

Topics

Stegosaur tracks and the persistence of facies – the Lower Cretaceous of Western Australia

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Sometime between January and June 1996, the only known stegosaur tracks were stolen from Broome in north-western Australia (Fig. 1). Vandalism or loss of any type material is always to be lamented, yet there is good cause to suspect that the trackmaker at Broome was not a stegosaur. The reasons why this should be so relate to some of the factors involved in the formation of dinosaur trace fossils and the difficulties encountered in their interpretation. The stratigraphy at Broome is notable for preserving evidence of potential Wealden-type deposition in Australia.

The Broome Sandstone Group is a sequence of sandstones, siltstones and soil horizons considered to be of freshwater or paralic* origin. The Group is Neocomian (Lower Cretaceous) in age and the similarity in lithofacies with the equivalent Wealden is striking. Dinosaur tracks are abundant throughout the Group, particularly around the type section at Gantheaume Point where sauropod trackways are found associated with large theropod tracks ascribed to *Megalosaurus*. The stegosaur track site is found 4 km north-east of the type section and is only briefly exposed at low tide.

Tracks

Figure 2 shows the 'stegosaur' tracks as they were in situ at Broome Harbour. The substrate is a mature palaeosol displaying extensive subhorizontal rooting

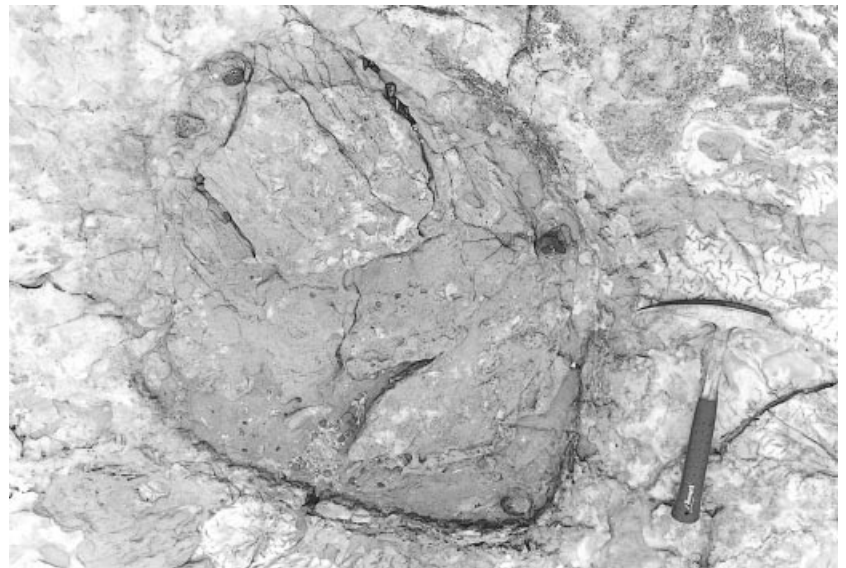
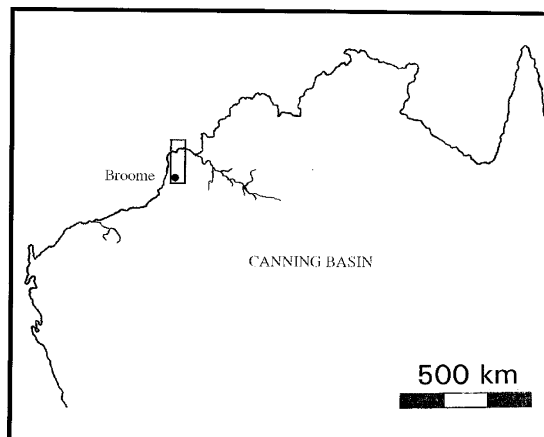


Fig. 2. Well-preserved dinosaur tracks in mottled soil horizon (uppermost unit C). Note void-filling concretion and rooting truncated by second partial track at bottom right (implies true track).

***Paralic:** literally, by the sea; it implies largely non-marine deposits formed near the coast.

Fig. 1. Outline map of coastal north-western Australia showing location of study area.

and secondary enrichment of clays washed down from the overlying topsoil. These features indicate that this is the subsoil and the print is a direct, or *true*, track, impressed via the topsoil alone. This is confirmed by exceptional soft-part preservation – a large bicusped pad preserved as positive relief, complete in outline.

If this is an accurate reflection of the ventral surface of the foot, what can be said of the trackmaker? The visual impression is of a 4- or 5-toed track, the central two digits (II and III) supported by a large hoof-like pad, and digit I offset at a pronounced angle to the rest of the foot. This lateral offset is due to irregular metapodial articulation. It is a characteristic restricted to the saurischia, and appears to rule out a stegosaur. Rarely is preservation good enough to make this kind of distinction (e.g. see Fig. 4). The print is almost certainly a forelimb, or manus, track and at 86 cm by 60 cm is far larger than any stegosaurian material so far discovered.

The marked indentation at the posterior margin and firmly compacted terminal pad indicate a heel striking the surface first, the weight borne equally by the ball of the foot. Such a gait, with heel flat on the ground, is termed plantigrade. It is generally accepted that most dinosaurs, including the large sauropods, were digitigrade – i.e. walking on the toes with wrist and heel raised from the ground. While this deep impression might be caused by a stationary animal sinking into soft substrate, it is difficult to see how a digitigrade animal could make this track.

It is worth remembering that there are no modern analogues for the largest dinosaurs, and almost nothing is known about the size or shape of the supporting soft-tissue structures. What little *is* known has come from exceptionally preserved tracks, detail that osteological studies cannot provide. Central to this is the role of the substrate in track formation.

Impressions transmitted to unlithified subsurface strata (undertracks) can distort the picture greatly and even indicate a different animal. The track evidence points to a large plantigrade saurischian, and we must look to the sauropods for a trackmaker. A likely candidate is one of the massive Titanosaurids which dominated the southern hemisphere during the Early Cretaceous, but with more than 20 genera and no body fossils yet found in Western Australia, further identification is not possible.

Stratigraphy

The Broome Sandstone Group bears such striking lithological similarity to the British Wealden as to merit direct comparison. Briefly, the lower Wealden (Hastings Group) comprises sandstones, mottled siltstones and soil horizons in overall coarsening-upwards sequences interpreted as alluvial-lagoonal mudplain deposits. The Broome stratigraphy is shown in Fig. 3.



Fig. 3. Broome Sandstone Group Type Section at Ganthaume Point (units are descriptive divisions). Basal white sandstone (A), mottled green mudstone (B), variegated sand-siltstones (C). Note sharp contact between units B and C.

The coarse white sands of unit A are poorly sorted, with thin parallel bedding and a lumpy pelleted appearance. Traversed by abundant dinosaur trackways but otherwise unfossiliferous, agitated shallow non-marine conditions are indicated. Unit B is a fissile, green, mottled, sandy siltstone with a very sharp upper contact (erosive?). Unit C alternates between variegated argillaceous sandstones and subordinate red siltstones, with occasional strongly developed soil horizons. The alternation of sands and muds with root traces and elliptical carbonate nodules marks these units as alluvium from meandering rivers, the vivid mottling a product of chemical weathering in a humid climate. The intense soil-forming activity of upper unit C, similar to that in modern middle latitudes, would require a considerable period of non-deposition, suggesting a site distal to the fluvial cross-bedded sandstones capping the sequence. Maximum exposed thickness is 13 m with a further 274 m proved in boreholes. Inferred palaeoenvironment is alluvial (lagoonal?) floodplain.

If these *are* Wealden-type deposits, then they are significant as the first major record of this facies in the southern hemisphere. Explanations for the change from paralic carbonate to terrigenous clastic deposition during Wealden times have included:

rapid sea-level fall and continental erosion (eustatic); rising sourcelands and increasing runoff (tectonic); progressive rifting and increasing maritime influence (climatic). Discussion of these topics is beyond the scope of this article, but the presence of this sequence in Australia has implications for the interpretation of this facies in general.

In 1984, Hallam reported Wealden deposits from North America, Europe, southern Russia, North Africa and Arabia. If Australia is included, deposition covers more than 120° (palaeo) longitude and 80° latitude. Early Cretaceous continental reconstructions show increasing maritime conditions, with all other areas of Wealden accumulation marginal to the newly forming Atlantic and Tethyan seaways. However, north-western Australia appears to have been fully coastal since Upper Palaeozoic times and was not directly affected by the break-up of Pangaea. Neither could any amount of local or regional tectonic activity account for such globally synchronous deposition.

In terms of rapid sea-level or climate change, it is tempting to speculate on the nature of the abrupt boundary between units B/C, and prominent erosional surfaces recently described from the basal Wealden of south Dorset by Hesselbo and Allen in 1991. Equally intriguing is the possibility that the Broome sequence spans the Jurassic-Cretaceous transition; the basal white sands of unit A could easily be the equivalent of Purbeckian lagoonal deposits. Chronology of the Broome Sandstone Group is poorly constrained, and the data presented herein too limited to attempt correlation, but it is clear that this site would repay more detailed investigation.

The assertion of 'Wealden' deposition is based on observed rock characteristics such as lithology, sequence and facies and is entirely lithostratigraphic.



Fig. 4. Detail of unit A. White pelleted sandstone with lightly impressed sauropod trackway. Tracks similar size to those in Fig. 2, but note the lack of detail and circular sand crescents – fluidic substrate/formation in shallow water?

Biostratigraphic detail is lacking, although plant remains reported from Broome are the familiar Weald cycad and fern genera *Otozamites*, *Sphenopteris* and *Cladophlebis*. There is no temporal control beyond Neocomian = Wealden and, as such, the suggested equivalence may be only approximate. Nevertheless, it seems reasonable, on the basis of this preliminary description, to propose extension of 'Wealden facies' to Australia.

Suggestions for further reading

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Fossils explained 21: Post-Palaeozoic ophiuroids

In comparison with our knowledge of most other fossil echinoderm groups, that of the ophiuroids (brittle stars and basket stars) is rather poor, despite the fact that their remains are quite common in some Mesozoic and Cenozoic deposits. Ophiuroids are mostly preserved as disarticulated ossicles of discs and arms only; localities which yield more or less complete specimens are, sad to say, few. The specific identification of dissociated ossicles is often difficult, but not impossible. However, more serious are the problems which arise when trying to assign fossil species to extant families. Ophiuroid classification relies primarily on morphological features of disc plating and the oral frame (jaw structure in particular; Figs 1 & 2). When considering living ophiuroids, most taxonomic characters can be readily seen in external view, which is why dissection is seldom needed. Such features are rarely sufficiently well preserved in

fossil ophiuroids and, even when they are, they have often suffered from sediment compaction and/or recrystallization. This holds especially true for specimens preserved in coarse-grained limestones.

Current classifications of ophiuroids are unsatisfactory and reflect grades of skeletal organization rather than true evolutionary relationships. A first attempt at a cladistic analysis of ophiuroids by Andrew Smith and colleagues has shown that a lot of work still needs to be done.

Having been the subject of numerous papers by Hans Hess, ophiuroids of Jurassic age are comparatively well known. Hess demonstrated that disarticulated ophiuroid ossicles could be identified to species and assigned, albeit often tentatively, to Holocene genera. In particular, lateral arm plates, preferably from all positions along the arm, may serve as the basis for new fossil species. Cretaceous species are less well known; however, my own research in progress at a number of north-west European localities will document an unexpectedly high ophiuroid diversity for the Campanian and Maastrichtian – that is, the last two stages of the Cretaceous.

Morphology of ophiuroids

At first sight, brittle stars appear to have much in common with the starfishes or asteroids (see *Geology Today*, v.12, p.230, 1996), but there are many differences. In ophiuroids, the simple or branched arms are sharply demarcated from the disc and have an internal row of ossicles, the vertebrae (Fig. 3). There are no ambulacral grooves (Figs 1 & 4). Covering the integument are disc ossicles of various types – for

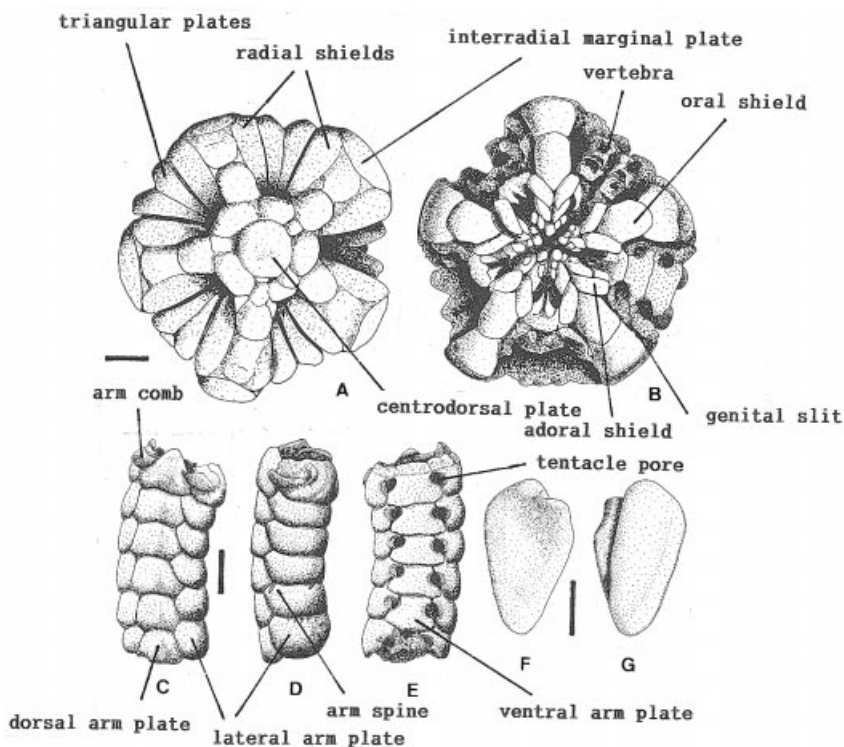
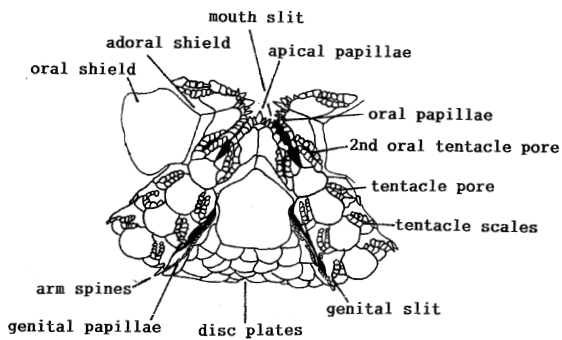


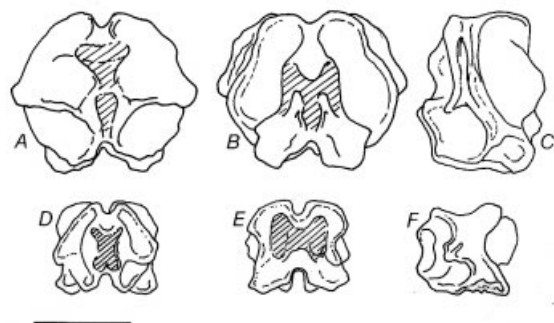
Fig. 1. General morphology of an ophiuroid, based on the holotype of *Felderophiura vanderhami* (modified after Jagt, *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Sciences de la Terre)*, v.61, text-figs 2, 3, 1991), from the late Maastrichtian (late Cretaceous) of The Netherlands. Scale bars represent 1 mm. (A,B) Dorsal and ventral views, respectively, of the disc. (C–E) Dorsal, lateral and ventral views of proximal arm fragment. (F,G) Internal and external view of highly distinctive radial shield, with indentation for associated triangular plates (see A).



example, shields, plates, scales, spines and granules. Adhesive tube feet along the arms (Fig. 1) are used to catch food particles, but also enable the animal to cling to slippery surfaces. In some forms, tube feet are used for locomotion as well, but most brittle stars move by muscular contractions, with the arms flexing and pushing the disc along. A few species are able to swim.

Disc: Conspicuous plates on the dorsal disc surface (Fig. 1A) include the centrodorsal plate, one or more circlets of disc plates and the paired radial shields above each arm base. At the arm base, the first dorsal arm plates are seen and, in some genera, arm combs are developed which articulate with the radial shields (Fig. 1C). All these plates may either be smooth or partially or completely covered with granules (Fig. 4C,E) and spines. In living ophiuroids, the stomach, gonads and bursae occur within the disc. The bursae open within the disc (genital slit; Figs 1B & 2), on opposite sides of the arm base, and serve in respiration and reproduction. Plates arranged around the mouth frame include the oral and adoral plates (Figs 1B & 2), with the latter in touch with the jaws. The jaws carry teeth as well as apical and oral papillae, which line the mouth slit (Fig. 2). In radial positions bordering the mouth slit are the first ventral and lateral arm plates, which conceal the vertebrae (Fig. 1B), as well as the second oral tentacle pore (Fig. 2), which either opens within or outside the mouth slit. A varying number of tentacle scales (Fig. 2) line the tentacle pores, leaving just a small opening for the tube foot.

Arms: Although it has often been claimed that the arms of most ophiuroid species can move in a horizontal plane only, all species are able to bend their arms vertically or coil them to some extent. The vertebrae are linked by muscles and connective tissues, and show either a dumbbell (streptospondyline) or ball-and-socket (zygospondyline) type of articula-



tion (Fig. 3); intermediate forms between these types are known. Arm spines are found on the proximal margins of lateral arm plates; these serve in feeding and defence, and are either appressed (lying flat on adjoining plates) or erect (Fig. 5).

Classification

Mike Simms and colleagues have recently pointed out that current ophiuroid classifications are unsatisfactory and do not reflect phylogenetic relationships. The classification proposed in a recent paper by Smith and co-workers presented a first cladistic analysis of the ophiuroids and calibrated this against the fossil record. Unfortunately, many fossil forms are still inadequately known, which is often due to their fragmentary preservation.

Despite these problems, it often proves possible to refer post-Palaeozoic ophiuroids to modern families and occasionally even genera, especially when well-preserved specimens are available. Details of dorsal disc plating are important, including the presence or absence of a centrodorsal plate, plate circlets, and the structure and size of the radial shields, as is the presence or absence of arm combs. The disc plates may either be smooth or sculptured to varying

Fig. 2. Part of the ventral surface of the disc of *Ophiura scomba* Paterson (modified after Paterson, *Bulletin of the British Museum of Natural History (Zoology)*, v.49, Fig. 46a, 1985), showing elements of the mouth frame and ventral disc plating.

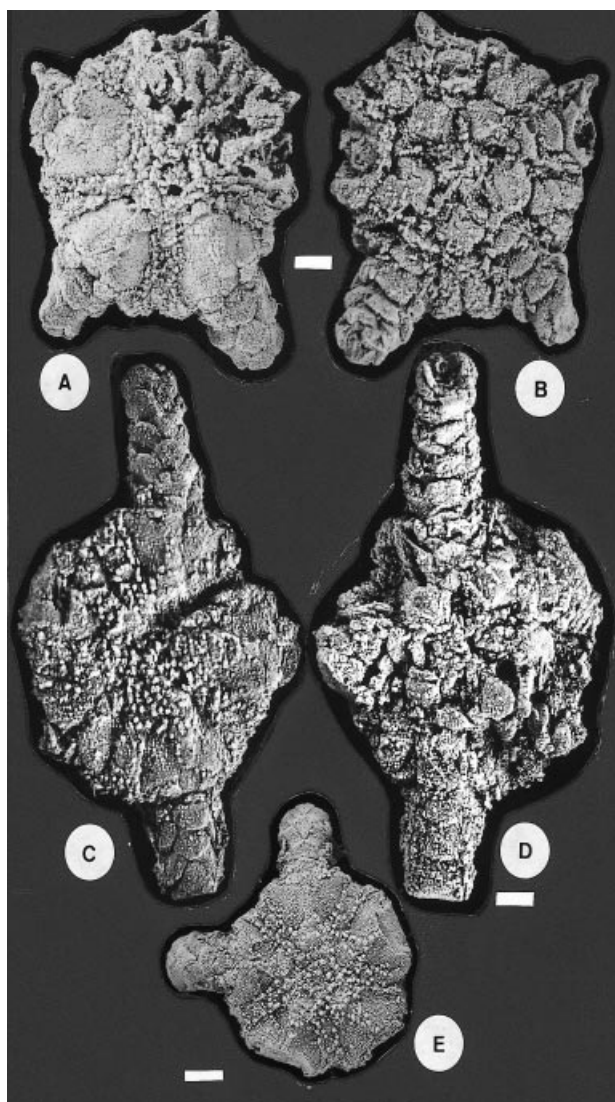


Fig. 5. Isolated ophiuroid lateral arm plates from the early Maastrichtian of Rügen (north-east Germany). (A)

Ophiacantha? danica (Rasmussen), with prominent articulation bases for erect arm spines. (B,C) *Ophiotitanos serrata* (Roemer), with partially concealed articulation bases for appressed arm spines, and representing proximal and distal positions along arm, respectively. All figures are scanning electron micrographs (courtesy of Saskia Kars, Vrije Universiteit Amsterdam).

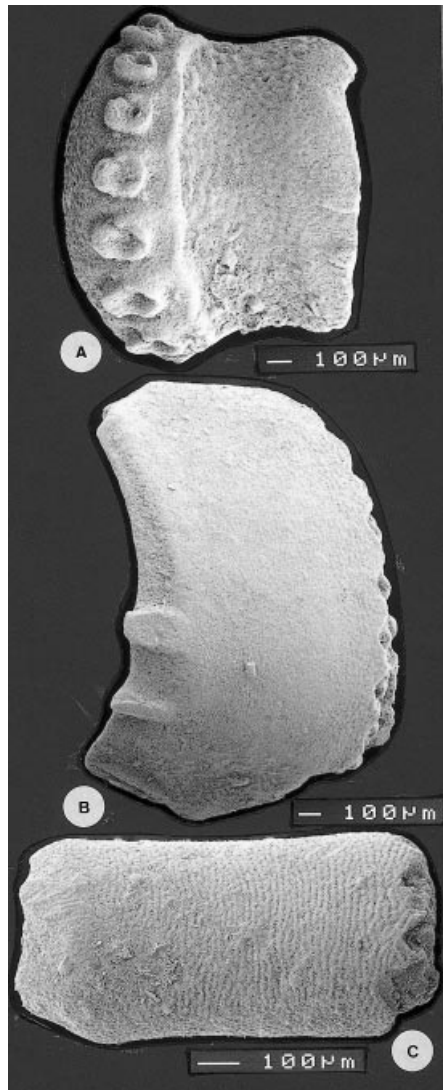


Fig. 3. (far left) Isolated ophiuroid vertebrae, illustrating the streptospondyline (A–C, modified after Hess, *Eclogae Geologicae Helvetiae*, v.59, Fig. 68, 1966) and zygospondyline (D–F, modified after Hess, *Eclogae Geologicae Helvetiae*, v.55, Fig. 87, 1962) types of articulation. A,D, proximal facets; B,E, distal facets; C,F, lateral views. Scale bar represents 20 mm.

Fig. 4. (left) ‘*Ophiura fuerstenbergii* Müller, silicified specimens preserving disc granulation, portions of arms and arm spines. Lower Campanian, Vaals-Eschberg (southern Limburg, The Netherlands). A–E show pear-shaped, paired radial shields; various circlets of smaller, granulated, disc plates; well-developed dorsal, ventral and lateral arm plates; as well as conspicuous oral shields bordering the mouth frame (refer to Figs 1 & 2 for identification). Photographs courtesy of W. Misear (Brussels). Scale bars represent 1 mm.

degrees, features which may also yield many clues concerning classification. On the ventral disc side, features of the mouth frame, particularly the number of apical and oral papillae, are of importance. The arm plating, especially the shape of the lateral arm plates, and the orientation and number of arm spine bases provide additional features upon which an assignment to family or genus may be based.

Heavy-plated, relatively large fossil forms with well-developed discs and arms, with or without a full complement of tentacle pores and with appressed spines, generally are referable to the families Ophiuridae and Ophiolepididae. More fragile forms, with erect spines and densely granulated discs, are classed in families such as the Ophiacanthidae, Amphiuroidae and Ophiothricidae. Thus more or less complete fossil ophiuroids often show a suite of characters, allowing them to be placed in extant families. However, generic assignment usually relies heavily on characters of the mouth frame, which are often poorly preserved through sediment compaction. In such cases, it may prove difficult to determine the shape and number of apical and oral papillae.

In cases where only dissociated ossicles of arms and discs are available, the shape of the radial shields (including the type of articulation between these

shields and the genital plates, visible on the internal surface), shape and curvature of the lateral arm plates (plus number and orientation of arm spine bases) and vertebral structure are of particular importance in identifying fossil ophiuroids. A direct comparison with representatives of the various modern families, many of which may be collected from the world’s beaches, is the best possible ‘first step’ in the identification of fossil brittle stars.

Preservation and palaeoecology

As outlined above, what generally remains of fossil ophiuroids are isolated ossicles only. More or less complete specimens – that is, discs with attached arms – are rare. However, from a number of localities, high-density ophiuroid populations have been recorded, especially of Jurassic age. Such occurrences generally result from rapid burial (obtrusion) of live animals through storms, and are found in deep- and shallow-water settings alike.

Naturally, species which actively burrowed in soft substrates stood a better chance of being preserved whole, in comparison with ophiuroids that lay on the sea floor, clung to objects (epizoic) or lived commensally. This may explain why the fossil record of Cretaceous brittle stars appears to have favoured heavy-plated, relatively robust forms, mostly with appressed spines. The well-preserved ophiuroids from the late Cretaceous succession in the United Kingdom, as described and illustrated by Spencer, are examples of this type. However, studies under way will document many diminutive and ‘brittle’ forms, mostly with erect spines. Thus many ecological types in highly diverse ophiuroid faunas (with up to 30 species) may be recognized and recorded.

Well-preserved specimens from the late Maastrichtian (= latest Cretaceous) of The Netherlands (Meerssen Member, Maastricht Formation) allow a preliminary assessment of predation pressure. Sublethal predation of ophiuroids results in self-mutilation (autotomy), during which one or more arms, or parts of an arm(s), are shed, the severed portion regenerating fairly rapidly. Despite the fact that the Meerssen Member represents a shallow-water (less than 10 m), subtropical setting with highly diverse decapod crustacean and teleost/chondrichthyan fish assemblages, very few ophiuroids have regenerating arms. Work done by Richard Aronson has suggested that predation on ophiuroids increased during the late Mesozoic when durophagous teleost fishes and decapod crustaceans underwent biotic radiations. The Maastricht example appears to contradict this conclusion. However, it is possible that large-scale displacement of sediment overwhelmed these ophiuroid faunas during several storms that were closely spaced in time. This sediment cover may thus have protected the ophiuroids from predation.

Identification of disarticulated ossicles

Working with rich and well-preserved ophiuroid material from the Jurassic of Switzerland and France, Hess showed that even disarticulated ossicles might serve as the basis for fossil species. He selected lat-

eral, rather than dorsal and ventral, arm plates to document ophiuroid diversity. For species recognition, it is preferable that plates from all positions along the arm should be considered. In this way, confusion of distal lateral arm plates of one species with the proximal plates of another, smaller form may be avoided. Details of (micro)sculpture (Fig. 5), structure and the number of arm spine bases can thus be used to recognize species, and permit the assignment of isolated plates to them. If external sculpture is particularly distinctive, other arm (and even disc) plates can be properly assigned to species. More than once, this method has been shown to yield reliable results, upon discovery of portions of arms and/or disc in which the ossicles are still in anatomical connection. The structure of vertebrae is less reliable in such taxonomic practice, except maybe for the distinction between zygospondyline and streptospondyline types of articulation. However, the curvature and internal structure of lateral arm plates may occasionally yield clues as to which type of vertebra was associated.

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