NORMAN MARSTON

Taxonomic Study of the Known Pupae of the Genus Anthrax (Diptera: Bombyliidae) in North and South America

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Smithsonian Institution
Norman Marston

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ABSTRACT

Norman Marston. Taxonomic Study of the Known Pupae of the Genus Anthrax (Diptera: Bombyliidae) in North and South America. Smithsonian Contributions to Zoology, number 100, 18 pages, 1971.—The pupae of fourteen species in the cephus, oedipus, and tigrinus groups of the genus Anthrax are described, and a key is given to separate these and four other species in the albofasciatus and trimaculatus groups. Photographs illustrate the cephalic and anal tubercles of sixteen species.

Contribution No. 896, Department of Entomology, Kansas Agricultural Experiment Station, Kansas State University, Manhattan.

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Introduction

For several years I have been studying the taxonomy of adults of the genus *Anthrax* Scopoli. During this time a number of reared specimens associated with the pupal skins have been assembled. Since very little information is available in the literature on the taxonomy of Bombyliid pupae, descriptions of the available pupae and a key for their separation are here published.

I am grateful to the various institutions and individuals listed in my previous papers (1962, 1970) for the loan of specimens for study, and to Dr. Carl W. Rettenmeyer for photographic help. The work was supported in part by National Science Foundation Grant G21291 to Dr. R. H. Painter and by Kansas Agricultural Experiment Station Project 546.

A previous study (Marston, 1964) dealing with the biology of the *Anthrax* species of the albofasciatus and trimaculatus groups included descriptions and keys to the pupae of four species. Otherwise, the only key to pupae of *Anthrax* is that of Malloch (1917) which separates four species (under Spogostylum Macquart and Argyramoeba Schiner) along with species in other genera. Several species have been described incompletely (Townsend, 1893; Malloch, 1915; Malloch, 1917; Brooks, 1952) due to lack of closely related species for comparison.

In this study descriptions are given for fourteen species in the cephus, oedipus, and tigrinus groups, together with a key to these and the four species of the albofasciatus and trimaculatus groups described previously. Photographs illustrate the cephalic and anal tubercles of sixteen of the species.

Taxonomic Characters

Pupae of species of *Anthrax* possess many excellent diagnostic characters. Particularly, consistent variation between each species has been noted in the shapes of cephalic and anal tubercles (see plates). Interspecific variations involve primarily forms of tubercles and their spatial relationships. No attempt was made to compare relative lengths of tubercles, as specimens emerging through hard clay or similar materials have abraded tubercles. The anterior and posterior facial tubercles (on the long, narrow sclerite on the ventral surface of the head) also vary between species.

The cephalic tubercles are peculiarly modified in the two species representing the tigrinus group. The two sets of tubercles are broadly separated mesally, rather than united on a common, raised cephalic area as in other groups. Also, the tubercles are broad basally and
Table 1.—Spines and Setae on Pupal Skins of Anthrax (Number of Skins Examined Shown in Parentheses).

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<tr>
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<th>Anthrax koebelei Marston (4)</th>
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broadly rounded apically, except for the anterior pair in *A. xylocopae* Marston. The anal tubercles in the tigrinus group are quite simple, represented by broadly separated, spurlike structures, whereas in species in other groups the tubercles show various combinations of denticles and do not taper evenly to the apices.

Several excellent characters have been noted on the posterior abdominal terga. Species of the cephus group and *A. trimaculatus* (Macquart) have several small, simple spines between setae on the sixth and seventh terga. Most species of the albofasciatus and oedipus groups have no such spines, although some specimens of *A. limatulus* Say have a few, especially on the sixth tergum. (Tables in my 1964 paper on the albofasciatus and trimaculatus groups omitted these spines and those on the eighth tergum). On the eighth tergum of *A. trimaculatus* and on all species of the cephus group except *A. analis* Say and *A. koebelei* Marston, are two pairs of triangular, spinelike processes, absent in other groups of the genus, which occur on each side of the dorsolateral tumidities (rounded tumorlike irregularities in the integument). In *koebelei* the mesal pair of processes is absent, while in *analis* both are absent.

Members of the oedipus and albofasciatus groups have a transverse row of setae on each side of the eighth tergum in front of the dorsolateral tumidities.

In the species representing the cephus group, setae are present on the tergum only in *A. hyalacrus* Wiedemann, and are on a line between the dorsolateral tumidities.

The numbers of sections (membranous parts) of the spiracles vary widely, but with considerable intraspecific variation. The flange around the spiracles varies from broad and well developed to entirely absent. In general, species of the cephus group have the least developed flanges, while species of the albofasciatus and oedipus groups have the broadest. In the oedipus group, the two species representing the pluto subgroup, *A. melanopogon* and *A. atriplax*, have the flanges broadly lobed posterodorsally on the anterior spiracles, while species of the oedipus subgroup have them evenly rounded.

Numbers of abdominal setae and spines differ greatly among species, as can be seen in Table 1, but there is considerable intraspecific variation. In general, smaller specimens have fewer setae and spines than larger specimens. The ranges of setae and tergal spines are tabulated. The number of tergal spines in the table is the total on the segment, but the number of setae is given for one side only. Only males have setae on the eighth sternum.

### Key to Known Pupae of *Anthrax* in North and South America

1. Anterior cephalic tubercles broadly separated mesally (Plate 2H); anal tubercles, acuminate, without denticles (Plate 3D) (tigrinus group) .................. 2

2(1). Anterior cephalic tubercles broadly connected mesally (Plate 2I); anal tubercles with at least mesal, preapical denticles .......................... 3

3(1). Seventh abdominal tergum with numerous small, simple spines between setae; eighth with one or two sharp processes on each side (except in *analis*); setae absent or, between dorsolateral tumidities (cephus and trimaculatus groups) .................. 4

4(3). Dorsal and ventral denticles at base of each anal tubercle, when present, not connected by sharp lateral ridge (Plate 3e), occasionally indistinctly joined by low ridge; mesal process on eighth tergum, when present, usually tapering to sharp apex (cephus group) ................................................................. 5

Dorsal and ventral denticles at base of each anal tubercle connected by sharp lateral ridge (Plate 3e); mesal process on eighth tergum bifid apically (trimaculatus group) ................................................................. *A. trimaculatus* Macquart

5(4). Anal tubercles without denticles basally, long, narrow, and broadly separated mesally (Plate 3a,b) .................................................. 6

Anal tubercles with more or less distinct denticles basally, separated by less than width of one tubercle mesally ........................................... 7
Key to Known Pupae of *Anthrax* in North and South America—Continued

6(5). Eighth tergum with one spine on each side lateral to dorsolateral tumidities; anterior facial tubercles sharply rounded apically. .......... *A. koebelai* Marston

Eighth tergum without spines; anterior facial tubercles long and acuminate. .......... *A. analis* Say

7(5). Eighth tergum without setae between innermost processes; dorsal, basal denticles on each anal tubercle arising at basal fourth or fifth (Plate 3r,a). .......... 8

Eighth tergum with a seta on each side mesad to innermost process; dorsal, basal denticles on each anal tubercle arising at basal third or half. (Plate 3n).

*A. hyalacrus* Wiedemann

8(7). Each anal tubercle with sharp denticle ventrally on mesal margin about one-third of distance to apex; medial facial tubercle formed on a line between anterior and posterior facial tubercles or slightly outside it (Plate 2r). .......... 9

Each anal tubercle with poorly defined, blunt-tipped ridge running about one-third of way to apex; medial facial tubercle formed slightly inside a line between anterior and posterior facial tubercles (Plate 3h). .......... *A. argyrogyrus argyrogyrus* Wiedemann

9(8). Each anal tubercle about six times longer than medial width (Plate 3r).

*A. pluricellus* Williston

Each anal tubercle about five times longer than medial width or shorter.

*A. aterrimus* (Bigot)

10(3). Anal tubercles with more or less distinct mesal denticles about two-thirds of distance to apices (Plate 4r). .......... 11

Anal tubercles without sharp denticles mesally, each with sharp ridge curving ventromesally from tip and then recurving dorsally to meet oblique ridge at sharp point two-thirds of distance to apex (Plate 4s). .......... *A. nidicola* Cole

11(10). Medial and posterior cephalic tubercles not widely separated from anterior pair, united less than halfway to apices (Plate 1h). .......... 12

Medial and posterior cephalic tubercles widely separated from anterior pair, united about two-thirds of distance to apices, about equal in length (Plate 2c).

*A. albofasciatus albofasciatus* Macquart

12(11). Mesal process on ninth tergum small, broad and low, or sharply tipped apically .......... 13

Mesal process on ninth tergum well developed, about as long as broad, bifid, truncate or broadly rounded apically. .......... subspecies of *A. limatulus* Say

13(12). Flange on anterior abdominal spiracles lobed posterodorsally. .......... 14

Flange on anterior abdominal spiracles evenly rounded posterodorsally .......... 15

14(13). Posterovalen ridge on each medial cephalic tubercle extending to posterior margin of cephalic area. .......... *A. atriplex* Marston

Posterovalen ridge on each medial cephalic tubercle becoming indistinct near base of tubercle. .......... *A. melanopogon* (Bigot)

15(13). Dorsal and ventral denticles at base of each anal tubercle connected by low ridge or unconnected (Plate 4o,v); ventrobasal denticles not connected by flanges to ventral denticles on mesial margins (when present) .......... 16

Dorsal and ventral denticles at base of each anal tubercle connected by high flange (Plate 4s); ventrobasal denticles connected by sharp flange to ventral denticles on mesal margin. .......... *A. peruianus* Marston

16(15). Sixth abdominal tergum with several spines between setae. .......... *A. cordillerensis* Marston

Sixth abdominal tergum without spines between setae. .......... *A. irroratus irroratus* Say and *A. cintalpa* Cole
**Anthrax tigrinus** (DeGeer)

Hurd (1959) has reviewed available biological information on *A. tigrinus*, a common parasite of *Xylocopa virginica virginica* (Linnaeus) in the eastern United States. Three pupal skins have been examined.

Integument of pupa brownish hyaline with yellow setae and reddish brown, black tipped tubercles and spines. Cephalic tubercles (Plate 2H) formed in straight line, anterior pair not joined mesally; anterior tubercle broad, flattened dorsoventrally, broadly rounded apically, little longer than medial tubercle, with sharp ventromesal and lateral edges; medial tubercle flattened dorsoventrally, broadly rounded apically, with sharp mesal and lateral edges, and ventral and ventrolateral ridges; posterior tubercle somewhat flattened dorsoventrally, with sharp mesoventral and dorsolateral edges, and anteromesal and posterior ridges. Length of facial sclerite about one and a half times width, posterior edge truncate; anterior facial tubercles simple, acuminate to blunt apices, broadly separated mesally; posterior facial tubercle undeveloped.

Thoracic spiracle with about twenty-seven sections, posterior ones undeveloped; flange undeveloped. Abdominal spiracles with about twelve to seventeen sections, anteroventral ones reduced; flange poorly defined, forming thick lobe anteroventrally. Setae on abdomen broad, flat, and finely pubescent.

Eighth tergum without setae or spines. Ninth tergum without mesal process. Anal tubercles (Plate 3c) without denticles, rounded basally, tapering to acute apices.

The three specimens examined do not vary significantly in basic structure. *A. tigrinus* may be readily separated from *xylocopae* by the structure of the anterior cephalic tubercles. In *tigrinus* they are broad, dorsoventrally flattened, and broadly rounded apically, whereas in *xylocopae* they are narrow, more or less terete, and acuminate apically.

Numerous characters separate *tigrinus*, *xylocopae*, and probably other species in the tigrinus group, from other groups of *Anthrax*. Probably the most readily observable is the distinct separation mesally between the anterior cephalic tubercles of *tigrinus* and *xylocopae*. In other groups the bases of the tubercles are broadly united mesally.

**Anthrax xylocopae** Marston

Two pupal skins of this species have been examined (see table). Adults were reared from nests of *Xylocopa californica arizonensis* Cresson in flower stalks of *Yucca elata* Engelmann at Rodeo, New Mexico. Hurd (1959) discussed the biology of the species (as *Anthrax simson* Fabricius).

Integument of pupa brownish hyaline with yellow setae and yellowish brown black-tipped tubercles. Bases of anterior cephalic tubercles (Plate 2o) not joined mesally; medial tubercle situated in nearly straight line between apices of anterior and posterior tubercles; anterior tubercle narrow, acuminate, curved posteromesally at apex, with high mesoventral and dorsolateral ridges; medial tubercle flattened dorsoventrally, broadly rounded apically, with sharp dorsal, ventral, and ventrolateral ridges; posterior tubercle compressed on dorsal side, with sharp mesal, lateral, and ventral ridges. Facial sclerite slightly less than twice its narrowest width, with broad, shallow emargination posteriorly; anterior facial tubercles simple, acuminate to blunt apices, broadly separated mesally; posterior facial tubercle undeveloped. Anterior facial setae arising slightly in front of level of anterior facial tubercles.

Thoracic spiracle with about fifteen sections, posterior ones reduced; indistinct flange present around anterodorsal fourth. Abdominal spiracles with about thirteen sections, anteroventral ones reduced, flange represented by low ridge around posterodorsal half, expanding as broad lobe anteroventrally.

Eighth tergum without setae or spines. Ninth tergum without mesal process. Anal tubercles (Plate 3c), acuminate, without denticles; bases of tubercles broadly separated, mesal margin tapering outward to apices, then slightly curved inward at tips.

The two pupal skins examined do not vary significantly in diagnostic characters. Characters for separating *A. xylocopae* from *tigrinus* and other species in the genus are discussed under *tigrinus*.

**Anthrax pluricellus** Williston

Seven pupal skins of *A. pluricellus* have been examined (see table). These were taken by Rau from nests of *Chalybion zimmermanni* Dahlbom. (Hymenoptera: Sphecidae) (Rau, 1940). The specimens are in the
collection of Dr. R. H. Painter and the National Museum of Natural History.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles and spines. Cephalic tubercles (Plate 2F) evenly spaced, in a straight line; anterior tubercle of moderate length, compressed dorsoventrally toward apex, with poorly defined mesal and lateral ridges; median tubercle nearly as long as anterior one, slightly bent forward, acuminate, with indistinct dorsolateral and ventromesal ridges, and sharp ventrolateral ridge connecting to posterior tubercle; posterior tubercle short, slightly curved anterodorsally, concave on anteromesal surface, with sharp anterolateral and postero mesal ridges and indistinct posterolateral ridge. Facial sclerite about two-and-half times longer than minimum width, posterior end with broad, semicircular emargination; anterior facial tubercles flattened anteroposteriorily, bent forward slightly, broad, short, bluntly rounded apically; posterior facial tubercle undeveloped, represented by rounded node. Facial setae arising just anterior to level of anterior facial tubercles.

Spiracles a little above level of integument, with out distinct flanges; thoracic spiracle with about 12 sections, posteroventral ones reduced; abdominal spiracles with about ten sections, anteroventral ones reduced.

Sixth and seventh terga with numerous, small spines between setae. Eighth tergum with two spines on each side, one on each side of dorsolateral tumidities, additional small spines sometimes present; setae absent. Medial process on ninth tergum broad, low, sharply rounded apically. Anal tubercles (Plate 3F) about six or seven times longer than medial width, separated medially by one-fourth or less of width of one lobe. Each tubercle with dorsal and ventral, sharp denticles near base unconnected or joined by low, poorly defined ridge; medial margin with sharp denticle ventrally about one-third of distance to apex and large mesal denticle about three-fourths of distance to apex; apex narrow, straight, and acuminate beyond preapical denticle.

The pupae of \textit{A. pluricellus}, \textit{aterrimus}, \textit{argyropygus} \textit{argyropygus}, and \textit{hyalacus} are quite similar and probably are typical of most species of the cephus group except for species closely related to \textit{analis}. The pupa of \textit{koebelei} seems to be intermediate between \textit{analis} and the first four, sharing some common characters with each, as does the adult. The pupa of \textit{koebelei}, and those of the first four, may be readily separated from pupae of all other species studied, except \textit{trimaculatus}, by the presence of spines on the eighth tergum. \textit{A. trimaculatus} may be readily distinguished by the high flange connecting the dorsal and ventral denticles on the anal tubercles.

In the cephus group, \textit{A. analis} is unique in that it lacks spines on the eighth tergum, while \textit{koebelei} is distinctive in that it has only one spine on each side, lateral to the dorsolateral tumidities. Other species have an additional pair mesad to the tumidities. In \textit{pluricellus}, the anal tubercles are distinctly longer than in \textit{argyropygus}, \textit{hyalacus}, and \textit{aterrimus}, about six or seven times the medial width of one lobe rather than five times the medial width of one lobe or less. \textit{A. hyalacus} may be distinguished from \textit{pluricellus}, \textit{argyropygus}, and \textit{aterrimus} by a pair of setae between the innermost spines on the eighth tergum. The setae are in a direct line between the dorsolateral tumidities rather than in front of them as on pupae of other groups. The cephalic tubercles of \textit{A. argyropygus} are distinctive in that the medial one is set slightly inside a line between the tips of the anterior and posterior ones, whereas in \textit{pluricellus}, \textit{aterrimus}, and \textit{hyalacus} they are in a straight line or the middle one is set slightly outside the line.

\textbf{Anthrax aterrimus} (Bigot)

Twenty-six pupal skins of this species from the National Museum of Natural History have been studied (see table). According to Krombein (1967), they were taken from nests of \textit{Trypargilum striatum} (Provancher), \textit{T. clavatum} (Say), \textit{T. collinum rubrocinctum} (Packard), and \textit{Isodontia auripes} (Fernald) (Hymenoptera: Sphecidae); \textit{Euodynerus megaera} (Lepeletier), \textit{Monobia quadridens} (Linnaeus), and \textit{Ancistrocerus spinolae} (Saussure) (Hymenoptera: Vespidae). An additional specimen was reared from a "mud dauber wasp."

Integument of pupa yellowish hyaline with yellow setae and reddish brown, black-tipped tubercles and spines. Anterior cephalic tubercle straight, tapering, with dorsomesal and ventrolateral ridges distally, without well-defined ridges basally; medial tubercle formed on or slightly outside a line between anterior and posterior tubercles, closer to posterior tubercle, slightly shorter than anterior tubercle, acuminate, with sharp ventrolateral ridge connecting to posterior tubercle;
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posterior tubercle short, slightly curved dorsomesally with sharp dorsal, ventromesal, and ventrolateral ridges. Facial sclerite about five and a half times longer than its narrowest width, with shallow, rounded emargination posteriorly. Anterior facial tubercles short, broad, anteroposteriorly flattened, tapering slightly to broadly rounded apices; posterior facial tubercle not developed.

Sixth and seventh terga with small spines between setae. Eighth tergum with two spines on each side, one on each side of dorsolateral tumidity (lateral spines sometimes bifurcate); setae absent on tergum (1 seta present adjacent to lateral spine on one specimen).

Medial process on ninth tergum short, broad to narrow basally, acuminate to sharp or narrowly bifurcate apex. Each anal tubercle three to five times longer than medial width of one tubercle, straight, separated mesally one-fourth to one-third of width of one tubercle; each tubercle with sharp dorsal and ventral, unconnected denticles near base; mesal margin with broad, sharp, preapical ridge, forming dorsal and ventral denticles, and sharp ventral denticles about one-third of distance to apex; each tubercle tapering outward from preapical ridge to sharp tip.

The pupae of *A. aterrimus* and *pluricellus* are quite similar. Differences are discussed under the latter species.

**Anthrax argyropygus argyropygus** Wiedemann

Twenty-seven pupal skins of *A. argyropygus* have been examined (see table). The species has been reared from *Trypargilum collinum collinum* Smith, *T. c. rubrocinctum* (Packard), *T. striatum* (Provancher), and *T. tridentatum archboldi* (Krombein) (Hymenoptera: Sphecidae); and from *Ancistrocerus catskill catskill* (Saussure), *Stenodynerus fulvipes fulvipes* (Saussure), *S. pulvinatus surrufus* Krombein, *S. secularis rufulus* Bohart, *S. beameri* Bohart, and *Pachodynerus erynnis* (Lepeletier) (Hymenoptera: Vespidae) (Krombein, 1967). An additional specimen was reared from the nest of a “trypoxylonid” (Hymenoptera: Sphecidae). Specimens are in the National Museum of Natural History and the R. H. Painter collection.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles and spines. Anterior cephalic tubercle (Plate 20) narrow, straight, and without definite ridges; medial tubercle closer to anterior one than to posterior one, formed slightly inside line between them, narrow, straight, with sharp posteroventral ridges connecting to posterior tubercle; posterior tubercle short, slightly curved anteriorly, with poorly defined anteromesal, anterior, and posteroventral ridges. Facial sclerite about eight times longer than narrowest width, with shallow, rounded emargination posteriorly. Anterior facial tubercles short, broad, anteroposteriorly flattened, produced slightly laterad and evenly rounded apically; posterior facial tubercle very short, flat, bent posteriorly, acute apically.

Spiracles produced slightly above margin of integument; thoracic spiracle with about thirteen sections, the posterior ones reduced; abdominal spiracles with eight to ten sections, anteroven tral ones reduced.

Sixth and seventh terga with numerous small spines between setae. Eighth tergum with two spines on each side, one on each side of each dorsolateral tumidity (one lateral spine bifurcate from base); no setae present or tergum. Medial process on ninth tergum short, broad basally, acuminate to sharp apex. Anal tubercles (Plate 30) short, thick basally, straight, separated mesally by about one-third to one-fourth width of one lobe; each tubercle with sharp dorsal and ventral, unconnected denticles near base; mesal margin with sharp dorsal and weak ventral denticles connected by a sharp ridge about three-fourths of distance to apex; apex broadly acuminate, slightly curved mesad apically.

The pupa of *A. argyropygus argyropygus* is most similar to *pluricellus*, *aterrimus*, and *hyalacrus*. Relationships of the four species are discussed under *pluricellus*.

**Anthrax hyalacrus** Wiedemann

Two specimens of *A. hyalacrus* were reared by Dr. Carl W. Rettenmeyer from nests of a trypoxylonid wasp (Hymenoptera: Sphecidae) on Barro Colorado Island, Canal Zone, Panama. The wasps were nesting in a cardboard carton in a clearing at the biological station.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles and spines. Cephalic tubercles (Plate 20) evenly spread, almost in a straight line; anterior tubercle short, com-
pressed dorsoventrally, bluntly rounded apically, and with poorly defined dorso- and ventrolateral ridges toward apex; medial tubercle short, acuminate to blunt apex, with well-defined dorso- and ventrolateral, and mesal ridges; posterior tubercle short, curved slightly forward and bluntly rounded apically, connected to medial tubercle by sharp dorso- and ventral ridges. Facial sclerite about eight times longer than narrowest width, with deep, square, narrow emargination at posterior end. Anterior facial tubercles short, broadly acuminate, flattened anteroposteriorly, narrowly separated or connected mesally. Posterior facial tubercle undeveloped, represented by rounded node.

Spiracles produced little above surrounding integument, without flanges; thoracic spiracle with about fifteen sections, posterior ones reduced; abdominal spiracles with about twelve sections, anteroventral ones reduced.

Sixth and seventh terga with numerous, small, single spines between setae. Eighth tergum with two spines on each side, one on each side of dorso- lateral timidities, one of dorsal pair sometimes absent; one seta also present on each side between timidities rather than anterior to them. Medial process on ninth tergum short, narrow, acuminate. Anal tubercles (Plate 3t) short and thick, slightly curved upward apically, separated mesally by about two-fifths of medial width of one lobe; each tubercle with short, spikelike, dorsal and ventral denticles about one- third of way to apex, ventral one sometimes reduced; ventromesal margin with sharp ridge extending about two-thirds of distance to apex, without denticles; dorso- and ventromesal margin with sharp denticle about three-fourths of distance to apex; apex bluntly acuminate beyond preapical denticle.

The pupa of *A. hyalacrus* is most similar to *pluricellus*, *aterimus*, and *argyropygus argyropygus*. Relationships of the four species are discussed under *pluricellus*.

**Anthrax analis** Say

Shelford (1913) gave an excellent account of the life history and habits of *A. analis*, which he reared from burrows of "*Cicindela scutellaria* Say, var. *lecontei* Hald." (Coleoptera: Cicindelidae). Malloch (1915) described the larva and pupa, utilizing specimens collected by Shelford. The specimen described here is from the R. H. Painter collection (see table). It agrees well with Malloch’s description, although the latter is rather incomplete, due to a lack of closely related species for comparison.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles and spines. Anterior cephalic tubercle (Plate 2a) broadly separated from middle and posterior ones, long, narrow, acuminate, and with sharp lateral, mesal, and ventral ridges; medial and posterior tubercules united about halfway to apex of posterior tubercle; medial tubercle formed well inside line between tips of anterior and posterior ones, narrow, acuminate, and with sharp dorsal, mesal, and posterolateral ridges; posterior tubercle slightly curved medially, acuminate, sharp, with sharp dorsal, ventral, and lateral ridges. Facial sclerite about seven times longer than narrowest width, posterior end shallowly emarginate. Anterior facial tubercles anteroposteriorly flattened, long, broad basally, tapering to sharp apexes, meeting at acute angle mesally. Posterior facial tubercles undeveloped, represented by rounded node.

Spiracles produced distinctly above surrounding integument; thoracic spiracle with about seventeen sections, posterior ones reduced; abdominal spiracles with about ten sections, anteroventral ones reduced. Flanges undeveloped.

Sixth and seventh terga with small, single spines between setae. Eighth tergum without spines or setae. Medial process on ninth tergum undeveloped, represented by low, acutely pointed node. Anal tubercles (Plate 3a) long, narrow, curved upward, and separated by about one and a half times width of one tubercle mesally. Each tubercle without denticles at base or on ventral side; dorso- and ventromesal side with poorly defined denticle about one-half of distance to apex formed by apical extension of thin, sharp dorso- and ventromesal ridge; apex narrow, curved slightly upward and mesal, sharp, and with poorly defined lateral, dorso-, and ventromesal ridges.

The pupa of *A. analis* is most similar to that of *koebelei*. *A. analis* may be readily recognized, however, by absence of spines on the eighth abdominal tergum and by acuminate rather than rounded anterior facial tubercles. These two species may be separated from all other species studied, except *xylocopa* and *tigrinus*, by the absence of denticles at the bases of the anal tubercles, and from the latter by being much smaller...
and having acuminate rather than rounded cephalic tubercles.

Anthrax koebelei Marston

Three pupal skins and one dried pupa associated with adults of this species are in the California Academy of Sciences collection. No host data were recorded with the specimens, however.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles. Anterior cephalic tubercle (Plate 2a) broadly separated from posterior ones, long, narrow, acuminate, slightly curved ventrad, and with indistinct lateral, mesal, and ventral ridges. Medial and posterior tubercles united basally about halfway to apices of posterior one; medial tubercle formed slightly mesad of line between apices of anterior and posterior ones, slightly curved anterodorsally, acuminate, and with sharp posterior and less distinct lateral and mesal ridges; posterior tubercle about two-thirds as long as medial one, curved anteromesally, flattened posterolaterally, and with distinct anteromesal, anterolateral and posteromesal ridges. Facial sclerite about six times longer than its narrowest width, shallowly emarginate posteriorly. Anterior facial tubercles broad, flattened anteroposteriorly, and with distinct lateral and mesal ridges; posterior tubercle undeveloped, represented by broad, low, transverse node.

Thoracic spiracle slightly produced above integument, without flange, composed of about fifteen sections, posterior ones reduced. Abdominal spiracles like thoracic, but with ventral sections reduced.

Sixth and seventh terga with small, single spines between setae. Eighth tergum without setae dorsally, with one spine on each side laterad of tumidities. Medial process on ninth tergum acuminate. Anal tubercles (Plate 3a) long, narrow, broadly separated mesally, and slightly curved upward; tubercles without denticles basally or on ventral surfaces at basal third; strong dorsal and weak ventral denticles present mesally two-thirds of distance to apices, connected by sharp, serrate ridge; tips curving slightly outward and recurving dorsomesally, narrow and acuminate.

The pupa of A. koebelei appears to be most closely related to that of analis Say. They may be readily separated, however, by the absence of spines on the eighth tergum in analis, and by the acuminate rather than rounded apices of the anterior facial tubercles of analis.
posteriorly. Anterior facial tubercles compressed anteroposteriorly, connected by sharp mesal ridge, with acute lateral apices. Posterior facial tubercle formed of two small anteroposteriorly flattened, apically rounded nodes. Anterior facial setae arising distinctly anterior to anterior facial tubercles.

Thoracic spiracle with about seven sections, with low, sharp flange around anterior two-thirds. Abdominal spiracles with about six sections, anteroventral ones reduced, sharp flange around anterodorsal three-fourths broad dorsally and especially anteroventrally, narrow otherwise.

Sixth and seventh terga without spines between setae. Eighth tergum without spines dorsally, with setae arising along line in front of dorsolateral humidities. Ninth tergum with short, simple transverse process, broad basally, tapering to bluntly rounded apex. Anal tubercles (Plate 4c) about four times longer than medial width of one lobe, separated mesally by about one-third medial width of one lobe or almost touching. Each tubercle basally with sharp dorsal and ventral denticles sometimes connected by low ridge; ventral denticle on mesal margin poorly defined or absent; strong dorsal and weak ventral denticles present preapically on meson from which tubercle tapers outward to sharp, slightly upturned apex.

The pupae of all available species of the oedipus subgroup show few good diagnostic characters. Also, in several species a wide intraspecific variation often serves to mask valid specific differences, particularly where pupae have been reared from unrelated hosts.

The pupa of A. peruvianus may be most readily separated from those of irroratus irroratus, cordillerensis, and cintalpa by presence of high lateral flange between the dorsal and ventral denticles on the anal tubercles and by presence of a flange between the ventral denticles at the base and the ventral denticles on the mesal margins of the tubercles about halfway to the apices. In irroratus irroratus, cordillerensis, and cintalpa some specimens may show a low ridge between the dorsal and ventral denticles, but none has a connection between the mesal ridge and the ventral denticles. A. cordillerensis may be readily distinguished from the other species by the presence of spines between the setae on the sixth abdominal tergum.

There are no constant taxonomic characters to separate all specimens examined of A. i. irroratus and cintalpa. All specimens of cintalpa have the medial cephalic tubercle situated farther outside a line between the anterior and posterior tubercles, however. In cintalpa, a line through the tips of the posterior and medial tubercles would be nearly parallel to the meson, whereas, in irroratus irroratus such a line would be at a distinct angle from the meson. Several specimens of the latter have fewer tergal setae on the first abdominal segment—only 9 or 10 compared with about 14 in all specimens of cintalpa examined. Also, two specimens of cintalpa show a greater number of pleural setae on the eighth abdominal segment—16 to 18 compared with the usual 3 to 7 on specimens of irroratus irroratus.

**Anthrax cintalpa Cole**

Cole (1957) stated that the type specimens of cintalpa were reared from nests of Melittoma euglossoides Lepeletier & Serville (Hymenoptera: Apidae). One paratype studied by the author has the pupal skin pinned with it. Additional specimens with pupal skins were reared from nests of Megachile concinna and Dianthidium sp. (Hymenoptera: Megachilidae). Specimens with pupal skins are in the collections of R. H. Painter, the author, and the University of California at Berkeley.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles. Medial cephalic tubercle (Plate 1c) formed outside a line between tips of anterior and posterior tubercles; line through tips of medial and posterior tubercles parallel to or at slight angle to meson; anterior tubercle slender, tapering to sharp apex, with sharp mesoventral and dorsolateral ridges and with indistinct dorsomesal ridge; medial tubercle broad basally, tapering to sharp apex, with sharp ventrolateral ridge; posterior tubercle short, curved upward, and tapering to sharp apex, with sharp dorsal and ventromesal ridges and blunt ventrolateral ridge. Facial sclerite about five times longer than narrowest width, with shallow emargination at posterior end; anterior facial tubercles antero-posteriorly flattened, with bluntly angled lateral apices, joined by sharp ridge mesally; posterior facial tubercle formed as low transverse ridge, rounded or indistinctly binodal. Anterior facial setae arising distinctly anterior to bases of anterior facial tubercles.

Thoracic spiracle with about seven sections, posterior ones reduced, with sharp flange around anterior two-thirds. Abdominal spiracles with about six sections, anteroventral ones reduced; flange arising posteriorly,
becoming broad dorsally, narrowing anteriorly and broadening again ventrally; flange evenly rounded posterodorsally.

Sixth and seventh terga without spines between setae. Eighth tergum without spines dorsally, with setae in front of line between dorsolateral tumidities. Medial process on ninth tergum high and broadly rounded apically or low and tapering to sharply rounded apex. Each anal tubercle (Plate 4H) four to five times longer than medial width, narrowly separated mesally or meeting at preapical denticles. Sharp dorsal and ventral denticles present at base of each tubercle, ventral denticle not connected by ridge; mesoventral ridge not forming denticles apically, not connected to ventrobasal denticles; dorsal preapical denticles well developed, sharp or bluntly rounded, ventral preapical denticles poorly developed, blunt; apices tapering outward from preapical denticles.

The similarities of the pupae of *A. cintalpa* to the pupae of *irroratus irroratus*, *cordillerensis*, and *peruvianus* are discussed under *irroratus*.

**Anthrax peruvianus** Marston

A number of pupal skins of this species were collected by R. H. Painter from nests of bees in ruins at Pachacamac, near Lima, Peru. Although no specimens were reared, adults were collected ovipositing in the same area. Pupal skins are in the collections of R. H. Painter and the author.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles. Medial cephalic tubercle located distinctly outside line between anterior and posterior terga, slightly closer to posterior tubercle (Plate 1a); each anterior tubercle narrow, acuminate, with sharp mesoventral ridge curving ventrally at base, sharp lateral ridge curving dorsally at base, and less distinct ventral ridge; medial tubercle acuminate to sharp apex, bent slightly forward at base, with well-defined posterolateral ridge connecting to posterior tubercle and poorly defined dorsolateral and mesal ridges basally; posterior tubercle short, thick, curved forward to sharp apex, with sharp ventromesal, ventrolateral, and dorsal ridges. Facial sclerite about four and a half times longer than narrowest width, shallowly emarginate at posterior end; anterior facial tubercles relatively long, flattened anteroposteriorly, tapering from meson to sharp lateral apices, barely meeting on meson; posterior facial tubercle composed of two short, anteroposteriorly flattened, sharply rounded nodes. Anterior facial setae arising distinctly anterior to anterior facial tubercles.

Thoracic spiracle with about seven segments, the posterior ones reduced; sharp, even flange present around anterior three-fourths. Abdominal spiracles with about six sections, ventral ones reduced; erect, broad dorsal flange narrowing to anterior end and to posterior connection with broad, recumbent, flaplike ventral flange.

Sixth and seventh terga without spines between setae. Eighth tergum without spines, with setae on line in front of dorsolateral tumidities. Ninth tergum with long mesal process tapering from broad base to sharply rounded apex. Anal tubercles (Plate 4b) about four times longer than medial width of one tubercle, separated medially by about one-fourth width of one tubercle. Base of each tubercle with large, acute, dorsal and ventral denticles connected by high, sharp lateral flange, ventromesal margin with sharp denticle about two-fifths of distance to apex which curves basally as sharp ridge to connect with ventrobasal denticle; mesal margin with blunt dorsal and ventral preapical denticles from which tubercle tapers laterally to sharp apex.

The relationships of *A. peruvianus*, *cordillerensis*, *irroratus irroratus*, and *cintalpa* are discussed under *irroratus*.

**Anthrax cordillerensis** Marston

One specimen reared from nest cells of *Hypodynerus* Saussure (Hymenoptera: Vespidae) in Santiago Province, Chile, has been studied (see table). It is in the author's collection.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles. Medial cephalic tubercle located distinctly outside line between anterior and posterior terga, closer to posterior tubercle; each anterior tubercle triangular in cross section; acuminate, with sharp dorsomesal, ventromesal, and lateral ridges; medial tubercle acuminate to sharp apex, bent slightly forward, with well-defined posterolateral ridge connecting to posterior tubercle and less well-defined dorsolateral and mesal ridges basally; posterior tubercle short, thick, acuminate, curving forward distally, with sharp dorsal ridge and poorly defined ventral and mesal ridges. Facial sclerite about four times longer than narrowest width, shallowly emargi-
nate at posterior end; anterior facial tubercles flattened anteroposteriorly, about as long as basal width of one tubercle, tapering from meson to sharp lateral apices, barely meeting on meson; posterior facial tubercle composed of two short, anteroposteriorly flattened and sharply rounded nodes. Anterior facial setae arising distinctly anterior to anterior facial tubercles.

Thoracic spiracle with about six segments, posterior ones reduced; sharp flange present around anterior half. Abdominal spiracles with about five sections, ventral ones reduced; erect, broad, dorsal flange narrowing to posterior end and to anterior connection with broad, recumbent, flaplike ventral flange.

Sixth tergum with spines between setae; seventh tergum with setae, but no spines. Eighth tergum with row of setae in front of each dorsolateral tumidity. Medial process on ninth tergum about as long as width at base, tapering to sharp tip. Anal tubercles (Plate 4D) short, broad, about four times longer than medial width of one lobe. Each lobe with strong dorsal and weak ventral denticles basally which are indistinctly connected by lateral ridge; bluntly rounded denticle present about halfway to apex as apical end of sharp ventromesal ridge; acute dorsal and blunt ventral denticles present mesally about three-fourths of distance to apex; tubercle tapering outward from preapical denticles to acuminate apex.

Relationships of *A. peruvianus, cintalpa, irroratus irroratus,* and *cordillerensis* are discussed under *irroratus*.

**Anthrax melanopogon** (Bigot)

One reared specimen of this species has been examined (see table). It is pinned with a nest cell of *Megachile gentilis* Cresson (Hymenoptera: Megachilidae). The specimen is in the collection of the author.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped tubercles and spines. Medial cephalic tubercle (Plate 1a) formed slightly outside line between anterior and posterior ones, and distinctly closer to posterior one; anterior tubercle long and acuminate, with sharp mesal ridge curving ventrally at base and lateral ridge curving dorsally at base; medial tubercle triangular in cross section, acuminate, with sharp dorsolateral and dorso-mesal ridges, and sharp ventrolateral ridge which extends basad laterally and does not join with dorsal

ridge of posterior pair; posterior tubercle short, curved dorsally from base, acute, with sharp dorsal and mesal ridge and less distinct ventrolateral ridge. Facial sclerite about five and one half times longer than narrowest width, truncate posteriorly; anterior facial tubercles short, tapering to acute apices, with mesal ridges meeting indistinctly on meson; posterior tubercle transverse, low, and indistinctly bifid.

Thoracic spiracle with about seven sections, the posterior ones reduced, with sharp flange around anterior half. Abdominal spiracles with six sections, the anteroventral ones reduced; sharp flange present around anterodorsal three-fourths, expanded as blunt lobe posterodorsally on anterior pairs.

Sixth and seventh terga without spines between setae. Eighth tergum without spines, with setae on line in front of dorsolateral tumidities. Ninth tergum with simple, transverse medial process. Anal tubercles (Plate 4b) short, broad, about four times longer than medial width of one lobe, separated mesally by about three-fifths of width of one lobe. Each lobe with strong dorsal and weak ventral denticles basally which are indistinctly connected by lateral ridge; bluntly rounded denticle present about halfway to apex as apical end of sharp ventromesal ridge; acute dorsal and blunt ventral denticles present mesally about three-fourths of distance to apex; tubercle tapering outward from preapical denticles to acuminate apex.

The pupae of *A. atriplex* and *melanopogon* differ little; probably the best character to separate them is the extension of the postero-mesal ridge on the medial cephalic tubercle of *atriplex* to the posterior margin of the cephalic area. The ridge becomes indistinct near the bases of the tubercle in the one specimen of *melanopogon* examined. Differences in the numbers of setae and spines may be attributed to the small size of the specimen of *melanopogon* examined.

Both *A. melanopogon* and *atriplex* differ from *cintalpa, peruvianus,* and *irroratus irroratus* in that the flange on the anterior abdominal spiracles is lobed rather than evenly rounded posterodorsally.

**Anthrax atriplex** Marston

Two specimens of this species from the National Museum of Natural History were reared by Krombein (1967) from the nests of *Megachile gentilis* Cresson...
(Hymenoptera: Megachilidae). Pupal skins are pinned with the specimens.

Integument of pupa yellowish hyaline with yellow setae and reddish brown black-tipped spines and tubercles. Medial cephalic tubercle (Plate IF) formed outside a line between anterior and posterior ones, and closer to posterior one; anterior tubercle of moderate length, tapering to acute apex, with sharp mesal ridge curving ventrally, sharp lateral ridge curving dorsally, and less distinct dorsal and ventral ridges basally; medial tubercle bent dorsolaterally from base at slight angle, broadly triangular basally, tapering to acute apex, with sharp ventrolateral ridge connecting to posterior tubercles, and sharp ventromesal ridge continuing around to posterior margin of cephalic area; posterior tubercle short, curving anteromesally to sharp apex, concave anteromesally, with sharp anterolateral, posterolateral, and posteromesal ridges. Facial sclerite about seven times longer than narrowest width, posterior end with shallow, broad emargination; anterior facial sclerites short, indistinctly united mesally, not flattened anteroposteriorly, with rugose surfaces tapering to sharp apices; posterior facial tubercle represented by low, binodal, transverse ridge. Bases of anterior facial setae distinctly in front of bases of anterior facial tubercles.

Thoracic spiracle with about eight sections, posterior ones reduced, with sharp flange around anterior two-thirds. Abdominal spiracles each with about six sections, the anteroventral ones reduced, with broad, sharp flange anteroventrally, narrowing anteriorly then broadening anterodorsally and forming sharp spur posteriorly.

Sixth and seventh terga without spines between setae. Eighth tergum without spines dorsally, with about three setae on each side in front of and mesad of dorsolateral tumidities. Ninth tergum with transverse, bifid, mesal process. Each anal tubercle (Plate 4G) about four times longer than medial width; tubercles separated mesally by about half the medial width of one tubercle. Each tubercle with strong dorsal and ventral denticles near base not connected by lateral flange (indistinct ridge sometimes present); ventromesal margin with denticle about halfway to apex extending basally as sharp flange; sharp dorsomesal and blunt, poorly defined, ventromesal denticles present about three-fourths of distance to apex; tubercle tapering outward from preapical denticles to bluntly acuminate, slightly incurved apex.

The relationship of *A. atriplex* to *melanopogon* and other species in the genus is discussed under *melanopogon*.

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Plate 1.—Anthrax species: A, Lateral view of pupal skin of A. limatulus fur (aft, anterior facial tubercles; atb, anal tubercle; ctb, cephalic tubercles; pft, posterior facial tubercle). Ventral views of cephalic tubercles of pupal skins: B, peruvianus; C, cintalpa; D, irroratus; E, nidicola; F, atriplex; G, melanopogon; H, limatulus fur.
PLATE 2.—Ventral views of cephalic tubercles of pupal skins of Anthrax species: A, analis; B, koebelei; C, albofasciatus albofasciatus; D, argyropygus argyropygus; E, hyalacrus; F, pluricellus; G, xylocopae; H, tigrinus; I, trimaculatus.
PLATE 3.—Dorsal views of caudal tubercles of pupal skins of Anthrax species: A, analis; B, koebelei; C, xylocopae; D, tigrinus; E, trimaculatus; F, pluricellus; G, argyropygus argyropygus; H, hyalaeus.
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