

THE DEMOSPONGE GENUS *LEPTOMITUS* AND A NEW SPECIES FROM THE MIDDLE CAMBRIAN OF SPAIN

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Abstract: Forty-five specimens of *Leptomitius conicus* sp. nov. have been collected from the base of the Murero Formation (Caesaraugustan, Middle Cambrian) in the Murero area of Zaragoza, north-east Spain. The new species is a small obconical sponge, which has coarse oxeas forming parallel rods that run the whole length of the specimens in the manner typical of the genus. The biostratigraphy and facies of the levels with *Leptomitius conicus* have been analysed. Palaeoecological information derived from associated trilobites, brachiopods and ichnofossils shows that *L. conicus* lived in a soft

substrate of a sublittoral environment of low to low/moderate energy. According to established Cambrian palaeogeographical reconstructions, a tropical distribution is inferred for the genus *Leptomitius*. Based on body shape, wall structure and stratigraphical distribution, a phylogenetic tree of the various *Leptomitius* species is proposed, with a central stock of simple cylindrical sponges branching out to other morphs.

Key words: *Leptomitius*, Demospongea, systematics, ecology, palaeobiogeography, Middle Cambrian.

THE occurrence of fossil sponges in the Cambrian of the Cadenas Ibéricas is very rare, despite a good record for groups such as trilobites, brachiopods and echinoderms. Liñán *et al.* (1996a) cited *Crumillospongia* sp. from the Valdemiedes Formation and García-Bellido Capdevila (1999, 2003) found *Leptomitius* cf. *L. lineatus* in the Murero Formation. Other additional poriferan references are based on isolated spicules (Álvaro and Vennin 1996).

We have recently found 45 specimens of *Leptomitius conicus* sp. nov. at the base of the Murero Formation in three locations in the province of Zaragoza (Murero, Villafeliche and Jarque). All the material represents a very short time interval within the *Badulesia granieri* Zone and the base of the *Pardailhania hispida* Zone (Lower–Middle Caesaraugustan; see Liñán *et al.* 2002, fig. 3.3).

Based on its simple wall structure and shape, *Leptomitius* is considered to be a possible central stock from which other protomonaxonid demosponges radiated in the Cambrian, as they developed new complex structures and specialized skeletons (Rigby 1986; Rigby and Collins 2004). Alternatively it could be regarded as a specialized form derived from the Hazeliidae (Botting 2003). The stratigraphic range of this possibly primitive genus is now

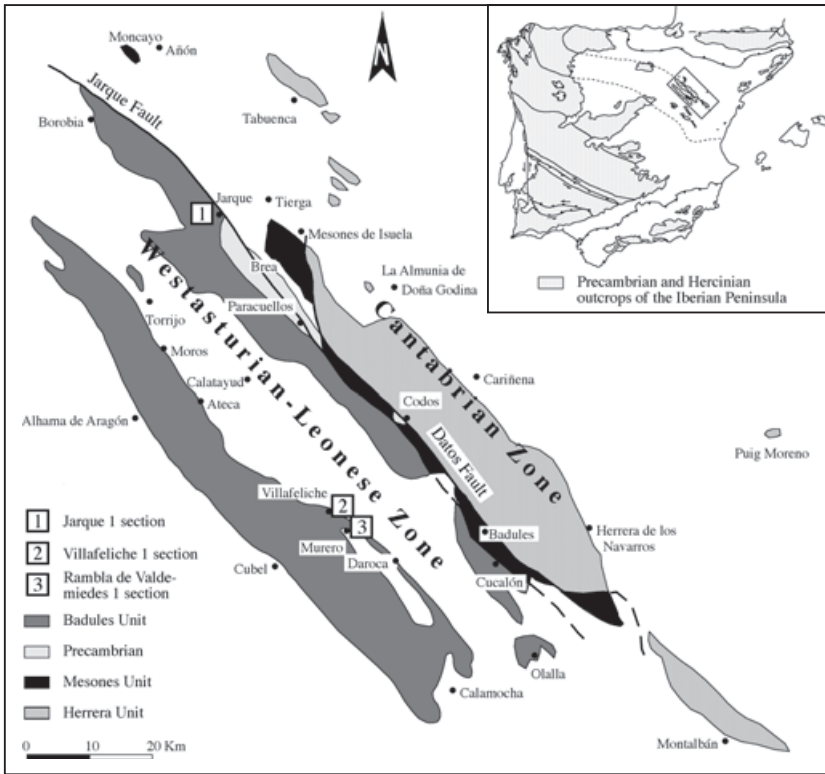
extended from the Lower Cambrian of China to the middle-Middle Cambrian of Spain.

GEOLOGICAL SETTING AND STRATIGRAPHY

The villages of Jarque, Murero and Villafeliche are located about 70 km west and south-west of Zaragoza city, in the Aragonese branch of the Cadenas Ibéricas (Text-fig. 1). From a geological point of view, these localities all belong to the Badules Unit, although the furthest ones were separated by at least 60 km in the Cambrian.

We have studied fossil material from the basal part of the Murero Formation in three sections: Jarque 1 (J₁ near Jarque), Rambla de Valdemiedes 1 (RV₁ near Murero) and Villafeliche 1 (Vi₁ near Villafeliche). These have been discussed previously in Liñán and Gozalo (1986), Gozalo *et al.* (1993, 1996, 2003a) and Liñán *et al.* (1996b).

The lithology of the Murero Formation in the levels with *Leptomitius conicus* sp. nov. comprises green lutites with scattered carbonate nodules (Text-fig. 2); some of the trilobites and echinoderms have been preserved as



TEXT-FIG. 1. Geological setting of the sections studied in the Cadenas Ibéricas; modified from Gozalo and Liñán (1988).

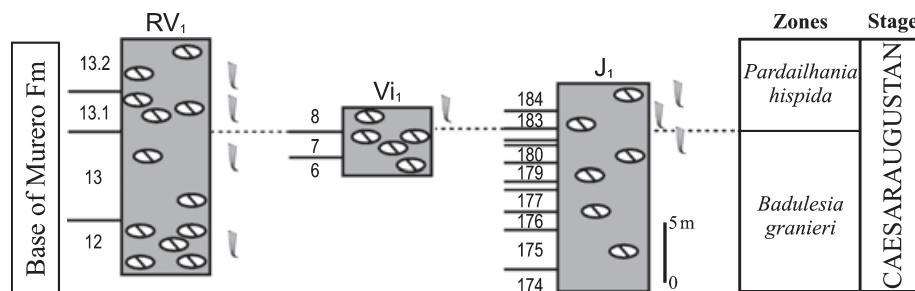
articulated specimens, which indicate a low-energy environment.

Leptomit *conicus* has been recorded in the *Badulesia granieri* Zone and at the base of the *Pardailhan* *hispid* Zone. The fossil assemblage of the former zone consists of trilobites [*Badulesia granieri*, *Conocoryphe* (*Parabailiella*) *languedocensis*, *Eccaparadoxides asturianus*], brachiopods, echinoderms (*Cincta*), algae and ichnofossils. The latter zone contains a greater diversity of fossils, with trilobites [*Agraulidae*, *Badulesia granieri*, *B. paschi*, *Ctenocephalus* cf. *terranovicus*, *Condylopyge* aff. *regia*, *Conocoryphe* (*Parabailiella*) *languedocensis*, *Eccaparadoxides asturianus*, *E. rouvillei*, *Pardailhan* *hispid* and *Pero* *nopsis acadica*], brachiopods, echinoderms (*Cincta*), algae and ichnofossils.

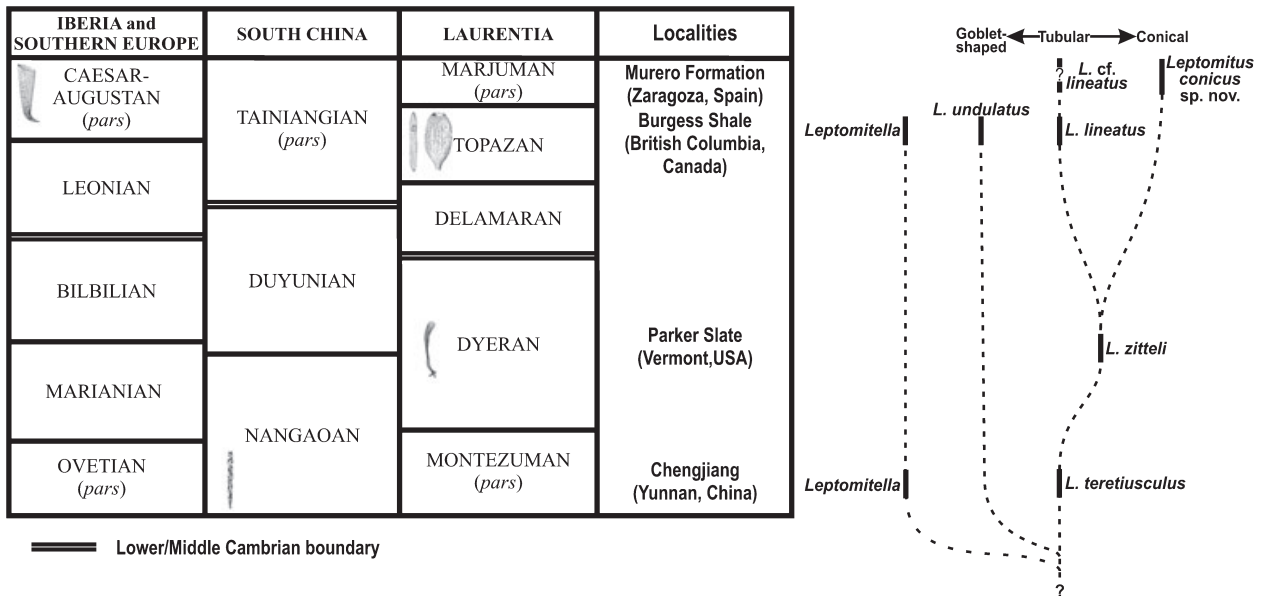
The first assemblage noted above belongs to the cosmopolitan polymeroid biofacies and the second to the miomeroid biofacies (*sensu* Liñán *et al.* 1993a; Liñán 1995). Both indicate an open sublittoral environment.

All of the levels with sponges contain brachiopods of the *Dictyonina-Acrothele* assemblage (formerly *Dictyonina-Redlichella*) *sensu* Liñán and Mergl (2001). This assemblage is characteristic of a relatively deeper sublittoral and low-energy environment.

Intercalated with the sponge-bearing levels are ichnofossils that belong to the *Sericichnus* and *Diplichmites* ichnoassemblage *sensu* Gámez Vintaned and Mayoral (1992, 1995). This assemblage has been included in the *Cruziana* ichnofacies (cf. Seilacher 1963), which is considered to represent relatively shallow sublittoral environments of



TEXT-FIG. 2. Stratigraphy of the base of the Murero Formation at the Rambla de Valdemedias 1 (RV₁), Villafeliche 1 (Vi₁) and Jarque 1 (J₁) sections, showing the distribution of *Leptomit* *conicus* sp. nov.



TEXT-FIG. 3. Correlation chart of the three regional scales with the distribution through the Cambrian of the different *Leptomitius* species (small reconstructions), and their phylogenetic relationships.

low/moderate energy, and a clastic substrate. In the case of the Murero Formation, the substrate was soft and mainly composed of mud.

The palaeoecological information derived from trilobites, brachiopods and ichnofossils is consistent, and indicates a soft substrate in a sublittoral environment. However, the energy of the intercalated levels with ichnofossils is inferred to have been slightly higher than that of the levels with sponges and trilobites. Thus, for the sections studied, the energy is regarded as low to low/moderate, and the depositional environment below storm-wave base level.

Age

The Caesaraugustan Stage is considered to be more or less equivalent to the *Paradoxides paradoxissimus* stage in Baltica (Sdzuy 1972; Liñán et al. 1993b). The *Pardailhania hispida* FAD (first appearance datum) is regarded as the marker of the beginning of the Middle Caesaraugustan (Liñán et al. 1993b). The Lower/Middle Caesaraugustan transition may be correlated with the *Tomagnostus fissus* and/or *Acidusus atavus* zones, which have been correlated with the lower part of the *Bolaspidella* Zone (Marjuman Stage) in the Laurentian scale (Text-fig. 3, and correlation chart in Geyer and Shergold 2000).

Palaeobiogeography

Leptomitius species are widely distributed in low latitudes (Text-fig. 4), when plotted on the palaeogeographical

reconstruction of McKerrow et al. (1992). This is generally the case for other Cambrian sponges, with the possible exception of *Protospongia* (Rushton and Phillips 1973; Baresi 2003) and *Diagoniella* (Baresi 2003). Thus, the distribution of *Leptomitius* is apparently restricted to tropical/subtropical regions and may have been controlled by climatic factors. This is also suggested by the data available for oryctocephalid trilobites (Shergold 1969; Gozalo et al. 2003b) and Cambriidae bradoriids (Siveter et al. 1996). The intercontinental distribution of *Leptomitius* in Laurentia and Gondwana may be interpreted as reflecting a planktonic mode of life during a parenchymella larval phase as well as asexual dispersal (Jablonski 1986; Vacelet 1999; García-Bellido and Rodríguez 2005).

Repository. The material studied is housed in the Museo de Paleontología de la Universidad de Zaragoza and recorded under numbers MPZ 2005/321–340, 2005/591–593 and 2006/595.

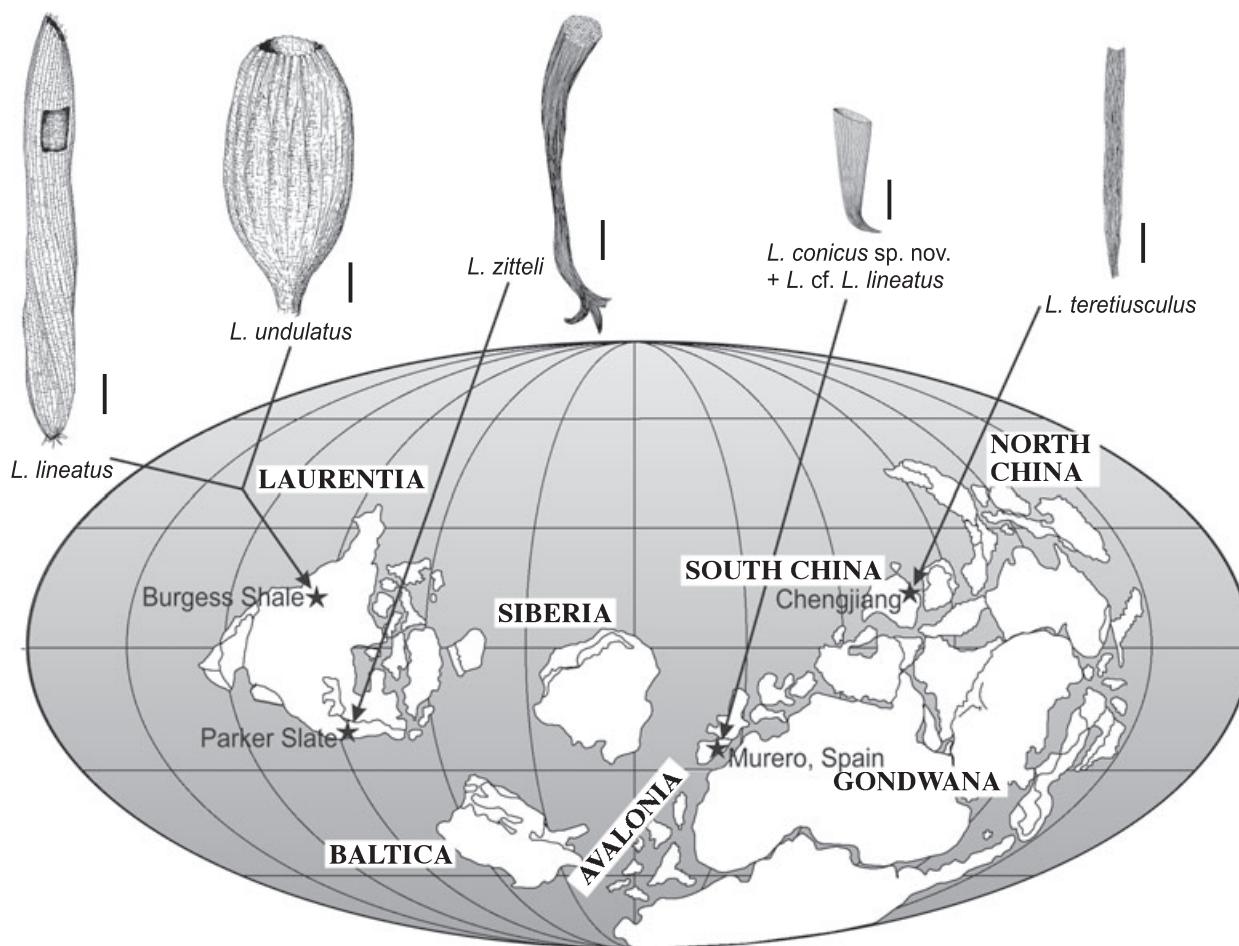
SYSTEMATIC PALAEONTOLOGY

Class DEMOSPONGEA Sollas, 1875
 Order PROTOMONAXONIDA Finks and Rigby, 2004
 Family LEPTOMITIDAE De Laubenfels, 1955

Genus LEPTOMITUS Walcott, 1886

Type species. *Leptomitius zitteli* Walcott, 1886.

Emended diagnosis. Elongate or goblet-shaped, tubular or obconical, very thin-walled sponges with double-layered



TEXT-FIG. 4. Palaeogeographical distribution of *Leptomitidae* species and their scaled reconstructions (*L. lineatus* from Rigby 1986; *L. undulatus* from Rigby and Collins 2004; *L. zitteli* modified from Walcott 1886). Palaeogeographical reconstruction based on McKerrow *et al.* (1992, fig. 1). Scale bars represent 10 mm.

skeleton. Coarse, moderately widely spaced, *en echelon* oxeas are dominant elements that extend as parallel rods virtually the entire length of the sponge in the outer skeletal layer. Spaces between rods filled with thatch of smaller vertical oxeas that combine with coarse rods to produce the outer skeletal layer. Inner layer a thatch of tiny horizontal, monaxial spicules. Vertical small spicules do not occur in bundles, while horizontal spicules are not clustered or cluster into ill-defined bundles. Walls lack parietal gaps and major canals.

Remarks. Although the previously described species of the genus fall within the diagnosis of Rigby (1986), the second Canadian species (Rigby and Collins 2004) and the one described here have widened the morphological spectrum of *Leptomitidae* in both shape and size (Table 1). When compared with other thin-walled fossil monaxonid sponges, the inner layer of small spicules, while occasionally presenting a faintly bundled appearance (Rigby and Collins 2004), never produces the well-defined reticulate pattern diagnostic of *Leptomitella* Rigby, 1986 nor the

EXPLANATION OF PLATE 1

Figs 1–5. *Leptomitidae conicus* sp. nov. from the Middle Cambrian Murero Formation, Cadenas Ibéricas, Spain. 1–2, MPZ 2005/321 (RV₁/13.1), holotype. 1, complete specimen showing the typical conical shape of the sponge; $\times 3.8$. 2, detail of the apical region of sponge, including slanted oscular margin; $\times 10$. 3, MPZ 2005/329 (RV₁/12baR), complete specimen showing the hooked base; $\times 9$. 4, MPZ 2005/323 (RV₁/13.1), paratype, detail of slanted oscular margin; $\times 10$. 5, MPZ 2005/332 (J₁/183), detail of specimen with horizontal oscular margin; $\times 9$. RV, Rambla de Valdemiedes locality; J, Jarque locality.

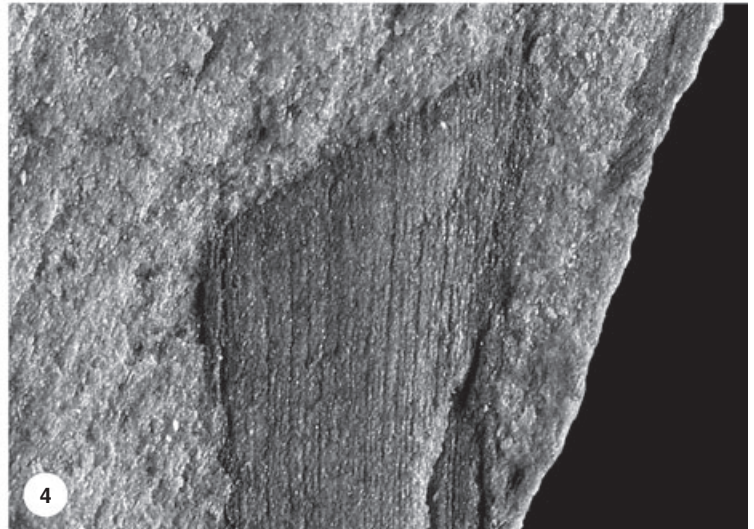
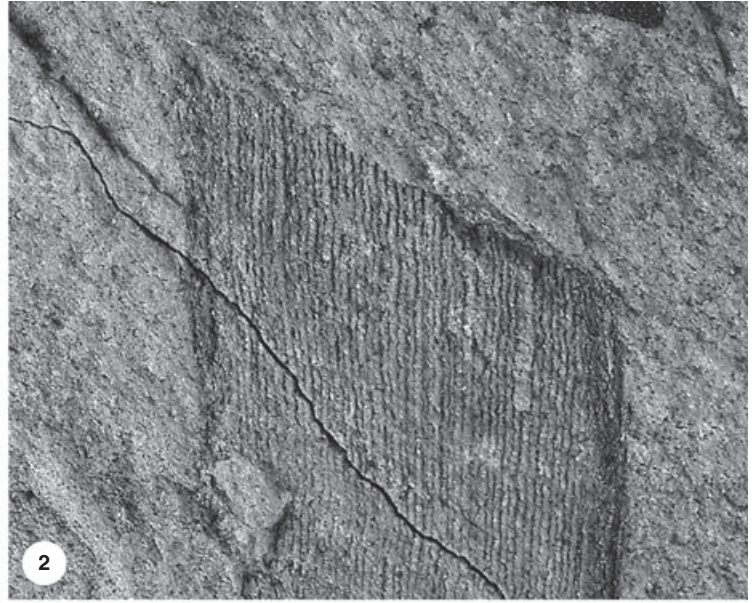


TABLE 1. Dimensions (in mm) of the species of *Leptomitius*.

	Length	Width (min.–max.)	Rod spacing	Coarse oxea		Fine oxea		Gastral oxea	
				Diameter	Length	Diameter	Length	Diameter	Length
<i>L. zitelli</i>	77	2–8	–	–	–	–	–	–	–
<i>L. lineatus</i>	360	4–14·5 (30)	0·6–1·1	0·05–0·10	8–10 (22)	0·02–0·025	0·7–0·8	0·007–0·015	0·12–0·15 (0·3)
<i>L. teretiusculus</i>	80	1–6	0·08–0·16	0·1	3–4	0·01	0·2–0·3	0·02	0·5
<i>L. teretiusculus</i> *	59	1·0–4·5	0·25–0·30	0·04–0·10	3–7	0·02–0·05	1–4	0·05–0·06	–
<i>L. undulatus</i>	78	6·5–38	0·1–0·4	0·06	25	0·015–0·020	–	0·015–0·020	0·3–0·5
<i>L. conicus</i>	11–36	3·5–9	0·045–0·12	0·015–0·075	–	–	–	–	–

* In Rigby and Hou (1995).

Dimensions in parentheses are extreme values.

diagonal net-like pattern of *Paraleptomitella* Chen, Hou and Lu, 1989.

Occurrence. The oldest species of *Leptomitius* is recorded from the *Eoredlichia-Wuttingaspis* Biozone, Qiongzhusian Stage (see Hou *et al.* 2004). This stage is equivalent to the lower part of the Nangaoan Stage in the new South China stage-scale proposed by Peng and Babcock (2001) and Peng (2003). The presence of *Eoredlichia* in the uppermost Lower Ovetian and Upper Ovetian (Liñán *et al.* 2002, 2005) allows a good correlation between South China and Iberia. The other Lower Cambrian species is *Leptomitius zitelli* from Vermont (USA), which belongs to the *Olenellus* Zone (see Walcott 1890), Dyerian Stage (Palmer 1998). The two *Leptomitius* species from the Burgess Shale (Canada) have been recorded in the *Bathyriscus-Elrathina* Zone (Fletcher and Collins 1998; Rigby and Collins 2004), within the Topazan Stage recently proposed by Sundberg (2005). Finally, the youngest record of *Leptomitius* is from the Caesaraugustan Stage (see above). Text-figure 3 presents a correlation chart for the three regions from which it has been recorded.

Geographical distribution. China, USA, Canada and Spain (see Text-fig. 4).

Leptomitius conicus sp. nov.

Plates 1–2; Text-figures 5–6; Table 2

Derivation of name. Latin, *conicus*, referring to the conical body shape of the sponge.

Type specimens. Holotype, MPZ 2005/321, and paratypes, MPZ 2005/322–325, from level 13.1 in the Rambla de Valdemiedes 1 section, base of the *Pardailhanian hispidus* Zone (Middle Caesaraugustan).

Other material. Forty other specimens of a small obconical *Leptomitius*, most of them with part and counterpart. Thirteen specimens are complete or almost complete (Table 2), and the rest are fragments of various sizes. The material comes from the Murero (Rambla de Valdemiedes), Jarque and Villafeliche localities, all within the Murero Formation, Caesaraugustan Stage, Middle Cambrian.

Diagnosis. Small obconical, double-walled sponge with wide apical osculum. Thin outer wall composed of a thatch of small oxeas, with evenly spaced, well-defined rods of single coarse, slightly overlapping oxeas producing a vertically striped appearance. Rods generally 0·012–0·075 mm in diameter, with intervals of 0·042–0·1 mm between them. Inner wall composed of very small, horizontal monaxial spicules.

Description. These sponges have a consistently obconical shape, with very narrow bases, when preserved (Pl. 1, figs 1, 3; Pl. 2, figs 1–3). Complete specimens range from 11 to 36 mm in length, but extrapolation from large fragments produces maximum sizes of almost 50 mm. All the specimens are considerably flattened owing to rock compaction. The widest sponge fragment is 10·4 mm (Pl. 2, fig. 4), but complete specimens have a flattened width of 3·5–9 mm at their oscular margins

EXPLANATION OF PLATE 2

Figs 1–7. *Leptomitius conicus* sp. nov., from the Middle Cambrian Murero Formation, Cadenas Ibéricas, Spain. 1, MPZ 2005/331 (J₁/181), complete specimen showing longitudinal rods as well as faint transverse lines corresponding to the moulds of the inner layer of oxeas; ×5. 2, MPZ 2005/334 (J₁/184), complete specimen with slightly hooked base; ×7·5. 3, MPZ 2005/322 (RV₁/13.1), paratype, complete specimen showing the hooked base; ×9. 4, MPZ 2005/335 (J₁/184), detail of widest specimen in the collection; ×5. 5, MPZ 2005/326 (RV₁/13), detail of specimen with varying widths between rods; ×8. 6, MPZ 2006/595 (J₁/183), detail of specimen showing the faint transverse lines of the horizontal inner oxeas; ×9. 7, MPZ 2005/336 (Vi₁/8), detail of specimen showing the undulation of the rods. J, Jarque locality; RV, Rambla de Valdemiedes locality; Vi, Villafeliche locality.

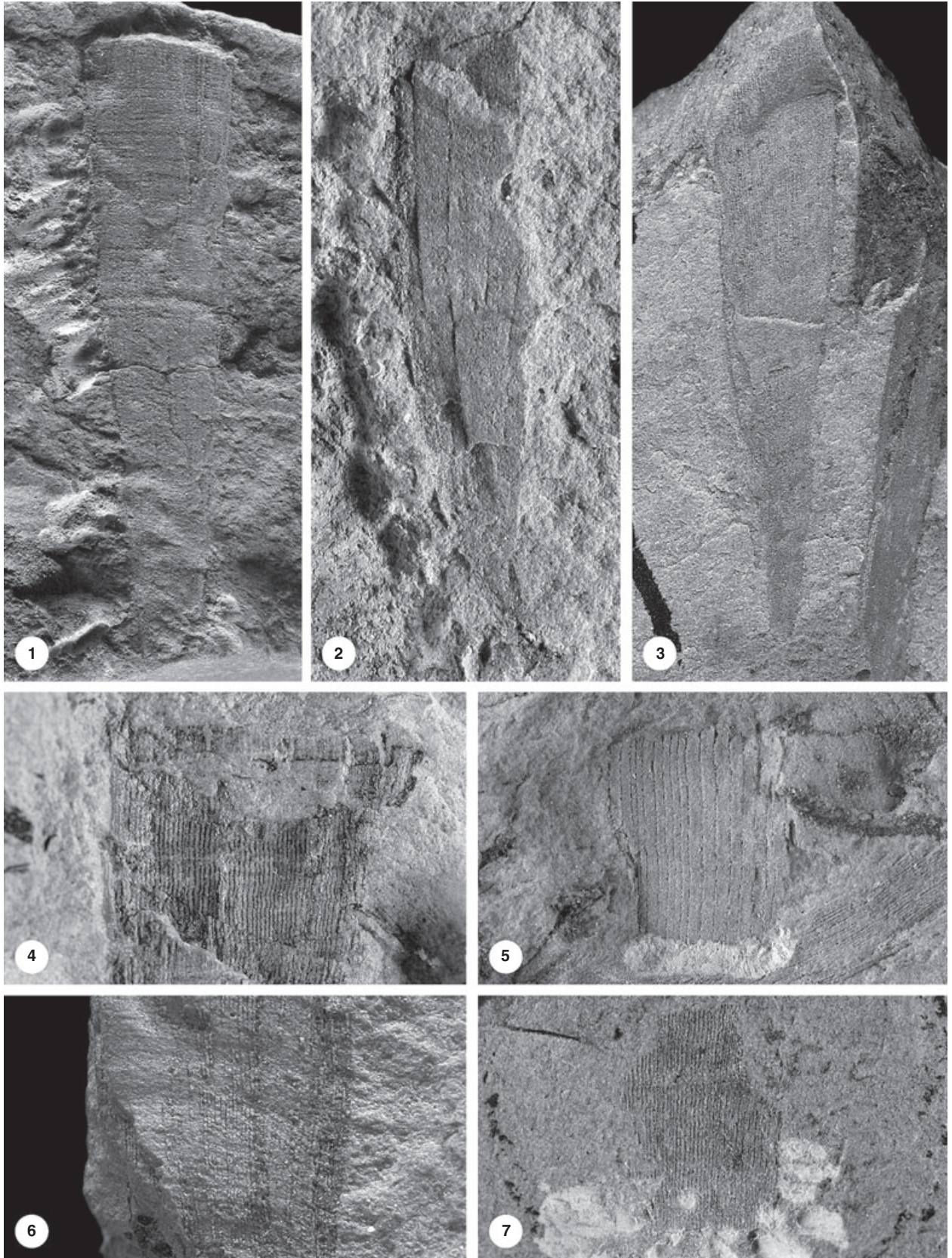


TABLE 2. Dimensions (in mm) of the best-preserved specimens of *Leptomitus conicus* sp. nov.

	Total length	Width (min.–max.)	Rod spacing	Coarse oxea diameter	Rods/mm basal–distal	Angle
MPZ 2005/321*	30	0.88–6.5	0.075–0.12	0.015–0.045	7.81	12°
MPZ 2005/322*	18.4	0.5–3.92	0.047–0.082	0.012–0.024 (0.036)	10.2	–
MPZ 2005/323	12.8	3.5	0.047–0.07	(0.035) 0.047–0.07	12.57	9°
MPZ 2005/324*	21.2	0.78–4.5	(0.059) 0.07–0.095	0.024–0.036	–	10°
MPZ 2005/325	20	3.15–5.2	(0.059) 0.083–0.12	0.024–0.036	8.8–7.11	–
MPZ 2005/326	7	4–5.5	0.12–0.37 (0.42)	0.024–0.036	1.99	–
MPZ 2005/327	15	1.5–4	0.03–0.075	0.015–0.03	10	–
MPZ 2005/328	12	4–5	0.06–0.15	0.015–0.03	6.94	12°
MPZ 2005/329*	11.2	0–3.5	0.045	0.024–0.036 (0.1)	7.14	13°
MPZ 2005/330*	13.6	0.48–3.5	–	–	–	12°
MPZ 2005/331	22	2–5	0.07–0.095 (0.12)	0.024	8.5–5	10°
MPZ 2005/332	10	3	0.045–0.075 (0.105)	0.015–0.03	10.62–10	–
MPZ 2005/333	17	2.8–6.4	0.045–0.075	0.015–0.03	15.70–13.03	15°
MPZ 2005/334*	13.5	0.15–2.95	–	–	–	10°
MPZ 2005/335	19	8.25–10.4	0.083–0.15 (0.177)	0.036–0.072	5.38	–
MPZ 2005/336	7	3.5	0.06–0.15	0.015–0.03	13.14	–
MPZ 2005/337*	36	1.24–9	0.075–0.105	0.06–0.075	8–6.88	15°
MPZ 2005/338*	29	1.47–6.5	0.06–0.105	0.03–0.06	9.2–8.62	10°
MPZ 2005/339*	35	0.68–9	0.06–0.09	0.06–0.075	–	12°
MPZ 2005/340*	28	0.6–6.5	0.075–0.15	0.03–0.06	11.6–8.28	9°
MPZ 2005/591*	17†	1.7–9	0.06–0.105	0.045–0.075	8.62	20°
MPZ 2005/592*	21	1.6–3.8	0.03–0.075	0.015–0.045	14.5–10.25	8°
MPZ 2005/593*	15	0.15–4.13	0.045–0.075	0.015–0.03	–	7°

* Complete or almost complete specimen.

† Obliquely compressed specimen.

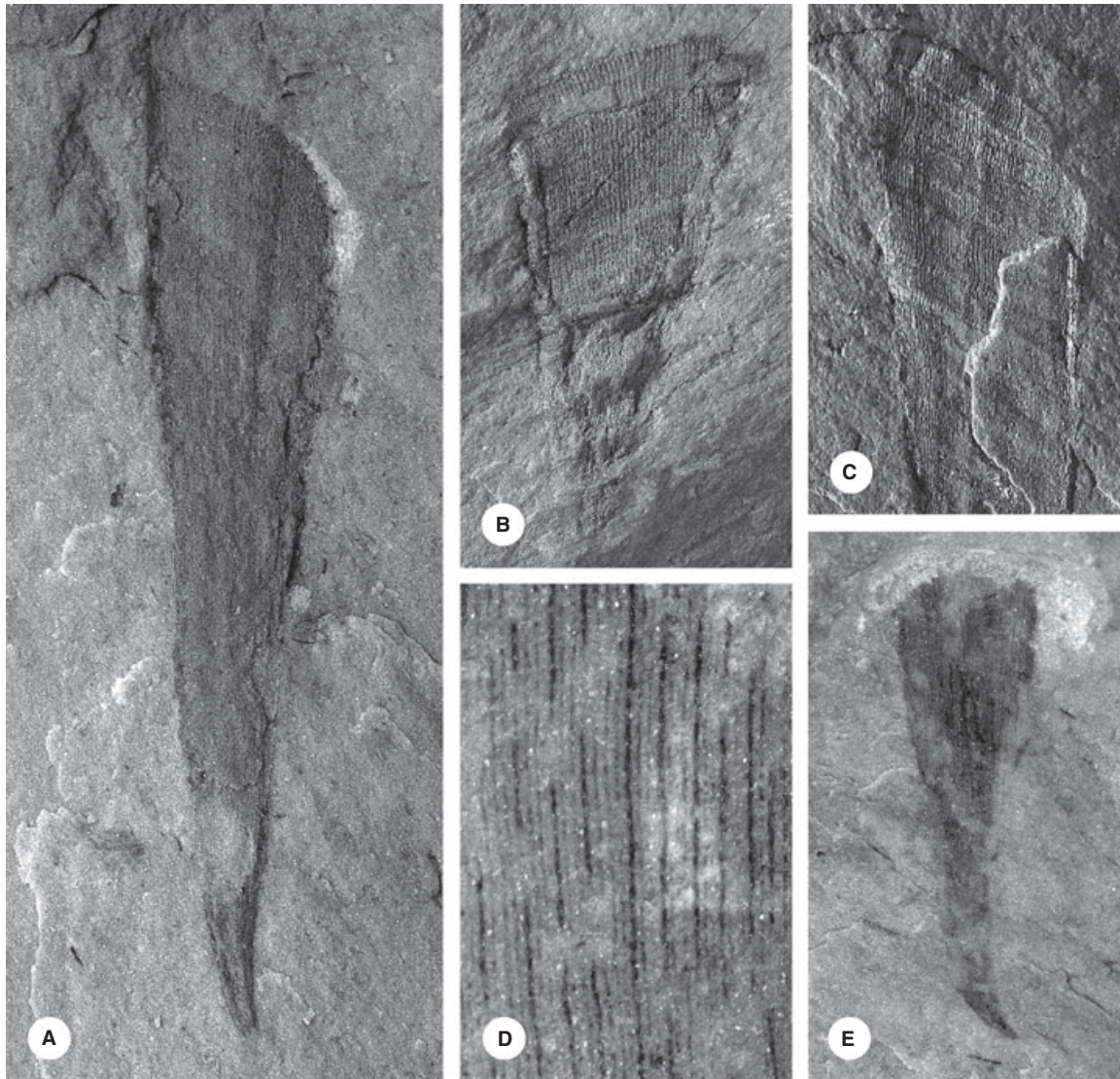
Dimensions in parentheses are extreme values.

(Table 2), which would correspond to diameters of 2.2–5.8 mm before compaction. Coarse oxeas form the vertical rods. These spicules appear to be single rather than bundled (Text-fig. 5D) and arranged tip to tip with a slight overlap. They have diameters of 0.015–0.075 mm, but one specimen has rods up to 0.10 mm in diameter (Pl. 1, fig. 3). These rods, preserved in the form of chlorite, sometimes weathered to limonite, are parallel to each other, producing the striped appearance typical of the genus, even when they occasionally wiggle (Pl. 2, fig. 6; Text-fig. 5B–C). These small undulations occur in both the lateral and the vertical axes, and are interpreted as taphonomic in origin. This is suggested by similar wrinkled surfaces in co-occurring *Paradoxides* trilobites. These are interpreted as having been produced during early diagenesis when organic acids from decay were present, making mineralized structures ductile. The spacing between rods increases slightly from the base to the upper areas of the sponge. Most specimens show spacing of between 0.045 and 0.12 mm, but it can be as narrow as 0.03 mm and as wide as 0.17 mm. The intervals between rods of one odd fragment vary laterally and reach up to 0.42 mm (Pl. 2, fig. 5). There are c. 6–13, in some cases up to 15, rods per millimetre and in the specimens where this parameter can be obtained in the basal and upper parts of the sponge, the rods are always more densely packed at the base (Pl. 2, figs 2–3). Complete specimens have a steeply obconical shape (Text-fig. 6) with an angle between 9 and 15 degrees. In an obliquely compressed specimen that was buried diagonal to

bedding, the angle reaches 20 degrees († in Table 2; Text-fig. 5B). Fragmentary specimens do not allow measurement of this angle but show slight tapering. This vertical increase in width is attained by larger rod intervals, plus the occasional bifurcation of a rod. In two partially eroded specimens some transverse relief is evident in low-angle light; this is interpreted as a mould of the inner wall spicules (Pl. 2, figs 1, 6). Some of the most complete specimens show a hooked base (Pl. 1, figs 1, 3; Pl. 2, fig. 2; Text-fig. 5E), which may have aided in keeping the sponge stabilized vertically on the sea-floor.

Owing to the state of preservation we cannot measure some features of this sponge, such as total lengths of the coarse oxeas, and dimensions of the fine oxeas between the rods and in the gastral layer. Some specimens have sediment filling their spongoecels, which has flattened thicknesses of 0.12–0.36 mm, depending upon how high up the body of the sponge the break in the wall occurs (Pl. 1, fig. 1; Pl. 2, figs 3–4).

Remarks. The shape and size of *Leptomitus conicus* sp. nov. is very consistent across the three localities where it has been found. Its small obconical body clearly differs from the elongated tubular aspect of the medium-sized *L. zitelli* Walcott, 1886 and *Leptomitus teretiusculus* Chen, Hou and Lu, 1989, and the larger *L. lineatus* (Walcott, 1920). It also lacks the goblet-shaped morphology of *Leptomitus undulatus* Rigby and Collins, 2004, but shares



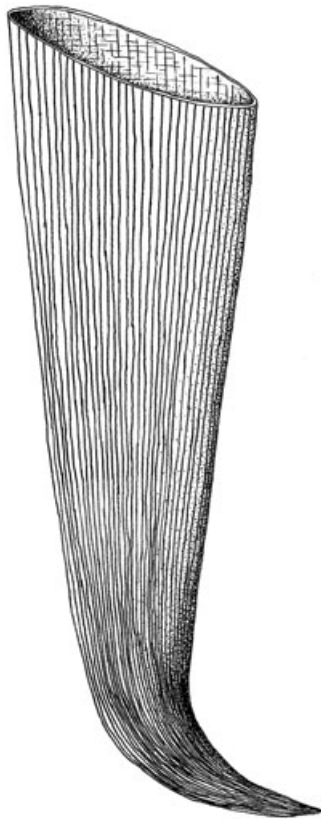
TEXT-FIG. 5. A–E, *Leptomitius conicus* sp. nov., from the Middle Cambrian Murero Formation, Cadenas Ibéricas, Spain. A, MPZ 2005/340 (RV₁/12b), complete specimen showing the typical obconical shape of the sponge and a slightly curved base; immersed in water; $\times 4.5$. B, MPZ 2005/591 (RV₁/12), complete specimen; note the corrugation at its base and the strong tapering as a result of having been buried tangential to bedding and subsequently compressed; $\times 3.5$. C, MPZ 2005/337 (RV₁/12), detail of upper part of specimen showing undulations affecting both sides of the flattened sponge; $\times 3$. D, MPZ 2005/592 (RV₁/12), detail of longitudinal rods in the middle part of specimen, preserved in the form of chlorite; immersed in water; $\times 50$. E, MPZ 2005/593 (RV₁/12), complete specimen with spicules weathered to limonite and hooked base; immersed in water; $\times 4.5$. RV, Rambla de Valdemiedes locality.

with it the thin double walls, the outer one of which has diagnostic vertical oxeas forming parallel rods that extend the whole length of the sponge.

Comparisons with dimensions of previously described species of *Leptomitius* (Table 1) show that *L. conicus* does not coincide with any of them. Its length, even extrapolating from the largest specimens, is still considerably less than that of any of the other species (Text-fig. 4). Its width, however, is similar to that of *L. zitteli* and *L. tereiusculus*. The spacing between the vertical skeletal rods is

in the lower end of the spectrum for the genus, while the diameter of the coarse oxeas of the new species is substantially less than that of the other species, overlapping only slightly with the specimen of *L. tereiusculus* described by Rigby and Hou (1995). *L. zitteli* in particular, but also *L. lineatus* and *L. tereiusculus* seem to preserve root tufts for anchoring to the soft substrate, while the Spanish species had a hooked base (Text-fig. 6).

This is not the only *Leptomitius* species present in Spain. A specimen of *Leptomitius* cf. *L. lineatus* has been



TEXT-FIG. 6. Reconstruction of *Leptomitus conicus* sp. nov., from the Middle Cambrian Murero Formation, Cadenas Ibéricas, Spain; $c. \times 3$.

described from the Rambla de Valdemiedes locality, also within the Middle Cambrian Murero Formation (García-Bellido Capdevila 2003).

There is a superficial resemblance between the spicule rods in *L. conicus* and the ribs of some early cephalopods and hyoliths (Malinky and Berg-Madsen 1999), but these have completely mineralized shells. In the Murero Formation, hyolith conchs are either conspicuously three-dimensional or show cracked walls owing to compaction, a process not present in these sponges. On the other hand, the operculum of this sponge, as can be observed in complete specimens, is straight (either perpendicular to the sponge axis or slanted), and not curved in the manner present in the groups mentioned above.

PHYLOGENETIC RELATIONSHIPS

The family Leptomitidae includes three Cambrian genera, *Leptomitus*, *Leptomitella* and *Paraleptomitella*, all of which appear in the Lower Cambrian, and the Silurian genus *Wareiella* Rigby and Harris, 1979. The tubular, elongated, simple-walled *Leptomitus*, with an inner layer of unbun-

dled monaxons, would be a reasonable origin for the group (Rigby and Collins 2004). *L. undulatus*, with its ill-defined horizontal inner-layer bundles, would have split early from the simple-walled, tubular shape represented by *L. teretiusculus*, close to the origin of the genus *Leptomitella*, which has well-defined inner horizontal, monaxon bundles (Text-fig. 3). The obconical shape of the Lower Cambrian *L. zitelli* could have developed from *L. teretiusculus*, later splitting into the linear *L. lineatus* and the obconical *L. conicus*. *Paraleptomitella* is markedly different in having curved cross-braced, coarse oxeas instead of parallel rods and an inner layer of bundled monaxons, and could have split from *Leptomitella*. According to Rigby and Collins (2004, text-fig. 11), leptomitids could have given rise to most other early monactinellid demosponges, while Botting (2003) suggested that they may be a side branch of the Hazeliids.

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