the gastral dorsum, but here the gaster is elongate and usually flattened, segments behind the first being apicoventral and reduced. The function here is one of protection (Bolton, 1974). When threatened Cataulacus species either grip firmly onto the bark and present an almost unbroken armoured surface to an aggressor, or roll into a protective ball. The modification of the gaster in this genus has not been for the same reasons as in Secostruma. Ankylomyrma shows a development of the first gastral tergite far beyond that seen in Secostruma. In this genus (Bolton, 1981) the first tergite forms almost the whole of the gaster; it is ball-like with an anteroventral orifice within which the remaining gastral segments are telescoped. The relatively powerful sting projects anteriorly. The modification here appears to have taken place for the same reasons as in Secostruma but in a very different habitat. As far as is known Ankylomyrma occurs only in the topmost branches of high rainforest trees in West and Central Africa; its prey and biology remains unknown.

## Affinities of Secostruma

Secostruma exhibits a combination of features characteristic of the Myrmica-group and the Tetramorium-group, and has a petiolar structure acquired by convergence or parallel evolution with a member of the Podomyrma-group, as discussed below.

Although it is certain that Secostruma should be included in either the Myrmica-group or the Tetramorium-group, it is difficult to decide which. The main synapomorphies of the Tetramorium-group include specialized mandibular dentition and the presence of a lamellate appendage apicodorsally on the sting in workers and females, and the presence of an elongate fusionsegment in the antennal funiculus of males (Bolton, 1980). Members of the Myrmica-group lack these features but have a characteristic pattern of forewing vein-reduction (Kusnezov, 1951; Bolton, 1988). None of these can be confirmed for Secostruma as the only available specimen is the holotype worker, which unfortunately has its sting completely withdrawn, and has evolved an autopomorphic mandibular structure.

The *Tetramorium*- and *Myrmica*-groups are very closely related, appearing to be linked at a

- higher level by a characteristic ventral alitrunk structure, form and position of propodeal spiracles, and construction of promesonotum, mandibles and clypeus, though work on these characters remains incomplete as yet. A review of the main characters of *Secostruma*, in an attempt to place the genus accurately, follows. The numbers duplicate the position in the generic diagnosis of *Secostruma* given above.
- 1. The palp formula count of 4, 3 is vastly predominant in *Tetramorium* (Bolton, 1980), but also occurs in *Hylomyrma* (Kempf, 1973), and in most *Ephebomyrmex*, and universally in *Pogonomyrmex* (Cole, 1968) of the *Myrmica*group.
- 2. form of The the mandibles autapomorphic in Secostruma, but their structure may be derived from a tetramoriine ancestral pattern or from a myrmicine one. In Tetramorium the dentition consists of an apical series of 3 larger teeth followed by a basal series of (usually) 4 smaller teeth (Bolton, 1980). In Myrmica and its allies the dentition consists of a series of 6 or more teeth which more or less regularly decrease in size from the apical tooth. The loss of a few preapical teeth from either of these would give a condition approximating that exhibited by Secostruma (Fig. 4). However, it seems that the most parsimonious alternative is to assume that the mandible in Secostruma has evolved from a tetramoriine form by the loss of two preapical teeth, leaving the apical and 4 small basals. This implies fewer and less dramatic modifications than would be necessary to obtain this mandibular form directly from a Myrmica-like ancestor.
- 3. Absence of an isolated strongly developed median clypeal seta (at the midpoint of the anterior clypeal margin) is common to both the tetramoriines and myrmicines, and is a plesiomorphic state. An indentation at the midpoint of the clypeal margin is a feature commonly encountered in *Tetramorium* (Bolton, 1977, 1980), but is apparently never developed in the *Myrmica*group.
- 4. Modification of the lateral portions of the clypeus into a shield-wall in front of the antennal insertions in universal in the tetramoriines. It is also widely and variably developed in the *Myrmica*-group in some species of *Hylomyrma*, *Pogonomyrmex* and *Myrmica*. However, in those members of the *Myrmica*-group showing this feature, the shield-wall is generally not as