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# OBSERVATIONS ON THE PUPAE OF BEES 

(Hymenoptera: Apoidea)

Charles D. Michener ${ }^{1}$
In the course of a recent study of bee larvae, pupae of a number of species have come to hand. The present investigation was undertaken in order to glean whatever information could be obtained on the pupal characters and the relationships of groups.

The pupae, as is well known, exhibit essentially the shape and form of adults, and the general features of pupae have been described and illustrated by many authors (e.g. Packard, 1897). From our standpoint the important pupal features are those not repeated in the adult, since the adult characteristics are well known. Unfortunately most authors have not systematically recorded these structures which are peculiar to pupae. As a result, most published accounts of pupae are of little value from the present standpoint.

Those pupal characters which are peculiar to pupae consist principally of spines and projections arising from various parts of the body. Their functions are unknown, although in some cases it is possible to see hairs of the adult projecting into them in older pupae. This is by no means always the case, spines being present (although small) in such relatively hairless bees as Neopasites. Nonetheless, the original function of these projections may have been to provide space for the development of the long hairs characteristic of bees and associated with their pollen collecting habits. On broad flat areas of the body these hairs can develop in a recumbent position, but at the ends of segments where the spines are of most frequent occurence long hairs cannot well develop in this position. Thus the long spines of the coxae and trochanters serve to house the long hairs arising on these segments in some bees (fig. 1). This explanation cannot well account for the scutal tubercles of Xylocopa or Melecta, for example, but does seem to be a possible explanation of most of the pupal projections.

It is interesting that certain adult spines and projections which have arisen repeatedly among the various bee groups correspond to the pupal projections. For example, anterior coxal spines,

[^0]found in adults of at least certain species of such unrelated genera as Colletes, Nomada, Megachile, and Xylocopa, but generally absent in adult bees, are formed inside of pupal spines which are found in virtually all bees but ordinarily contain only hair. Thus it would seem that the pupal spines provide a potentiality for the development of adult spines.

Table I summarizes the characteristics peculiar to pupae of bees. The characters require explanation as follows:

1. "Scape"-When the antennal scape bears a small median tubercle, it is marked + .
2. "Vertex"-The symbol + indicates that a pair of tubercles are present on the vertex more or less in the position of the lateral ocelli.
3. "Frons"-The symbol + indicates the presence of a pair of low tubercles, one in front of the summit of each eye.
4. "Lateral angles of pronotum"-The symbol + indicates that these angles are produced to spines.
5. "Posterior lobes of pronotum"-The symbol + indicates that these lobes are produced.
6. "Mesoscutum"-The symbol + indicates that paired tubercles are present.
7. "Scutellum"-The symbol ++ indicates a pair of large erect protuberances while + indicates a pair of smaller, anteriorly directed ones. (See Melecta, excluded from table since specimens are not available.)
8. "Metanotum"-The symbol + indicates a median protuberance.
9. "Tegulac"-The symbol + indicates a protuberance, ++ a spine, $\pm$ a protuberance present or absent.
10. "Wings"-The symbol + indicates a small median tubercle on each forewing and usually a small basal tubercle as well.
11-13. "Coxae"-The symbol + indicates an inner apical coxal spine; ++ is used if the spine is unusually long.
14-16. "Trochanters"-The symbol + indicates a posterior apical spine; ++ is used if the spine is unusually long.
17-18. "Femora"-The symbol + indicates a posterior or inferior basal protuberance on the femur while ++ indicates a spine in this position.
11. "Hind tibiae (base)"-The symbol + indicates a protuberance near the base of each hind tibia, at about the position of the apex of the basitibial plate, while ++ indicates a spine in this position.
12. "Hind tibiae (apex)"-The symbol + indicates an outer apical spine at the apex of the hind tibia.
13. "First tergum spiculate"-The numerals indicate the anteriormost metasomal tergum to bear a transverse subapical row of spicules. Commonly spicules are found from the tergum indicated in this row back to the fifth (females) or sixth (males) tergum, but this is not universal.
14. "Size of tergal spicules"-The symbol + indicates minute spicules, giving rise to setae which are more conspicuous than the spicules; ++ indicates larger spicules, while +++ indicates very large spicules.
15. "Long setae"-The symbol + indicates long setas on vertex, mesoscutum, and metasomal terga.

|  | \% |  |  |  |  | $\frac{\stackrel{\pi}{\ddot{u}}}{\frac{\pi}{\tilde{u}}}$ | $\begin{aligned} & \text { gig } \\ & \text { ig } \end{aligned}$ |  | $\begin{array}{\|l\|l} \tilde{y} \\ \stackrel{8}{2} \\ \frac{6}{\lambda} \end{array}$ | $\begin{aligned} & \frac{0}{2} \\ & \frac{2}{4} \\ & \frac{2}{8} \\ & \frac{8}{2} \end{aligned}$ |  |  |  |  | 号 | $\frac{\square}{4}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1. Scape |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  |
| 2. Vertex |  | $+$ |  | + | + | + | + | $\pm$ |  |  |  |  |  |  |  |  |
| 3. Frons |  |  |  | + | $\pm$ |  |  |  |  |  |  |  |  |  |  |  |
| 4. Lateral angles of pronotum | $+$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 5. Posterior lobes of pronotum | $+$ | + |  |  |  |  |  |  |  |  |  | + | $+$ |  |  |  |
| 6. Mesoscutum |  |  | $2+$ |  |  |  |  |  | $2+$ |  | 4+ | $2+$ | $2+$ |  |  |  |
| 7. Scutellum | $+$ | $+$ |  | $+$ | $\begin{aligned} & + \\ & + \end{aligned}$ | $+$ | $\begin{aligned} & + \\ & + \end{aligned}$ |  |  |  |  | + | + |  |  |  |
| 8. Metanotum | $+$ | + |  | + | $+$ | + | + |  |  |  |  |  |  |  |  |  |
| 9. Tegulae |  | $+$ |  |  | $\pm$ | + | $+$ |  |  |  |  |  |  |  |  |  |
| 10. Wings |  |  |  | + | $+$ | + | + |  |  |  |  |  |  |  |  |  |
| 11. Fore coxae | $+$ | $+$ | + | + | $+$ | $+$ | + | + | $+$ | + | + | + | + | $+$ | + | + |
| 12. Mid coxae | $+$ | $+$ | + | + | $+$ | $+$ | + | + | $+$ | + | + | + | + | $+$ | $+$ | + |
| 13. Hind coxae | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $+$ | $+$ | + | + | $+$ | + | + | $+$ | + | + | + | + | + | $+$ | + |
| 14. Fore trochanters | $+$ | $\begin{aligned} & + \\ & + \end{aligned}$ | + | $+$ | + | + | $+$ | $+$ | $+$ | + | + | + | + | $+$ | + | $+$ |
| 15. Mid trochanters | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $+$ | + | $+$ | + | + | + | + | $+$ | + | + | + | + | + | + | $+$ |
| 16. Hind trochanters | $+$ | $+$ | + | + | $+$ | + | + | + | $+$ | + | + | + | $+$ | + | + | $+$ |
| 17. Fore femora | $+$ | $+$ | + | $+$ | + | $+$ | $+$ |  |  |  | + | $\begin{aligned} & + \\ & + \end{aligned}$ | $+$ |  | $+$ | $+$ |
| 18. Mid femora |  |  |  |  |  |  | $+$ |  |  |  |  |  | $+$ |  | $+$ | $+$ |
| 19. Hind tibiae (base) |  |  |  | $+$ | $+$ | + | $+$ |  |  |  |  |  |  |  |  |  |
| 20. Hind tibiae (apex) |  |  |  |  |  | $+$ |  |  |  |  |  |  |  |  |  |  |
| 21. First tergum spiculate |  |  | 2 | 1 | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |  |
| 22. Size of tergal spicules |  |  | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $\begin{aligned} & + \\ & + \\ & + \\ & \hline \end{aligned}$ | $\begin{aligned} & + \\ & + \\ & + \\ & \hline \end{aligned}$ | $\begin{aligned} & + \\ & + \\ & + \\ & \hline \end{aligned}$ | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $+$ | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $+$ | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | $\begin{aligned} & + \\ & + \\ & \hline \end{aligned}$ | + | $+$ |  |
| 23. Long setae |  |  |  |  |  |  |  | + |  |  |  |  |  |  |  |  |

It is evident from a study of Table I that, so far as the few bee pupae available are concerned, considerable support for existing classifications (see Michener, 1944) is provided. Thus the
family Colletidae is distinguishable by the absence of tergal spicules, a character shared only with Apis. The family Halictidae is recognizable by the numerous and very strong protuberances, the tubercles on the wings and the spine or tubercle at the base of the hind tibiae being found only in this family. Nomia falls clearly with the Halictidae on the basis of pupal characters, although some authors have put it with the Andrenidae. Megachile differs from all other known bee pupae in the presence of long setae. It is interesting that megachilid larvae are the principal bee larvae having setose bodies. The larger anthophorine bees (Emphor, Diadasia, Anthophora, Melecta) are distinguished from the Apinae by the presence of mesoscutal tubercles, and in this respect they resemble Xylocopa.


Fig. 1. Fore leg of Anthophora linsleyi Timberlake, pupa, showing by broken lines the developing adult leg within and by dotted lines some of the hairs inside the pupal spines.

The following descriptive comments are limited to those features of the pupa not shared by adults. For example, inner apical spines of the tibiae are not mentioned since the tibial spurs of the adults form inside of them and their position and number is re-
flected by the adult structures. Spines and other projections are absent unless stated to be present.

Colletes fulgidus Swenk
Lateral angles of pronotum and posterior lobes of pronotum produced; mesoscutellum with a pair of large protuberances; metanotum with large median protuberance; coxae, trochanters, and bases of anterior femora with long spines.

Montara, California, September, 1940 (J. W. MacSwain).

## Policana herbsti Friese

As described for Colletes but vertex with distinct pair of tubercles (in positions of lateral ocelli); lateral angles of pronotum not produced; tegulae produced; posterior margins of metasomal terga swollen.

Correo Nuñoa, Chile (Claude-Joseph).
Nomadopsis euphorbiae (Cockerell)
Mesoscutum with pair of very small tubercles, one on either side of midline, in front of middle; coxae and trochanters with spines; bases of fore femora each with inferior projection; metasomal terga, beginning with the second, with subapical rows of spicules, the rows interrupted medially.

Riverside County, California, August 17, 1946 (J. W. MacSwain).

## Augochlora pura (Say)

Vertex with pair of protuberances (in positions of lateral ocelli) and pair of lower ones just in front of upper ends of eyes; antennal scapes each with small protuberance; scutellum with pair of high protuberances; metanotum with median broad protuberance; middle of each forewing with protuberance; smaller one at base of each wing; coxae and trochanters each with small spine; bases of fore femora each with protuberance; base of hind tibia with short spine; metasomal terga with large subapical spicules, only a few on first tergum and these unusually large.

Short Mountain, Shenandoah, Virginia, June 6, 1941, in rotten $\log$ (A. B. Gurney) .

Lasioglossum (Chloralictus) sparsum (Robertson)
As Augochlora pura but pair of protuberances in front of upper ends of eyes and on antennal scapes absent; tegulae somewhat protuberant.

Lawrence, Kansas, June 24, 1951 (C. D. Michener). Lasioglossum (Evylaeus) kincaidii (Cockerell)
As Augochlora pura but small protuberances on antennal scapes absent; spicules of first metasomal tergum like those of second.

Montara, California, June 12, 1940 (J. W. MacSwain).

## Halictus tripartitus Cockerell

As in Augochlora pura but pair of protuberances in front of upper ends of eyes and on antennal scapes absent; tegulae somewhat protuberant; basal spine of each rear tibia a mere protuberance but apex of rear tibia with long spine on outer side (in addition to usual tibial spurs on inner side) ; spicules of first tergum similar to those of second.

Chino, Arizona, July 4, 1950 (J. G. Rozen, R. H. Beamer).
Nomia melandri Cockerell
Vertex with pair of small tubercles (in positions of lateral ocelli) ; scutellum with pair of high tubercles; metanotum with median projection; tegulae each with sharp spine; forewing with weak median and basal projection; coxae and trochanters with spines, those of former rather short, especially on rear coxae; fore and middle femora with protuberances at bases; base of hind tibia with spine; metasomal tergum three and following with subapical spicules.

Delta, Utah, June 27, 1950 (G. E. Bohart, C. D. Michener).
Megachile (Chelostomoides) sp.?
Coxae and trochanters with spines; metasomal sterna produced apically (female); vertex and median region of mesoscutum with long setae; metasomal terga two and following with subapical rows of long setae.

Blythe, California, April 2, 1941, in old Colletes burrow (E. G. Linsley, J. W. MacSwain).

Megachile (Litomegachile) brevis Say
As in the species of Chelostomoides but vertex with three small tubercles representing positions of ocelli.

Lawrence, Kansas (C. D. Michener).

## Xylocopa virginica (Linnaeus)

Mesoscutum with a pair of tubercles in front of middle, one on each side of midline; coxae and trochanters with long spines; metasomal terga two and following with small subapical tubercles; last tergum produced to a hard spine.

Veitch, Virginia, July 7, 1914 (T. E. Snyder). Neopasites sp.?
Coxae and trochanters with small spines; metasomal terga two and following with subapical rows of spicules.

The specimen is in poor condition and there may be more pupal structures than indicated.

Lawrence, Kansas, April 5, 1951, from nest of Calliopsis andreniformis Smith (C. D. Michener).

Emphor bombiformis (Cresson)
Mesoscutum with two pairs of tubercles, the anterior pair in front of middle, the posterior pair behind middle, the latter closer together than the former; scutellum swollen; coxae and trochanters with spines, anterior femora each with basal projection; metasomal terga two and following with subapical spicules.

Hattiesburg, Mississippi, August 20, 1944 (C. D. Michener).
Diadasia enevata (Cresson)
Posterior lobes of pronotum produced; mesoscutum with a pair of tubercules behind middle; scutellum with two tubercles, large and directed forward; coxae and trochanters with spines, those of rear trochanters short; anterior femora each with spine at base; metasomal terga two and following with subapical rows of spicules.

Delta, Utah, June 27, 1950 (G. E. Bohart, C. D. Michener).
Anthophora linsleyi Timberlake
Posterior lobes of pronotum produced to spines; mesoscutum with a pair of tubercules behind middle; scutellum with a pair of anteriorly directed tubercles; coxae and trochanters each with a spine; bases of fore and middle femora each with a long spine; metasomal terga two and following with subapical rows of spicules.

Twenty miles east of Bakersfield, California, March 29, 1941 (E. G. Linsley, J. W. MacSwain).

Anthophora (Clisodon) furcata syringae (Cockerell)
As above, but no long spine at base of middle femur.
Mineral King, Tulare County, California, August 10, 1939 (G. E. Bohart).
Melecta spp.
Semichon (1922) has described the pupa of Melecta armata Panzer. It is said to be similar to that of its host, Anthophora personata Erickson, except that the pair of mesoscutal tubercles are erect, each forming a multidentate crest, and the scutellar tubercles are much larger and directed posteriorly to form spines. The mesoscutal tubercles are shown to be similarly modified in Melecta miranda Fox by Porter (1951).

## Bombus americanorum (Fabricius)

Coxae and trochanters with apical spines; metasomal terga two and following each with subapical row of short setae.

Lawrence, Kansas, August, 1950 (C. D. Michener).
Bombus vosnesenskii Radoszkowski
Agrees with B. americanorum.

Hat Creek, Lassen County, California, June 4, 1941 (E. G. Linsley, C. D. Michener).

## Trigona cupira Smith

Coxae and trochanters with spines, those of fore and hind coxae very short; fore and middle femora each with projection at base; metasomal terga two and following with subapical rows of setae.

Juan Mina, Canal Zone, May 4, 1945 (C. D. Michener).

## Apis mellifera Linnaeus

Coxae and trochanters with spines, those of front coxae short, of front trochanters unusually long; fore femora each with a spine at base, middle femora with a blunt projection, hind femora with a broad rounded projection.

Lawrence, Kansas, June 1, 1952 (M. H. Michener).

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