where their margins meet. This arrangement is considered plesiomorphic as it represents the closest approximation to a simple reduced segment, without any superimposed or secondarily derived specialisation.

In contrast the apex of the sternite is complex in ponerines and often highly specialized. It may be truncated, concave, or bilobate; the tergal apex may flare outwards from the sternite; clefts or incisions may be developed on each side between tergite and sternite; complex internal inflections or lobes from the sternite may develop; or combinations of these may occur. Dissociation of segments 2 and 3 in ponerines shows that the posterior foramen of segment 2 is complex and modified away from the simple reduced segment state seen in cerapachyines. All these specializations in ponerines are regarded as apomorphic.

(ii) *Sternite of helcium* (Figs 1–11, 13–15, 17–23)

The cerapachyine helcium, seen in profile, shows a large convex and prominent sternite which is very conspicuous. It is so large that it can be seen in normally mounted specimens, without dissection (Figs 3, 4, 9, 10, 14, 15), and appears to play an important part in the articulation of segments 2 and 3. In front view the helcial sternite is attached (fused) low down on the inner sides of the tergal arch and is strongly convex ventrally (Figs 1, 6, 7, 11, 15). Its lowest point always projects well beyond the lower margins of the helcial tergite.

The ponerines show a much reduced helcial sternite which is not nearly so convex. In profile the sternite is invisible and the helcium appears to consist solely of the tergite. Frontal view reveals that the sternite is small, only weakly convex to flat, and runs transversely between the inner walls of the tergal arch, being attached (fused) well above the lower tergal margins.

The state of the helcium in cerapachyines is regarded as plesiomorphic, that of the ponerines as apomorphic. The cerapachyine condition reflects the closest approximation of the ancestral segment shape, with a simple arched tergite and sternite and with both sclerites visible.

(iii) *Spiracles of segments 5–7* (Figs 1, 6, 7, 11, 15, 17–23)

The spiracles of segments 5–7 are all visible in cerapachyines without artificial distension or dissection of the gaster. In general they are situated on the posttergite of each segment, just behind the posterior margin of the preceding tergite. In some species the spiracle may be very close to the pre-posttergal boundary. (This condition also occurs in the subfamilies Dorylinae and Ecitoninae.)

In ponerines the spiracles of segments 5–7 are not visible without artificial distension or dissection of the gaster. The spiracle of segment 5 is on the pretergite but very close to the pre-posttergal boundary; it may be revealed with only a slight retraction of the posttergite of segment 4. The spiracles of segments 6–7 are far forward on each pretergite and are fully concealed by the posttergites of the preceding segments.

Examination of 'lower' poneroid groups such as Myrmeciinae and Pseudomyrmecinae, considered primitive on many morphological grounds, and of lower aculeates such as *Tiphia*, indicates that the plesiomorphic condition in poneroid ants is that exhibited by the Ponerinae; and hence the cerapachyines are apomorphic in these characters.

(iv) *Tergosternal fusion of segment 4*

The tergite and sternite of segment 4 are unfused in the cerapachyines, fused in the ponerines. The fused condition is apomorphic and thus the cerapachyines express the plesiomorphic condition.