THE DEMOSPONGE GENUS \textit{LEPTOMITUS} AND A NEW SPECIES FROM THE MIDDLE CAMBRIAN OF SPAIN

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Abstract: Forty-five specimens of \textit{Leptomitus 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 \textit{Leptomitus conicus} have been analysed. Palaeoecological information derived from associated trilobites, brachiopods and ichnofossils shows that \textit{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 \textit{Leptomitus}. Based on body shape, wall structure and stratigraphical distribution, a phylogenetic tree of the various \textit{Leptomitus} species is proposed, with a central stock of simple cylindrical sponges branching out to other morphs.

Key words: \textit{Leptomitus}, 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 \textit{Crumillospongia} sp. from the Valdemiedes Formation and García-Bellido Capdevila (1999, 2003) found \textit{Leptomitus} cf. \textit{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 \textit{Leptomitus 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 \textit{Badulesia granieri} Zone and the base of the \textit{Pardailhania hispida} Zone (Lower–Middle Caesaraugustan; see Liñán et al. 2002, fig. 3.3).

Based on its simple wall structure and shape, \textit{Leptomitus} 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 (J 1 near Jarque), Rambla de Valdemiedes 1 (RV 1 near Murero) and Villafeliche 1 (Vi 1 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 \textit{Leptomitus conicus} sp. nov. comprises green lutites with scattered carbonate nodules (Text-fig. 2); some of the trilobites and echinoderms have been preserved as...
articulated specimens, which indicate a low-energy environment.

*Lepomitus conicus* has been recorded in the *Badulesia granieri* Zone and at the base of the *Pardailhania hispida* 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, *Condylomyge aff. regia, Conocoryphe (Parabailiella) languedocensis, Eccaparadoxides asturianus, E. rouvillei, Pardailhania hispida and Pero-

*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.

Interlayered with the sponge-bearing levels are ichnofossils that belong to the *Sericichnus and Diplichnites* 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
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

*Leptomitus* 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 *Protopspongia* (Rushton and Phillips 1973; Baresi 2003) and *Diagoniella* (Baresi 2003). Thus, the distribution of *Leptomitus* 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 Cambridae bradoriids (Siveter et al. 1996). The intercontinental distribution of *Leptomitus* 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. Leptomitus zitteli* Walcott, 1886.

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

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**TEXT-FIG. 3.** Correlation chart of the three regional scales with the distribution through the Cambrian of the different *Leptomitus* species (small reconstructions), and their phylogenetic relationships.
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 *Leptomitus* 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
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TABLE 1. Dimensions (in mm) of the species of Leptomitus.

<table>
<thead>
<tr>
<th>Species</th>
<th>Length (min.–max.)</th>
<th>Rod spacing</th>
<th>Coarse oxea Diameter</th>
<th>Length</th>
<th>Fine oxea Diameter</th>
<th>Length</th>
<th>Gastral oxea Diameter</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. zitelli</td>
<td>77</td>
<td>2–8</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>L. lineatus</td>
<td>360</td>
<td>4–14 5</td>
<td>0:6–1:1</td>
<td>0:05–0:10</td>
<td>8–10</td>
<td>0:02–0:025</td>
<td>0:07–0:08</td>
<td>0:007–0:015</td>
</tr>
<tr>
<td>L. teretiusculus</td>
<td>80</td>
<td>1–6</td>
<td>0:08–0:16</td>
<td>0:1</td>
<td>3–4</td>
<td>0:01</td>
<td>0:2–0:3</td>
<td>0:02</td>
</tr>
<tr>
<td>L. teretiusculus*</td>
<td>59</td>
<td>1:0–4:5</td>
<td>0:25–0:30</td>
<td>0:04–0:10</td>
<td>3–7</td>
<td>0:02–0:05</td>
<td>1–4</td>
<td>0:05–0:06</td>
</tr>
<tr>
<td>L. undulatus</td>
<td>78</td>
<td>6:5–38</td>
<td>0:1–0:4</td>
<td>0:06</td>
<td>25</td>
<td>0:015–0:020</td>
<td>–</td>
<td>0:015–0:020</td>
</tr>
<tr>
<td>L. conicus</td>
<td>11–36</td>
<td>3:5–9</td>
<td>0:045–0:12</td>
<td>0:015–0:075</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Dimensions in parentheses are extreme values.


Occurrence. The oldest species of Leptomitus is recorded from the Eoredlichia-Wuttingaspis Biozone, Qionghzhuan 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 posed by Peng and Babcock (2001) and Peng (2003). The youngest record of Leptomitus is from the Burgess Shale (Canada), which belongs to the Olenellus Zone (see Walcott 1890), Dyerian Stage (Palmer 1998). The two Leptomitus species from the Burgess Shale (Canada) have been recorded in the Bathyuriscus-Elrathina Zone (Fletcher and Collins 1998; Rigby and Collins 2004), within the Topazan Stage recently proposed by Sundberg (2005). Finally, the youngest record of Leptomitus 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).

Leptomitus 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.

EXPLANATION OF PLATE 2

Figs 1–7. Leptomitus 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, MPZ 2005/322 (RV1/131), 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 (V1/8), detail of specimen showing the undulation of the rods. J, Jarque locality; RV, Rambla de Valdemedes locality; Vi, Villafeliche locality.
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an obliquely compressed specimen that was buried diagonal to the shape (Text-fig. 6) with an angle between 9 and 15 degrees. In the sponge, the rods are always more densely packed at the base to 15, rods per millimetre and in the specimens where this angle varies laterally and reach up to 0ÆÆ between rods of one odd fragment vary as wide as 0ÆÆ. The spacing between rods increases slightly from the base to the upper areas of the sponge. Most specimens show a hooked base (Pl. 1, figs 1, 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 gastric layer. Some specimens have sediment filling their spongocoels, which has flattened thicknesses of 0Æ12–0Æ36 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

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

<table>
<thead>
<tr>
<th>Total length (min.–max.)</th>
<th>Width</th>
<th>Rod spacing</th>
<th>Coarse oxea diameter</th>
<th>Rods/mm basal–distal</th>
<th>Angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPZ 2005/321*</td>
<td>30</td>
<td>0Æ88–6Æ5</td>
<td>0Æ075–0Æ12</td>
<td>0Æ015–0Æ045</td>
<td>7Æ81</td>
</tr>
<tr>
<td>MPZ 2005/322*</td>
<td>18Æ4</td>
<td>0Æ5–3Æ92</td>
<td>0Æ047–0Æ082</td>
<td>0Æ012–0Æ024 (0Æ036)</td>
<td>10Æ2</td>
</tr>
<tr>
<td>MPZ 2005/323</td>
<td>12Æ8</td>
<td>3Æ5</td>
<td>0Æ047–0Æ07</td>
<td>(0Æ035) 0Æ047–0Æ07</td>
<td>12Æ57</td>
</tr>
<tr>
<td>MPZ 2005/324*</td>
<td>21Æ2</td>
<td>0Æ78–4Æ5</td>
<td>(0Æ059) 0Æ07–0Æ095</td>
<td>0Æ024–0Æ036</td>
<td>–</td>
</tr>
<tr>
<td>MPZ 2005/325</td>
<td>20</td>
<td>3Æ15–5Æ2</td>
<td>0Æ083–0Æ12</td>
<td>0Æ024–0Æ036</td>
<td>8Æ8–7Æ11</td>
</tr>
<tr>
<td>MPZ 2005/326</td>
<td>7</td>
<td>4Æ–5Æ5</td>
<td>0Æ12–0Æ37 (0Æ42)</td>
<td>0Æ024–0Æ036</td>
<td>1Æ99</td>
</tr>
<tr>
<td>MPZ 2005/327</td>
<td>15</td>
<td>1Æ5–4</td>
<td>0Æ03–0Æ075</td>
<td>0Æ015–0Æ03</td>
<td>10</td>
</tr>
<tr>
<td>MPZ 2005/328</td>
<td>12</td>
<td>4Æ–5</td>
<td>0Æ06–0Æ15</td>
<td>0Æ015–0Æ03</td>
<td>6Æ94</td>
</tr>
<tr>
<td>MPZ 2005/329*</td>
<td>11Æ2</td>
<td>0Æ3–3Æ5</td>
<td>0Æ045</td>
<td>0Æ024–0Æ036 (0Æ1)</td>
<td>7Æ14</td>
</tr>
<tr>
<td>MPZ 2005/330*</td>
<td>13Æ6</td>
<td>0Æ48–3Æ5</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>MPZ 2005/331</td>
<td>2Æ2</td>
<td>2Æ–5</td>
<td>0Æ07–0Æ095 (0Æ12)</td>
<td>0Æ024</td>
<td>8Æ5–5</td>
</tr>
<tr>
<td>MPZ 2005/332</td>
<td>10</td>
<td>3</td>
<td>0Æ045–0Æ075 (0Æ105)</td>
<td>0Æ015–0Æ03</td>
<td>10Æ62–10</td>
</tr>
<tr>
<td>MPZ 2005/333</td>
<td>17</td>
<td>2Æ8–6Æ4</td>
<td>0Æ045–0Æ075</td>
<td>0Æ015–0Æ03</td>
<td>15Æ70–13Æ03</td>
</tr>
<tr>
<td>MPZ 2005/334*</td>
<td>13Æ5</td>
<td>0Æ15–2Æ95</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>MPZ 2005/335</td>
<td>19</td>
<td>8Æ25–10Æ4</td>
<td>0Æ083–0Æ15 (0Æ177)</td>
<td>0Æ036–0Æ072</td>
<td>5Æ38</td>
</tr>
<tr>
<td>MPZ 2005/336</td>
<td>7</td>
<td>3Æ5</td>
<td>0Æ06–0Æ15</td>
<td>0Æ015–0Æ03</td>
<td>13Æ14</td>
</tr>
<tr>
<td>MPZ 2005/337*</td>
<td>36</td>
<td>1Æ24–9</td>
<td>0Æ075–0Æ105</td>
<td>0Æ06–0Æ075</td>
<td>8Æ9–6Æ88</td>
</tr>
<tr>
<td>MPZ 2005/338*</td>
<td>29</td>
<td>1Æ47–6Æ5</td>
<td>0Æ06–0Æ105</td>
<td>0Æ03–0Æ06</td>
<td>9Æ2–8Æ62</td>
</tr>
<tr>
<td>MPZ 2005/339*</td>
<td>35</td>
<td>0Æ68–9</td>
<td>0Æ06–0Æ09</td>
<td>0Æ06–0Æ075</td>
<td>–</td>
</tr>
<tr>
<td>MPZ 2005/340*</td>
<td>28</td>
<td>0Æ6–6Æ5</td>
<td>0Æ075–0Æ15</td>
<td>0Æ03–0Æ06</td>
<td>11Æ6–8Æ28</td>
</tr>
<tr>
<td>MPZ 2005/591*</td>
<td>17†</td>
<td>1Æ7–9</td>
<td>0Æ06–0Æ105</td>
<td>0Æ045–0Æ075</td>
<td>8Æ62</td>
</tr>
<tr>
<td>MPZ 2005/592*</td>
<td>21</td>
<td>1Æ6–3Æ8</td>
<td>0Æ03–0Æ075</td>
<td>0Æ015–0Æ045</td>
<td>14Æ5–10Æ25</td>
</tr>
<tr>
<td>MPZ 2005/593*</td>
<td>15</td>
<td>0Æ15–4Æ13</td>
<td>0Æ045–0Æ075</td>
<td>0Æ015–0Æ03</td>
<td>–</td>
</tr>
</tbody>
</table>

* Complete or almost complete specimen.
† Obliquely compressed specimen.
Dimensions in parentheses are extreme values.
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 *Leptomitus* (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. teretiusculus*. 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. teretiusculus* described by Rigby and Hou (1995). *L. zitteli* in particular, but also *L. lineatus* and *L. teretiusculus* 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 *Leptomitus* species present in Spain. A specimen of *Leptomitus* cf. *L. lineatus* has been
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 unbulged 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 Haziellids.

**REFERENCES**


