Microconchid tubeworms from the Jurassic of England and France

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The Bajocian tubeworm *Spirorbis midfordensis*, previously regarded as a spirorbid polychaete, is reinterpreted as a microconchid and assigned to *Punctaconchus* gen. nov. along with two new species, *Punctaconchus ampliporus* sp. nov. (Toarcian?, Aalenian–Bathonian), the type species of the new genus, and *Punctaconchus palmeri* sp. nov. (Bathonian). Microconchids are a mostly Palaeozoic group of tubeworms that are probably more closely related to modern lophophorate phyla than they are to polychaetes. *Punctaconchus*, the youngest unequivocal microconchid, is characterised by having large pores (punctae) penetrating the tube wall, which has a fibrous or platy lamellar microstructure, and ripplemark-like transverse ridges on the tube interior. In both morphology and ecology it is a remarkable homeomorph of the polychaete *Spirorbis*.

Key words: Microconchida, morphology, Jurassic, England, France.

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Introduction

Small, spirally-coiled calcareous worm tubes are common in the Palaeozoic and Triassic (e.g., Brönnimann and Zaninetti 1972; Burchette and Riding 1977; Weedon 1990), but rare in the Jurassic. Such tubeworms are traditionally assigned to the polychaete genus *Spirorbis*. However, pre-Cretaceous examples have been reinterpreted as microconchids (Class Tentaculitoidea Bouček, 1964) on the basis of the early ontogeny and microstructure of their tubes (Weedon 1991, 1994; Dreesen and Jux 1995; Taylor and Vinn 2006). Microconchids (Figs. 1–4) differ from polychaete tubeworms (Filogranidae, Spirorbidae, and Serpulidae) principally in having lamellar (e.g., Fig. 4F), pseudopunctate or punctate tubes (e.g., Figs. $2A_2$, D, E, $3A_3$, E, $4E_2$), and a bulb-like tube origin (Weedon 1991; Taylor and Vinn 2006; Fig. $3A_2$).

In the Jurassic, *Spirorbis*-like tubeworms have been recorded from the Yorkshire coast (*Serpula cirriformis* Young, 1828; *Serpula compressa* Young, 1828), the Bajocian Upper Coral Bed (*Spirorbis midfordensis* Richardson, 1907) and the Bathonian White Limestone Formation of Gloucestershire (*Spirorbis* sp. in Taylor 1979), and Caillasses de la Basse Ecarde Formation of Normandy (*Spirorbula* sp. in Palmer and Fürsich 1981). Another putative spirorbid, *Spirorbis imprimus* Ziegler and Michalik, 1998, described from the Upper Jurassic of the Pieniny Klippen Belt of the western Carpathians, resembles neither microconchids nor spirorbids and is most likely to be a coiled serpulid, which are very common in the Jurassic (e.g., Parsch 1956).

Spirorbiform tubeworms from the Jurassic have not previously been studied in detail and their microstructures have never been described. Using well-preserved material principally from the Middle Jurassic of England and France, and aided by SEM, we here document the morphologies and microstructures of supposed *Spirorbis* and *Spirorbula*, providing evidence for their microconchid affinities. Consequently, a new genus (*Punctaconchus*) and two new species (*P. ampliporus* and *P. palmeri*) are introduced.

Institutional abbreviation.—NHM, Natural History Museum, London, UK.

Geological setting

The western Anglo-Paris Basin was a major site of shallow marine carbonate sedimentation during Middle Jurassic times. The sequence stratigraphy of the region has been studied by Rioult et al. (1991) who recognized 18 depositional cycles in the Middle to Upper Jurassic related to short-term changes in sea-level. Fossil invertebrates are very abundant and diverse in the Middle Jurassic of England and Normandy. They have been the subject of numerous monographic studies beginning in the early 19th century, along with several palaeoecological studies in more recent years.

The tubeworms used in the current study come from five stratigraphical horizons spanning Upper Aalenian to Upper Bathonian, the names of the tubeworm species recorded being given in brackets. In ascending order the horizons are:

(1) Upper Aalenian, *Ludwigia murchisonae* Zone; Inferior Oolite Group, Birdlip Limestone Formation, Crickley Member (including the former "Pea Grit"); Stroud-Cheltenham area of Gloucestershire, England (see Barron et al. 1997). This material encrusts articulated shells of large terebratulid brachiopods, at least some of which are from an oncolitic limestone believed to have been deposited in a shallow water, open shelf environment where the sea-bed was stabilised by dense vegetational cover (Mudge 1995). (*Punctaconchus ampliporus* sp. nov.).

(2) Lower Bajocian, *Witchellia laeviuscula* Zone; Lincolnshire Limestone Formation, Kirton Shale Member (see Ashton 1980); Kirton-in-Lindsey, Lincolnshire, England. All specimens are detached from their original substrates. (*Punctaconchus midfordensis* [Richardson, 1907]).

(3) Upper Bajocian, *Parkinsonia parkinsoni* Zone; Inferior Oolite Group, Salperton Limestone Formation, *Clypeus* Grit Member (see Parsons 1976; Barron et al. 1997); around Midford, Avon and Stroud, Gloucestershire, England. These detached specimens belong to the Lindsall Richardson Collection, are labelled "Bradfordian (Truellii), Upper Coralbed", and possibly include syntypes of *Spirorbis midfordensis* Richardson, 1907. (*Punctaconchus midfordensis* [Richardson, 1907]).

(4) Middle or Upper Bathonian, *Morrisiceras morrisi* or *Procerites hodsoni* zones; Great Oolite Group, White Limestone Formation; Foss Cross Quarry, Gloucestershire. Recorded as *Spirorbis* sp. by Taylor (1979), most of this material encrusts shells of the bivalve *Plagiostoma*. (*Punctaconchus ampliporus* sp. nov.).

(5) Upper Bathonian, *Aulacosphinctes hollandi* Zone; Caillasses de la Basse Ecarde Formation (see Rioult et al. 1991); St Aubin-sur-Mer, Calvados, Normandy, France. Most of the spirorbiform tubeworms here encrust a lithistid sponge, *Platychonia magna*, which forms small patch reefs (Palmer and Fürsich 1981). (*Punctaconchus palmeri* sp. nov.).

In addition to these Middle Jurassic localities, a tubeworm-encrusted intraclast allegedly from the Lower Jurassic was studied. The specimen is labelled as Whitbian (= Toarcian) in age and is apparently a derived fossil obtained by dredging the River Nene at Stebbington, Huntingdonshire, England. The tubeworms—*Punctaconchus ampliporus* sp. nov.—are partly decalcified, revealing casts of the pores or punctae that penetrate their walls.

Material and methods

All of the studied material has been registered into the fossil worm collections of the Natural History Museum, London.

After initial study using optical microscopes, selected specimens were examined with a low-vacuum scanning electron microscope (LEO VP-1455). This enabled back-scattered electron imaging of uncoated specimens, including large substrates encrusted by small tubeworms. A few specimens were detached from their substrates using a blade and embedded in epoxy resin. These were either thin sectioned, or polished and etched with 1% acetic acid for a few seconds to enable SEM of skeletal ultrastructures.

Morphology

The striking homeomorphy between microconchids and spirorbid polychaetes is reflected in the frequent misidentification of Ordovician–Jurassic microconchids as *Spirorbis* (Taylor and Vinn 2006). Both groups have small, spirally coiled, calcareous tubes that attach to hard or firm substrates (Fig. 1). Tightness of coiling may vary between species in each group, and the apertures of the tubes sometimes become elevated above the substrate by upward growth during late ontogeny. Mass recruitment in dense aggregations characterises both groups and they very often occur as opportunistic foulers of organic substrates.

Set against these morphological and ecological similarities are contrasts that indicate a radical dissimilarity in the mode of tube formation and betray the different phylum-level affinities of microconchids and spirorbids. Microconchid tubes have a closed origin with a bulb-like initial chamber (Fig. $3A_2$), whereas tubes of spirorbid polychaetes have an open origin without a bulbous initial chamber. The tube ultrastructure of microconchids is microlamellar. In contrast, that of spirorbids usually comprises finely prismatic crystallites that lie in various orientations and are never arranged to form laminae. Microconchids have either pseudopunctate tubes, in which the laminae contain regular inflections, or punctate tubes penetrated by pores up to 20 μm in diameter (Figs. $2A_2$, D, E_2, $3A_3$, $4E_2$). Spirorbids are never pseudopunctate (Taylor and Vinn 2006) and, although the tubes of *Paradexiospira* and some species of the subfamily Januinae may contain pores called alveoli (Rzhavsky 1994), these are much larger than the punctae of microconchids and have rounded edges. There are usually only two lateral rows of alveoli, unlike the punctae in microconchids which are spread evenly over the entire tube surface.

Systematic palaeontology

Class Tentaculita Bouček, 1964

Order Microconchida Weedon, 1991

Genus *Punctaconchus* nov.

Type species: *Punctaconchus ampliporus* sp. nov.

Derivation of the name: Combination of puncta and conch (tubicolous shell).

Species included: *Punctaconchus ampliporus* sp. nov., *P. midfordensis* Richardson, 1907, *P. palmeri* sp. nov.

Diagnosis.—Minute calcitic tubes, planispiral, up to three whorls, dextrally coiled (clockwise), diameter of tube increasing rapidly and evenly, last whorl almost totally enveloping inner whorls, umbilicus narrow. Tube wall microlamellar, penetrated by large, circular or elliptical punctae distributed over entire surface, lamellae deflected outwards around pores. Tube exterior smooth or ornamented by longitudinal or oblique ridges. Tube interior covered by ripplemark-like transverse ridges that bifurcate and may anastomose.

Discussion.—*Punctaconchus* differs from serpulid and spirorbid polychaetes in its microlamellar shell structure, the presence of numerous small pores (punctae) in the tube wall and the closed origin of the tube. The new genus resembles the type species of the Microconchida, *Microconchus carbonarius* Murchison, 1839, in its size, spirally coiled tube, microlamellar structure and punctae. However, it differs in having much larger punctae and an internal surface ornamented by a pattern of ridges resembling ripplemarks. *Punctaconchus* tubes also increase in diameter more rapidly than those of *Microconchus* and the inner whorls are more extensively overlapped by the outer whorls.

The only punctate Mesozoic microconchid hitherto described is *Pseudobrachidium germanicum* Grupe, 1907 from the Late Triassic of Germany (Warth 1982). It differs from the new genus in having much smaller pores, and in this respect resembles *Microconchus*. Unlike *Punctaconchus*, tubes of *Pseudobrachidium* can become uncoiled during late growth stages, as in some *Microconchus*. Indeed, it is possible that *Pseudobrachidium* is a junior synonym of *Microconchus*.

The new genus resembles *Palaeoconchus* Vinn, 2006, and *Annuliconchus* Vinn, 2006, both from the early Palaeozoic of Baltoscandia. However, both of these genera lack punctae and *Annuliconchus* also has an annulated tube. Neither *Palaeoconchus* nor *Annuliconchus* has the distinctive, ripplemark-like tube interiors characteristic of *Punctaconchus*.

Spirorbis midfordensis Richardson, 1907 is reassigned to *Punctaconchus* because of its microlamellar shell structure characteristic of microconchids, the presence of large punctae penetrating the tube wall at regular intervals and the ripplemark-like ornament of the tube interior.

The three species of *Punctaconchus* (*P. ampliporus*, *P. midfordensis,* and *P. palmeri*) can be distinguished using the characters of external ornamentation and porosity. *P. ampliporus* has relatively smooth tubes with large, dense punctae, *P. midfordensis* has tubes with sharp longitudinal striations, and *P. palmeri* tubes have oblique ornamentation in early ontogeny and sparse punctae.

Stratigraphic and geographic range.—Middle Jurassic, Late Aalenian to Late Bathonian of England, and Normandy, France; also questionably occurring in the Early Jurassic, Toarcian of England.

Punctaconchus ampliporus sp.nov.

Figs. 1, 2.

Derivation of the name: In reference to the large (Latin *amplus*) pores (Latin *pori*).

Holotype: NHM A12009(1), tube attached to bivalve shell.

Type locality: Foss Cross Quarry, Gloucestershire, England.

Fig. 1. Microconchid *Punctaconchus ampliporus* sp. nov. Several individuals, including the holotype (NHM A12009; arrowed), encrusting a bivalve shell together with a serpulid, thecidacean brachiopods and a bryozoan. Bathonian, White Limestone Formation, Foss Cross Quarry, Gloucestershire, UK. Scale bar 2 mm.

Type horizon: Middle or Upper Bathonian, *M. morrisi* or *P. hodsoni* zones; Great Oolite Group, White Limestone Formation.

Material.—Holotype: A12009(1). Paratypes: A12009(2)–A12009(13), twelve individuals on same substratum as holotype; AN747, polished, etched section; Other material: AN748–AN757, numerous individuals encrusting other shells from the same locality as the types. AN758, six individuals associated with a paratype of the bryozoan *Reptoclausa porcata* Taylor, 1980 (NHM D7526) and encrusting a brachiopod shell, Upper Aalenian, *L. murchisonae* Zone, Inferior Oolite Group, Birdlip Limestone Formation, Crickley Member, near Stroud, Gloucestershire, England; A7698, more than 50 individuals encrusting a derived pebble dredged from the River Nene at Stebbington, Huntingdonshire, England, and reputedly Toarcian, *Lytoceras jurense* Zone, *Haugia variabilis* Subzone.

Diagnosis.—Tube small, dextrally coiled, cemented to the substrate over its entire length, lacking a free distal part. External surface smooth, evenly pitted by closely spaced, very large punctae. Diameter of tube increasing rapidly and regularly, umbilicus relatively narrow.

Description.—Tube small in size, dextrally coiled (clockwise), containing up to three whorls (Fig. 2A–C). Outline approximately circular. Diameter of tube increasing rapidly and regularly, umbilicus relatively narrow. Broad base of tube cemented to the substrate over its entire length, lacking a free distal portion. Tube external surface smooth, convex, pitted by pores (Fig. $2A_2$), umbilical part moderately sloping, tube aperture subpentagonal, lumen oval in cross section. Tube interior covered by faint ripplemark-like ridges perpendicular to growth direction, numbering about six per 0.1 mm,

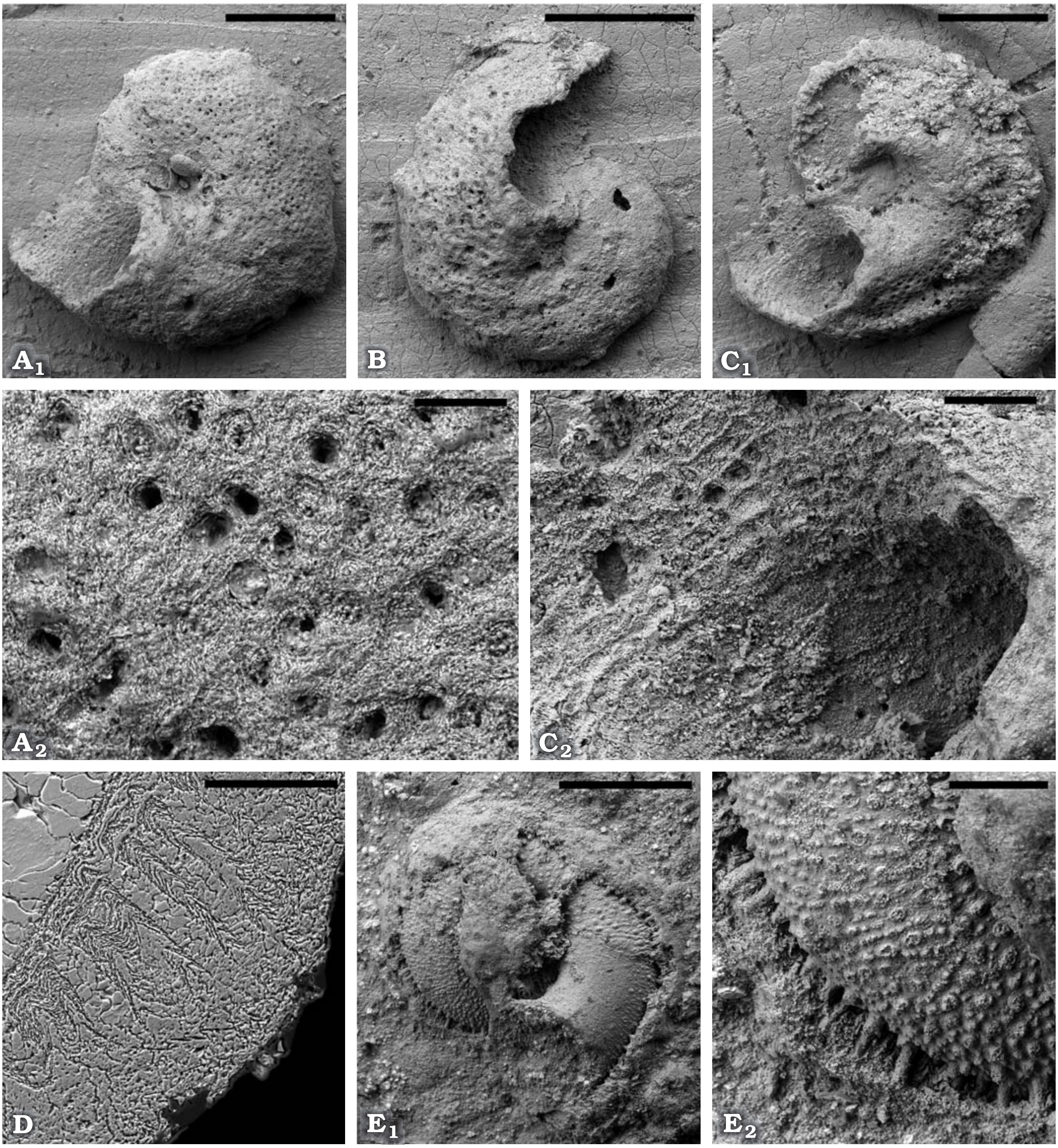

Fig. 2. Microconchid *Punctaconchus ampliporus* sp. nov. Scanning electron micrographs (back-scattered electron images) of uncoated specimens. **A**–**D**. Bathonian, White Limestone Formation, Foss Cross Quarry, Gloucestershire, UK. **A**. Holotype, NHM A12009(1), entire individual (A_1) and detail of tube surface showing pores, many partly infilled (A_2). **B**. Paratype with broken aperture, NHM A12009(2). **C**. Worn paratype, NHM A12009(3), entire individual (C_1) and detail of ornament on tube interior near aperture (C_2). **D**. Paratype, NHM AN747, polished, etched section of tube wall showing large punctae filled by calcite, with wall laminae deflected outwards towards tube exterior (bottom right) around punctae, and coarse diagenetic infill of tube interior (top left). **E**. Toarcian, Stebbington, Huntingdonshire, UK, NHM A7698, corroded specimen (E_1) with natural casts of punctae (E_2). Scale bars 500 μm (A_1, B, C_1, E_1), 100 μm (C_2, E_2), 50 μm (A_2, D).

sometimes bifurcating and anastomising to give a net-like appearance (Fig. 2C_2). Tube wall relatively thick (0.10–0.15 mm), microlamellar. Punctae very large (15–20 μm wide), closely and evenly spaced, distances between neighbouring punctae 10–20 μm (Fig. 2E). Shell laminae deflected outwards by about 5 μm around edges of punctae (Fig. 2D). In longitudinal section wall laminations appear wavy, individual laminae averaging 1.4 μm in thickness.

Dimensions.—Maximum diameter of tubeworm: 1.08–1.65 mm; diameter of aperture: 0.54–0.66 mm. Number of specimens measured: 5.

Discussion.—This new species resembles *Punctaconchus midfordensis* in the size of the tubes and presence of large punctae in the tube walls. However, it differs in having a smooth tube exterior and slightly fainter ridges on the tube interior, as well as more densely packed punctae. The very dense porosity of the tubes of *P. ampliporus* is particularly evident in a specimen (Fig. 2E) in which the punctae have been cast naturally by diagenetic minerals. Whereas the microlamellar tube of the new species appears to be composed of calcite platelets or laths, that of *P. midfordensis* is fibrous (Fig. 3C), although this apparent difference may be diagenetic.

In his description of *Spirorbis midfordensis*, Richardson (1907) mentioned being shown a specimen of the brachiopod *Pseudoglossothyris simplex* from the Pea Grit (Upper Aalenian) encrusted by numerous *Spirorbis*. These are likely to have been *Punctaconcus ampliporus* which is represented at this stratigraphical level in the NHM collections.

Stratigraphic and geographic range.—Middle Jurassic, Late Aalenian–Middle/Late Bathonian of Gloucestershire, England. Questionably Toarcian of Huntingdonshire, England (probably a derived fossil).

Punctaconchus midfordensis (Richardson, 1907)

Fig. 3.

1907 *Spirorbis midfordensis* sp. nov.; Richardson 1907: 435, fig. 7.
2006 *Microconchus midfordensis* (Richardson); Taylor and Vinn 2006: fig. 1F, G.

Material.—NHM A1814–1816 (five specimens, possibly syntypes), Upper Bajocian, *Parkinsonia parkinsoni* Zone, Inferior Oolite Group, Salperton Limestone Formation, *Clypeus* Grit Member (labelled "Bradfordian [Truellii], Upper Coralbed"), road section, Midford, near Bath, Avon (Lindsall Richardson Colln, purchased March 1915). NHM A1817–1819, AN764 (sample), Upper Bajocian, *P. parkinsoni* Zone, Inferior Oolite Group, Salperton Limestone Formation, *Clypeus* Grit Member (labelled "Bradfordian [Truellii], Upper Coralbed"), Worgan's Quarry, near Stroud, Gloucestershire, England (Lindsall Richardson Colln, purchased March 1915). NHM A11925–A11929, eleven specimens, Lower Bajocian, *Witchellia laeviuscula* Zone, Lincolnshire Limestone Formation, Kirton Shale Member, Kirton-in-Lindsey, Lincolnshire, England.

Emended diagnosis.—Tube small, dextrally coiled (clockwise). External surface with strong longitudinal ridges, pitted regularly by large punctae. Internal surface with transverse ridges, sometimes bifurcating, forming a ripplemark-like pattern. Tube diameter increasing rapidly and regularly, umbilicus relatively narrow.

Description.—Tube small, dextrally (clockwise) coiled, comprising up to three whorls (Fig. $3A_1$, B). Outline approximately circular. Tube diameter increasing rapidly and regularly. Umbilicus relatively narrow, moderately sloping. Broad base of tube cemented to the substrate commonly over its entire length but in some specimens the aperture is slightly raised. Tube exterior with sharp, strong longitudinal ridges (10–20 μm wide) spaced 30–100 μm apart, convex, pitted by punctae (Fig. $3A_3$). Aperture subpentagonal to oval, lumen oval in cross section. Tube interior covered with well developed ridges (about four per 0.1 mm) perpendicular to growth direction, sometimes bifurcating, resembling ripplemarks (Fig. 3D). Tube wall relatively thick (0.10–0.15 mm), laminated (Fig. 3E), microstructure comprising fibres 8–13 μm long, 1–2 μm thick and oriented transversely (Fig. 3C). Laminations wavy in longitudinal section, individual laminae about 1.4 μm thick on average. Pores large (12–15 μm wide), spaced 10–20 μm apart. Shell lamellae deflected outwards by 5–7 μm around pores.

Dimensions.—Maximum diameter of tubeworm: 0.90–1.89 mm; diameter of aperture: 0.42–0.81 mm. Number of specimens measured: 9.

Remarks.—*Punctaconchus midfordensis* resembles the Triassic species *Microconchus phlyctaena* Brönnimann and Zaninetti, 1972, but differs in having strongly developed longitudinal ridges and large punctae. All known specimens of this species are detached from their substrates, unlike the other two species of *Punctaconchus* in which all specimens are preserved firmly cemented to hard substrates. The identity of the substrates used by *P. midfordensis* is unknown. Possibilities include plants or soft bodied animals, or alternatively molluscs with aragonitic shells which are typically lost through leaching in these Middle Jurassic carbonates.

Stratigraphic and geographic range.—Middle Jurassic, Lower–Upper Bajocian, Avon, Gloucestershire and Lincolnshire, England.

Punctaconchus palmeri sp. nov.

Fig. 4.

1981 *Spirorbula* sp.; Palmer and Fürsich 1981: 7, pl. 2: 12.

Derivation of the name: After Timothy J. Palmer who, along with Franz T Fürsich, described the palaeoecology of the sponge reefs in which the new species is found.

Holotype: NHM AN759(1), tube attached to bivalve shell.

Type locality: St Aubin-sur-Mer, Calvados, Normandy, France.

Type horizon: Upper Bathonian, *Aulacosphinctes hollandi* Zone; Caillasses de la Basse Ecarde Formation, sponge reefs.

Material.—Holotype: NHM AN759(1). Paratypes: AN759(2)–AN759(7) (six individuals on same substrate as holotype), AN760–762 (22 individuals on three substrates), AN763 (polished and etched section).

Diagnosis.—Tube small, dextrally coiled, cemented to the substrate over its entire length, aperture slightly raised in some specimens. Diameter of the tube increasing rapidly and regularly, umbilicus relatively narrow. External surface with

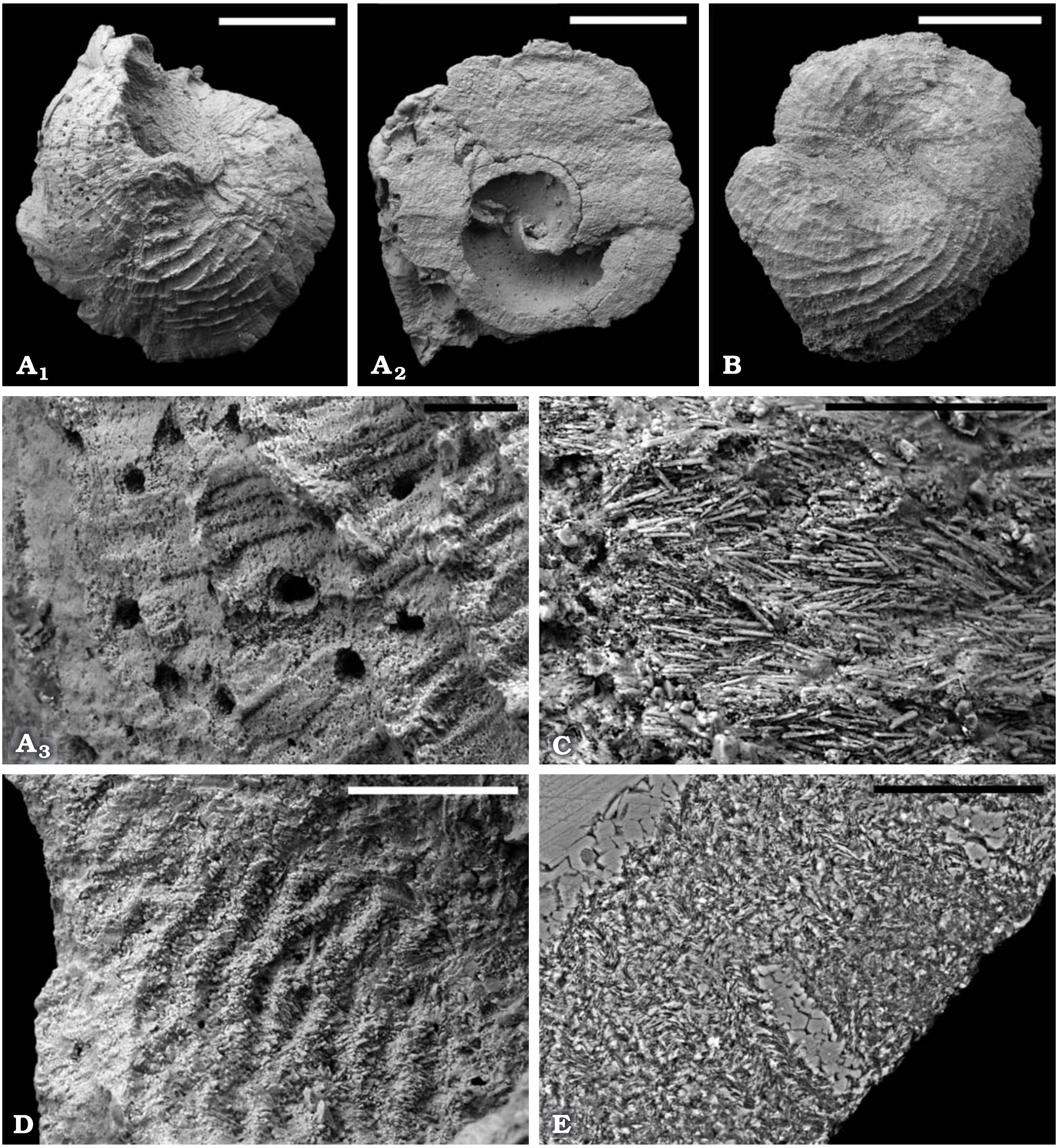

Fig. 3. Microconchid *Punctaconchus midfordensis* (Richardson, 1907). Scanning electron micrographs (back-scattered electron images) of uncoated specimens. **A**, **D**, **E**. Bajocian, *Clypeus* Grit Member, Worgan's Quarry, Gloucestershire, UK. **A**. NHM A1817, detached individual from upper side (A_1) showing longitudinal ridges on tube exterior, underside (A_2) showing closed tube origin exposed by erosion of basal wall, and detail of punctate tube surface (A_3). **D**. NHM A1818, ornament on tube interior near aperture. **E**. NHM A1819, polished, etched section of tube wall showing a few punctae filled by calcite, and diagenetic mineral infilling of tube interior (top left). **B**, **C**. Bajocian, Kirton Shale Member, Kirton-in-Lindsey, Lincolnshire, UK. **B**. NHM A11925, tube with external ornament of longitudinal ridges. **C**. NHM A11926, transversely oriented fibres on tube exterior. Scale bars 500 μm (A_1, A_2, B), 100 μm (D, E), 50 μm (A_3, C).

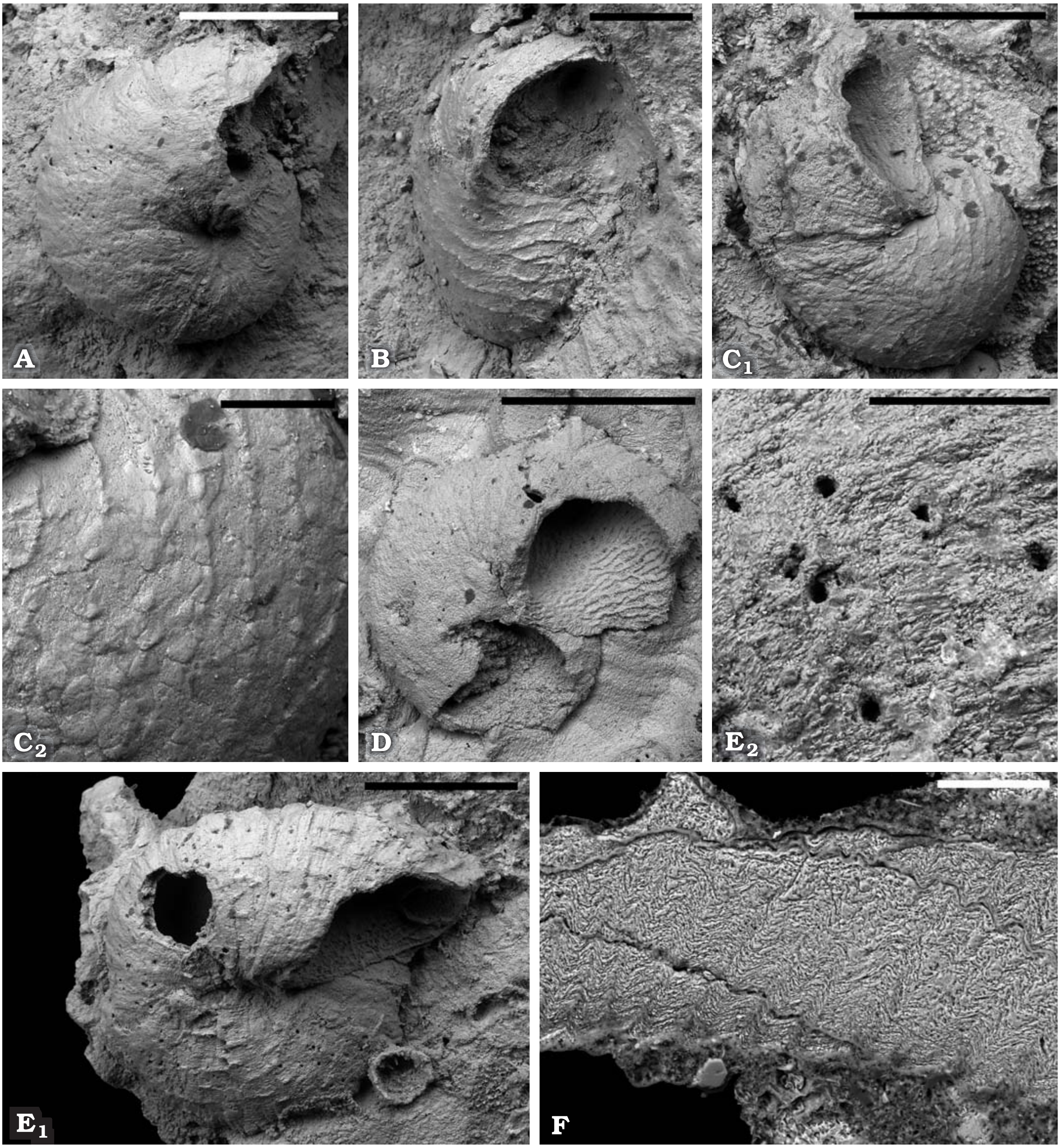

Fig. 4. Microconchid *Punctaconchus palmeri* sp. nov. Scanning electron micrographs (back-scattered electron images) of uncoated specimens. Bathonian, Caillasses de la Basse Ecarde Formation, St Aubin-sur-Mer, Normandy, France. **A**. Holotype, NHM AN759(1). **B**. Paratype, NHM AN759(2), small specimen viewed obliquely to show aperture and ornament on initial whorl. **C**. Paratype, NHM AN760, entire specimen (C_1) and detail of external ornamentation (C_2). **D**. Paratype, NHM AN761, broken tube with ripplemark-like ornament visible on interior of basal wall. **E**. Paratype, NHM AN762, bored individual (E_1) and detail of punctae on tube outer surface (E_2). **F**. Paratype, AN763, polished and etched section of tube wall showing wavy wall lamination and growth increment bounded by deeply etched laminae; tube exterior is at top of image. Scale bars 500 µm (A, C_1, D, E_1), 200 µm (B), 100 µm (C_2, E_2), 50 µm (F).

strong semiperpendicular ridges in juveniles, becoming faint in adults, pitted by transversely elliptical punctae. Tube interior with well developed ripplemark-like ridges transverse to growth direction.

Description.—Tube small, dextrally coiled (clockwise), comprising up to three whorls (Fig. 4A, B, C_1, D, E_1). Outline approximately circular. Tube diameter increasing very rapidly and regularly. Umbilicus relatively narrow, moderately sloping. Broad base of tube cemented to the substrate commonly over its entire length, but in some specimens the aperture is slightly raised. Tube exterior of juveniles (Fig. 4B, C_2) with strong oblique ridges (10 μm wide) spaced 30–40 μm apart, often broken into nodes. Mature specimens externally covered with weakly developed, faint perpendicular ridges, 6–8 per 0.1 mm. Tube convex, sparsely pitted by punctae (5–10 μm wide), transversely elliptical (Fig. 4E). Aperture oval, lumen oval in cross section. Tube interior covered with well developed ripplemark-like ridges (about five per 0.1 mm) perpendicular to growth direction, sometimes bifurcating (Fig. 4D). Tube wall 0.08–0.10 mm thick at the aperture in mature specimens. Lamellae of tube wall wavy (Fig. 4F), reflecting the ripplemark-like ridges on the tube interior, heights of the waves being 5–6 μm. Growth increments mollusc-like in longitudinal sections of tubes (Fig. 4F).

Dimensions—Maximum diameter of tubeworm: 0.66–1.50 mm; diameter of aperture: 0.33–0.66 mm. Number of specimens measured: 10.

Discussion.—*Punctaconchus palmeri* is similar to both *P. ampliporus* and *P. midfordensis* in having punctate tube walls and a ripplemark-like ornament on the interior surface of the tube. It resembles *P. ampliporus* in lacking prominent longitudinal ridges on tube exteriors, but differs in having sparser and much smaller pores and a stronger ripplemark-like ornament on the tube interior. It also differs in showing a more rapid increase in tube diameter. *Punctaconchus palmeri* differs from *P. midfordensis* in lacking prominent longitudinal ridges, and in having sparser and much smaller punctae.

This species was assigned by Palmer and Fürsich (1981) to the genus *Spirorbula* Nielsen, 1931. The original material of *Spirorbula* comes from the Danian of Denmark and comprises two species, *S. cingulata* Nielsen, 1931, and *S. tortilis* Nielsen, 1931, which are either spirorbids or coiled serpulids. They are unrelated to microconchids.

Stratigraphic and geographic range.—Middle Jurassic, Late Bathonian, Calvados, Normandy, France.

Discussion

Small, spirally coiled tubeworms from the Middle Jurassic, previously assigned to the polychaete spirorbid genera *Spirorbis* and *Spirorbula,* are the youngest known examples of the problematical Microconchida, a group that is more common in Palaeozoic and Triassic deposits. Three species are recognized, all assigned to the new genus *Puntaconchus*. In overall morphology, they represent remarkable homeomorphs of spirorbid polychaetes. However, their porous tubes and skeletal microstructure imply a very different mode of growth from that of true spirorbid polychaetes which are first recorded unequivocally from the Cretaceous (Taylor and Vinn 2006). Whereas the tubes of spirorbids are formed from a mucus paste containing calcium carbonate crystallites that is applied episodically around the tube aperture, those of microconchids were apparently formed as continuous secretions from an epithelium that lined the interior of the tube.

The Jurassic microconchid *Punctachonus* differs from its Palaeozoic–Triassic predecessors in having walls with very large pores, contrasting with the imperforate or minutely porous tubes found in older taxa. At least some species of *Punctachonus* have a fibrous tube ultrastructure, a feature not yet recorded among Palaeozoic or Triassic microconchids. Microconchid tubes, by analogy with brachiopods, bryozoans and molluscs, are inferred to have possessed an outer organic layer (periostracum or cuticle). Maintenance of this layer may have been aided by the pores in the calcareous skeleton which would have permitted a direct link between the outer organic layer and the soft tissues of the animal within the tube. The fibrous tube ultrastructure and the large pores probably indicate a high organic content in the skeleton compared to Palaeozoic microconchids that lack pores and possess tabular crystallites with lower surface areas than the fibres of *Punctaconchus*. Thus, the tubes of *Punctaconchus* may have been more flexible and easier to repair in the event of damage.

Punctaconchus is not only the youngest known microconchid, but also the youngest tentaculitoid, a class that includes tentaculitids, cornulitids, and trypanoporids. These vermiform, calcareous tube-building animals flourished in the Palaeozoic and were a distinctive, if minor, component of Palaeozoic marine faunas. Uniquely among tentaculitoids, some microconchids were able to inhabit reduced salinity environments (Taylor and Vinn 2006). The youngest non-marine microconchids are recorded from the Triassic (e.g., Ball 1980). However, the Jurassic genus *Punctaconchus* is known only from marine strata.

More research is needed on Mesozoic tubeworms to determine the timing of the switchover from spirorbiform microconchids to spirorbid polychaetes. The youngest known microconchids, described in this paper, date from the Late Bathonian. None of the supposed spirorbid polychaetes recorded from the pre-Cretaceous seem actually to belong to this group: some are microconchids and others are likely to be spirally coiled serpulids. True spirorbids are, however, present in the Cretaceous, at least as early as the Cenomanian. Therefore, current evidence suggests that there was no overlap in the ranges of spirorbiform microconchids and spirorbid polychaetes, implying extinction of the former group before origination of the latter. It may be notable that, according to the data of Parsch (1956), there is a fivefold increase in the number of spirally coiled serpulid species between the Middle and Upper

Jurassic. This suggests a major diversification of annelid tubeworms immediately after the presumed extinction of spirorbiform microconchids at the end of Middle Jurassic. Ecospace vacated by spirally coiled spirorbiform microconchids could thus have been reoccupied by spirally coiled serpulid polychaetes and eventually by true spirorbids.

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