

Brown (1954) presented a summary of all taxonomic information regarding Formicidae and proposed the first explicit phylogeny of the family. Brown's diagram shows a basal divergence within the ants into two main groups that he termed the poneroid and the myrmecioïd complexes. His poneroid complex included a basal group of 'primitive ponerines' with the 'advanced ponerines' budding out, together with the army ants (Dorylinae s.l.) and the myrmecines. The myrmecioïd complex included all other subfamilies, and was named after the genus *Myrmecia* Fabricius that appears at the base. Later, Wilson et al. (1967) proposed the same phylogenetic arrangement with the addition of the fossil *Sphecomyrma freyi* Wilson & Brown at the base of the myrmecioïd complex. Taylor (1978) presented a slightly modified diagram; he put *S. freyi* as the ancestor of all the ants and, based on the tubulation of the fourth abdominal segment, transferred the genus *Myrmecia* from the myrmecioïd complex to the poneroid complex, renaming the former as the formicoid complex.

Baroni Urbani (1989) published the first cladogram for all the subfamilies of Formicidae. His analysis is unreliable because of problems in character coding and search strategy (Carpenter 1990). In addition, he treated Ponerinae as a terminal clade in the analysis even though admittedly paraphyletic due to the lack of clear autapomorphies suggesting otherwise. In summary, Ponerinae has been recognized as a paraphyletic assemblage of genera since the phylogenetic relationships between ant subfamilies were considered for the first time by Brown (1954).

Bolton (1990a; 1990b; 1990c) discovered many potential taxonomically informative characters from a detailed study of abdominal plate morphology across the poneroid group of subfamilies. Bolton's discoveries are of great importance, nevertheless the methods of interpretation he used were neither fully cladistic nor consistent. He identified sets of synapomorphies for various groups of genera and decided that those groups deserved subfamily status. Consequently, he unified *Cerapachys* F. Smith, *Acanthostichus* Mayr, *Ctenopyga* Ashmead, *Cylindromyrmex* Mayr, *Leptanilloides* Mann, *Simopone* Forel and *Sphinctomyrmex* Mayr and revived the subfamily Cerapachyinae. He transferred *Apomyrma* Brown, Gotwald & Lévié from Ponerinae to Leptanillinae. He also proposed the tergo-sternal fusion of the IV abdominal segment as a synapomorphy for the remaining

Ponerinae genera and dismissed as parallelism all the characters shared between some 'advanced' ponerines and members of the revived Cerapachyinae and the doryline section (all army ants). Finally, he placed Ponerinae, Leptanillinae, Cerapachyinae and the army ant subfamilies into an informal 'poneroid group', defined by the fusion of the presclerite and postsclerites of the third abdominal segment. Despite Bolton's usage of cladistic terminology, these reclassifications were done without a test of congruence among data.

Baroni Urbani et al. (1992) performed a cladistic analysis using subfamilies of Formicidae as terminal taxa. This analysis was based on Bolton's recent reclassifications, but with the following further modifications: *Aenictogiton* Emery, a genus known only from males with a history of uncertain placement between Ponerinae and the army ants (s. s.) was treated as a separate terminal; *Apomyrma*, was also treated as a separate terminal, despite Bolton's recent reclassification; *Leptanilloides*, one of the genera placed by Bolton in Cerapachyinae, was also treated as a separate entry. Ponerinae is polymorphic for 41.3 % of the informative characters in the matrix. This situation reflects the heterogeneity of the ants placed inside this taxon. Figure 1 shows the resulting cladogram. This result supports the separation of the ants into Bolton's poneroid group (but see Grimaldi et al. 1997). The cladogram shows a basal polytomy inside the poneroid group involving Ponerinae along with *Apomyrma*, Leptanillinae and the rest of the poneroids. Based on that result, Baroni Urbani et al. (1992) decided to place *Aenictogiton*, *Apomyrma* and *Leptanilloides* in subfamilies of their own.

Lattke's analysis

Lattke (1994) was concerned not with the relationships among members of the poneroid group, but rather with the monophyly of the Ponerinae tribe Ectatommini. For this purpose he included all but one of the genera considered by Brown (1958) as members of Ectatommini. He explicitly excluded *Aulacopone* because of the lack of information: about 38.8% of the characters he used in the matrix. To test the monophyly of Ectatommini, he sampled representative genera from 3 out of 5 of the remaining ponerine tribes. He performed two analyses using either *Cerapachys* (Cerapachyinae) or *Myrmecia* (Myrmeciinae) as outgroups, each in a separate analysis. His matrix contained 36 morphological characters and the following taxa: