TEREBELLID POLYCHAETE BURROWS FROM THE LOWER PALAEOZOIC

by A. T. THOMAS *and* M. P. SMITH

ABSTRACT. *Trachyderma*, as established by Phillips for specimens from the Upper Silurian of the Welsh Borderland, was triply preoccupied. Chapman described supposedly congeneric material from the Silurian of Victoria, but that material is generically distinct and *Keilorites* Allan was erected to accommodate it. *Oikobesalon* nom. nov. is erected as a replacement name for *Trachyderma* Phillips, which has been regarded variously as either a body fossil or a trace fossil. Based on its distinctive structure, it is interpreted here as the thin organic lining of a terebellid polychaete dwelling burrow. New illustrations and descriptions are given both of Phillips' original specimens and of *O. citrimorion* from England and Canada. Chapman's material of *Keilorites* is also redescribed to include burrows with a thick sediment wall. Putative gill plumes of *Keilorites* described by Chapman in a later paper are reinterpreted as ichnofossils comparable with certain *Zoophycos*. Unlike typical modern terebellids, the agent responsible for *Oikobesalon* may have been able to produce a new burrow after exhumation, or when required during growth. This capacity explains the morphological contrasts between *Oikobesalon* and previously described terebellid burrows.

THE Much Wenlock Limestone Formation of Wren's Nest (Dudley, West Midlands) is well known for its diverse and well-preserved body fossil biota. The best, articulated, material comes from obrution deposits which occur at certain levels, particularly towards the top of the Nodular Beds Member (see Dorning (1983) for formalization of Butler's (1939) lithostratigraphy). Trace fossils also occur in the formation, but these have been studied less, and none has been formally described. Mr R. Foxall originally brought the Dudley specimen of *Oikobesalon citrimorion* (Pl. 1, figs 2–3) to us for identification, but it remained undetermined until Dr A. W. A. Rushton suggested that it might have affinities with *Keilorites* or *Trachyderma* (= *Oikobesalon* nom. nov.): the latter suggestion proved to be correct. However, study of the type specimens and the related literature revealed a number of problems concerning the interpretation of the material and matters of nomenclature.

The taxa dealt with here have been variously interpreted by previous authors: some have considered body fossils to be represented, others traces. In first describing specimens now referred to *Oikobesalon*, Phillips (1848, p. 331) erected two species of *Trachyderma* to include annelid remains differing from those of serpulids in having a large, long and flexible free external tube or covering which is membraneous or 'coriaceous' (= leathery) rather than calcareous: clearly, Phillips considered his specimens to be ichnofossils. By contrast, Williams (1916, p. 17) thought that he recognized a small head in *T. coriacea*, interpreting that species as a small, but more complete, form of *T. squamosa*, and the latter as an adult lacking the head and tail. Chapman (1910, p. 103) considered his Australian material to be congeneric with Phillips', and interpreted it as the parchment-like tube of a polychaete. It was for this material that the name *Keilorites* Allan, 1927 was erected. Chapman (1919) later reinforced his interpretation by describing what he considered to be the 'gill plumes' of the same animal. Howell (1962, p. W155) dealt with *Keilorites* (*Trachyderma* was not recognized as an independent taxon), and Keiloritidae Allan, 1927, in the section of the *Treatise* dealing with worms, diagnosing those taxa to include worms producing perpendicular or diagonal burrows lined with membraneous material. It is therefore not clear whether Howell regarded *Keilorites* as a body fossil or as a trace. Neither *Trachyderma* nor *Keilorites* was mentioned in the second edition of the *Treatise* dealing with trace fossils (Häntzschel

1975), presumably because they were believed to be body fossils. Brood (1980, p. 279) considered *Keilorites* to represent the mucous tube of a sedentary annelid. Study of the type material of both taxa, and its re-interpretation in the context of comparable Pleistocene and Recent specimens, demonstates unequivocally that they are ichnofossils.

TERMINOLOGY

For convenience, the term 'lining' is used here in a restricted sense to refer to the layer of organic material forming the burrow wall in *Oikobesalon*. 'Wall' is used to refer to the construct of sediment externally bounding *Keilorites* burrows. Simple excavated burrows, where no construction has occurred at burrow boundaries, are termed 'unwalled'. See Keighley and Pickerill (1994, p. 306) for a general discussion of burrow terminology.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus OIKOBESALON nom. nov. [*pro* TRACHYDERMA Phillips, 1848]

*non*1829	*Trachyderma* Latreille, p. 7 [a coleopteran].
*non*1829	*Trachyderma* Gravenhorst, p. 283 [a hymenopteran].
*non*1829	*Trachyderma* Wiegmann, p. 421 [a reptile].

Derivation of name. From the Greek '*oikos*', house and '*besalon*', brick; alluding to the inferred method of burrow formation. Neuter gender.

Remarks. Phillips (1848, p. 331) proposed the genus *Trachyderma* for *T. coriacea* and *T. squamosa* from the Ludlow of the Welsh Borderland. Chapman (1910, p. 102) described supposedly congeneric material from the Silurian of Victoria, Australia, assigning his material to the new species *T. crassituba* and to *T.* cf. *squamosa*. Allan (1927, p. 240) noted that the name *Trachyderma* was a junior homonym on three counts: the senior homonym (see also Wiegmann (1834, pp. 7, 23); Sherborn (1932, p. 6554)) was used by Latreille (1829) for a genus of Coleoptera. Allan (1927) considered Phillips' and Chapman's specimens to be congeneric and this has been followed by most subsequent authors (e.g. Howell 1962, p. W155; Brood 1980, p. 279). Re-examination of Phillips' and Chapman's types, however, indicates that they are not.

Both of Phillips' species comprise elongate tubes, at least partly sediment-filled, but with a thin black lining of carbonized organic material preserved locally (e.g. Pl. 2, fig. 3). The outer surfaces of the specimens show transversely fusiform wrinkles. On relatively unweathered specimens, fine, sometimes bifurcating extensions of the organic layer extend outwards into the sediment. These extensions are orientated at right angles to the tube axis (Pl. 2, fig. 3). By contrast, Chapman's specimens have a thick sediment wall (Pl. 2, figs 1–2, 8) and, although some are transversely corrugated externally, they lack an organic lining with fusiform markings, and there is no trace of fine lateral projections into the surrounding sediment. These differences are here regarded as sufficient to justify separate ichnogenera.

Ichnopecies included. O. coriaceum Phillips, 1848; *O. citrimorion* sp. nov.; *O. liljevalli* (Brood, 1980); *O. squamosum* Phillips, 1848; *O.* cf. *squamosum* Phillips (of Brood 1980).

'*Type*' *ichnospecies.* The *Code* of the ICZN states that genus-group ichnotaxa do not require a type species and that any type designation should be disregarded [Articles 42(b), 67(m); Ride *et al.* (1985)]. This has not been followed universally [e.g. Keighley and Pickerell (1994)], however, because ichnologists can find the concept of a type species just as useful as those who study body fossils. The following notes concerning the 'type' species of *Oikobesalon* are included should the relevant articles be changed in the future.

Following Allan's (1927, p. 240) erection of *Keilorites* for *Trachyderma sensu* Chapman, Bather (1927, p. 286) nominated *T. squamosa* as the type species of *Trachyderma* Phillips. However, Williams (1916, p. 17) had implicitly selected *Trachyderma coriacea* as the type species of the genus (ICZN Article 69a iv), a selection overlooked by subsequent authors.

Diagnosis. Burrow (up to 30 mm across in compressed specimens studied) with thin organic lining. Locally, lining is linearly thickened to define transverse fusiform bands. Marginally, branched extensions of organic material extend outwards into the sediment from the thickened zones.

Remarks. It is the structure of the lining that is particularly characteristic of *Oikobesalon*. No other ichnogenus possesses an organic lining of fusiform construction, while lacking a differentiated sedimentary wall. On the basis of Gotland material, Brood (1980, fig. 3, p. 281) reconstructed *Oikobesalon* as blind-ended and J-shaped. None of our specimens is complete, so we do not know if that shape is characteristic of the ichnogenus. We regard the lining structure as more significant than overall shape, however, because burrows thought to have been produced by similar means vary considerably in gross morphology. Like Brood's material, none of our specimens shows any indication of branching, so we are satisfied that an unbranched morphology is typical of *Oikobesalon*.

In his reconstruction of the burrow, Brood (fig. 3, p. 281) did not show the characteristic fine extensions of the organic layer into the surrounding sediment, though these are very clear in his photographs (figs 1A, E, 2A–B). Brood also argued that the lining of *O. liljevalli* was vesicular close to its blind end. The absence of such structures from our specimens could be due to their fragmentary condition.

The morphology of the organic lining, and its likely mechanism of formation, are discussed separately below.

Distribution. Lower Cambrian, Oxfordshire; Wenlock and Ludlow series of the Welsh Borderland, Gotland and Ontario.

On the assumption of the synonymy of *Trachyderma* Phillips and *Keilorites*, *Oikobesalon* has been widely reported from sedimentary rocks ranging from Cambrian to Silurian in age: few published records seemingly refer to material closely resembling Phillips' species, however. In an early detailed discussion of *Trachyderma*, Williams (1916, pp. 17–18) noted the organic lining and fusiform bands of *T. coriacea* and indicated their absence from many species referred by him to the genus. We have not attempted a monographic revision of the ichnogenus, but faunal lists (e.g. Holland *et al.* 1963, p. 156) suggest that it is widely distributed in the regressive Ludfordian facies of the Welsh Borderland. The only non-Silurian specimen we have studied which is certainly referable to *Oikobesalon* is BGS BDF9523 (Pl. 1, fig. 5), from the Lower Cambrian of the Withycombe Farm Borehole, Oxfordshire.

Oikobesalon coriaceum Phillips, 1848

Plate 1, figures 1, 4; Text-figure 1A–C

1839	*Serpulites longissimus* Sowerby, *in* Murchison, p. 608, pl. 5, fig. 1.	
v*.1848	*Trachyderma coriacea* Phillips, pp. 230, 331, pl. 4, figs 1–2.	
1888	*Trachyderma coriacea* Phill.; Etheridge, p. 37 [list].	
1910	*T. coriacea* Phillips; Chapman, p. 316.	
1916	*Trachyderma coriacea* Phillips; Williams, p. 17.	
v.1938	*Trachyderma coriacea* Phillips; Stubblefield, p. 30 [referred to *Keilorites*?].	

Type material. T. coriacea is based on two figured syntypes, both from the 'Upper Ludlow' (= Whitcliffe Beds) of Hillside Farm, Woodbury Hill, Abberley district, Hereford and Worcester. BGS GSM38370 (Pl. 1, fig. 1; Text-fig. 1B) compares quite closely with the original illustrations (Phillips 1848, pl. 4, fig. 2–2a), and this specimen is here selected as lectotype. Stubblefield identified BGS GSM38369 as the second figured syntype. That specimen is a slab with numerous fragmentary specimens, none of which resembles Phillips' plate 4, figure 1, although the lithology suggests that the provenance is correct. Mr S. P. Tunnicliff informs us that the

specimen can be traced back to the 1865 BGS catalogue, where it bears a tablet number adjacent to that for GSM38370. This is good circumstantial evidence that GSM38369 was available to Phillips, and may well have formed part of the type series, but we doubt that the slab includes the figured syntype. The paralectotype status of the material is therefore subject to some doubt. Phillips' collection includes additional specimens (BGS GSM105335–105337) from the type locality. These may also be paralectotypes but, again, none matches his plate 4, figure 1.

Other material. BGS GSM661, block with numerous specimens, 'Upper Ludlow (Downton Passage Beds)' (presumably = Whitcliffe Beds/Downton Castle Sandstone transition), north of Chances Pitch, Malvern area. BGS GSM105333; Whitcliffe Beds, Whitcliffe, Ludlow.

Description. Specimens 2·8–4·9 mm wide, and preserved as internal and external moulds in brown weathering, decalcified siltstone. All lie parallel to bedding and are interpreted as exhumed fragments. Most are straight or only gently curved, but occasional specimens are flexed more strongly. The specimens are crossed transversely by fine lines delimiting fusiform bands. These lines occur as sharp negative impressions on external moulds, and as slightly more round-topped positive features on internal ones. Hence they apparently represent places where the original organic lining, now largely weathered away, was thicker. Counting along the longitudinal mid-line, 20–24 bands occur in 10 mm. Disruption of the bands in strongly flexed specimens (Text-fig. 1A, C) implies breakage. The maximum sagittal length of the bands remains essentially constant across the size range of material studied. Locally, at specimen margins, branched extensions of organic material extend outwards into the sediment from the thickened zones (Text-fig. 1C). There, the extensions are seen in section: in three dimensions, they would form transversely orientated flanges.

Remarks. The exhumed nature of the specimens implies that the *Oikobesalon* tube was quite robust when fresh. Breakage of the strongly flexed specimens suggests significant rigidity. See below for comparisons with other species.

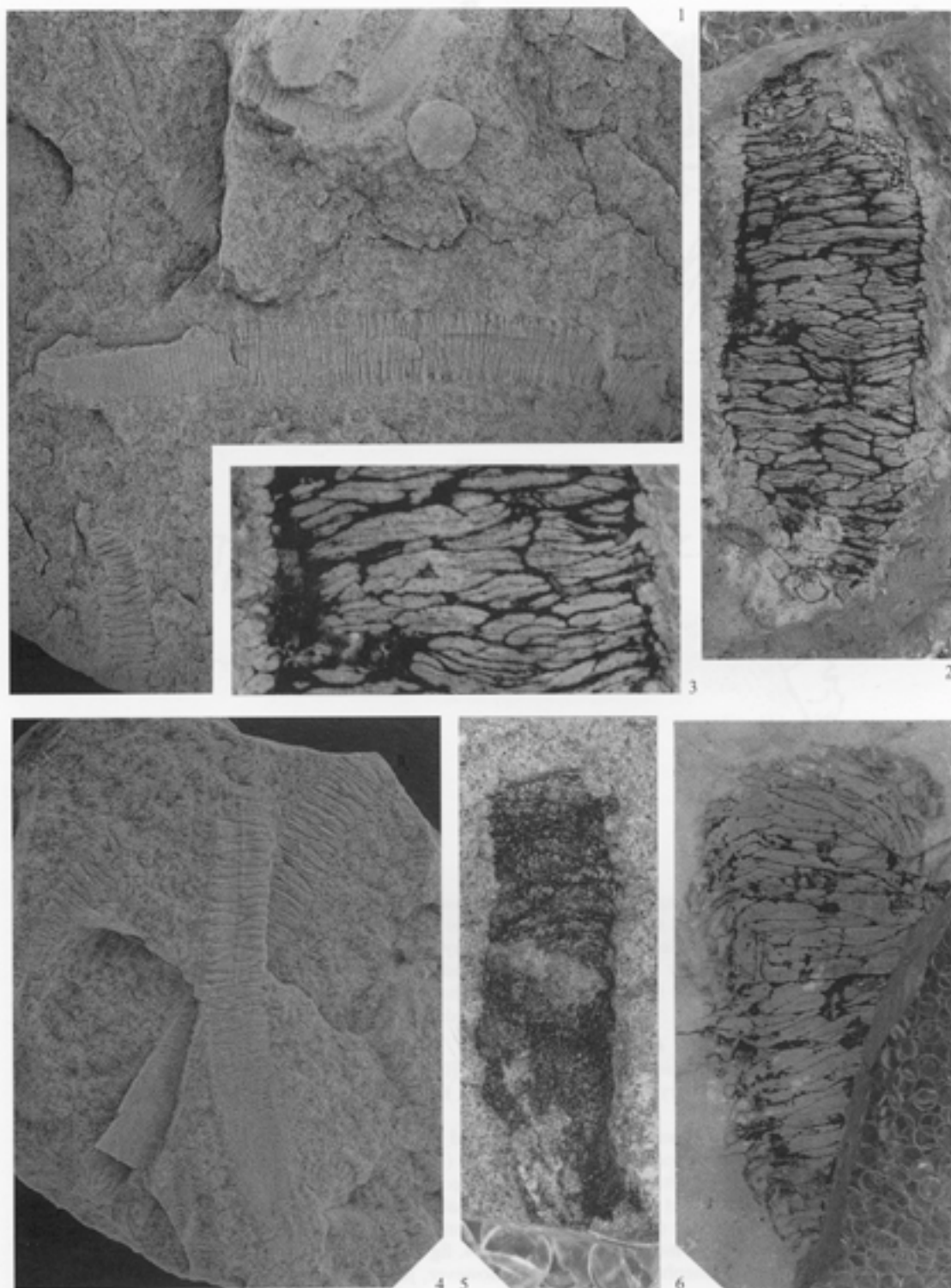## *Oikobesalon squamosum* Phillips, 1848

Plate 2, figures 3–4

| v*.1848 | *Trachyderma squamosa* Phillips, pp. 230, 332, pl. 4, figs 3–4. |
non 1888	*Trachyderma* (*squamosae* Phill. aff.); Lindström, p. 6 [= *O. liljevalli*].
v non 1910	*Trachyderma* cf. *squamosa* Phillips; Chapman, p. 104, pl. 27, fig. 5 [burrow possesses neither an organic lining nor a thick sediment one].
1927	*T. squamosa* Phillips; Allan, p. 286.
v.1938	*Trachyderma squamosa* Phillips; Stubblefield, p. 32 [referred to *Keilorites*?].
non 1979	*K. squamosus* Phillips; Brood, p. 252 [= *O. liljevalli*].

Type material. Bather (1927, p. 286) selected BGS GSM38371 (figured Phillips 1848, pl. 4, fig. 3), from the Upper Ludlow (presumably Whitcliffe Beds) of Gorstley (common north-east of Linton), Hereford and

---

EXPLANATION OF PLATE 1

Figs 1, 4. *Oikobesalon coriaceum* Phillips, 1848; Whitcliffe Beds, Hillside Farm, Woodbury Hill, Abberley district, Hereford and Worcester. 1, lectotype, BGS GSM38370. 4, possible paralectotype, BGS GSM105335. Both ×2.

Figs 2–3, 6. *Oikobesalon citrimorion* sp. nov. 2–3, holotype, DUDMG G14076; loose block from Nodular Beds Member of Much Wenlock Limestone Formation (Wenlock, Homerian), Wren's Nest Inlier, Dudley, West Midlands; ×1·5 and ×3 6, paratype, NHM P6938; Niagara Group (Wenlock), Ontario, Canada; ×1·5.

Fig. 5. *Oikobesalon* sp. indet.; BGS BDF9523; Lower Cambrian, Withycombe Farm Borehole, Oxfordshire; ×4.

Specimens shown in figs 1 and 4 whitened with ammonium chloride sublimate; other specimens photographed under alcohol.

PLATE 1

THOMAS and SMITH, *Oikobesalon*
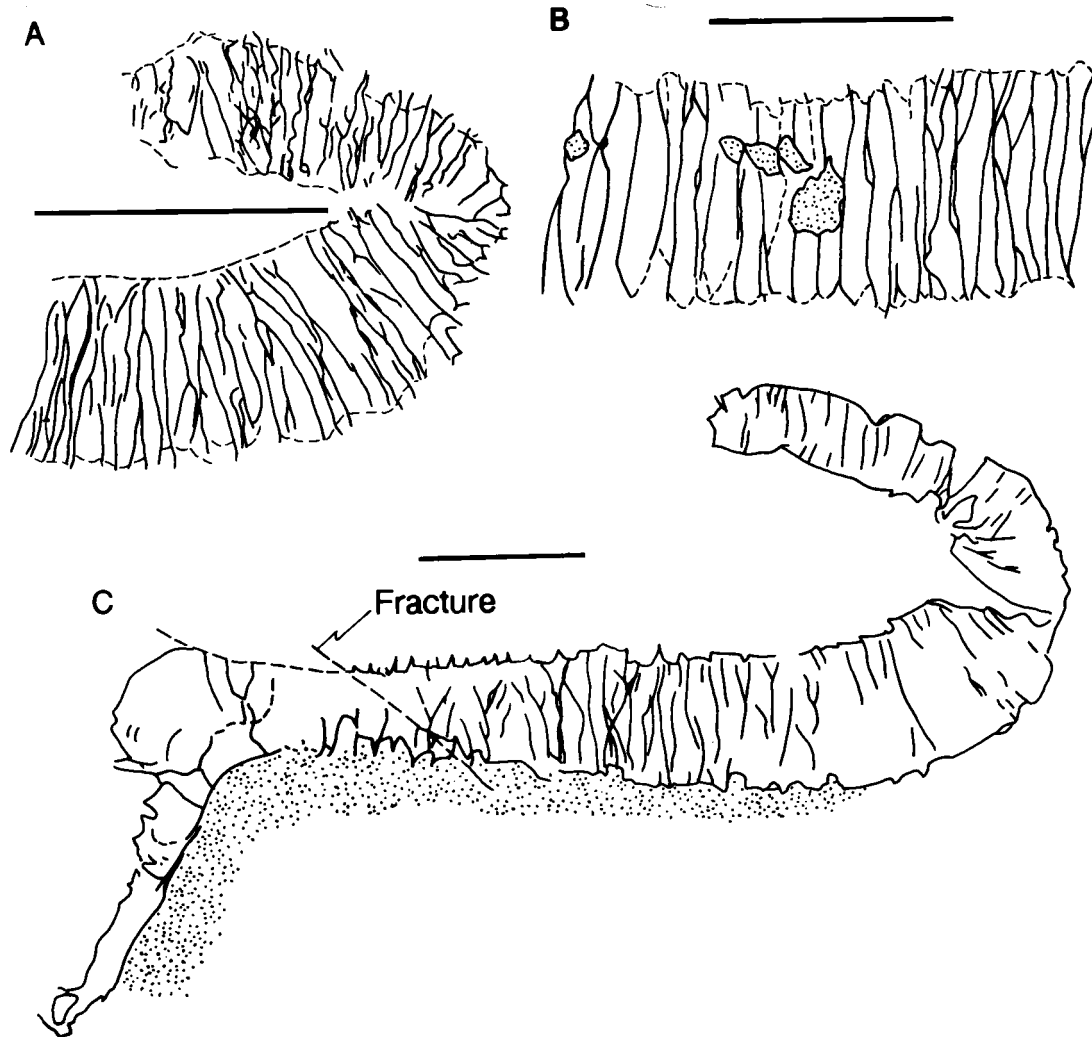
TEXT-FIG. 1. *Camera lucida* drawings of *Oikobesalon coriaceum* Phillips, 1848. A, C, two probable paralectotype specimens on BGS GSM661; note the disrupted banding on the right side of A, suggesting breakage of the tube during flexure, and the lateral extensions of the organic layer preserved locally in C. The spinose structure at the left of C is at a slightly higher level in the sediment and probably represents a fortuitously superimposed fragment. B, portion of lectotype (BGS GSM38370) to show fusiform banding. Scale bars represent 5 mm; stippling indicates sediment cover.

Worcester, as lectotype of *T. squamosa*. BGS GSM38372 (figured Phillips 1848, pl. 4, fig. 4), from the Upper Ludlow, Hillside Farm, Woodbury Hill, Abberley district, Hereford and Worcester, is thus the paralectotype.

Description. The following is based on the lectotype, and focuses on comparisons with *O. coriaceum*. The specimen is much less strongly compressed, having an oval (*c.* 4 × 10 mm) cross section, reflecting preservation in a more competent calcareous siltstone [uncompressed specimens of an *Oikobesalon* species (Pl. 3, fig. 4), from the Ludlow of Ireland, show that the burrow was originally circular in cross section]. Transverse fusiform annulations are apparent, but are difficult to measure. Along the mid-line, and parallel to the tube axis, band width ranges between *c.* 0·5–1·0 mm. Phillips (1848, pl. 4, fig. 3) reconstructed the lectotype as comprising a single burrow shaped like a shepherd's crook. It is, however, just as likely that two separate specimens are

represented on the slab (Pl. 2, figs 3–4). The carbonized lining is more extensively preserved, and lateral extensions into the sediment are seen locally (see arrowed area on Pl. 2, fig. 3). The paralectotype shows a thin carbonized lining, with fine transverse wrinkles on the external mould (Pl. 2, fig. 7), but these are finer, much more closely spaced than in the lectotype, and are not clearly fusiform in shape.

Remarks. Because of the contrasts described, we consider it unlikely that the lectotype and paralectotype are congeneric, and therefore base our conception of the ichnotaxon on the former specimen.

O. squamosum differs from *coriaceum* in its greater tube width and coarser-scale transverse banding. It is possible that only a single ichnospecies is represented, and that these contrasts simply reflect differences in the size of the producing organism. Because of the preservational contrasts and the nomenclatural confusion which has surrounded these taxa in the past, we think it prudent to defer the question of possible synonymy until more material of *squamosum* becomes available.

O. liljevalli, from the Wenlock (Högklint Formation and Slite Group) of Gotland, is known from better, and more completely preserved, material. It resembles *squamosum* in overall dimensions. Brood (1980, p. 280) distinguished *liljevalli* by its thicker lining and by the presence of large sediment-filled vesicles posteriorly. Both these contrasts could be due to differences in quality and completeness of preservation, however. Those specimens recorded as *Keilorites* cf. *squamosus* (Brood p. 281, figs 1A, 4), from the Ludlow (Hemse Group) of Gotland, more closely resemble the lectotype of *squamosum* in preservation. The transverse extensions of the organic lining are longer in the Gotland specimens but, again, this could be attributed to more complete preservation.

Oikobesalon citrimorion sp. nov.

Plate 1, figures 2–3, 6; Text-figure 3D

Derivation of name. From the Latin '*citrinus*', of citron, and Greek '*morion*', piece or portion; fancied resemblance between the holotype (Pl. 1, fig. 2) and a grapefruit or orange segment. Noun in apposition.

Material. Holotype, DUDMG G14076; loose block from Nodular Beds Member of Much Wenlock Limestone Formation, Wren's Nest Inlier, Dudley, West Midlands. Paratype, NHM P6938; Niagara Group (Wenlock), Ontario, Canada.

Description. The British specimen (Pl. 1, figs 2–3) is approximately 20 mm wide. This is likely to approximate to the original tube diameter (Briggs and Williams 1981). Large-scale fusiform bands occur; these have a maximum length of 1·6–1·7 mm measured parallel to the tube axis. Each of these larger bands includes smaller-scale components, also transversely fusiform in shape and typically 5–8 mm wide. The Canadian specimen is slightly more weathered, but is similar in all essential respects. Its maximum width is c. 30 mm, with larger-scale fusiform bands 1·6–3·2 mm long. Again, these contain traces of finer-scale banding within.

Remarks. These specimens are substantially bigger than any of those assigned to previously described *Oikobesalon* ichnospecies: this probably accounts for the larger scale banding. However, specimens of *O. citrimorion* are distinguished by having the larger bands made up of smaller-scale subunits.

Ichnogenus KEILORITES Allan, 1927

Remarks. Allan (1927, p. 240) erected the genus *Keilorites*, with *Trachyderma crassituba* Chapman as type, and included it within his family Keiloritidae. Bather (1927, p. 286) questioned whether *Keilorites* was intended for the Australian material alone or for all specimens previously referred to *Trachyderma* Phillips. However, a straightforward reading of Allan's (1927) note indicates that he based his taxon on the Australian species and not the English specimens. The main purpose of this paper is to clarify the morphology and nomenclature of *Oikobesalon*. We therefore redescribe and diagnose *Keilorites* on the basis of the original material, without attempting a comprehensive revision of the ichnogenus.

Diagnosis. Unbranched, J-shaped burrow, with thick sediment wall. Transverse rugations present externally.

Keilorites crassitubus (Chapman, 1910)

Plate 2, figures 1-2, 8-9

v*p.1910   *Trachyderma crassituba* Chapman, p. 103, pl. 27, figs 1a-b, 2-3, *non* pl. 29, fig. 1 [= unwalled burrow].

1927   *Trachyderma crassituba* Chapman; Allan, p. 240 [referred to *Keilorites*].

1927   *T. crassituba* Chapman; Bather, p. 286.

Type material. Holotype specimen broken into two portions (Pl. 2, figs 8-9), NMV P10330–P10331 (figured Chapman 1910, pl. 27, fig. 1a-b); Yarra improvement works, South Yarra. Paratypes: NMV P10333 (Pl. 2, fig. 2), between Hoyte's Paddock and Punt Road, South Yarra; P10332 (Pl. 2, fig. 1), P10343 (Pl. 2, fig. 10), type locality; respectively figured Chapman (1910, pl. 27, figs 2-4; pl. 29, fig. 1). All from Melbourne Formation (Lower Ludlow, *nilssoni* graptolite Biozone), excavations along Yarra River, South Yarra, 2-3 km east of Melbourne city centre, Victoria.

Description. The holotype is shaped overall like a reclining J, with a short vertical tube and a longer horizontal one. The tube is circular in cross section, with a maximum diameter of about 17 mm. The holotype and two paratypes show a distinct sediment wall, < 5 mm thick in the holotype (Pl. 2, figs 1-2, 8). Another paratype differs in being unlined (Pl. 2, fig. 10). Externally, the tube surface bears coarse and irregular transverse rugations (Pl. 2, fig. 9).

Remarks. The lack of a sediment wall suggests that one paratype belongs to a different ichnospecies from the remainder of the type series. Material compared by Chapman (1919, p. 317) with *K. crassitubus* and by Chapman (1910, p. 104) with *O. squamosum* (Pl. 2, figs 5-6, 11) similarly shows neither sediment wall nor organic lining, and we would not assign these specimens to either ichnogenus. Chapman (1910, p. 104) noted the absence of a wall in some of his specimens, attributing this to dissolution of a tube wall that he regarded as originally membraneous and compressible. When present, the burrow wall is clearly composed of sediment, so this explanation is incorrect.

EXPLANATION OF PLATE 2

Figs 1-2, 8-9. *Keilorites crassitubus* (Chapman, 1910); Melbourne Formation (Lower Ludlow, *nilssoni* graptolite Biozone), excavations along Yarra River, South Yarra, 2-3 km east of Melbourne city centre, Victoria. 1, paratype, NMV P10332; Yarra improvements, South Yarra; ×2. 2, paratype NMV P10333; between Hoyte's Paddock and Punt Road, South Yarra; ×2. 8-9, holotype (broken into two portions) NMV P10330–P10331; locality as fig. 1. 8, dorsal view of the vertical portion of the burrow and the proximal part of the horizontal portion. 9, ventral view of the horizontal portion of the tube; triangular section of wall at top left corresponds with triangular exfoliated section at bottom right of fig. 8. Both ×1·5.

Figs 3-4. *Oikobesalon squamosum* Phillips, 1848; lectotype, BGS GSM38371; Upper Ludlow, Gorstley (common north-east of Linton), Hereford and Worcester; ×1. Arrow in fig. 3 points to lateral extensions of organic lining.

Figs 5-6, 10-11. Unassigned unwalled burrows. 5-6, NMV P10334 (*Trachyderma* cf. *squamosa* of Chapman 1910, pl. 27, fig. 5); Humevale Formation (Lower Devonian), junction of Woori Yallock Creek and Yarra River, c. 50 km east of Melbourne city centre; ×1·5. 10, NMV P10343 (paratype of *T. crassituba* Chapman); Melbourne Formation (Lower Ludlow, *nilssoni* graptolite Biozone), Yarra improvements, South Yarra, excavations along Yarra River, 2-3 km east of Melbourne city centre, Victoria; ×1·5. 11, NMV P10335 (*T.* cf. *crassituba* of Chapman 1910, pl. 27, fig. 4); locality as fig. 10; ×2.

Fig. 7. Unassigned burrow with carbonized lining; BGS GSM38372 (paralectotype of *O. squamosum*); Upper Ludlow, Hillside Farm, Woodbury Hill, Abberley district, Hereford and Worcester; ×2.

Specimen shown in fig. 3 photographed under alcohol; other specimens whitened with ammonium chloride sublimate.

PLATE 2
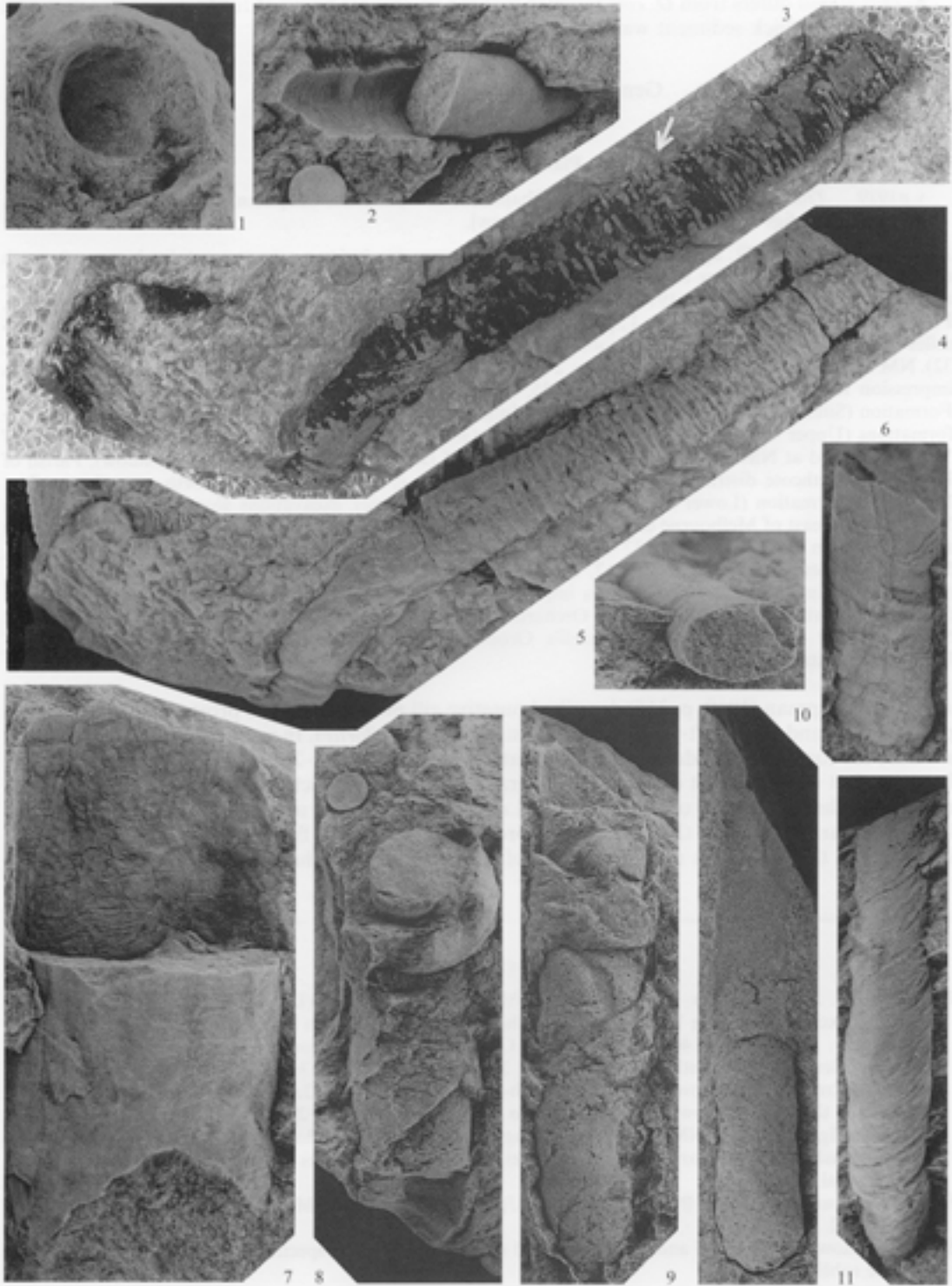
THOMAS and SMITH, *Keilorites*, *Oikobesalon*, unassigned burrows

K. crassitubus differs from *O. coriaceum* in lacking an organic lining of fusiform construction and in possessing a thick sediment wall.

Genus ZOOPHYCOS Massalongo, 1855?

Zoophycos? sp.

Plate 3, figures 1–3, 5–7

v.p1919   *Trachyderma*, sp. cf. *crassituba*, Chapm., *et alii specierum* Chapman, p. 317, pl. 13, figs 1–3, pl. 14, figs 6–12, *non* fig. 5 [tubular burrow].

Material. NMV P140079; Springfield Formation (Llandovery, *turriculatus–crispus* graptolite biozones), north of eastern end of old Keilor township reserve, Maribyrnong River, Keilor district. NMV P13118–P13119, respectively figured Chapman (1919, pl. 14, figs 6, 10), P13120 (Chapman 1919, pl. 13, fig. 2; pl. 14, fig. 7), P13121 (Chapman 1919, pl. 13, fig. 1; pl. 14, fig. 11); Deep Creek Siltstone (Llandovery), Jackson's Creek, 4 miles (6·4 km) north-west of Keilor (probably James's worm impression locality; see James 1920, p. 330, pl. 32). NMV P58214, P140076; same section, *c.* 2 km downstream (east south-east) of Organ Pipes (James's worm impression locality), Sydenham. NMV P13135, figured Chapman (1919, pl. 14, fig. 5); Anderson Creek Formation (Silurian), near Scotchman's Creek, Mulgrave. NMV P140081; Anderson's Creek or Melbourne formations (Upper Wenlock–Lower Ludlow), Plenty Gorge, south of Morang. GSV (Geological Survey of Victoria, housed at NMV) 38945; probably lower part of Dargile Formation (Wenlock–Ludlow), Parish of Redcastle, Heathcote district, central Victoria, mine dumps *c.* 1 mile (*c.* 1·6 km) north-east of township. Melbourne Formation (Lower Ludlow, *nilssoni* graptolite Biozone), excavations along Yarra River, South Yarra, 2–3 km east of Melbourne city centre: NMV P58217–P58218, P58229–P58230, (103 feet (31 m) below surface, Domain Road sewer); P13122–P13123, figured Chapman (1919, pl. 14, figs 9, 8), (Domain Road sewer, South Yarra Sewerage Works); P13117, figured Chapman (1919, pl. 13, fig. 3; pl. 14, fig. 12), P58242, (Hawthorn main drain); P140082, (Yarra improvements); P140080, P58237, (Melbourne district). Silurian (exact age uncertain): P140077 (Russell's Orchard, 1¼ miles (2 km) north-north-east of Langwarrin (railway) Station, Keilor district); P140078 (Russell's Ground, pipetrack 1½ miles (2·4 km) north-north-east of Langwarrin Station).

Remarks. Chapman (1919, p. 315) described putative gill plumes (cephalic prostomial appendages), possible eyes, and other soft-part structures, attributed to *Keilorites*. In most specimens that we have studied, the fossils appear darker than the matrix (e.g. Pl. 3, figs 1–2, 5). They are not carbonized, however, but rather consist of darker, finer grained, sediment, which contrasts with the paler host material. Other specimens occur in bleached sediment, and these are paler than the background instead of darker. Most of the material is more-or-less completely flattened, but relief is preserved in some and this facilitates reinterpretation of the specimens as ichnofossils.

EXPLANATION OF PLATE 3

Figs 1–3, 5–7. *Zoophycos*? sp. indet. 1, P58242; Melbourne Formation (Lower Ludlow, *nilssoni* graptolite Biozone), excavations along Yarra River (Hawthorn main drain), South Yarra, 2–3 km east of Melbourne city centre; ×2. 2, NMV140081; Anderson's Creek or Melbourne formation (Upper Wenlock–Lower Ludlow), Plenty Gorge, south of Morang; ×1. 3, 7, NMV P140076; Deep Creek Siltstone (Llandovery), Jackson's Creek, *c.* 2 km downstrean (east-north-east) of Organ Pipes (James's worm impression locality), Sydenham; the main burrow is interpreted as a hypichnial ridge; ×1·25. 5, NMV P13117; locality and horizon as fig. 1; ×1·5. 6, NMV P140079; Springfield Sandstone (Llandovery), north of eastern end of old Keilor township reserve, Maribyrnong River, Keilor district; the grooves are interpreted as natural moulds of hypichnial ridges; ×2.

Fig. 4. *Oikobesalon* sp. indet.; BGS GSM105334; Upper Ludlow, Croagh Martin, Doonquin, Dingle, western Ireland; ×2.

Specimens shown in figs 1–2, 5 and 7 photographed under alcohol; other specimens whitened with ammonium chloride sublimate.

PLATE 3
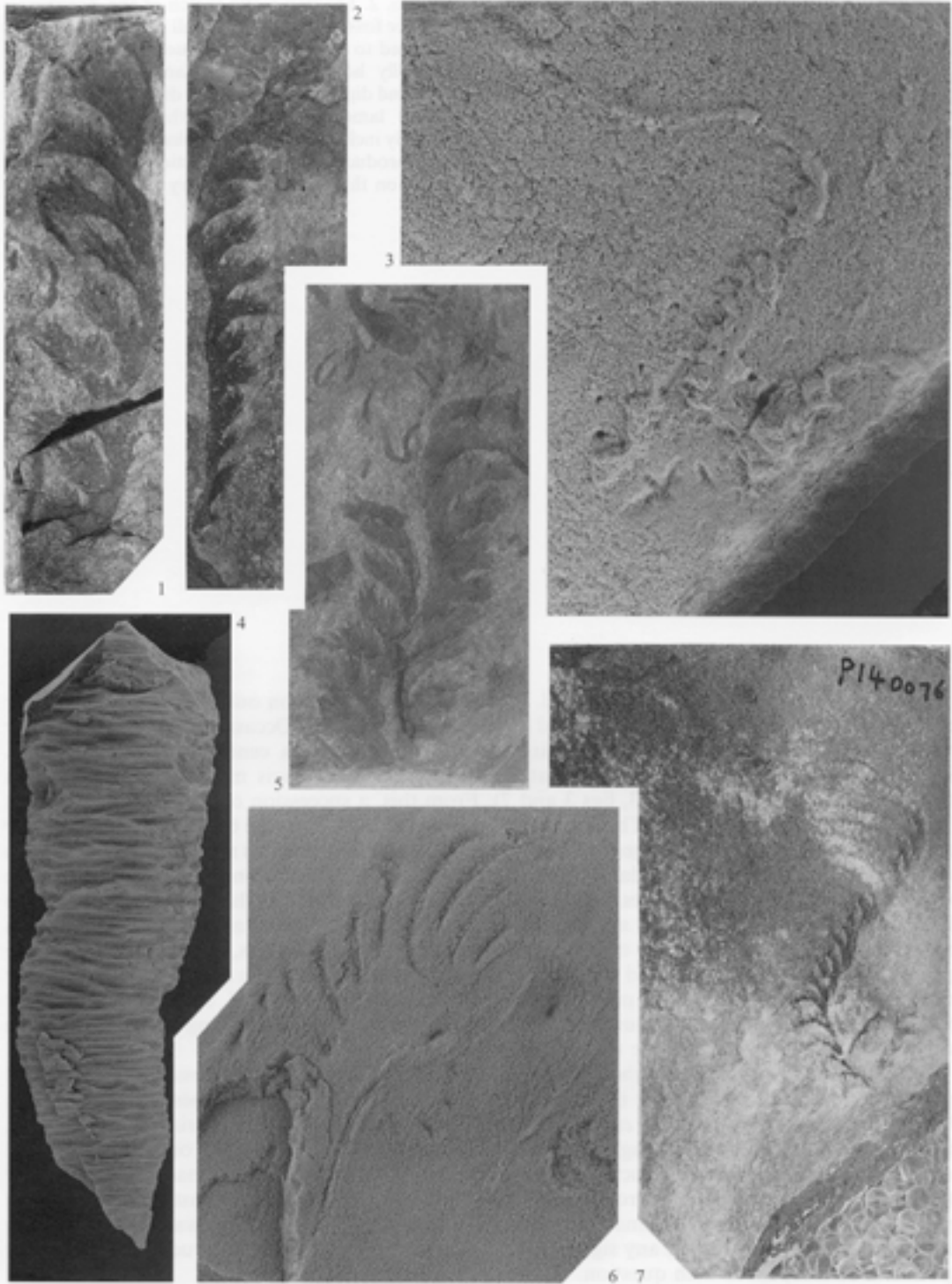
THOMAS and SMITH, *Zoophycos?, Oikobesalon*
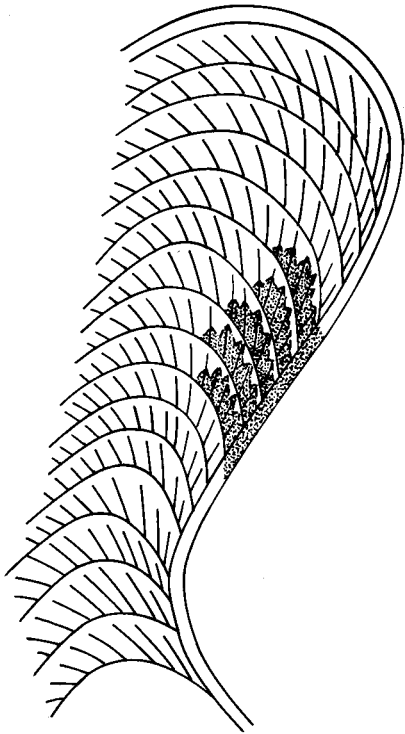
TEXT-FIG. 2. Diagrammatic sketch of the *Zoophycos*-like trace fossil producing the 'gill plumes' previously attributed to *Keilorites*. The sinuous main burrow is essentially horizontal. Major lamellae extend leftwards and dip gently in the same direction. Secondary (minor) lamellae arise from these and are also obliquely inclined. The fine stippled area indicates the shape produced by the intersection of a horizontal surface on this complex geometry of dipping planes.

The 'plumes' are typically gently curved, having a simple margin on one side, and on the other bearing branches which have one feathered margin (Pl. 3, figs 1–2). Occasionally specimens occur back-to-back, with the two branched margins facing away from a central axis (Pl. 3, fig. 5). Specimens which preserve relief show that the simple margin or axis marks the position of a horizontal burrow (compare Pl. 3, figs 3 and 7). From this, a succession of gently inclined planes (major lamellae) arises laterally. The specimen illustrated in Plate 3, figure 6 shows that each major lamella bears a pattern of fine ridges and grooves orientated obliquely to its margins: these are taken to indicate the positions of secondary (minor) lamellae. It is the intersection of this complex surface with essentially flat bedding planes, combined with the contrast between the host sediment and the fill, that results in the frond-like appearance. In summary: the 'plume' axis represents the main burrow, the proximal parts of the major lamellae form the lateral branches, and the minor lamellae give rise to the one finely feathered margin on each branch. The plume-like appearance is especially marked when only the proximal parts of the major lamellae are preserved. Specimens that occur back-to-back could represent fortuitous associations or the successive reworking of sediment by the same animal on either side of the main burrow.

The structure described is matched in certain types of *Zoophycos*, an ichnofossil in which lateral growth takes place by successive branching probings along nearly parallel lines (Simpson 1970). Arcuate forms (often termed '*Z. cauda galli*') most resemble the present material (Simpson 1970, p. 508, fig. 1b), but these are thought to represent incomplete specimens which originally belonged to larger and more complex structures. In our material, the secondary laminae point obliquely backwards towards the main burrow in plan view, whereas in Simpson's reconstruction of '*cauda galli*' many of the secondary laminae are inclined obliquely outwards and backwards. Whilst we do not see why this should reflect any significant behavioural contrast, it seems prudent to assign our specimens to *Zoophycos* with question.

CONSTRUCTION OF THE *OIKOBESALON* BURROW

We have been able to match the essential features of *Oikobesalon* only in burrows produced by members of the Terebellidae, a family of rather large, strongly cephalized, sedentary polychaetes. Recent terebellids mostly live in blind-ended tubes (Nara 1995, p. 176), and are suspension or detritus feeders, taking diatoms and other unicellular algae, and small invertebrates (see Grassé (1959) and Fauchald and Jumars (1979) for overview of morphology and biology). The similarities in tube morphology are such that we do not doubt that *Oikobesalon* was produced by a terebellid. Nevertheless, contrasts exist which suggest significant differences between the *Oikobesalon* animal and the agents responsible for producing previously described terebellid burrows. In this section, we discuss published accounts of Recent and Pleistocene terebellid burrows, the structure of the organic lining of *Oikobesalon*, and then make comparisons between them.

Previously described terebellid burrows

Aller and Yingst (1978) studied the tube dwellings of the extant sedentary terebellid polychaete *Amphitrite ornata* from the Cape Cod area of Massachusetts. Specimens of *A. ornata* commonly range from 80 to 200 mm long, and occur in intertidal sands and sandy muds. They usually construct U-shaped tubes with an internal diameter of 5–10 mm (Aller and Yingst 1978, p. 203). The burrow wall generally consists of four or more thin (1·5–2 mm) concentric cylinders or elongated cones each of which is lined on its inner side with an organic sheet about 5 μm thick (Aller and Yingst 1978, p. 211, fig. 3). The tube wall is formed by the successive packing of fusiform, brick-like structures, made of mucus-bound sediment, which separate from each other when the burrow is dried. The bricks vary in size, commonly being 2–4 mm transversely and 0·2–0·7 mm long (parallel to the tube axis), and may extend partly or wholly through the *c.* 2 mm thick external sediment cylinder. Extensions of the inner, organic, burrow lining occasionally extend outwards between the bricks (Aller and Yingst 1978, p. 213).

Aller and Yingst (1978, p. 231) inferred the mechanism of burrow formation using direct observation, published descriptions, and analogy with other terebellids. Sediment particles are collected by the tentacles and coated with mucus. They are then taken between the unusually pliable and muscular (Fauchald and Jumars 1979, p. 252) outer lips, worked into a small parcel with additional mucus, and packed and shaped by the lower lip onto the accreting end of the tube. The animal subsequently rotates slightly in its tube and repeats the procedure. Each of the small parcels represents one of the fusiform bricks. By this means, *A. ornata* can extend its tube at a rate of *c.* 10 mm/hour. However, the animal cannot reburrow if completely exhumed.

An almost identical method of tube construction (involving the collection of mud, kneading with mucus, and shaping before construction) is known for *Neoamphitrite figulus*, a terebellid known from North Sea tidal flats and down to depths of 60 m (Schäfer 1972, p. 345). As well as using shaped bricks, however, *N. figulus* may incorporate foreign fragments and mud pebbles into its tube. A tube composed of fusiform bricks is known also for *N. cirrosa* (Schäfer 1972, fig. 204, p. 346). Schäfer (1972, p. 364) briefly described a broadly similar mechanism of burrow formation in the sabellid *Sabella pavonina*, but in this species components are added as complete rings and so lack the distinctive fusiform shape.

The multiple layered construction of the *A. ornata* tube reflects several episodes of tube construction: only the innermost tube and its lining represent the primary dwelling structure. The outer layers result either from slight lateral or vertical movement, or may reflect the walls of older, smaller tubes mechanically split by the animal as it grew. The latter seems particularly likely in those cases where the arc length of the outer layers in radial cross section is smaller than the next inner one (Aller and Yingst 1978, p. 232). Although the burrow of *A. ornata* is U-shaped, it is used much of the time as two separate vertical burrows (Aller and Yingst 1978, p. 233). The U-morphology may increase the animal's options for escape, for switching feeding areas, or for changing its respiratory position. Other terebellids may construct U-shaped, multibranched or vertical tubes.
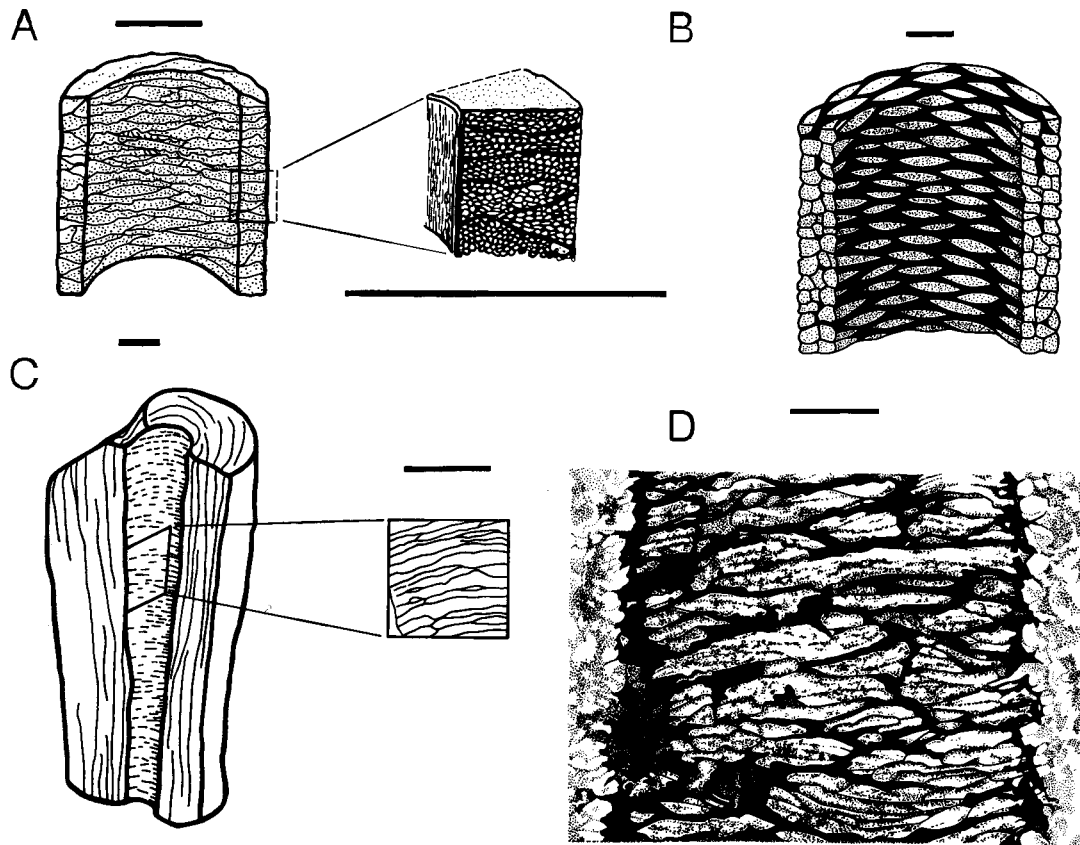
TEXT-FIG. 3. A, portion of *Amphitrite ornata* burrow and enlarged view of burrow wall (modified after Aller and Yingst 1979, fig. 3c–d, p. 211). B, portion of *Neoamphitrite cirrosa* burrow (from Schäfer 1956, text-fig. 13, p. 211; scale from Schäfer 1972, fig. 204, p. 346). C, portion of *Rosselia socialis* burrow and enlarged view of inner surface (modified after Nara 1995, fig. 7B, p. 177; partly from observations by Kikuchi). D, *Oikobesalon citrimorion* sp. nov.; DUDMG G14076; tracing of part of holotype. Scale bars represent 5 mm.

The ichnospecies *Rosselia socialis* was originally described from the Lower Devonian of Germany, and subsequently has been recorded widely in strata ranging from Early Cambrian to Pleistocene in age. It was redescribed and interpreted by Nara (1995), based on well preserved material from the Middle Pleistocene of the Boso Peninsula, central Japan. There, *R. socialis* is abundant in shoreface to offshore deposits of the Kongochi Formation.

R. socialis burrows are walled, with a central diameter of 3–11 mm and an outer diameter of 8–16 mm (Nara 1995, p. 172). The wall is concentrically laminated and consists mainly of mud (specimens associated with an ash layer contain ash in the burrow lining, suggesting that sediment particles were collected at the surface; Nara 1995, p. 173, fig. 6B). The burrows are often *c*. 0·2 m long (more rarely < 1 m) and may be vertical or inclined at angles up to 60°. Reworked specimens occur, which may be broken into blocks. The concentric lamination of the burrow wall reflects an internal variation in grain size, attributed by Nara (1995, fig. 5, p. 175) to changes in the grain size of surface sediments (from which particles were collected) caused by alternating low and high energy conditions in the environment. Each lamina in the wall consists of a hollow spindle or cone. The overall shape of the burrow is spindle- or funnel-shaped: the funnel-shaped forms occur below erosion surfaces and formed as a result of truncation.

Nara did not observe the brick-like wall structures described by Aller and Yingst or Schäfer (1972, p. 346). However, he noted that they were recorded by Kikuchi, in structures reassigned by Nara to *R. socialis* from the younger Narita Formation (Middle Pleistocene) of the Boso Peninsula (Nara 1995, p. 177, fig. 7B). Nara's drawing represents an area less than 10 mm square, and some of the fusiform bands are incomplete. However, they range from rare examples only *c.* 1 mm in maximum dimension to others apparently more than 10 mm across.

The supposed terebellid remains from the Ordovician of Bohemia described by Prantl (1950) consist of small shelly fossils arranged in narrow zones in the sediment. These may represent some kind of agglutinated tube, but they do not closely resemble the material dealt with here.

The organic lining of Oikobesalon

The existence of exhumed and broken specimens indicates that, when fresh, the lining of *Oikobesalon* possessed significant mechanical strength and rigidity. Because of weathering, it is not possible to estimate the original thickness of the lining in our material. However, from *O. liljevalli* specimens, Brood (1980) argued that the organic lining was collapsed in the fossil state, and estimated its original thickness from the thickness of spar-filled cavities left after shrinkage of the tube. The complex but regular shape of the outer surface (now preserved as a sediment mould) he figured certainly suggests that that surface was biogenically produced (Brood 1980, p. 280, fig. 2). The organic lining appears as a very thin film largely separated from the surrounding sediment by carbonate spar. In places, the surrounding spar is absent, yet the organic layer is equally thin: presumably this reflects local compaction prior to precipitation of the cement. Brood (1980, p. 279) estimated the lining thickness of *liljevalli* at 1 mm for a tube about 100 mm long and 10 mm wide.

The organic layer in specimens of *Oikobesalon* is highly carbonized, and its original composition unknown. Aller and Yingst (1978, p. 233) suggested that the organic layer of *A. ornata* might consist principally of sulphated or phosphate-rich mucopolysaccharides. They noted that such burrow linings sometimes contain enzymes which help to inhibit colonization by other organisms.

Comparisons between Oikobesalon and described terebellid burrows

The distinctive fusiform banding of the organic lining of *Oikobesalon* and the brick-like structures found in terebellid tubes are similar in both size and shape. Characteristic of the ichnogenus are the projections of the organic layer into the sediment. These we interpret as defining brick boundaries similar to those of the modern *A. ornata*. As in *Oikobesalon*, the organic linings described from Recent material occur principally on inner surfaces and sometimes between adjacent bricks. Exhumed specimens of *Oikobesalon* have no sediment wall preserved in association with the lining: this may be because the sediment separated as easily from the organic layer as Aller and Yingst described for *A. ornata* tubes. The absence of an identifiable sediment wall from *in situ* specimens is more surprising, although it would be difficult to recognize if the animal was indiscriminate in its choice of grain size, and if the amount of mucus used to bind the sediment was small. It is notable that Brood's (1980) estimate of 1 mm for the lining thickness in *O. liljevalli* greatly exceeds the 5 μm recorded for *A. ornata*. We propose that the *Oikobesalon* animal relied more on the thickened organic lining to maintain the integrity of its burrow, and that the surrounding sediment layer was more loosely consolidated.

The mode of growth of *Oikobesalon* must have differed from that of *Rosselia socialis* and *A. ornata* tubes. If the agent responsible for forming *Oikobesalon* had lived permanently in its burrow, either a concentric pattern of organic/sediment laminae would be expected due to burrow enlargement during growth, or disruption of the organic lining would be seen where it was split to allow new packages of mucus-bound sediment to be inserted. We propose that the *Oikobesalon*-producing organism did not inhabit one burrow throughout life. Rather it may have been able to construct a new burrow after exhumation, or when required during growth. Although the literature sometimes reports terebellids as being entirely sessile, Fauchald and Jumars (1979, pp. 252–253) noted that some may leave their tubes when necessary, and may swim or move on the substrate by

peristaltic crawling or by using their tentacles. Evidently terebellids have the potential for locomotion, but few use this capacity regularly, preferring a sessile or discretely motile existence.

REFERENCES

ALLAN, R. S. 1927. *Keilorites*, a new generic name for a Silurian annelid from Australia. *Geological Magazine*, **64**, 240.

ALLER, R. C. and YINGST, J. Y. 1978. Biogeochemistry of tube dwellings: a study of the sedentary polychaete *Amphitrite ornata* (Leidy). *Journal of Marine Research*, **36**, 201–254.

BATHER, F. A. 1927. *Keilorites*. *Geological Magazine*, **64**, 286.

BRIGGS, D. E. G. and WILLIAMS, S. H. 1981. The restoration of flattened fossils. *Lethaia*, **14**, 157–64.

BROOD, K. 1979. Organic tubes. 252. *In* JAANUSSON, V., LAUFELD, S. and SKOGLUND, R. (eds). Lower Wenlock faunal and floral dynamics – Vattenfallet Section, Gotland. *Sveriges Geologiska Undersökning, Serie C*, **762**, 1–294.

—— 1980. Two species of *Keilorites* from the Silurian of Gotland. *Geologiska Föreningens i Stockholm Förhandlingar*, **102**, 279–282.

BUTLER, A. J. 1939. The stratigraphy of the Wenlock Limestone of Dudley. *Quarterly Journal of the Geological Society, London*, **95**, 37–74.

CHAPMAN, F. 1910. New or little-known Victorian fossils in the National Museum. Part X. Some Palaeozoic worms and crustacea. *Proceedings of the Royal Society of Victoria, New Series*, **22**, 101–112, pls 27–29.

—— 1919. New or little-known Victorian fossils in the National Museum. Part XXII. Palaeozoic worms; with evidence of soft parts. *Proceedings of the Royal Society of Victoria, New Series*, **31**, 315–324, pls 13–14.

DORNING, K. J. 1983. Palynology and stratigraphy of the Much Wenlock Limestone Formation, Dudley, central England. *Mercian Geologist*, **20**, 31–40.

ETHERIDGE, R. 1888. *Fossils of the British Islands*: 1. *Palaeozoic*. Clarendon Press, Oxford, viii + 468 pp.

FAUCHALD, K. and JUMARS, P. A. 1979. The diet of worms: a study of polychaete feeding guilds. *Annual Review of Oceanography and Marine Biology*, **17**, 193–284.

GRASSÉ, P.-P. (ed.) 1959. *Traité de zoologie: anatomie, systématique, biologie. Tome V, premier fascicule. Annélides, Myzostomides, Sipunculiens, Echiuriens, Priapuliens, Endoproctes, Phoronidens*. Masson et cie, Paris, ml–mcxvi + 1053 pp.

GRAVENHORST, J. L. C. 1829. *Ichneumenologia europaea*. Vratislaviae, 1097 pp.

HÄNTZSCHEL, W. 1975. *In* TEICHERT, C. (ed.). *Treatise on invertebrate paleontology. Part W. Miscellanea, Supplement 1, trace fossils and problematica*. University of Kansas Press and Geological Society of America, Boulder, Colorado, and Lawrence, Kansas, xxi + 259 pp.

HOLLAND, C. H., LAWSON, J. D. and WALMSLEY, V. G. 1963. The Silurian rocks of the Ludlow district, Shropshire. *Bulletin of the British Museum (Natural History), Geology Series*, **8**, 93–171, pls 1–7.

HOWELL, B. F. 1962. Worms. W144-W177. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part W. Miscellanea – conodonts, conoidal shells of uncertain affinities, worms, trace fossils and problematica*. University of Kansas Press and Geological Society of America, Boulder, Colorado and Lawrence, Kansas, xxv + 269 pp.

JAMES, A. V. G. 1920. The physiography and geology of the Bulla-Sydenham area. *Proceedings of the Royal Society of Victoria, New Series*, **32**, 323–349, pls 32–34.

KEIGHLEY, D. G. and PICKERILL, R. K. 1994. The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology*, **37**, 305–337.

LATREILLE, P. A. 1829. *In* CUVIER, G. L. C. F. D. *La règne animal, distribué d'après son organisation, pour service de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée*. Nouvelle edition, revue et augmentee tom. 4, 5, by P. A. Latreille. 5 vols. Fortin, Masson et cie, Paris.

LINDSTRÖM, G. 1888. *List of the fossil faunas of Sweden: II. Upper Silurian*. Palaeontology Dept, State Museum of Natural History, Stockholm, 29 pp.

MASSALONGO, A. 1855. *Zoophycos, novum genus plantorum fossilium.* Antonelli, Verona, 53 pp., 7 pls.

MURCHISON, R. I. 1839. *The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester and Stafford; with descriptions of the coalfields and overlying formations.* John Murray, London, xvi + 523 pp., 37 pls.

NARA, M. 1995. *Rosselia socialis*: a dwelling structure of a probable terebellid polychaete. *Lethaia,* **28,** 171–178.

PHILLIPS, J. 1848. *In* PHILLIPS, J. and SALTER, J. W. Palaeontological appendix to Professor John Phillips' memoir on the Malvern Hills, compared with the Palaeozoic districts of Abberley, &c. *Memoirs of the Geological Survey,* **2** (1), viii–xiv + 331–386.

PRANTL, F. 1950. Some terebelloid remains from the Ordovician of Bohemia. *Věstnik královské české Spolecnosti Nauk,* **8** (for 1948), 1–8, pls 1–2.

RIDE, W. D. L., SABROSKY, C. W., BERNARDI, G., MELVILLE, R. G., CORLISS, J. O., FOREST, J., KEY, K. H. L. and WRIGHT, C. W. 1985. *International code of zoological nomenclature.* 3rd edition. International Trust for Zoological Nomenclature, xx + 338 pp.

SCHÄFER, W. 1956. Wirkungen der Benthos-Organismen auf den jungen Schichtverband. *Senckenbergiana lethaea,* **37,** 183–263, pls 1–2.

—— 1972. *Ecology and paleoecology of marine environments.* Oliver and Boyd, Edinburgh, xii + 568 pp.

SHERBORN, C. D. 1932. *Index animalium 1801–1850,* vol. T–Z. Cambridge University Press, 6363–7056.

SIMPSON, S. 1970. Notes on *Zoophycos* and *Spirophyton.* 505–514. *In* CRIMES, T. P. and HARPER, T. C. (eds). Trace fossils. *Geological Journal Special Issue,* **3,** 1–547.

STUBBLEFIELD, C. J. 1938. The types and figured specimens in Phillips and Salter's palaeontological appendix to John Phillips' memoir on 'The Malvern Hills compared with the Palaeozoic districts of Abberley, etc. *Mem. Geol. Surv.* Volume II, Part I, June 1848)'. *Summary of progress of the Geological Survey of Great Britain and the Museum of Practical Geology* (for 1936, part 2), 27–51.

WIEGMANN, A. F. A. 1829. *Isis oder encyclopadische Zeitung von Oken.* Band 22, Heft 4, 418–424.

—— 1834. *Herpetologia Mexicana, seu descriptio amphibiorum Novae Hispanae, quae itineribus Comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum zoologicum berolinese pervenerunt. Pars prima, saurorum species amplectens. Adiecto systematis saurorum prodromo, additisque multis in hunc amphiborum ordinem observationibus.* C. G. Lüderitz, Berolini. vi + 54 pp., 10 pls.

WILLIAMS, H. S. 1916. The fauna of the Chapman Sandstone of Maine including descriptions of some related species from the Moose River Sandstone. *Professional Paper of the United States Geological Survey,* **89,** 1–347, pls 1–27.

A. T. THOMAS

M. P. SMITH

School of Earth Sciences
The University of Birmingham
Birmingham B15 2TT, UK