



Figure 2

Armaniidae imprint fossils from Cretaceous of Siberia, Russia. (a) *Armania robusta*. (b) *Pseudarmania rasnitsyni*. Both fossils are from 95 myo mudstone of Obeschayuschiy. (Images courtesy of G. Dlussky)

antenna is formed by the elongation of the first segment (the scape) and the distinct bend that separates it from the remainder of the antenna (the segmented funiculus). The petiole is the modification of abdominal segment II and in some ant groups segment III is further developed into a postpetiole. The metapleural gland is often considered the major feature used to define the Formicidae (52) because it is unique to ants and nothing even closely equivalent exists in any other group of hymenopterans. The gland appears to secrete antimicrobial and, in some cases, alarm substances (117). It has been secondarily lost in some, largely arboreal or socially parasitic, groups, particularly in the subfamilies Formicinae and Myrmicinae (6). The metapleural gland is usually absent in male ants. A nonmorphological synapomorphy for ants is eusocial behavior, which is expressed morphologically in females by the differentiation of the queen and worker castes (although in some socially parasitic taxa, the worker caste has been secondarily lost).

The Cretaceous specimens have elicited the most debate because with these fossils we can ask, When do the first “true” ants appear? In other words, what among bizarre Cretaceous ant-like hymenopterans is a true ant? Dlussky (19) first described the Armaniidae as an intermediate link between ants and scoliid wasps. There has been considerable discussion of whether this group should be given family rank (1, 6, 19, 26, 41, 42, 83, 89, 108, 114), but the most recent action by Bolton (6) classified them as a subfamily. Here we do not follow this recommendation and consider them at the family rank for the remainder of our discussion (see reasons below). Armaniids are known exclusively as imprint fossils that are poorly preserved (**Figure 2**), making the critical areas of the body difficult or impossible to observe (e.g., seeing whether a metapleural gland is present or not). Still, what we know of them is that armaniids possessed a broadly attached, but poorly developed, petiole, very short scapes, and females do appear queen-like (19). Although Dlussky (19) reported the presence of a metapleural gland in some armaniids, others have questioned this interpretation (41, 77). It is this lack of a definitive metapleural gland that has led some authors to consider the armaniids at the family rank and therefore not true ants (35, 84, 116). In addition to only being known from fragmentary imprint fossils, another major complicating factor in determining whether armaniids are true ants is that no specimens have been found with individuals