have the completely retractile genitalia characteristic of army ant males. Petersen's (1968) excellent review of leptanilline males shows just how different they are from the males of army ants.

Other considerations

A number of characters at first considered useful in this survey later proved to be of little or no value, and a couple of these merit a comment.

I first thought that the lack of a stridulatory system (dorsally on posttergite of abdominal segment 3 and pretergite of segment 4) in leptanillines may have value in the phylogenetic analysis. Unfortunately this is a character which comes and goes with baffling irregularity, not just in ants but in the Vespoidea (*sensu* Gauld & Bolton, 1988) in general. The stridulatory system occurs in all Myrmicinae examined so far, but appears to be universally absent in the army ant subfamilies and the cerapachyines, as well as the leptanillines. Among the Ponerinae it is present in Ponerini, Platythyreini, and the 'lower' Ectatommini, but seems wholly absent from the Amblyoponini and also missing from some 'higher' ectatommine genera.

Some characters important in the diagnosis of tribe Leptanillini are of no value at subfamily level as they are autapomorphies of the tribe. Included here are the larval characters mentioned above and the reduced wing venation. Even within the Leptanillini in its older sense the reduced venation, supposedly characteristic of the males, has been compromised, as *Yavnella* (Kugler, 1987: 54, Fig. 14) shows a much fuller vein system than is usually encountered in *Leptanilla* (Baroni Urbani, 1977: 473, Figs 43, 44). *Apomyrma* has an even more complete venation in the female (Brown *et al.*, 1971: 267, Fig. 7).

The occurrence of dichthadiiform females in genus *Leptanilla* and in the army ant subfamilies is not a synapomorphy. It seems most likely that the condition has arisen independently in each group as a nomadic and mass-predatory lifeway was evolved. Outside the aenictines, dorylines, ecitonines and genus *Leptanilla*, dichthadiigynes also occur in some *Leptogenys* (Ponerinae) (e.g. Wilson, 1958; Bolton, 1975), in *Onychomyrmex* (Ponerinae) (Brown, 1960), in *Simopelta* (Ponerinae) (Gotwald & Brown, 1967), and in at least one species of *Sphinctomyrmex* (Cerapachyinae) (Brown, 1975), where nomadism is known or suspected. Standing apart from this, other leptanillines such as *Apomyrma* and *Anomalomyrma* have normal alate females, although the peculiar fusion of abdominal sternites 2 and 3 in *Anomalomyrma* females (Fig. 7) may indicate the beginnings of yet another independent evolution of dichthadiigyny.

The leptanilline tribes and genera

Until now this subfamily has only contained the single tribe Leptanillini, but the current study indicates that three tribes are present: Leptanillini, Apomyrmini (transferred here from subfamily Ponerinae) and Anomalomyrmini, a new tribe from the Oriental and Indo-Australian regions, which is closer related to Leptanillini than either is to Apomyrmini.

A synopsis of the subfamily is given below, followed by a discussion of the phylogenetic relationships of the three tribes, and preliminary keys to genera have been drawn up. Following this the tribes are diagnosed and descriptions of their abdominal external morphologies are given.

Synopsis of subfamily

Leptanillinae Emery
Tribe Leptanillini Emery
Genus *Leptanilla* Emery (=*Leptomesites* Kutter)
Genus *Noonilla* Petersen
Genus *Phaulomyrma* Wheeler & Wheeler
Genus *Scyphodon* Brues
Genus *Yavnella* Kugler
Tribe Apomyrmini Dlussky
Genus *Apomyrma* Brown, Gotwald & Levieux
Tribe Anomalomyrmini Taylor
Genus *Anomalomyrma* Taylor
Genus *Protanilla* Taylor

Phylogeny of the leptanilline tribes

The characters cited below are necessarily based on the worker caste. Worker-associated females and males are scanty and far too poorly known to provide characters which can be proved to be universal. In queens, however,