to accept that it has arisen only once during the course of poneroid evolution, and to conclude that Leptanillinae and Ponerinae diverged after the evolution of this specialised articulation.

The helcium in Leptanillinae and Ponerinae consists of a thickened, inverted U-shaped collar formed from the pretergite (Figs 5, 10, 14). The helical sternite is reduced to a thin transverse strip, which may be shallowly convex to concave, running between the arms of the U-shaped tergal collar, some distance up from their apices and completely fused to the inner face of the tergite on each side. In both anterior and profile view the helcial sternite does not project ventrally below the apices of the tergite.

The two subfamilies within this clade are distinguished as follows in workers and females. After each apomorphy the corresponding plesiomorphic state, applicable to the alternative subfamily, is given in square brackets.

1 Apomorphies of Ponerinae.
Abdominal segment 4 with tergosternal fusion. [Tergosternal fusion of abdominal segment 4 absent in Leptanillinae.]
Metapleural lobes present. [Metapleural lobes absent in Leptanillinae.]

2 Apomorphies of Leptanillinae.
Spiracles of abdominal segment 3 large and far forward, very close to or on anterior face of post-tergite (Figs 2, 5, 9, 10, 13, 14). [Spiracles small and more posteriorly sited in Ponerinae.]

Apart from the above, the Leptanillinae have closed metacoxal cavities, with a complete cuticular annulus (Figs 1, 8, 12), and eyes are universally absent in all known workers (Figs 3, 4, 9, 11, 13, 15). In the Ponerinae the metacoxal cavities are open or, more usually, the cuticular annulus is interrupted by a mobile suture. Metacoxal cavities are closed only in a few very specialized small genera. Among the Ponerinae eyes are generally retained, being lost only in individual species of a few genera and lost independently in one or two extremely specialized small genera.

Separation from army ant subfamilies

The morphological characters which underlie the decision to uncouple Leptanillinae from its traditional association with the army ant subfamilies are as follows. First and foremost, the helcium in the army ant subfamilies (and in Cerapachyinae) is differently specialized. The helcial sternite in these groups is large, thick, and strongly convex, so much so that it bulges ventrally and is clearly visible in profile without dissection; it can normally be seen in ordinarily point-mounted specimens. In this condition it bears a strong resemblance to a reduced, fused, but otherwise normally constructed dorsal and ventral pair of abdominal sclerites, and hence is plesiomorphic at this level of analysis. The condition seen in leptanillines and ponerines, described above, is a modification of this state, with enlargement of the tergite and reduction and specialization of the sternite, and hence is apomorphic.

Apomorphic developments common to workers of the army ant subfamilies (and also the Cerapachyinae), but lacking in the Leptanillinae and Ponerinae, include the posterior migration of the spiracles of abdominal segments 5–7 so that all abdominal spiracles are visible. Specialization of the army ant pygidium (tergite of abdominal segment 7) has taken place, either by extreme reduction in size, development of a transverse furrow subapically, or by flattening its dorsum and arming it with teeth or denticles. Leptanillines and ponerines retain the plesiomorphic state here, having abdominal spiracles 5–7 concealed by the preceding tergite (Figs 3, 9, 13) and having a simple large pygidium which is convex and evenly curved.

Apart from these features, which cover all the subfamilies concerned, it should also be pointed out that the Ecitoninae and the aenictines have the poststernite of abdominal segment 3 much reduced (apparently independently) relative to the third posttergite, and that the Dorylinae and Ecitoninae both retain the plesiomorphic state of having the propodeal spiracles situated far forward. In leptanillines the poststernite of abdominal segment 3 is not drastically reduced relative to the size of posttergite 3, and the propodeal spiracles are shifted backwards on the sclerite.

Finally, leptanilline males, whilst unique in several ways (lobate mandibles, strange to bizarre genitalia, much-reduced venation), do not show any of the 'sausage-fly' habitus associated with the army ant subfamilies, nor do they