

MIDDLE TRIASSIC HOLOTHURIANS FROM NORTHERN SPAIN

by ANDREW B. SMITH and J. GALLEMÍ

ABSTRACT. An abundant fauna of well-preserved holothurians is described from the Middle Triassic (Ladinian) of Collbató, northern Spain. Three new genera and species are represented, *Strobilothyone rogenti*, a heterothyonid, *Monilipsolus mirabilis*, a psolid, and *Collbatothuria danieli* an aspidochirote of uncertain familial affinities. A new subfamily, Monilipsolinae, is created for *Monilipsolus*. Holothurians had clearly achieved considerable diversity by the Middle Triassic; at least four of the six currently recognized orders were established by this time. Holothurians were also ecologically diverse by the Middle Triassic with epibenthic, deposit-feeding species, infaunal, suspension-feeding species and epifaunal, attached, suspension-feeding species all represented.

Of the five classes of echinoderm alive today, none has a poorer fossil record than the holothurians. There are some 1160 named species alive today (Pawson 1982), and these are found in virtually all marine habitats. Yet only a handful of complete specimens of fossil holothurians have ever been discovered. This is partially explained by the relatively low fossilization potential of holothurians, since the great majority have their skeleton reduced to microscopic spicules. However, the holothurian fossil record is considerably worse than might be expected. For example, although several families of dendrochiroitids possess an imbricate skeleton of large calcite plates and might be expected to be preserved in Konservat Lagerstätten, none has ever been reported as fossils. Complete fossil holothurians have been reported from just six localities:

1. Hunsrückschiefer, Lower Devonian of Budenbach, West Germany. This has yielded seven specimens of *Palaeocucumaria hunsrueckiana* Lehmann, described by Seilacher (1961).
2. Francis Creek Shale, Middle Pennsylvanian of Illinois, USA. Over two thousand specimens of an *Achistrum* sp., only a preliminary description of which has so far been published (Sroka 1988).
3. Muschelkalk, Middle Triassic, of Tarragona, Spain. One specimen each of the elasipod *Oneirophantites tarragonensis* Cherbonnier and the aspidochirote *Bathysynactites viai* Cherbonnier, preserved as impressions in calcareous silts (Cherbonnier 1978).
4. Upper Hauptrogenstein, Upper Bajocian, Middle Jurassic of Schinznach, Switzerland. A single specimen of the stichopid *Holothuriopsis pawsoni* Hess (Hess 1973) which preserves body wall spiculation but little else.
5. Solenhofen Limestone, Kimmeridgian, Upper Jurassic of Solenhofen, West Germany. Two species have been identified as holothurians, *Proholothuria armata* Giebel and *Pseudocaudina brachyura* Broili, the latter based on a single specimen (Frizell and Exline 1966). *P. armata* is a worm-shaped fossil that shows no details and is indeterminate to phylum. *P. brachyura* shows longitudinal banding and might be a holothurian, though Hess (1973) has questioned this.
6. Lower Cretaceous (Albian) of Tepexi de Rodriguez, Puebla, Mexico. A complete holothurian is recorded from here (Seibertz 1988), but no description of this has yet been published.

The lack of complete specimens creates major problems in investigating the evolutionary history of holothurians. Holothurian spicules are relatively common as microfossils and a parataxonomy has been established on spicule morphology alone (e.g. Frizell and Exline 1955, Deflandre-Rigaud 1962). However, this may bear little correlation with natural biological groupings and it is difficult to deduce much about the mode of life of extinct holothurians from spicule morphology. Further problems arise because higher taxa of holothurians are defined to a large degree on soft tissue

anatomy, such as the shape of the feeding tentacles or the arrangement of gonads, characters that are unknown even in those few fossil species preserved as complete specimens. Complete fossil holothurians can, however, generally be placed within a biological classification and provide direct information about the ecological diversification of the group.

The discovery of a new assemblage of well-preserved fossil holothurians belonging to three families from the Middle Triassic of Catalonia, north-east Spain is thus totally unexpected. The locality was discovered in 1986 when David Brusi, a lecturer at the Teacher's College of the Universidad Autónoma de Barcelona, collected two ophiuroids from a disused limestone quarry at Pedrera d'en Rogent. These specimens were shown to one of us (J.G.) who later visited the locality with Brusi. On this trip several fossil holothurians were found and photographed but not collected because it was felt that this was a difficult operation and required a portable rock-saw. A second visit by J.G. was made in November 1987, equipped with power tools, and many fossil holothurians were collected together with other fossils. Just prior to this second visit a number of specimens had been collected from this quarry by an amateur palaeontologist, Dr Daniel Gutiérrez. The ophiuroids collected by him were later described (Calzada and Gutiérrez 1988) but the holothurians were given to us for study. A preliminary account of this holothurian fauna was presented at the Fourth Annual Meeting of the Spanish Palaeontological Society in Salamanca (Gallemí 1990). Supplementary material has been collected subsequently from this quarry in February 1989 by J.G.

LOCALITY AND GEOLOGICAL SETTING

The holothurians described here come from a steeply dipping bedding surface in an abandoned limestone quarry locally known as 'La Pedrera d'en Rogent' (Rogent's quarry), some 200 metres east of the village of Collbató, Catalonia, north-eastern Spain (Text-fig. 1). It is Middle Triassic in age and represents the most westerly outcrop of Triassic in the Llobregat River area. Collbató is situated in the 'Pre-littoral Range', the innermost of the three tectonic belts into which the Catalan Mountain Ranges are divided; the others being the Vallès-Penedès Depression and the Littoral Range (Text-fig. 1). In the region of Collbató the succession is tectonically complex.

The Triassic of this region overlies Palaeozoic basement and resembles the succession seen in southern Germany with Buntsandstein facies succeeded by Muschelkalk facies. Three units (M1–M3) are recognized within the Muschelkalk here. The upper and lower units (M1 and M3) are carbonates clearly of marine origin, while the middle unit (M2) is composed mainly of sandstones and clays of continental facies. Masachs (1981) had previously suggested that beds equivalent to those at La Pedrera d'en Rogent belong to the M1 unit (Anisian). However, in the most recent geological mapping of this region (Rosell *et al.* 1975), the outcrop at Collbató was placed within unit M3 (Ladinian) and Calzada and Gutiérrez (1988) accepted a Ladinian age for the echinoderm fossil horizon. The holothurian horizon corresponds to the La Riba Reef Formation (F. Calvet, personal communication, July, 1989) and is indeed Ladinian.

Associated fauna at this horizon include sponges, indeterminate internal moulds of gastropods, bivalves, and ammonids, echinoids (some with spines attached) and crinoids. Isolated vertebrae and a single tooth have also been found. The crinoid is a species of *Encrinus* in which the lowest six or seven secundibrachs are uniseriably arranged. It comes closest to *E. aculeatus* Meyer, from the Lower Muschelkalk of Germany. The echinoid test material all belongs to *Miocidaris sensu stricto* and the associated spines are of three forms attributable to '*Cidaris*' *wissmanni* Bather [*C. roemeri* of Jekelius (1936) and Mihaly (1981)], '*C.*' *ecki* Assmann and a smooth-shafted, slightly fusiform spine of uncertain affinity. All are relatively long-ranging morphotypes in the Middle Triassic (Smith 1990).

At La Pedrera d'en Rogent 16–20 metres of micritic, finely laminated, almost lithographic, limestones with more marly intercalations are exposed. The section includes at least one layer covered in the trace fossil *Fucoides* and several thin levels of bioclastic limestone, composed largely of echinoderm debris. Sedimentary structures are limited to some megaripples and some scour

TEXT-FIG. 1. Map showing the fossil localities discussed in the text and their regional setting. 1, regional setting and location of map 2. 2, Barcelona region showing position of map 3. 3, simplified geological map of the Collbató district showing the fossil localities (stars) that have yielded holothurians: P = La Pedrera d'en Rogent; R = El Pujolet; T = Tertiary; Q = Quaternary; B = Buntsandstein (Lower Triassic); M1-3 = Lower, Middle and Upper Muschelkalk (Middle Triassic). Simplified from Rosell *et al.* (1975).



troughs associated with bioclastic influx. The detailed succession is very difficult to follow because of the dense network of small-scale faults that cross-cuts the quarry.

Most of the holothurians come from bedding planes that are covered in sponges distributed as small rounded discs or as more continuous mats (Pl. 1, fig. 1). The palaeoenvironment of these precise beds has not been investigated, but Calvet *et al.* (1987) and Calvet and Tucker (1988) have interpreted the palaeoenvironmental setting of the La Riba Reef facies as representing deposition in relatively tranquil marine habitat below fair weather wave-base on an intracratonic carbonate ramp.

A second quarry, 'El Pujolet' lies just to the north west of the village of Collbató (Text-fig. 1). Here a steeply-dipping bedding surface covered in *Fucoides* dominates nearly all of the quarry face. *Encrinurus* and ophiuroids have been collected from here, but as yet only a single articulated holothurian (*Strobilothyone rogenti*) has been found.

SYSTEMATIC PALAEOLOGY

Class HOLOTHUROIDEA

Order DENDROCHIROTIDA Grube, 1840

Family HETEROthyonidae Pawson, 1970

Diagnosis. Body completely covered in plates lacking spires; spicules in the form of cups may also be present. Plates not pierced for tube feet. Mouth anterior, anus at end of a posterior tail. Calcareous ring composed of five radial and five interradial elements; radial elements not composite, with well developed posterior processes.

Type genus and species. *Heterothyone alba* (Hutton), from fine sands or muds around New Zealand and the Chatham Islands [Recent].

Taxa included. *Strobilothyone rogenti* sp. nov. [Middle Triassic, Spain]; *Heterothyone ocnoides* (Dendy) [Recent, New Zealand].

Remarks. *S. rogenti* clearly belongs to the Dendrochirotida because of its well developed calcareous ring and complete body covering of imbricate plates lacking spires. Pawson (1982) recognized several extant families within this order. Three of these (Phyllophoridae, Sclerodactylidae and Cucumariidae) are soft bodied with their skeleton reduced to microscopic spicules. In addition the former two have complex calcareous rings that are made up of a mosaic of plates, unlike that of *Strobilothyone*. The four remaining families all possess a skeleton of large imbricate plates as does *Strobilothyone*. Psolidae are very easily distinguished because their mouth is displaced dorsally and they have a differentiated sole that is uncalcified: *Strobilothyone* clearly does not belong to that family. Paracucumidae are fully plated and cylindrical in shape but unlike *Strobilothyone* have a simple calcareous ring lacking posterior processes and their plates are spired. Placothuriidae are also fully plated and cylindrical in shape like *Strobilothyone*, but their calcareous ring is very different. Radial elements of the calcareous ring in Placothuriidae have long posterior processes that are composed of a mosaic of small plates. *S. rogenti* comes closest to members of the family Heterothyonidae. Heterothyonids have simple well-defined posterior processes on the radial elements of the calcareous ring that are only slightly shorter than those seen in *S. rogenti*. They are cylindrical in form and fully plated with a slightly differentiated anal tail (Pawson 1970, pl. 1, figs 2 and 3). The family contains only two living species, placed in a single genus, *Heterothyone*. The principal difference between *Heterothyone* and *Strobilothyone* is that in *Heterothyone* there are microscopic ossicles in the form of cups overlying the plates of the body wall. Cups are absent in *Strobilothyone*, which may represent the primitive condition. It is worth noting that in a closely related family, Placothuriidae, there are two species of *Placothuria*, one with scales overlain by microscopic buttons (*P. huttoni* (Dendy)) and the other lacking buttons (*P. squamata* Pawson). Thus the presence of microscopic sclerites in addition to body wall plating appears to be a character of low taxonomic value.

Genus STROBILOTHYONE nov.

Derivation of name. From the Latin *strobilus* a pine-cone, in allusion to its superficial appearance.

Diagnosis. Body plates 1–2 mm broad and undifferentiated; no cup deposits present. Mouth directed ventrally. Anus pentagonal, situated on a posterior tail. Radial elements of calcareous ring with deep anterior notch; posterior processes longer than rest of ossicle.

Type species. *Strobilothyone rogenti* sp. nov.

Age. Ladinian, Middle Triassic.

Taxonomic remarks. *Strobilothyone* has a very similar calcareous ring structure to *Heterothyone*, but differs in having a deeper anterior notch in radial elements and slightly longer posterior processes.

EXPLANATION OF PLATE I

Preservational style of holothurians from the Ladinian at La Pedrera d'en Rogent, Collbató, MGB 32383, × 1. There are eleven specimens of *Strobilothyone rogenti* gen. et sp. nov., including the holotype (arrowed), and a single specimen of *Collbatothuria danieli*, gen. et sp. nov. (C). Small oval masses of sponge cover the surface.



SMITH and GALLEMÍ, *Strobilothya*, *Collbatothuria*

The principal difference between these two genera is in the complete absence of any spicular deposits in addition to the plates in *Strobilothyone*. In *Heterothyone* cup-elements are present in the body wall (Pawson, 1970, text-fig. 3). Furthermore, in *Strobilothyone*, the mouth appears to be directed slightly ventrally, rather than being terminal as in *Heterothyone*.

Functional morphology and mode of life. This holothurian has an elongate body form with a distinct caudal process which was apparently retractable, since it is not seen in contracted specimens. The mouth and anus open at opposite poles and papillae and other projections are entirely wanting. The smooth vermiform appearance, lack of a clearly differentiated sole and tube feet and the apical position of the mouth all suggest that *Strobilothyone* was an infaunal holothurian. Furthermore, the fact that plates imbricate in two directions (i.e. towards the mouth anteriorly and towards the anus posteriorly) strongly suggests that *Strobilothyone* was U-shaped, since this is precisely the condition seen in modern U-shaped heterothyonids and placothuriids (D. L. Pawson, personal communication, August, 1989). Thus *Strobilothyone* probably lived much like many modern heterothyonids with both anterior and posterior extremities projecting from the sediment (Pawson 1982). Feeding tentacles must have been well developed, to judge from the calcareous ring, and *Strobilothyone* was presumably an infaunal, benthic, suspension-feeder. None of the specimens, however, is preserved in inferred life position, nor is there any evidence of possible holothurian burrows at this horizon.

Strobilothyone rogenti sp. nov.

Plate 1, fig. 1; Plate 2, figs 1–5; Plate 3, figs 1–3; Text-figs 2–6

Types. Holotype MGB 32383 (Pl. 1, fig. 1, arrowed; Pl. 2, fig. 1) paratypes MGB 30556, 30578, 30562, 32320, 32322, 32336, 32338, 32372, BMNH E27540–1.

Other material studied. MGB 30563, 30564 (sectioned), 30566, 30573, 30679–82, 30684 (sectioned), 32321, 32357, 32361, 32364, 32366.

Age and distribution. Middle Triassic, Ladinian, known from La Pedrera d'en Rogent and El Pujolet, near Collbató, Catalonia, north-eastern Spain.

Diagnosis. As for the genus.

Description. Individuals are up to 30 mm in length and are fusiform in shape, the widest point being about mid-length in most cases. The posterior tends to be more pointed than the anterior (Pl. 2, figs 3 and 4; Pl. 3, fig. 3). Some individuals (Pl. 2, fig. 1; Text-fig. 2) have a distinct caudal appendage which is considerably narrower than the rest of the body. This is at most only 25% of the total length of the body and is absent in obviously contracted specimens (Pl. 3, fig. 1; Text-fig. 3). Contracted specimens are circular in cross-section and there is no differentiated sole. Maximum diameter ranges from about 30–70% of the length.

The entire body is sheathed in imbricate plates up to 2 mm wide, 0.6 mm in length and about 0.1 mm in thickness. These plates are tightly stacked in contracted specimens (Text-fig. 3) but show much less overlap in extended specimens (Text-fig. 2). They appear to be only two or three stereom layers thick. Most specimens

EXPLANATION OF PLATE 2

Figs 1–5. *Strobilothyone rogenti* gen. et sp. nov. 1, MGB 32383 (specimen arrowed in Pl. 1, fig. 1), holotype, × 4 (see Text-fig. 2 for interpretation). 2, MGB 30562, paratypes, × 4 (see also Text-fig. 3); note the change in the direction of imbrication between the oral and anal poles. 3, MGB 32338, paratype, almost complete specimen showing anal appendage in contracted state, × 2. 4, MGB 32372, paratype, a juvenile, × 4. 5, MGB 32320, paratype, showing calcareous ring in side view, × 4 (see Text-fig. 4 for interpretation). All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.



SMITH and GALLEMÍ, *Strobilothyone*



TEXT-FIG. 2. *Strobilothyrone rogenti* gen. et sp. nov., MGB 32383; camera lucida drawing of the holotype (see also Pl. 2, fig. 1). Relatively uncontracted specimen in ventral view showing anal appendage.

TEXT-FIG. 3. *Strobilothyone rogenti* gen. et sp. nov., MGB 30562; camera lucida drawing of paratype (see Pl. 2, fig. 2). Specimen in contracted state.



show a change in the sense of imbrication about mid-length, plates towards the anterior imbricate backwards while those in the posterior half imbricate towards the anterior (Pl. 2, fig. 2; Pl. 3, fig. 3; Text-figs 2 and 3). The plating close to the anus becomes virtually pentagonal in some specimens (Pl. 3, fig. 1; Text-fig. 6) suggesting that there might be a pentagon of internal, anal valve plates making this region more rigid. No other spicules are associated with the body wall.

The calcareous ring is seen in MGB 30578 (Pl. 3, fig. 2) and MGB 32320 (Pl. 2, fig. 5). It consists of ten elements, five radial and five interradial pieces (Text-figs 4 and 5). The radial pieces are the larger and have both anterior and posterior processes. Anterior processes are relatively short and two or three in number. The posterior processes are much longer, forming more than half of the radial length of the ossicle. There are two processes to each element and these are simple. The interradial pieces are as broad as the radial pieces but lack posterior processes. They have a small central anterior projection and possibly an adjacent anterior notch.

A small plate about 0.3 mm in diameter with a spongy appearance is seen close to the calcareous ring in MGB 30578 (Text-fig. 5). This may be the madreporite.

Family PSOLIDAE Perrier, 1902

Diagnosis. Plated dendrochirotes with a differentiated sole and both mouth and anus opening on the dorsal surface. Calcareous ring simple; radial elements with shallow anterior notch but without posterior processes.

Subfamily MONILIPSOLINAE nov.

Diagnosis. Body oval in outline and flattened, with double marginal row of stout, perforate bead-like ossicles arranged radially. No oral valve plates.

Type species. *Monilipsolus mirabilis* sp. nov.

Age. Middle Triassic, Ladinian.

Remarks. This subfamily is erected for the new species *Monilipsolus mirabilis*. It is fully plated with differentiated dorsal and ventral plating, the ventral surface taking the form of a sole. In general body organization it closely resembles extant psolid dendrochirotes, having the mouth displaced dorsally and the anus also dorsal and at the end of a short tail. The calcareous ring of *Monilipsolus* resembles that of living psolids, being composed of radial and interradian elements that are moderately stout and lack posterior processes. The presence of an almost complete plated integument over the peristome and a solid calcareous ring suggests that *Monilipsolus* possessed an introvert and could withdraw its tentacles. *Monilipsolus* differs from extant psolids in having a strongly calcified sole and in having a remarkable double ring of stout, perforate, bead-like ossicles around the periphery. This last character easily distinguishes *Monilipsolus* from all extant species of Psolidae and is an excellent autapomorphy for the subfamily.

Genus MONILIPSOLUS nov.

Derivation of name. From the Latin *monile*, a necklace, in allusion to the appearance of the peripheral band of bead-like ossicles.

Type species. *Monilipsolus mirabilis* sp. nov.

Age. Middle Triassic, Ladinian.

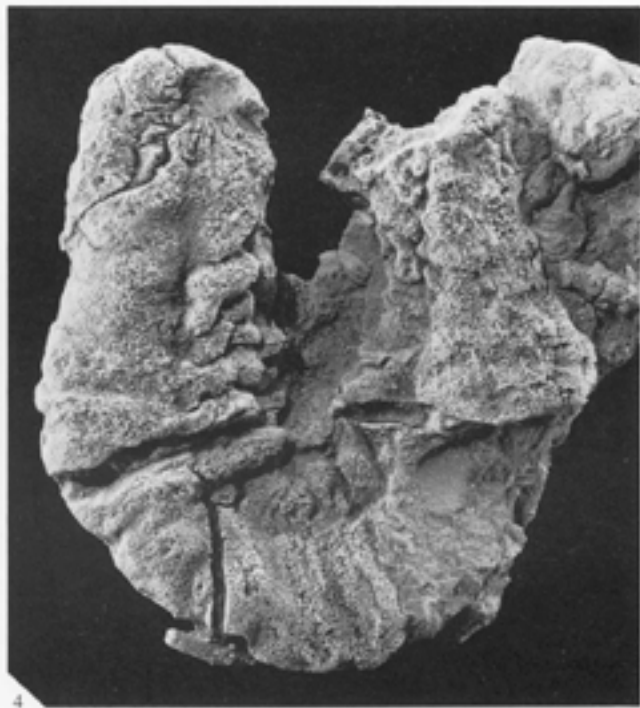
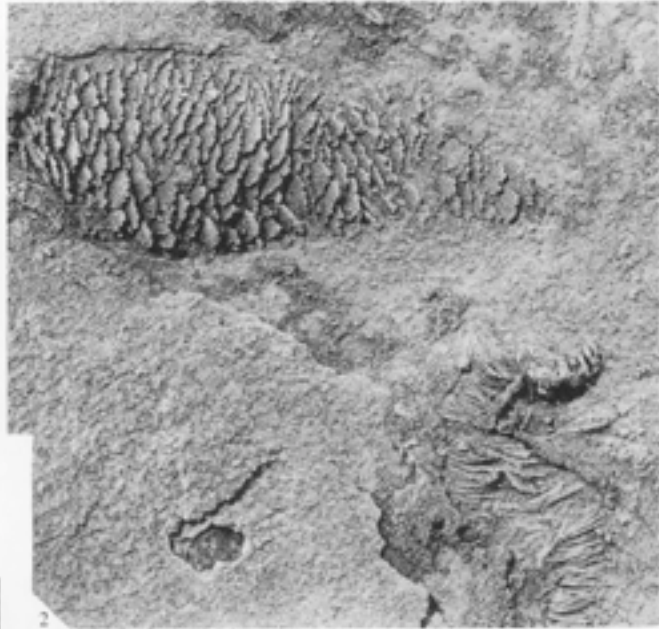
Diagnosis. Body oval, up to 55 mm in length and about $\frac{1}{3}$ rd as wide; depressed. Sole of thin imbricate plates; dorsal surface of thicker plates with two irregular biserial bands of single pores perforating plates. Tube-feet absent from sole but probably present around margin. Peristome large, occupying most of the anterior end of the dorsal surface, largely covered by a peristomial membrane of radially-arranged plates. Periproct at end of small tail. Well developed anterior notch on radial elements of calcareous ring.

Description. See description of *M. mirabilis* below.

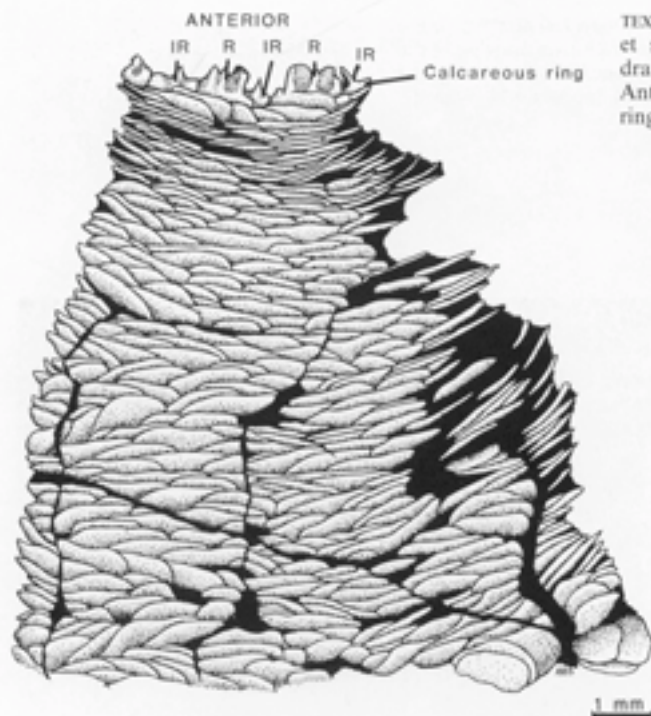
Remarks. *Monilipsolus* is a most remarkable holothurian genus. No other holothurian possesses any structure comparable with the large perforate calcite ossicles that rim the body. The function of these ossicles is unknown. It seems probable that *Monilipsolus* was a suspension feeder, like modern psolids, since it has a dorsally directed mouth and ventral sole for attachment. The large size of the

EXPLANATION OF PLATE 3

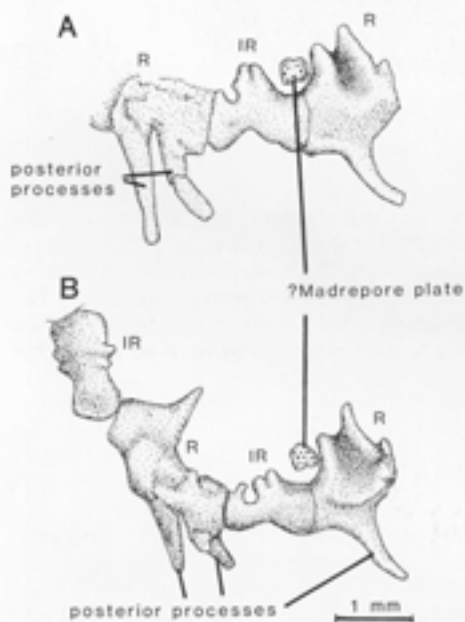
Figs 1-3. *Strobilothyrone rogenti* gen. et sp. nov. 1, MGB 32322 (paratype), juvenile (see also Text-fig. 6). 2, MGB 30578 (paratypes); two specimens, the lower of which shows part of the calcareous ring (see Text-fig. 5). 3, MGB 30556 (paratype). All $\times 4$.
Fig. 4. *Collbatothuria danieli* gen. et sp. nov., MGB 32274 (paratype), $\times 3$ (see also Text-fig. 18).
All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.



SMITH and GALLEMÍ, *Strobilothyone*, *Collbatothuria*

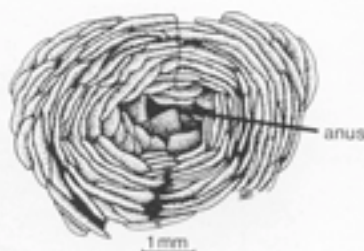


TEXT-FIG. 4. *Strobilothyrone rogenti* gen. et sp. nov., MGB 32320; camera lucida drawing of paratype (see Pl. 2, fig. 5). Anterior portion showing the calcareous ring elements in side view; note the apical position of the mouth.



TEXT-FIG. 5. *Strobilothyrone rogenti* gen. et sp. nov., MGB 30578; paratype; camera lucida drawings of calcareous ring elements in a partially disarticulated specimen. A, lateral aspect showing two radial (R) and one interradial (IR) elements. B, same in more anterior aspect. Both to same scale.

TEXT-FIG. 6. *Strobilothyrone rogenti* gen. et sp. nov., MGB 32322; paratype. Camera lucida drawing of the posterior region showing the anus and the pentagonal arrangement of plates surrounding it (see Pl. 3, fig. 1).



TEXT-FIG. 7. *Monilipsolus mirabilis* gen. et sp. nov., MGB 32385, holotype; dorsal surface, $\times 8$. See Text-fig. 8 for an interpretation.

peristome, the fact that it is mostly covered by a flexible plated membrane, and the presence of a well developed calcareous ring whose radial elements have deep anterior notches for the attachment of tentacle retractor muscles all point to there being an introvert; the tentacles could presumably have been more or less fully retracted and protected by the peristomial plated membrane. The periproct lies on the dorsal surface at the end of a short tail. The flattened profile and broad, differentiated sole suggest that *Monilipsolus* was adapted to grip onto firm or hard bottoms. Oral tube-feet may have been present but uncalcified, or might have been absent; none is preserved. However, there are rather large circular spaces found around the periphery of the sole, adjacent to each perforate ball, which might mark the sites of large tube-feet (Text-figs 13 and 14). Tube feet were definitely present dorsally, but were small and have not been preserved. There are two irregular bands of small perforations, about 0.1 mm in diameter, on dorsal plates that run along the length of the animal (Text-fig. 12) and which mark the site of the tube feet.

Thus in general body organization and mode of life *Monilipsolus* closely resembles modern psolid, suspension feeders which cling to pebbles and other such solid substrata.

The stout perforate ossicles that form a marginal rim to *Monilipsolus* are unique and of unknown function. These are sometimes slightly faceted to fit closely together and are developed around the



TEXT-FIG. 8. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 32385 (holotype), dorsal aspect (see Text-fig. 7).

entire periphery, without a break. The perforations are narrow, 0.5–0.6 mm in diameter in ossicles 1.5–1.6 mm in diameter and expand slightly towards the interior. The interior opening of these pores lies within the body cavity, inside the plated mesoderm, and so must have connected to some internal coelom or organ. The exterior opening is directed laterally and slightly downwards (ventrally), so that it is generally not seen in dorsal view and can just be seen in ventral view.

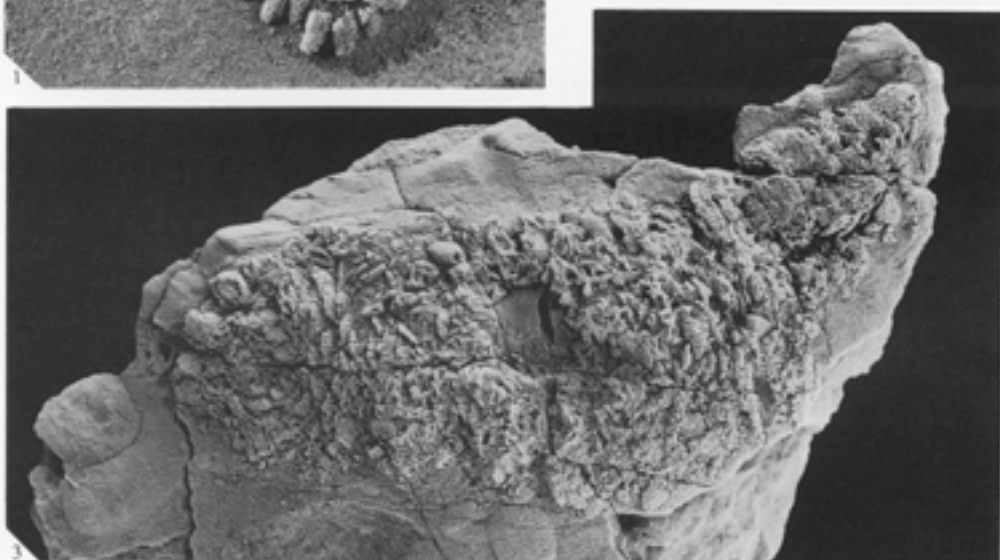
The functional significance of this peripheral ring of perforate ossicles can be assessed by considering its possible role with respect to the various vital functions that a holothurian must perform. These are to do with feeding, sensory reception, defence, locomotion/adhesion, reproduction and respiration.

It seems highly improbable that the perforate ossicles played any part in feeding since they are well removed from the mouth and digestive tract. Comparative morphology suggests that *Monilipsolus* fed using tentacles, like psolids.

EXPLANATION OF PLATE 4

Figs 1–3. *Monilipsolus mirabilis* gen. et sp. nov. 1, MGB 32367 (paratypes); both individuals show dorsal surfaces (incomplete), the upper is illustrated in Text-fig. 11. 2, MGB 30671 (paratype), dorsal surface showing tube foot pores (see also Text-fig. 12). 3, MGB 32325 (paratype), dorsal surface, mouth to the left (see Text-fig. 10 for interpretation). All $\times 3$.

All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.



SMITH and GALLEMÍ, *Monilipsolus*



TEXT-FIG. 9. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of BMNH E27543; paratype (see Pl. 5, fig. 2). Dorsal surface.

They are also almost certainly not associated with reproduction, simply because of their multiplicity and distribution around the entire periphery. In holothurians the gonads open through a single pore close to the tentacle ring. No holothurian has multiple gonopore openings and their distribution and orientation are difficult to explain in functional terms.

Gaseous exchange is another possible function. The pores would then be inhalant or exhalant (or both) orifices through which sea water would be drawn inside the mesodermal skeleton to allow efficient gaseous exchange, presumably across a thin membrane. Although some Palaeozoic cystoids have developed a comparable system, no holothurian is known that has any system remotely comparable. Furthermore, the positioning of the pores around the periphery of the animal pointing

TEXT-FIG. 10. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 32325; paratype (see Pl. 4, fig. 3). Dorsal aspect.



slightly downwards would only make sense if these were exhalant orifices and no obvious inhalant orifice can be identified. We do not favour this interpretation.

They cannot be locomotory in function, because they have no articulation at the base and seem to fit together very closely, often being slightly faceted. The perforations might conceivably be associated with some form of secretion to enhance adhesion. However, it must be pointed out that the environment in which *Monilipsolus* is preserved shows no evidence of strong current activity. Another possibility is that they are in some way associated with defence, possibly openings for extruding some form of sticky substance as the Cuvierian tubules do. However, although they form a continuous ring around the periphery of the animal, which gives all round protection, the openings are directed slightly downwards and one might expect structures associated with defensive

secretions to be scattered over the entire dorsal surface rather than being restricted to the very periphery.

The most likely interpretation is that these structures were sensory in function, for example housing long tube-feet that formed a sensory frill around the entire margin of the animal. However, this fails to explain why the ossicles themselves are so massive and we assume that tube-feet were needed to provide grip and on the ventral surface were directed downwards, not laterally.

The stout perforate ossicles that rim this species are highly distinctive and should be recognizable even from disarticulated debris. Interestingly, no such ossicles have ever been recorded from the St Cassian Beds (Cassian, late Middle Triassic) of the Cortina d'Ampezzo district of Italy, where a very rich echinoderm fauna has been documented by Zardini (1976). Zardini has carefully identified a large number of isolated skeletal elements, many of them very small, including echinoid spines, asteroid and ophiuroid ossicles, crinoid columnals and even somphocrinid cups. The absence of monilipsolid ossicles in the St Cassian Beds is thus unlikely to be due to collection failure.

Monilipsolus mirabilis sp. nov.

Plate 4, figs 1–3; Plate 5, figs 1–4; Text-figs 7–14

Diagnosis. As for the genus.

Types. Holotype MGB 32385 (Text-fig. 7); paratypes MGB 30561, 30565, 30569, 30572, 30576, 30671, 30674, 32319, 32325, 32367, 32384, BMNH E27542–3.

Other material studied. MGB 32365, 32369 (sectioned).

Age and distribution. Middle Triassic, Ladinian, known only from La Pedrera d'en Rogent, Collbató, Catalonia, north-eastern Spain.

Description. Body flattened in profile and oval in outline with the skeleton differentiated into a lower (ventral) sole of thin imbricate plates, a marginal band of stout perforate ossicles arranged into two irregular rows anteriorly, and an upper domed surface of thicker imbricate plates some of which are perforated for tube feet. Individuals range from about 25 mm long by 8 mm wide to 55 mm by 18 mm. Anterior and posterior end are uniformly rounded, the anterior (Pl. 5, fig. 1) being generally slightly wider than the posterior (Pl. 5, fig. 3). The body is usually parallel-sided but tapers slightly in the posterior third (Text-figs 9 and 10).

The ventral surface is composed of a series of thin, imbricate plates that are laterally elongate (Pl. 5, figs 1, 3, 4). Plates are widest down the median part of the sole and become more equant in outline towards the edge (Text-fig. 13). Very rarely one or more of the sole plates around the margin may be perforated like the marginal ossicles (Text-fig. 14). The ventral plates usually have a high degree of overlap and imbricate towards the posterior. None of the ventral plates is perforated for tube feet but around the edge of this surface, immediately adjacent to the stout marginal ossicles, are found small (0.3 mm) gaps that in places appear almost circular. These may mark the sites of ventral tube feet. Although no definite remains of tube feet are preserved, vague tubular structures in between marginal ossicles (Text-fig. 14) may possibly represent tube feet.

Marginal ossicles are shaped like the beads of a necklace and are slightly tapered distally (Pl. 4, fig. 1). In larger individuals these ossicles are about 2.0–2.3 mm in length and 1.1–1.2 mm in width. Each is perforated by a 0.5 mm diameter cylindrical pore that expands very slightly towards the interior. The ossicles have a smooth surface and form a continuous ring to the margin of the body (Text-fig. 8). They are irregularly arranged into

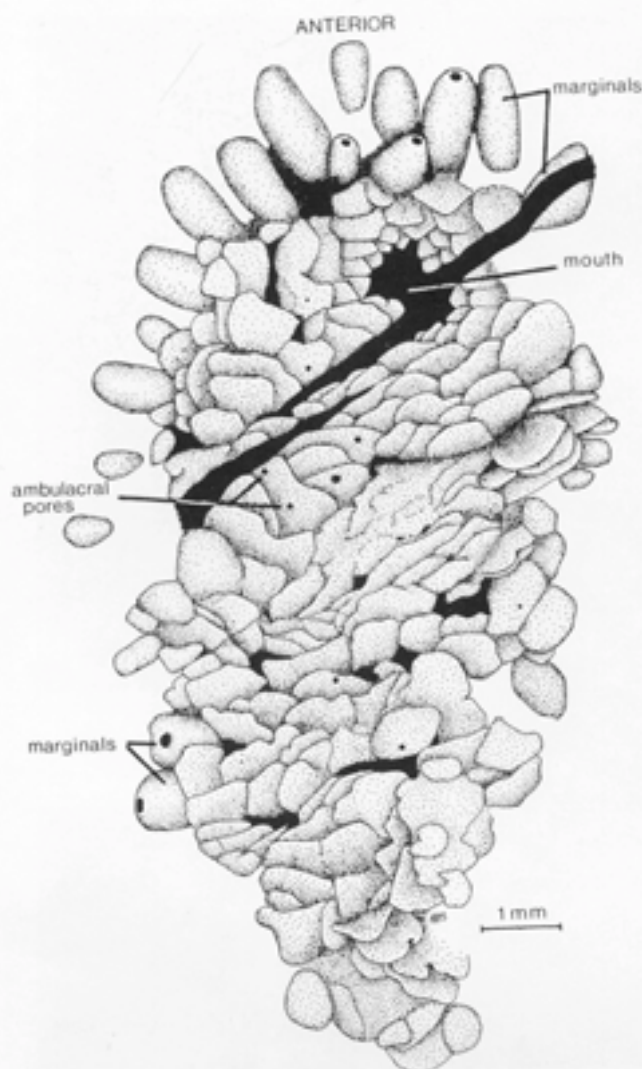
EXPLANATION OF PLATE 5

Figs 1–4. *Monilipsolus mirabilis* gen. et sp. nov. 1, MGB 30674 (paratype), ventral surface, anterior to top. 2, BMNH E27543 (paratype), juvenile, dorsal surface, anterior to the right (see also Text-fig. 9). 3, MGB 30576 (paratype), ventral surface, posterior to top (see also Text-fig. 13). 4, MGB 30561 (paratype), ventral surface, anterior portion, (see also Text-fig. 14). All $\times 4$.

All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.



SMITH and GALLEMÍ, *Monilipsolus*



TEXT-FIG. 11. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 32367; paratype (see Pl. 4, fig. 1). Anterior portion seen in dorsal aspect showing peristome and tube foot pores.

an upper and lower alternating series, but this becomes better defined around the anterior and posterior borders where two distinct rows of marginals are present (Text-fig. 11). The pores on marginal ossicles open distally and are usually just visible in ventral aspect (Pl. 5, fig. 4) but not in dorsal aspect (Pl. 4, fig. 1).

The dorsal surface was domed in life but is now usually collapsed. It is composed of imbricate plates that are thicker than those of the sole (about 0.15–0.2 mm in thickness) and show a much smaller degree of overlap (Text-figs 11 and 12). There is no recognizable organization to this surface. Both the mouth and anus lie on this surface. The peristome is recognizable as a large area of concentrically arranged platelets around a central hole situated close to the anterior (Pl. 4, figs 1 and 3; Text-figs 7–11). Platelets decrease in size towards the opening and there are no larger valve-like plates protecting the mouth. The peristome occupies most of the anterior end of the body. The anus lies near the posterior end of the body and in some specimens appears to form a small tail-like projection (Text-figs 9 and 10; Pl. 4, fig. 3; Pl. 5, fig. 2). In between the peristome and anal tail many of the dorsal plates are perforated for tube feet (Pl. 4, fig. 2; Text-figs 11 and 12). These pores

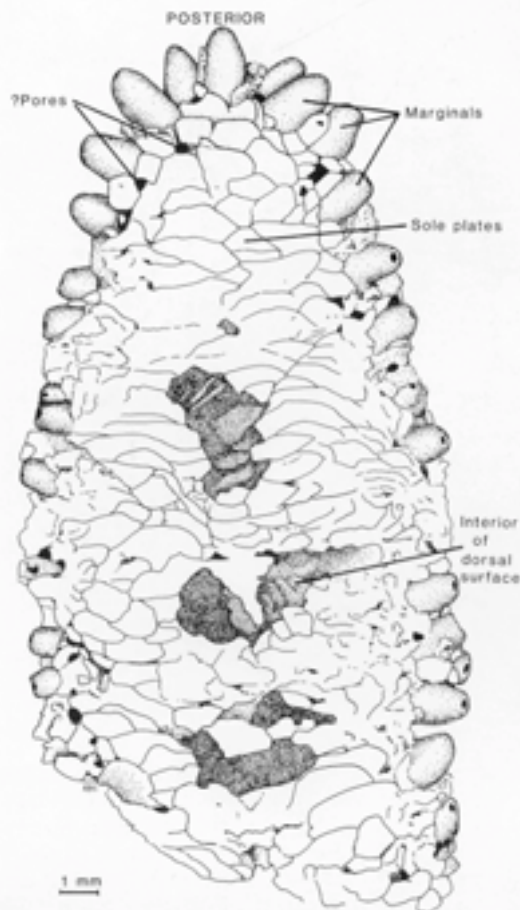
TEXT-FIG. 12. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of dorsal plating in MGB 30671 (paratype) showing the distribution of the tube foot pores (see Pl. 4, fig. 2).



are more or less scattered over the entire surface with a tendency to be concentrated into two bands, one on each side of the mid-line (Text-fig. 12).

The complete calcareous ring is not seen in any specimen but elements of it are exposed in a slightly disaggregated specimen, MGB 30674. The interradial elements are narrow and spade-shaped, lacking posterior processes but with a large anterior projection. The radial elements are broader than long and also lack posterior processes, the posterior border being distinctly concave. There is a moderately deep anterior notch centrally which in effect defines two small anterior processes. This notch may in fact become closed over anteriorly so as to form a pore.

Remarks. Like other holothurians from this locality, specimens of this species commonly display a mid-ventral groove due to early diagenetic compaction and collapse of the skeleton above the digestive tract.



TEXT-FIG. 13. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 30576; paratype (see Pl. 5, fig. 3). Ventral surface showing sole plating.

Order ASPIDOCHIROTIDA Grube, 1840
 Family uncertain
 Genus COLLBATOTHURIA NOV.

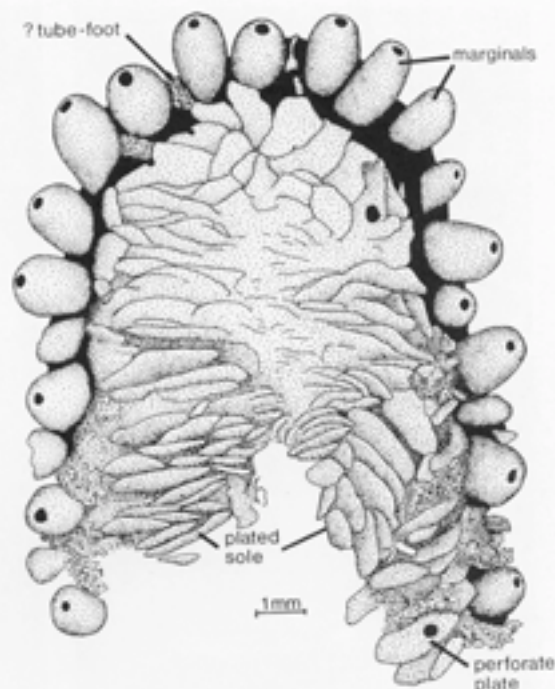
Derivation of name; after the village of Collbató near where the species was found.

Type species. *Collbatothuria danieli* sp. nov.

Age and distribution. Middle Triassic, Ladinian, known only from La Pedrera d'en Rogent, Collbató, Catalonia, north-eastern Spain.

Diagnosis. Small (up to 50 mm in length), vermiform, differentiated dorso-ventrally into a sole with many tube-feet and a latero-dorsal surface lacking tube-feet and without warts. Mouth large, open, at anterior but slightly ventral. Anus at posterior terminus. Body wall thick and heavily calcified but not plated. Form of body-wall spiculation unknown. Calcareous ring present, but form unknown; apparently simple without anterior projections.

TEXT-FIG. 14. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 30561; paratype (see Pl. 5, fig. 4). Ventral surface showing sole plating and marginals.



Remarks. The systematic position of this genus remains uncertain. Its thick wrinkled body wall, obviously heavily calcified with spicules, its straight cylindrical body and differentiated sole, and simple calcareous ring are all suggestive of Aspidochirotida. Three families are currently recognized within the Aspidochirotida (Pawson 1982), but unfortunately they are differentiated solely on soft tissue, anatomical structures (arrangement of gonads, presence/absence of tentacle ampullae). It is therefore impossible to be more specific about the taxonomic placement of *Collbatothuria*. In general body form and organization it resembles several genera within the Holothuriidae and Stichopidae. *Collbatothuria* has relatively smooth dorsal and lateral surfaces with only circumferential crenulations associated with contraction. Wart-like projections are absent from dorsal and lateral surfaces and there is also no evidence of tube feet in this region, though they are clearly developed over the sole. These characters differentiate *Collbatothuria* from extant genera of Holothuriidae and Stichopidae.

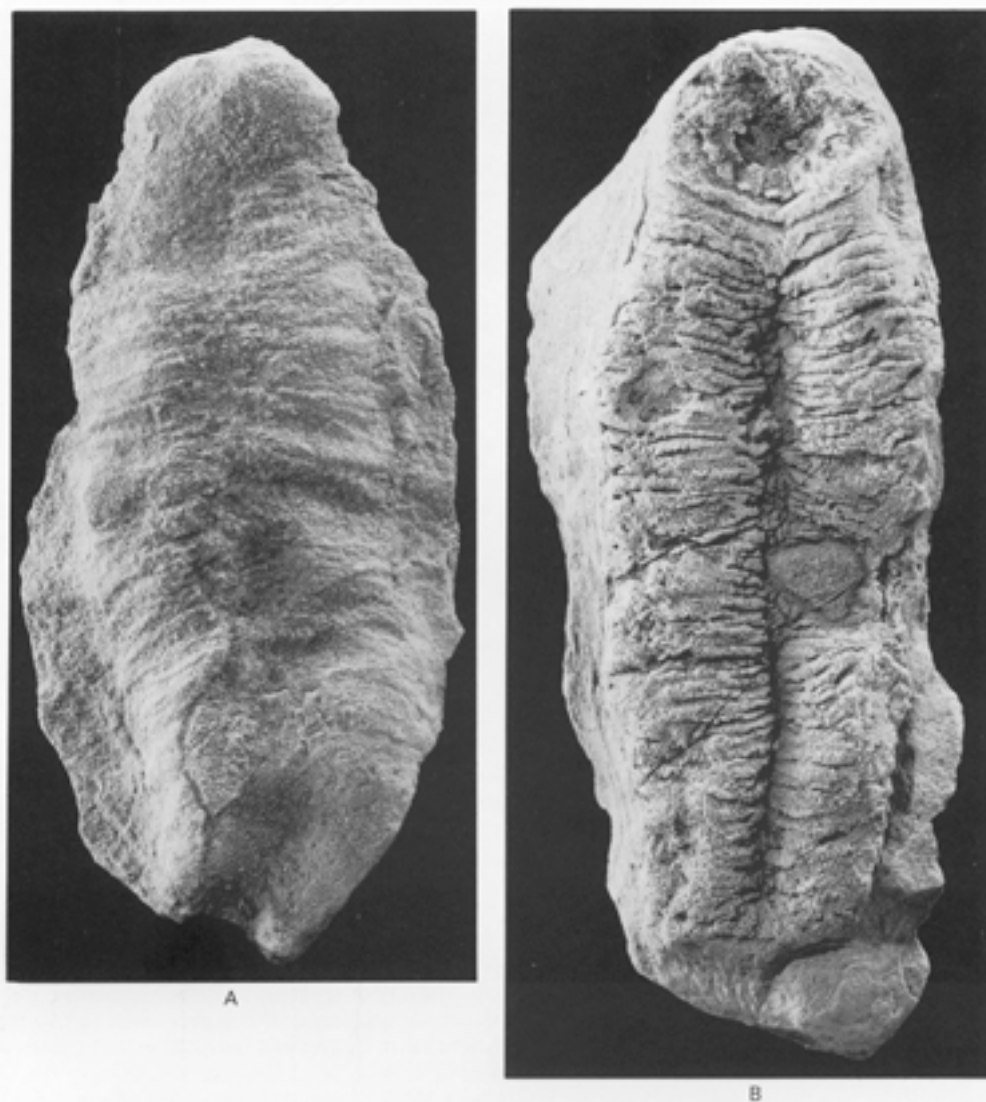
The well differentiated sole with its numerous tube feet indicate that *Collbatothuria* was an epifaunal benthic crawler with a locomotory sole. Its downward-opening mouth suggests that it was a deposit-feeder, using its tentacles to pick up suitable detritus from the sea floor. Its mode of life was, therefore, similar to that of modern Holothuriidae and Stichopidae.

Collbatothuria danieli sp. nov.

Plate 3, fig. 4; Text-figs 15-18

Derivation of name; in honour of Dr Daniel Gutiérrez, an amateur palaeontologist who discovered the holotype and other specimens.

Diagnosis. As for the genus.



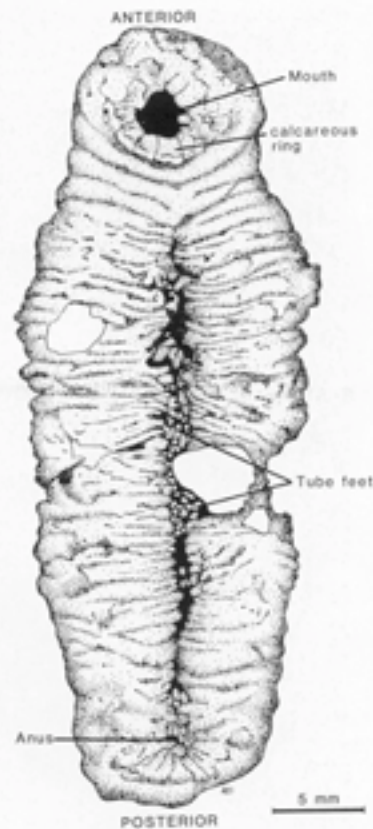
TEXT-FIG. 15. *Collbatothuria danieli* gen. et sp. nov.: A, dorsal surface, BMNH E27544 (see Text-fig. 17); B, ventral surface of holotype, MGB 32273 (see Text-fig. 16). Both specimens $\times 4$.

Types. Holotype MGB 32273; paratypes MGB 32274, 32377, 32383 (Pl. 1, fig. 1; 'C'), BMNH E27544.

Age and distribution. Middle Triassic, Ladinian, known only from La Pedrera d'en Rogent, Collbató, Catalonia, north-eastern Spain.

Description. Specimens, which are sausage-shaped, are 35 mm to 52 mm long. They were presumably ovoid in cross-section, but are now flattened due to diagenetic compression with a median furrow marking the digestive tract (Text-fig. 15). Their overall shape varies with the state of contraction. Contracted specimens are rather

TEXT-FIG. 16. *Collbatothuria danieli* gen. et sp. nov., camera lucida drawing of MGB 32273 (holotype). Ventral surface.



short and fat, with a maximum width that is almost 50% of the length (Pl. 1, fig. 1; 'C'). Others are more elongate with a width that is only about 20% of the length (Pl. 3, fig. 4). One specimen is preserved in a U-shaped position (Text-fig. 18), but other specimens are all straight.

The mouth lies anteriorly facing downwards (Text-figs 15 and 16). It is a large circular opening, some 2.5 mm in diameter in a 35 mm long specimen. This opening is surrounded by a ring-like structure of individual elements which represents the calcareous ring (Text-fig. 16). The precise structure of the calcareous ring cannot, however, be made out since it is covered by thick integument. There appear to be only ten elements and none has strong anterior projections. There is no visible body wall plating, the body being a wrinkled integument (Pl. 3, fig. 4; Text-fig. 15). This integument is relatively thick and presumably must have been heavily spiculated to be preserved, but the silicification has destroyed any original spicules that were present. The dorsal surface is virtually smooth and wrinkle-free (Text-figs 15a and 17) and has no papillae, tube feet or warty projections. The ventral surface is generally concave and presumably contracted prior to death. It is differentiated as a sole and there are numerous small tube feet on this surface (Text-figs 15b, 16). The ventral surface is much more strongly wrinkled than the dorsal surface and papillae are well developed along the margin of the sole (Pl. 3, fig. 4; Text-fig. 18). The anus is terminal and in MGB 32273 is marked by a concentric valvular appearance to the integument (Text-figs 15b and 16). In MGB 32274 there appear to be a few larger papillae developed around the anus (Text-fig. 18).

EVOLUTIONARY IMPLICATIONS OF THE FAUNA

The Collbató fossil bed is uniquely important in yielding a fauna of holothurians in relative

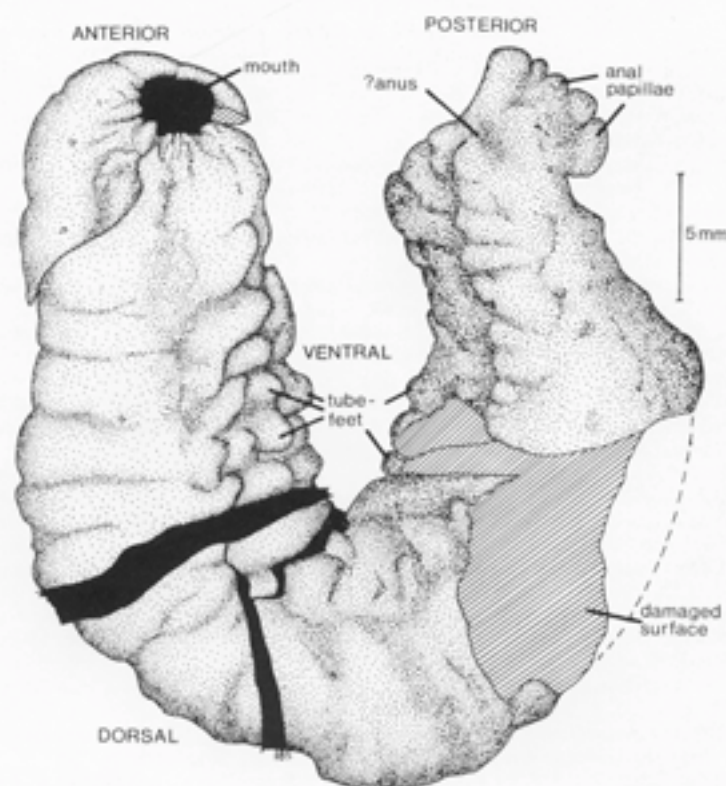


TEXT-FIG. 17. *Collbatothuria danieli* gen. et sp. nov., camera lucida drawing of BMNH E27544 (paratype). Dorsal surface: cross-hatching = sediment covered areas.

abundance, belonging to three separate families. What is more, these are by far the best preserved, complete specimens of fossil holothurians that have ever been discovered. Only in one other fossil holothurian can details of general anatomical arrangement, body-wall plating and the structure of the calcareous ring be documented and that is the synaptid apodan *Achistrum* from the Middle Pennsylvanian of Illinois. The information available on these species makes it possible to place them within a biological classification established on Recent species with a fair degree of certainty.

Two other species, *Oncirophantites tarragonensis* Cherbonnier and *Bathysynactites viai* Cherbonnier, have been reported from the Middle Triassic of Tarragona, Spain (Cherbonnier 1978). Neither is well preserved or reveals as much anatomical information as the three species described here, since they are preserved only as decalcified impressions. However, *Oncirophantites* was tentatively assigned to the order Elasipoda on account of its long lateral papillae and the position of the mouth, and *Bathysynactites* was assigned to the Aspidochirotida. Both were preserved in anoxic facies of Middle Triassic (Muschelkalk) age.

Taking the Tarragona and Collbató fossil holothurians together, gives a Middle Triassic fauna of five species. These belong to three orders, namely Elasipodida, Aspidochirotida and Dendrochirotida. Members of a fourth order, Apodida, must have been present since the group had already differentiated by the Upper Carboniferous, as shown by the *Achistrum* sp. from the Mazon Creek Shale. Thus, of the six extant orders of Holothurioida, only Molpadiida and Dactylochirotida have no fossil record by the early Mesozoic. Considerable taxonomic diversity of holothurians had therefore been achieved by the Middle Triassic. Furthermore, a certain amount of ecological



TEXT-FIG. 18. *Collbatothuria danielli* gen. et sp. nov., camera lucida drawing of MGB 32274; paratype (see Pl. 3, fig. 4). Specimen in lateral view with ventral surface towards the interior.

diversification is also evident. In the Middle Triassic we can recognize epibenthic, deposit-feeding forms with well developed soles (*Collbatothuria*, ?*Bathysynactites*, ?*Onciophantites*), burrowers (*Strobilothyrone*) and epibenthic, psolid-like suspension-feeders that attached to firm bottoms (*Monilipsolus*). Considering how well skeletized some of these taxa are and how diverse holothurians had become by the Middle Triassic, it is surprising to us how rarely they have been reported in the fossil record.

Acknowledgements. Field trips have been covered with funds of the MGB's Project 'Work on fossiliferous localities' (1988 and 1989) financed by the Ajuntament de Barcelona (Area de Cultura-Secretaria Technica de Museus). A British Council's Academic Travel Grant allowed one of us (J.G.) to carry out research for the paper. We thank also D. Brusi for presenting the first material from Collbató, Dr J. M. Pons, E. Vicens and J. Muñoz (Universitat Autònoma de Barcelona) for their help in previous phases of the study, Mr E. Rogent for allowing us access to his quarry and D. Gutiérrez, R. Mañé and I. Gurrea for donating important specimens. Dave Pawson, Chris Paul and Paul Gilliland provided helpful comments on an earlier draft of the paper, for which we are grateful.

REFERENCES

- CALVET, F., MARCH, M. and PEDROSA, A. 1987. Estratigrafía, sedimentología y diagénesis del Muschelkalk superior de los Catalánides. *Cuadernos Geología Ibérica*, **11**, 171–197.
- and TUCKER, M. E. 1988. Outer ramp cycles in the Upper Muschelkalk of the Catalan Basin, northeast Spain. *Sedimentary Geology*, **57**, 185–198.
- CALZADA, S. and GUTIÉRREZ, D. 1988. Ofiuras (Echinodermata) del Ladinense catalán. *Batalleria*, **1**, 31–38.
- CHERBONNIER, G. 1978. Note sur deux empreintes d'holothuries fossiles du Trias moyen de la region de Tarragone (Espagne). *Thalassia Jugoslavica*, **12** [for 1976], 75–79.
- DEFLANDRE-RIGAUD, M. 1962. Contribution à la connaissance des sclerites d'holothurides fossiles. *Mémoires du Muséum d'Histoire naturelle de Paris*, **11**, 1–123.
- FRIZZEL, D. L. and EXLINE, H. 1955. Monograph of fossil holothurian sclerites. *Missouri University School of Mines and Metallurgy Bulletin, Technical Series*, **89**, 1–204.
- 1966. Holothuroidea – fossil record. U646–672. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part U. Echinodermata 3*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 695, pp.
- GALLEMI, J. 1990. Nuevos equinodermos del Muschelkalk superior (Ladinense) de Cataluña. In CIVIS, J. and FLORES, J. A. (eds), *Actas de Paleontología (Actas de las IV Jornadas de Paleontología, Salamanca 1988); Acta Salmanticensis, Bibliotheca de las Ciencias* **68**, 141–147.
- GRUBE, A. E. 1840. *Actinien, Echinodermen und Würmer des Adriatischen und Mittelmeers*. J. H. Bon, Königsberg, 92 pp., 1 pl.
- HESS, H. 1973. Neue Echinodermen-Funde aus dem mittleren Dogger des Aargauer Juras. *Eclogae geologicae Helvetica*, **66**, 625–656.
- JEKELIUS, E. 1936. Der Weisse Triaskalk von Brasov und seine Fauna. *Anularul Institutului Geologic al Romaniei*, **17**, 1–106.
- MASACHS, V. 1981. Itinerari M2-C. Manresa-Monistrol de Montserrat-Collbató. 70–72. In MASACHS, V. (ed.). *Itineraris Geològics. Bages, Berguedà, Anoia, Solsonès*. Centre d'Estudis Geològics 'Valenti Masachs', Manresa, 103 pp.
- MIHALY, S. 1981. Az Aggteleki-Karszt középső-Triász Echinoidei. *Magyar Állami Földtani IntézevÉvi Jelentése*, (1979), 297–331.
- PAWSON, D. L. 1970. The marine fauna of New Zealand: sea cucumbers (Echinodermata: Holothuroidea). *New Zealand Department of Scientific and Industrial Research, Bulletin*, **201**, 7–69.
- 1982. Holothuroidea. 791–818. In PARKER, S. P. (ed.). *Synopsis and classification of living organisms*, vol. 2. McGraw-Hill, New York, 1232 pp.
- PERRIER, R. 1902. Holothuries, in *Expédition scientifique de la Travailleur et du Talisman*. G. MASSON, Paris, 273–554 pp., pls 12–22.
- ROSELL, J., TRILLA, J., OBRADOR, A., PEON, A., ALONSO, F., RAMIREZ, J. and CABAÑAS, J. 1975. Mapa Geològica de España. E. 1:50,000. Sabadell (392). *Instituto Geológico y Minero de España*, 31 pp., 1 folded map.
- SEIBERTZ, E. 1988. Symposium report: 1er Congreso Nacional de Paleontología, Mexico City, 16–20 November 1987. *Cretaceous Research*, **9**, 391 only.
- SEILACHER, A. 1961. Holothurien im Hunsrückschiefer (Unter-Devon). *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, **89**, 66–72.
- SMITH, A. B. 1990. Echinoid evolution from the Triassic to the Lower Jurassic. *Cahiers de l'Institut Catholique de Lyon, séries Science* **3**, 79–117.
- SROKA, S. D. 1988. Preliminary studies on a complete fossil holothurian from the Middle Pennsylvanian Francis Creek Shale of Illinois. 159–160. In BURKE, R.D., MLADENOV, P. V., LAMBERT, P. and PARSLEY, R. L. (eds). *Echinoderm Biology*. A.A. Balkema, Rotterdam, 818 pp.
- ZARDINI, R. 1976. *Fossili di Cortina: Atlante degli Echinodermi Cassiani Trias Medio superiore della regione Dolomitica attorno a Cortina d'Ampezzo*. Foto Ghedina, Lugglio, 29 pp., 22 pls.

ANDREW B. SMITH

Department of Palaeontology
British Museum (Natural History)
Cromwell Road, London SW7 5BD

JAUME GALLEMI

Museu de Geologia
Parc de la Ciutadella s/n
08003 Barcelona, Spain

Typescript received 25 October 1989

Revised typescript received 8 January 1990