

result of the adoption of similar lifeways.

Strong doubts about the doryline affinity of *Leptanilla* first arose when Wheeler & Wheeler (1965) gave detailed descriptions of the larvae of three species. These larvae showed striking differences from the dorylines and exhibited some remarkable apomorphies not shown in any other poneroid group. So impressive were these characters that Baroni Urbani (1977), in his revision of the Leptanillinae as it was then understood, stated that the larvae were the main reason for separating leptanillines from dorylines. The apomorphies, as given by Wheeler & Wheeler (1965), were '(1) the peculiar projection from the ventral surface of the prothorax; (2) the reduction of the spiracles from the normal ten pairs to a single pair, which is located on abdominal somite III; and (3) the shape and stance of the mandibles.' Masuko (1987) has since discovered the function of some of these characters, as mentioned in the discussion of leptanilline larvae, below.

These strong characters isolating larval leptanillines from larval army ants prompted a closer look at the adult morphology of the leptanillines. As with the cerapachyines (Bolton, 1990) the abdominal segments of workers and females were quickly seen to display a wealth of previously unnoticed characters. As the analysis advanced it became apparent that not only were the leptanillines not particularly close to the dorylines, but that they were in fact the sister-group of the Ponerinae. Further, *Apomyrma*, a West African genus originally placed in the ponerine tribe Amblyoponini, was found to be a leptanilline. My current concept of subfamily Leptanillinae is completed by the inclusion of a third, new, tribe which contains two genera from the Oriental and Indo-Australian regions.

Thus the concept of subfamily Leptanillinae outlined below is much expanded and considerably different from earlier understanding. Previous phylogenies have all tended to place leptanillines somewhere near the army ant groups, although most of them clearly indicate that such a placement was tentative and dubious, and lacking adequate characterization. Brown (1954) summed it up quite nicely when he said that the Leptanillinae, in the sense of *Leptanilla* alone, 'has suffered such drastic anatomical reduction in most of the usually valuable phylogenetic characters that it is doubtful whether we

shall ever be certain of its true affinities.' He concluded that opinion at the time 'seems to favor relating the group to the Dorylinae.'

Later phylogenies, such as those of Wilson *et al.* (1967), Taylor (1978) and Dlussky (1988), all bring out the Leptanillinae with the army ant subfamilies, but all indicate clearly that the decision is not supported by strong evidence.

Another major problem which has dogged our understanding of the group, as also in the dorylines, has been the development of a dual taxonomy. By this I mean that one system has been developed for workers (and females where known), and a separate and unrelated system has been adopted for males. Within the Leptanillini this has resulted in the description of many isolated species-level taxa based solely on males, and has also led to the diagnosis of whole genera based solely on individuals of this sex, a process which unfortunately is still continuing (Kugler, 1987). Petersen (1968) and Baroni Urbani (1977) give systematic notes on these male-based genera. This is an unhappy state of affairs which needs to be cleared up by the acquisition of whole-colony samples, so that the various castes and sexes can be associated. I feel sure that when this has been accomplished the number of nominal species-level taxa now recognized in Leptanillini (thirty-six) will fall to a lower figure, and a number of names currently assigned generic status within Leptanillini will fall as synonyms.

The biology of the leptanillines is little understood. All presently known species are hypogaeic and, for the most part, that is all that is known. *Leptanilla* has been claimed to be a nomadic mass-forager for many years (e.g. Wheeler, 1910), probably because of its doryline-like dichthadiiform female, but published evidence showing details of such a lifeway has been lacking until relatively recently.

Masuko (1987) has found that *Leptanilla japonica* feeds exclusively on geophilomorph centipedes, in the soil. Colonies are small, with only about 100 workers, a single queen, and 100–200 brood. Perhaps the strangest biological feature he discovered is that queens feed only on exudations of larval haemolymph, secreted from a special gland on abdominal segment 3. This gland was thought to be a spiracle by Wheeler & Wheeler (1965), as discussed below in the notes on leptanilline larvae. The colony cycle is summarized thus by Masuko (1987). 'In