiacanthins. In addition, *Ophiotitanos moravica* sp. nov. from Štramberk could be related to *Ophiotitanos* sp. from Serre de Bleyton. It is also interesting that both Serre de Bleyton and Municipal Quarry No. 2 are probably of coeval Barremian age. The deep-water fauna from Blake Nose also bears some resemblance to the assemblage from the Municipal Quarry No. 2: both faunas include ophiomusines and representatives of the suborder Ophiacanthina.

Our evaluation of the ophiuroid distribution in the Kopřivnice Formation shows that ossicles are rare, yet taphonomically similar (*i.e.* no size and shape selection and sorting, equally low abrasion and fragmentation) components in local echinoderm (crinoid, echinoid, asteroid) taphocoenoses.

Echinoderms of the Kopřivnice Formation, at least in some sections, seem to be a mixture of autochthonous and redeposited specimens coming from immediately underlying older deposits (Olivetská Hora, Čupek, and Gloriet formations). However, new comparative data supporting these proceses are still necessary. Regarding the species diversity, this looks very similar to identical in both echinoderm components.

Acknowledgements

The authors are grateful to reviewers Ben Thuy (Natural History Museum Luxembourg) and John W.M. Jagt (Natural History Museum Maastricht) for their helpful suggestions that greatly improved the manuscript and also acknowledge Jan Sklenář for his kind help at the National Museum (Prague). This work was supported by the Czech Science Foundation (Project No. 23-06075S).

References

Alexander, C.I. 1931. A new Lower Cretaceous ophiuroid. *Journal of Paleontology 5*, 152–153.

Cornell, W.C., Lemone, D.V. & Norland, W.D. 1991. Albian ophiuroids from Cerro de Cristo Rey, Dona Ana County, New Mexico. *Journal of Paleontology 65*, 1009–1012. DOI 10.1017/S0022336000033321

Eliáš, M. 1970. Litologie a sedimentologie slezské jednotky v Moravskoslezských Beskydách. *Sborník Geologických Věd, Řada G 18*, 7–99.

Eliáš, M. 1997. Geologie slezské jednotky v okolí Štramberka. *Zprávy o Geologických Výzkumech v Roce 1996*, 72–73.

Ewin, T. & Thuy, B. 2017. Brittle stars from the British Oxford Clay: unexpected ophiuroid diversity on Jurassic sublittoral mud bottoms. *Journal of Paleontology 81(4)*, 781–798. DOI 10.1017/jpa.2016.162

Fernández, D., Giachetti, L., Stöhr, S., Thuy, B., Pérez, D., Comerio, M. & Pazos, P. 2019. Brittle stars from the Lower Cretaceous of Patagonia: first ophiuroid articulated remains for the Mesozoic of South America. *Andean Geology 46(2)*, 421–432. DOI 10.5027/andgeoV46n2-3157

Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. & Skupien, P. 2013. First record of paguroid anomurans (Crustacea) from the Tithonian-lower Berriasian of Štramberk, Moravia (Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 269(3)*, 251–259. DOI 10.1127/0077-7749/2013/0348

Gray, J.E. 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias* Linn.). *Annals and Magazine of Natural History 1(6)*, 175–184, 275–290. DOI 10.1080/03745484009443296

Hertz, M. 1927. Die Ophiuroiden der Deutschen Tiefsee-Expedition. I. Chilophiurida Matsumoto (Ophiolepididae, Ophioleucidae, Ophiodermatidae, Ophiocomidae). *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898–1899 22(3)*, 59–122.

Hess, H. 1962. Mikropaläontologische Untersuchungen an Ophiuren. I. Einleitung. II. Die Ophiuren aus dem Lias (Pliensbachien-Toarcien) von Seewen (Kt. Solothurn). *Eclogae geologicae Helvetiae 55*, 595–656.

Hess, H. 1964. Die Ophiuren des englischen Jura. *Eclogae geologicae Helvetiae 57*, 756–801.

Hess, H. 1966. Mikropaläontologische Untersuchungen an Ophiuren V: Die Ophiuren aus dem Argovien (unteres Ober-Oxford) vom Guldental (Kt. Solothurn) und von Savigna (Dépt. Jura). *Eclogae geologicae Helvetiae 59*, 1025–1063.

Hess, H. 1970. Schlangensterne und Seesterne aus dem oberen Hauterivien "Pierre jaune" von St Blaise bei Neuchâtel. *Eclogae geologicae Helvetiae 63*, 1069–1091.

Hess, H. 1975a. Mikropaläontologische Untersuchungen an Ophiuren VI: Die Ophiuren aus den Günsberg-Schichten (oberes Oxford) vom Guldental (Kt. Solothurn). *Eclogae geologicae Helvetiae 68(3)*, 591–601.

Hess, H. 1975b. Mikropaläontologische Untersuchungen an Ophiuren VII: Die Ophiuren aus den Humeralis-Schichten (Ober-Oxford) von Raedersdorf (Ht-Rhin). *Eclogae geologicae Helvetiae 68(3)*, 603–612.

Houša, V. 1959. Předběžná zpráva o výzkumu desetinohých korýšů (Crustacea, Decapoda) štramberských vrstev. *Zprávy o geologických výzkumech v roce 1957*, 75–76.

Houša, V. 1961. Stáří štramberského a kopřivnického vápence. *Časopis pro Mineralogii a Geologii 6*, 410–418.

Houša, V. 1964. Úložné poměry štramberského vápence v lomu Kotouč u Štramberka podle vrstevnaté výplně dutin. *Věstník Ústředního Ústavu geologického 39*, 429–434.

Houša, V. 1974. Stopy vrtavé činnosti organismů a výskyty epifauny na povrchu štramberských a olivetských vápenců ve Štramberku. *Časopis pro Mineralogii a Geologii 19(4)*, 403–414.

Houša, V. 1976. Spodnokřídové formace doprovázející tělesa tithonských vápenců u Štramberka. *Časopis Slezského Musea A 25*, 63–85, 119–131.

Houša, V. 1990. Stratigraphy and calpionellid zonation of Stramberg Limestone and associated Lower Cretaceous beds, 365–370. *In* Pallini, G., Cecca, F., Cresta, S. & Santantonio, M. (eds) *Atti del secondo convegno internazionale* "*Fossili, Evoluzione, Ambiente*". *Pergola 25–30 ottobre 1987*.

Houša, V. & Nekvasilová, O. 1987. Epifauna cemented to corals and bivalves from the Tithonian of Štramberk (Czechoslovakia). *Časopis pro Mineralogii a Geologii 32(1)*, 47–58.

Houša, V. & Vašíček, Z. 2004. Ammonoidea of the Lower Cretaceous deposits (Late Berriasian, Valanginian, Early Hauterivian) from Štramberk, Czech Republic. *Geolines 18*, 7–57.

Jagt, J.W.M. 1985. Opmerkingen over enkele slangsterren uit het Luiks-Limburgse Boven-Krijt. Deel 1: ?*Asteronyx ornatus* H.W. Rasmussen, 1950. *Grondboor & Hamer 39*, 98–100.

Jagt, J.W.M. 1999. Ophiuroid diversity in the type area of the Maastrichtian Stage. *Geologie en Mijnbouw 78*, 197–206. DOI 10.1023/A:1003795318464

Jagt, J.W.M. 2000a. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 3: Ophiuroids; with a chapter on Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark) by M. Kutscher & J.W.M. Jagt. *Scripta Geologica 121*, 1–179.

Jagt, J.W.M. 2000b. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 6: Conclusions. *Scripta Geologica 121*, 505–577.

Kočí, T., Veselská-Kočová, M., Gale, A.S., Jagt, J.W.M. & Skupien, P. 2015. Late Jurassic-Early Cretaceous stalked barnacles (Cirripedia, genus *Eolepas* Withers, 1928) from Štramberk, Moravia (Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 275(2)*, 233–247. DOI 10.1127/njgpa/2015/0464

König, C. 1825. *Icones Fossilium Sectiles*. 44 pp. Privately published, London. DOI 10.5962/bhl.title.157008

Kowal-Kasprzyk, J., Waśkovska, A., Golonka, J., Krobicki, M., Skupien, P. & Słomka, T. 2021. The Late Jurassic-Palaeogene carbonate platforms in the Outer Western Carpathian Tethys. A regional overview. *Minerals 11*, 1–26. DOI 10.3390/min11070747

Kristan-Tollmann, E. & Gramann, F. 1992. Paleontological evidence for the Triassic age of rocks dredged from the northern Exmouth Plateau (Tethyan foraminifers, echinoderms and ostracodes), 463–474. *In* Rad, U., Haq, B.U. et al. (eds) *Proceedings of the Ocean Drilling Program, Scientific Results 122*. DOI 10.2973/odp.proc.sr.122.186.1992

Kristan-Tollmann, E., Tollmann, A. & Hamedani, A. 1979. Beiträge zur Kenntnis der Trias von Persien. *Mitteilungen der Österreichischen geologischen Gesellschaft 70*, 119–186.

Kroh, A. 2003. First record of gorgonocephalid ophiuroids (Echinodermata) from the Middle Miocene of the Central Paratethys. *Cainozoic Research 2*, 143–155.

Kroh, A. 2004. First fossil record of the family Euryalidae (Echinodermata: Ophiuroidea) from the Middle Miocene of the Central Mediterranean, 447–452. *In* Heinzeller, T. & Nebelsick, J.H. (eds) *Echinoderms: München*. *Proceedings of the 11th International Echinoderm Conference, 6–10 October 2003, Munich, Germany.* DOI 10.1201/9780203970881.ch73

Kroh, A. & Jagt, J.W.M. 2004. Notes on North Sea Basin echinoderms, Part 3. Pliocene gorgonocephalid ophiuroids from borehole IJsselmuiden-1 (Overijssel; the Netherlands). *Cainozoic Research 4*, 67–70.

Kutscher, M. 1987. *Aspidura streichani* sp. n. – eine neue Ophiuren-Art aus dem Muschelkalk von Rüdersdorf. Zeitschrift für geologische Wissenschaften *15*, 703–707.

Kutscher, M. 1996. Echinodermata aus dem Ober-Toarcium und Aalenium Deutschlands II. Ophiuroidea. *Stuttgarter Beiträge zur Naturkunde Serie B 242*, 1–33.

Kutscher, M. 2011. Neue Lateralschild-Typen von Schlangensternen (Ophiuroidea) aus der Rügener Schreibkreide (Ob. Unter-Maastrichtium). *Geschiebekunde aktuell 27(3)*, 83–88.

Kutscher, M. & Jagt, J.W.M. 2000. Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark), 45–179. *In* Jagt, J.W.M. (ed.) *Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 3: Ophiuroids*. *Scripta Geologica 121*.

Lamarck, J.P.B.A. de 1816. *Histoire naturelle des animaux sans vertèbres 2, Edition 1*. 568 pp. Verdière, Paris.

Ljungman, A.V. 1867. Ophiuroidea viventia huc usque cognita enumerata. *Öfversigt af Kongelige Vetenskaps-Academiens Förhandlingar, Stockholm 1866(23)*, 303–336.

Martin-Medrano, L., Thuy, B. & García-Barrera, P. 2009. New Albian (Early Cretaceous) ophiuroids from the Tlayúa Quarry, Puebla, Mexico. *Palaeontology 52(1)*, 83–94. DOI 10.1111/j.1475-4983.2008.00836.x

Maryańska, T. & Popiel-Barczyk, E. 1969. On the remains of Ophiuroidea from the Uppermost Maastrichtian and Danian deposits at Nasiłów near Puławy, Poland. *Prace Muzeum Ziemi 14*, 131–139.

Matsumoto, H. 1913. Evolutionary history of the class Ophiuroidea and a note on the new classification of the class. *Zoological Magazine 25*, 521–527.

Matsumoto, H. 1915. A new classification of the Ophiuroidea: with descriptions of new genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia 67*, 43–92.

Menčík, E. et al. 1983. *Geologie Moravskoslezských Beskyd a Podbeskydské pahorkatiny.* 304 pp. Ústřední ústav geologický, Praha.

Mikuláš, R. 1992. Early Cretaceous borings from Štramberk. *Časopis pro Mineralogii a Geologii 37(4)*, 297–312.

Müller, A.H. 1950. Die Ophiuroideenreste aus dem Mucronatensenon von Rügen. *Geologica 5*, 1–35.

Müller, J. & Troschel, F.H. 1840. Über die Gattungen der Asteriden und Ophiuren. *Wiegmanns Archiv für Naturgeschichte 6*, 318–326, 328–368.

Nekvasilová, O. 1974. The genus *Thecidiopsis* (Brachiopoda) from the Lower Cretaceous of Štramberk (Czechoslovakia). *Časopis pro Mineralogii a Geologii 19(3)*, 239–244.

Nekvasilová, O. 1980. Terebratulida (Brachiopoda) from the Lower Cretaceous of Štramberk (north-east Moravia), Czechoslovakia. *Sborník geologických Věd, řada Paleontologie 23*, 49–81.

O'Hara, T.D., Hugall, A.F., Thuy, B., Stöhr, S. & Martynov, A.V. 2017. Restructuring higher taxonomy using broad-scale phylogenomics: the living Ophiuroidea. *Molecular Biology and Evolution 107*, 415–430. DOI 10.1016/j.ympev.2016.12.006

O'Hara, T.D., Stöhr, S., Hugall, A.F., Thuy, B. & Martynov, A.V. 2018. Morphological diagnoses of higher taxa in Ophiuroidea (Echinodermata) in support of a new classification. *European Journal of Taxonomy 416*, 1–35. DOI 10.5852/ejt.2018.416

Okanishi, M. & Fujita, T. 2009. A new species of *Asteroschema* (Echinodermata: Ophiuroidea: Asteroschematidae) from southwestern Japan. *Species Diversity 14*, 115–129. DOI 10.12782/specdiv.14.115

Okanishi, M., O'Hara, T. & Fujita, T. 2011. A new genus *Squamophis* of Asteroschematidae (Echinodermata, Ophiuroidea, Euryalida) from Australia. *ZooKeys 129*, 1–15. DOI 10.3897/zookeys.129.1202

Picha, F.J., Stráník, Z. & Krejčí, O. 2006. Geology and hydrocarbon resources of the Outer Western Carpathians and their foreland, Czech Republic, 49–175. *In* Picha, F.J. & Golonka, J. (eds) *The Carpathians and their foreland: geology and hydrocarbon resources. Memoir of the American Association of Petroleum Geologists 84*. DOI 10.1306/985607M843067

Rasmussen, H.W. 1950. Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark. *Danmarks Geologiske Undersøgelse 2(77)*, 1–134. DOI 10.34194/raekke2.v77.6866

Rasmussen, H.W. 1952. Cretaceous Ophiuroidea from Germany, Sweden, Spain and New Jersey. *Meddelelser fra Dansk Geologisk Forening 12*, 47–57.

Rasmussen, H.W. 1972. Lower Tertiary Crinoidea, Asteroidea and Ophiuroidea from Northern Europe and Greenland. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 19*, 1–83.

Remeš, M. 1902. Nachträge zur Fauna von Stramberk. I. Die Fauna des rothen Kalksteins. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients 14(4)*, 195–217.

Roemer, F.A. 1840–1841. *Die Versteinerungen des norddeutschen Kreidegebirges.* 1–48 pp. (1840), 49–145 pp. (1841). Hahn'sche Hofbuchhandlung, Hannover.

Skupien, P. & Smaržová, A. 2011. Palynological and geochemical response to environmental changes in the Lower Cretaceous in the Outer Western Carpathians; a record from the Silesian unit, Czech Republic. *Cretaceous Research 32*, 538–551. DOI 10.1016/j.cretres.2011.04.001

Skupien, P. & Vašíček, Z. 2002. Lower Cretaceous ammonite and dinocyst biostratigraphy and paleoenvironment of the Silesian Basin (Outer Western Carpathians). *Geologica Carpathica 53(3)*, 179–189.

Spencer, W.K. 1905–1908. A monograph on the British fossil Echinodermata from the Cretaceous formations, 2. The Asteroidea and Ophiuroidea. *Monograph of the Palaeontographical Society of London 3–5*, 67–90 (1905), 91–132 (1907), 133–138 (1908).

Spencer, W.K. & Wright, C.W. 1966. Asterozoans, u4–u107. *In* Moore, R.C. et al. (eds) *Treatise on Invertebrate Paleontology*, *Part U, Echinodermata 3(1).* The Geological Society of America, Boulder & The University of Kansas Press, Lawrence.

Svobodová, M., Hradecká, L., Skupien, P. & Švábenická, L. 2004. Microfossils of the Albian and Cenomanian shales from the Štramberk area (Silesian Unit, Outer Western Carpathians, Czech Republic). *Geologica Carpathica 55*, 371–388.

Svobodová, M., Švábenická, L., Skupien, P. & Hradecká, L. 2011. Biostratigraphy and palaeoecology of the Lower Cretaceous sediments in the Outer Western Carpathians (Silesian Unit, Czech Republic). *Geologica Carpathica 62*, 309–332. DOI /10.2478/v10096-011-0024-9

Štorc, R. 1996. Zpráva o výzkumu hadic (Ophiuroidea, Echinodermata) ze svrchního cenomanu-spodního turonu české křídové pánve. *Zprávy o geologických výzkumech v roce 1995*, 168–169.

Štorc, R. 1997. Ophiuroid remains from the nearshore environments of the Bohemian Cretaceous Basin (Cenomanian-Turonian boundary interval). A preliminary report. *Bulletin of the Czech Geological Survey 72(2)*, 171–174.

Štorc, R. 2002. *Ophiuroidea in the Bohemian and Tunisian Cretaceous*. 521 pp. Ph.D. thesis, Charles University, Prague, Czech Republic.

Štorc, R. 2004a. The ophiuroid *Amphiura*? *plana* in nearshore settings of the Bohemian Cretaceous Basin (Czech Republic). *Geologica Carpathica 55(1)*, 37–41.

Štorc, R. 2004b. The Late Cretaceous brittle star *Ophiosmilax*? *alternatus* from Europe and northern Africa. *Geobios 37*, 395–401. DOI 10.1016/j.geobios.2003.01.010

Štorc, R. & Benyoucef, M. 2021. Brittle stars from the upper Cenomanian of the Preafrican platform: First ophiuroid

remains for the Cretaceous of Algeria. *Annales de Paléontologie 107(3)*, 1–11.
DOI 10.1016/j.annpal.2021.102489

Štorc, R. & Žítt, J. 2008. Late Turonian ophiuroids (Echinodermata) from the Bohemian Cretaceous Basin, Czech Republic. *Bulletin of Geosciences 83(2)*, 123–140.
DOI 10.3140/bull.geosci.2008.02.123

Taylor, B.J. 1966. Taxonomy and morphology of Echinodermata from the Aptian of Alexander Island. *British Antarctic Survey Bulletin 8*, 1–18.

Thuy, B. 2013. Temporary expansion to shelf depths rather than an on shore-offshore trend: the shallow-water rise and demise of the modern deep-sea brittle star family Ophiacanthidae (Echinodermata: Ophiuroidea). *European Journal of Taxonomy 48*, 1–242. DOI 10.5852/ejt.2013.48

Thuy, B. 2015a. Unravelling the origin of the euryalid brittle stars: a preliminary report, 185–188. *In* Zamora, S. & Rábano, I. (eds) *Progress in Echinoderm Palaeobiology 19*. Instituto Geológico y Minero de España, Madrid.

Thuy, B. 2015b. A peri-reefal brittle-star (Echinodermata, Ophiuroidea) assemblage from the Middle Jurassic of the northeast Paris Basin. *Ferrantia 71*, 87–106.

Thuy, B. & Kroh, A. 2011. Barremian ophiuroids from the Serre de Bleyton (Drôme, SE France). *Annalen des Naturhistorischen Museums in Wien, Serie A 113*, 777–807.

Thuy, B. & Stöhr, S. 2018. Unravelling the origin of the basket stars and their allies (Echinodermata, Ophiuroidea, Euryalida). *Scientific Reports 8*, 8493.
DOI 10.1038/s41598-018-26877-5

Thuy, B., Gale, A.S., Kroh, A., Kucera, M., Numberger-Thuy, L.D. et al. 2012. Ancient origin of the modern deep-sea fauna. *PLoS ONE 7(10)*, e46913.
DOI 10.1371/journal.pone.0046913

Thuy, B., Gale, A.S., Stöhr, S. & Wiese, F. 2014. Shallow-water brittle-star (Echinodermata: Ophiuroidea) assemblages from the Aptian (Early Cretaceous) of the North Atlantic: first insights into bathymetric distribution patterns. *Göttingen Contributions to Geosciences 77*, 163–182.
DOI 10.3249/webdoc-3927

Thuy, B., Numberger-Thuy, L.D. & Jagt, J.W.M. 2018. An unusual assemblage of ophiuroids (Echinodermata) from the late Maastrichtian of South Carolina, USA. *Swiss Journal of Palaeontology 137(2)*, 337–356.
DOI 10.1007/s13358-018-0166-9

Vašíček, Z. & Skupien, P. 2013. Early Berriasian ammonites from the Stramberk Limestone in the Kotouč Quarry (Outer Western Carpathians, Czech Republic). *Annales Societatis Geologorum Poloniae 83*, 329–342.

Vašíček, Z., Skupien, P. & Jagt, J.W.M. 2018. Curreent knowledge of ammonite assemblages from the Štramberk Limestone (Tithonian–lower Berriasian) at Kotouč Quarry, Outer Western Carpathians (Czech Republic). *Cretaceous Research 90*, 185–203. DOI 10.1016/j.cretres.2018.04.016

Wyville Thomson, C. 1873. *The Depth of the Sea. An Account of the General Results of the Dredging Cruises of the H.M.SS. 'Porcupine'and 'Lightning During the Summers of 1868, 1869, and 1870, Under the Scientific Direction of Dr. Carpenter, F.R.S., J. Gwyn Jeffreys, F.R.S. and Dr. Wyville Thomson, F.R.S.* 527 pp. Macmillan and Co., London.
DOI 10.5962/bhl.title.54574

Žítt, J. 1983. Spoon-like crinoids from Štramberk (Lower Cretaceous, ČSSR). *Sborník Národního Muzea 39B*, 69–113.

Žítt, J. 1986. *Magnosia* Michelin and *Magnosiopsis* gen. n. (Echinoidea) from the Lower Cretaceous of Štramberk (Czechoslovakia). *Časopis pro Mineralogii a Geologii 31*, 371–385.