in the subfamily both castes have the same number of separated waist segments, namely one in *Apomyrma* and two in *Anomalomyrma* (the female of *Protanilla* remains unknown).

Male

Apart from a single pharate male of *Apomyrma* noted by Brown *et al.* (1971), no worker-associated males have ever been described in Leptanillinae. Numerous isolated males (eighteen species), assumed to belong in Leptanillini, have been described in *Leptanilla* and its satellites *Phaulomyrma*, *Noonilla*, *Scyphodon* and *Yavnella*. Indubitably some of these will eventually be found to be conspecific with worker-based species within *Leptanilla* when collections containing workers in association with males are made. Petersen (1968) gives a good synopsis of this sex; see also Baroni Urbani (1977) and Kugler (1987).

Males of *Protanilla* and *Anomalomyrma* remain unknown, or just possibly may be represented by one of the male-based genera mentioned above, and the pharate male of *Apomyrma* provides very little information. Thus the diagnosis below is both tentative and unsatisfactory, and applies with certainty only to members of tribe Leptanillini, in the sense of this publication.

1 Mandibles usually reduced, represented by a pair of small, apparently non-opposable lobes; more rarely the lobes larger and plate-like.
2 Antennal sockets exposed; antennae with 13 segments.
3 Alate; venation absent or reduced to a single vein just behind the leading edge (probably a fusion of *Sc+R+Rs*), or with apical abscissa of *Rs* free. More rarely *Cu* and the basal abscissae of *Rs* and *M* may be visible as spectral veins.
4 Pterostigma absent.
5 Waist with only abdominal segment 2 (petiole) separated.
6 Abdominal segment 4 without tergosternal fusion.
7 Genitalia large to enormously hypertrophied, often bizarre; not retractile.

Larva

As with the males, larval descriptions have only been accomplished for a few species of *Leptanilla* (five), and for *Apomyrma stygia*. For details see Wheeler & Wheeler (1965, 1971, 1989), Kugler (1987), and the synoptic larval study by Wheeler & Wheeler (1976).

Larvae belonging to genus *Leptanilla* are very distinctive, possessing the three remarkable characters mentioned in the introduction. Masuko (1987) has recently discovered the function of two of these. The peculiar projection from the ventral surface of the larval prothorax is now known to be a specialized carrying device, which workers grip with their lower mouthparts, but not the mandibles. Masuko also notes that the enlarged 'spiracle' on abdominal segment 3, as described by Wheeler & Wheeler (1965, 1976), is not a spiracle at all but a specialized organ for feeding haemolymph to the queen, as mentioned in the introduction to this paper. Masuko adds that under SEM observation normal spiracles can be seen.

Larvae of *Apomyrma* are leptanilline in shape but lack the diagnostic features of *Leptanilla*. Despite the sterling efforts of the Wheelers' it is apparent that comparative studies of many more leptanilline larvae need to be undertaken before authoritative synapomorphies can be worked out.

Phylogeny of Leptanillinae

The construction of the helcium (articulatory pretergite and presternite of abdominal segment 3) is proposed here as a strong synapomorphy of the clade Ponerinae + Leptanillinae. The Ponerinae in this instance excludes the cerapachyine tribes Cerapachyini, Cylindromyrmecini, and Acanthostichini, which are now regarded as a discrete subfamily Cerapachyinae (Bolton, 1990).

The Ponerinae and the Leptanillinae share the same very specialized and characteristic helcial structure, which is unique among all the poneroid subfamilies. It may be postulated that this structure has evolved twice, once in each subfamily, but as it appears exactly the same in both subfamilies and is unlike that of any other poneroid subfamily, it seems most parsimonious to accept a common origin for the articulation,