

To W. L. Brown, with compliments

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MORPHOLOGICAL CONSIDERATIONS AFFECTING THE
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(HYMENOPTERA, FORMICIDAE)

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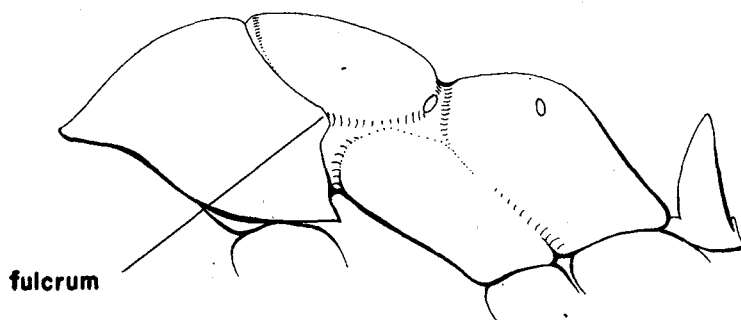
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In the course of identifying series of ants from Colorado and other western areas, the writer's attention was drawn to a peculiar structural feature of the genus *Formica*. The significance of this structure for the classification of these ants has not been appreciated. The morphological trait in question involves the thorax and particularly the promesonotal suture. In a great many ants, this suture is but a crease between the first two segments of the thorax, and in others it is even obsolete so that the two segments are immovably united. It has been assumed that the latter situation (thoracic rigidity) obtains in *Formica*, probably as a result of the fact that most

myrmecologists have dealt only with dried and fixed specimens mounted on pins. Inasmuch as all my specimens are preserved in alcohol, and are therefore still pliable, I have noticed for a long time past that the promesonotal suture of *Formica* is actually an articulated or movable joint. Until recently, no particular attention was paid to this fact, but when using the keys in Dr. Creighton's book on North American Ants, I found the thoracic structure of *Formica* could no longer be ignored.



F. cinerea lepida

Fig. 1, profile of the thorax of *Formica cinerea lepida* Wheeler, showing the promesonotal joint with articular surface exposed.

The above mentioned keys pertaining to the identification of the *fuscata* group contain a couplet for the separation of the forms of *cinerea* (p. 529, couplet No. 8), which states that in *F. montana* the anterior edge of the mesonotum stands distinctly above the pronotum and descends to the latter in an abrupt slope, and that in *F. altipetens* no such structural feature is to be seen, the pronotum and mesonotum usually forming a smooth convexity with little or no rise in the anterior level of the mesonotum. Examination of the type specimens upon which these differences are based (dried specimens), confirms Dr. Creighton's split in the key, but it will be observed that the key uses qualified statements, to wit, "usually form a single convexity . . ." and, "slightly or not at all raised above the level of the pronotum . . . etc." This was calculated to cover presumably exceptional instances. There is nothing unusual about such an approach to taxonomic

characters (in fact it is highly desirable), but in the case in point, the writer noticed that by moving the prothorax and the remainder of the thorax behind the promesonotal joint, it was possible to make any individual ant pass to either "lug" of the key with perfect ease, and thus vitiate the value of the key split. Incidentally, the articular surface exposed by these manipulations is very shiny and therefore easily distinguished from the adjacent subopaque and pubescent external surface of the thoracic dorsum. The articular surface also represents the steep decline from mesonotum to pronotum mentioned in Creighton's key. The fulera for this articulation are located, one on each pleuron, midway between dorsal and ventral surfaces of the thorax, in this way producing a hinged joint, fig. 1.

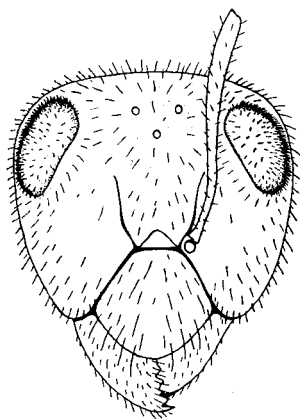
The character thus destroyed was employed by Dr. Creighton as the primary trait, but a secondary one was also given. At first it seemed we had no reliable method of separating *montana* from *lepida*, but further study serves to salvage these forms from synonymy and I believe we now have adequate means for recognizing them. The secondary characters given in Creighton's treatment concern pilosity and in reality are the best available; in fact they are the ones previously used in part by Wheeler in his revision of *Formica* in 1913. By arranging the *cinerea* complex on the basis of hair pattern, it is possible to recognize all forms without difficulty, and the characters, moreover, seem to be sufficiently constant. Pilosity as a separatory trait may be objected to by some, but it appears, so far, to be the only adequate criterion in the species involved. Hairiness, like color, is a minor characteristic in ants, but there is no intrinsic reason why these cues should be discarded as long as they can be shown to have constancy and geographic significance in any given case. Accordingly, the arrangement followed for detecting the species herein concerned is given below (see fig. 2):

Formica pilicornis Emery—covered with abundant, short, erect blunt hairs, the pilosity extending also to all parts of the head including very obvious hairs on the eyes and all surfaces of the antennal scapes.

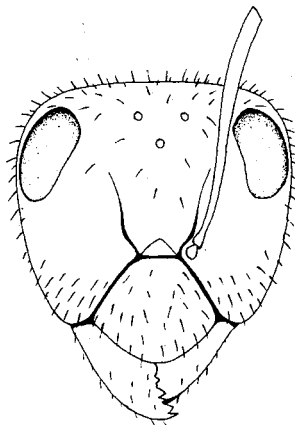
Formica cinerea lepida Wheeler—abundant, long, erect hairs present on most surfaces of the body including thoracic dorsum, petiolar scale, the gula, occipital border of the head and the genae, on the latter particularly near the insertions of the mandibles.

Formica cinerea montana Emery—hairs present on most parts of the body, but not so abundant as on *lepida*, including the gula and occipital border, but noticeably absent on the genae. Normally the cheeks are free of any hairs.

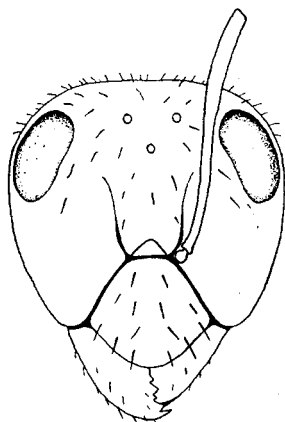
Formica altipetens Wheeler—hairs relatively sparse on the body with



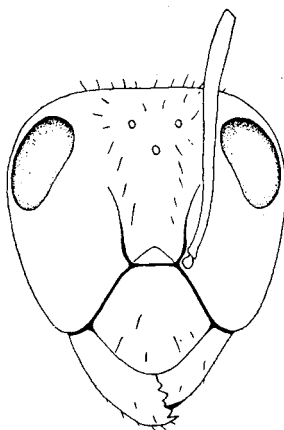
Formica pilicornis



F. cinerea lepida



F. cinerea montana



Formica altipetens

Fig. 2, frontal views of the heads of ants in the *cinerea* complex, arranged in the order of decreasing pilosity.

a few present on the gula, clypeus, front, and middle of the occiput. The genae and most of the head free of any hairs.

It will be seen from this list that there is a definite and consistent trend from a condition of dense pilosity (*pilicornis*) to one in which hairs are very sparse (*altipetens*). Study of an adequate series convinces me that these facts hold true, and that the relatively hairless condition of *altipetens* is not merely traceable to rubbed specimens. It will also be noticed that the nomenclature has been changed slightly to agree with what is considered to be the relationships of these forms, but it departs from Dr. Creighton's handling only in that *montana* is reduced from full species rank to that of a subspecies of *cinerea*. In my opinion, the fact that the typical *cinerea* is palaeartic does not make it impossible for its subspecies to occur in North America. The typical form and the American forms are so close morphologically, it does not seem proper to separate them specifically. That *pilicornis* is a full species, I have no doubt, for its dense pilosity extending to the scapes, makes it a very different ant, and its restriction to the Pacific Coast areas lends support to this view. *Montana* and *lepida* appear to be relatively slight departures from the European type, and seem to represent New World variants occupying respectively the eastern and the western portions of the United States, with a broad overlap in the Rocky Mountains of Colorado. (For distribution of all these ants see Creighton, 1950, pp. 531, 534, and 538.) Intergrades between *montana* and *lepida* are frequent in material coming from Colorado, as evidenced primarily by the fact that specimens with moderate pilosity and in all other respects referable to *montana*, may have 1 to 3 hairs on the lower genae near the mandibular insertions.

Altipetens blankets most of the range of *lepida*, and extends further south even as far as the Mexican border. It occurs fairly abundantly in the Colorado mountains, but is not known to reach as far east as *lepida*, that is, to the western Dakotas. *Altipetens* is the least pilose member of the series and therefore quite unlike *F. cinerea*. Since it is largely sympatric with *lepida*, it should for these reasons be regarded not as a geographic race of the true *cinerea*, but as a full species.

The author has no further information on the form described by Santschi as *F. cinerea canadensis*, and agrees with Creighton that it may be necessary, after examination of the types, to conclude that it belongs either to *altipetens* or to *lepida*. As it was described from a relatively low altitude (plains of Saskatchewan), I am inclined to believe it may be a northern sample of the *lepida* population.

The discovery of a movable thoracic joint in *Formica* has made certain other sections of Dr. Creighton's keys suspect, and with this in mind the point was pursued further. An articulation of the same sort exists in *Lasius*, *Acanthomyops*, *Camponotus*, *Myrmecocystus*, *Brachymyrmex*, *Oecophylla*, *Cataglyphis*, *Plagiolepis*, *Prenolepis*, *Paratrechina*, and *Polyergus*, as ascertained from an examination of specimens in my collection, and while a similar joint seems to be present in *Polyrhachis*, the

amount of movement obtainable in this genus may be infinitesimal. I have examined several species of *Polyrhachis* in alcohol belonging to Dr. Creighton, and have found a surprising situation. Two species, in the subgenera *Hagiomyrma* and *Hedomyrma*, have a definitely mobile thorax, four species, in the subgenera *Polyrhachis*, *Campomyrma*, and *Hagiomyrma*, have a joint showing limited movement, and one belonging to the subgenus *Chariomyrma* has the suture evident but no movement whatever is obtainable. It would appear, however, that this feature is broadly evident in the subfamily *Formicinae* as far as the genera observed are concerned, and will probably prove true in others as well. Other subfamilies were tested also with the following results. Among the *Dolichoderinae*, the genera *Tapinoma*, *Iridomyrmex*, *Dorymyrmex*, *Asteca*, *Liometopum*, and *Dolichoderus* all showed a very easily moved promesonotal articulation. In the *Myrmicinae*, the genera *Aphaenogaster*, *Myrmica*, *Manica*, *Pogonomyrma*, *Crematogaster*, *Pheidole*, *Solenopsis*, *Leptothorax*, *Myrmecina*, *Monomorium*, and *Stenammas* all demonstrated that the thoracic segments are firmly ankylosed into a single tagma. Among the *Dorylinae*, the genera *Eciton*, *Dorylus* and *Cheliomyrmex* also have absolutely immovable thoraces with hardly any trace of sutures visible dorsally. The only example of the *Pseudomyrminae* available, *Pseudomyrmex* itself, presented a movable promesonotal joint. And in the subfamily *Ponerinae*, (*sens. lat.*) we observe an inconstant condition of the articulation. *Ponera*, *Neoponera*, *Euponera*, *Leptogenys*, *Odontomachus*, *Anochetus*, *Pachycondyla*, and *Stigmatomma* all possess easily moved joints, while *Ectatomma*, *Proceratium*, *Sysphincta*, *Paraponera*, *Cylindromyrmex* and *Cerapachys* have no motion, and their thoraces are as immovable as in the *myrmecines*. The genus *Paraponera* possesses a definite suture, even dorsally, but the joint seems to be completely fixed as all attempts to elicit movement failed.

These genera represent only a random sampling of the conditions to be found in ants, and no doubt other genera would throw additional light on the question. But enough have been investigated to make it reasonably certain that the use of such a character as we encounter in the keys of the Ant Book can only be valid if the genus involved possesses a rigid thorax. With this fact clearly in sight, it is gratifying to state that couplet No. 18, p. 141, for the species of *Aphaenogaster* should cause no trouble. Unfortunately, as much cannot be said for the reliability of couplet No. 10, p. 441-2 for the genus *Myrmecocystus*, since the level at which the epinotum lies with respect to the anterior edge of the pronotum will depend entirely upon the angle assumed by the pronotum at its junction with the mesonotum. This angle in pinned specimens, though fixed by drying, is bound to vary from ant to ant, depending, of course, on its degree when the ants were killed.

It should also be pointed out that the advantage to be gained from linear measurements of the thorax of an ant when drawing up its description, as compared to total length of the specimen, is not as great as we might have expected, in genera that have a movable thoracic

suture. Such thoracic measurements will always have their value, but the taking of these data and their interpretation will have to be made with extra caution and due care to insure uniformity of procedure.

The apparently trivial structure discussed in this paper would seem to be of importance only for the separation of a rather small number of species, but when we regard the array of genera which have, or do not have, a movable joint, we are faced with a character that is of more fundamental nature. All the genera examined in Formicinae, Dolichoderinae, Myrmicinae, and Pseudomyrmecinae are consistent, that is to say, they possess or they lack, an articulating promesonotal junction, and only the Ponerinae show much variation with respect to this feature.

If we consider the Arthropods as a whole, and the insects in particular, it is evident that a multiplicity of separate, though repeated parts, is a primitive condition, and that as one progresses upward through these groups there is a tendency for replicative structures to fuse, and therefore suffer reduction in their numbers. This behavior can be shown to have occurred probably on numerous occasions and may consequently be interpreted as a polyphyletic phenomenon. Then if this reasoning can be extended to the present situation, it may be suggested that the mobile condition of the thoracic juncture in ants is primitive (or perhaps generalized), and the immobilized state a derived or advanced condition. It will be recalled that in the Ponerinae both phases are observable, with some genera showing evolution toward fixity of the thorax. The ankylosed or fused state turns up again in the army ants and the myrmecine genera, possibly as independently evolved phenomena, while in the dolichoderines and formicines, though in many ways admittedly highly specialized groups, the relatively primitive mobility has been retained. What correlation these structural aspects may have with the behavior and physiology of various ants, and with the causes of such evolutionary divergences, is not apparent at this time. It might be emphasized, however, that a correlation exists between the presence of a mobile thorax, and the agility and tempo of behavior of ants. In general it may be said that dolichoderine and formicine ants are very active and responsive insects, and this is true of *Pseudomyrmex* also, while as a rule myrmecine species by comparison are stolid and show a more plodding behavior. It must be recognized, of course, that there are degrees in either one of these categories. To what extent the ponerine genera would conform to this characterization is uncertain, but it would be worthy of investigation.

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