III. *Notes on the biology of some inquilines and parasites in a nest of* Bombus derhamellus *Kirby; with a description of the larva and pupa of* Epuraea depressa *Illig.* (= aestiva *Auctt.*: *Coleoptera, Nitidulidae*).

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[Read February 4th, 1920.]

I. Introduction.

The purpose of this paper can be gathered from the list of headings above. While working temporarily at the Imperial College of Science, London, I received from Miss L. E. Cheesman, on July 19, 1918, part of a nest of *Bombus derhamellus* Kirby, the "Red-shanked Carder-bee," containing a number of insects of more than one Order which are frequently found as inmates of humble-bees' nests (20). The nest had been sent to Miss Cheesman at the Zoological Society's Gardens from Hoo, near Rochester, and the species of bee was determined from some dead workers in the nest. The other inmates were living, and were as follows: (*a*) two larvae of *Volucella sp.*, which died without completing their metamorphosis; (*b*) several larvae from which adults of the Tachinid fly, *Brachycoma devia*, were bred; (*c*) pupae from which emerged a Phorid fly, *Aphiochaeta rata*, and a Braconid parasite, *Orthostigma pumilum*; (*d*) several larvae from which adults

of the Cryptophagid beetle *Antherophagus pallens*, were reared; and lastly, (*e*) numerous larvae of the Nitidulid beetle *Epuraea depressa* (= *aestiva*).

Thus, the portion of the nest sent to me contained a good selection of the inmates enumerated by Mr. F. W. L. Sladen in his book on "The Humble-Bee" (**20**, chap. iv). The one which he mentions first was, however, absent; namely, the humble-bee wax-moth, *Aphomia sociella*, to the attacks of which he states that *Bombus derhamellus* is specially liable. This insect may have been present in the parts of the nest which I did not see.

My thanks are due to Miss Cheesman, for giving me the material, to Mr. A. W. Rymer Roberts, for advice on several points connected with the description of the larva of *Epuraea depressa*, and to Mr. K. G. Blair, who took charge of the pupae of that insect for some time during my absence.

II. **Brachycoma devia** Fallen.

This Tachinid fly is stated to devour the bees' brood (**20**, p. 75). Four larvae were present in the nest, one of which was killed and preserved, while the other three pupated on or shortly before July 30, 1918. The puparia were kept through the winter in sand which was moistened periodically, the conditions being identical with those described below under *Antherophagus*. One adult emerged May 15–16, the other two May 18, 1919. Sladen writes that the adult flies emerge in two or three weeks. This probably refers to a summer generation; in my material the pupal stage lasted nine months and a half. Sladen also describes the puparia as at first yellowish-brown, afterwards dark red; my three examples are very dark. The determination of the fly was confirmed by Mr. C. J. Wainwright.

III. **Aphiochaeta rata** Wood *and its parasite* **Orthostigma pumilum** Nees.

I am indebted to Mr. J. E. Collin for determining this Phorid fly. Two puparia found in the litter of the nest were isolated, and adults emerged from them respectively Aug. 12, (♀), and some time between Aug. 18 and Sept. 1, 1918 (♀). A male of the fly was found alive in the nest, Aug. 16, 1918.

Dr. Keilin has not studied this species in particular,

but he considers that the larvae of *Aphiochaeta* and of *Phora* are in general saprophagous, feeding especially on dead insects and snails. There are several published records of their being bred from the bodies of other insects, but it is doubtful whether any of these were cases of true parasitism, and whether the insects from which they were bred were not already decomposing (**16,** pp. 61–62 and 79–80). Be this as it may, Mr. Donisthorpe has recorded the rearing of 4 examples of *Aphiochaeta rata* from larvae which came out of the body of a Clerid beetle, *Thanasimus formicarius*, taken in Sherwood Forest (**8**). He also found one specimen in an observation nest of *Formica exsecta* (**9,** p. 61; **10,** p. 280). Mr. Collin tells me that he has seen specimens bred from a nest of *Vespa norvegica* by Mr. C. Nicholson of Chingford in 1915.

From another puparium of the *Aphiochaeta*, found in the nest of *B. derhamellus* and isolated, there emerged some time between Aug. 18 and Sept. 1, 1918, a female of the Braconid (Alysiid) parasite, *Orthostigma pumilum*, determined by Mr. R. E. Turner. It has been bred from other Phoridae. The Cambridge Museum contains a series bred from puparia of *Aphiochaeta rufipes* Meigen, which were found in a vase in a house at Parkhead, near Sheffield, June 1910 (in this case the flies were identified by Mr. F. J. H. Jenkinson and the parasites by Mr. G. T. Lyle). T. A. Marshall (**17,** p. 373) mentions that the parasite was bred in multitudes from *Aphiochaeta rufipes* by Ratzeburg in 1840.*

IV. **Antherophagus pallens.**†

The only representatives of this Cryptophagid beetle found in the nest were three larvae, one of which was

* In 1919 these two species of *Aphiochaeta* were found frequenting the burrows of a solitary wasp, *Crabro cavifrons* Thoms., in an elm log at Grantchester, Cambridge. On Aug. 16 a ♀ *A. rufipes* was taken flying about the log. On Aug. 22 a ♂ *A. rata* was seen by Mr. C. Warburton to enter one of the burrows: it remained inside about five minutes and was caught on emerging. Mr. J. E. Collin determined both flies.

† Fowler refers to this species as "*A. pallens* Gyll." Ganglbauer (**12,** p. 704) gives "*pallens* Oliv.," adding references to Herbst, Erichson, Sturm, Thomson, and Reitter, but not to Gyllenhal. Reitter (Fauna Germanica, Käfer, iii, p. 58, 1911) also has "*pallens* Oliv." Gemminger and Harold (iii, 1868, p. 882) have "*pallens* Fabr.," and add references to Olivier, Gyllenhal, and Sturm. I have not tried to decide which is strictly correct.

killed and preserved; the other two excavated cells for pupation early in Aug. 1918, in which they remained as resting larvae all the winter, not pupating till late April or early May 1919, and emerging as adults late in May. Therefore, as far as could be ascertained, the resting-larva condition endured about nine months, while the pupal period occupied twelve days or more.

Detailed observations of wintering and pupation.—The following is a more detailed account of the behaviour of these two larvae. For several days they were observed wandering restlessly about the vessel containing the nest-fragments, as though seeking a place for pupation. Therefore on Aug. 8, 1918, they were isolated in a small glass vessel containing sawdust to a depth of about half an inch. The very next day both had excavated cells, one against the side of the vessel, the other in the angle formed by its side and bottom (cf. *Epuraea depressa*). As in the case of *Epuraea depressa*, the cells were not lined with any secretion.

In these cells the larvae remained the whole winter. The sawdust was slightly moistened about every second day. Ordinarily the vessel was only covered with fine gauze, but when its contents became very dry it was sometimes lightly covered with a glass cover for about 24 hours after moistening the sawdust, to allow the moisture to diffuse through the contents. The vessel had to be moved from one place to another several times, owing to my leaving London. It was kept in rooms where fires were only burning exceptionally, and under these conditions changes in the weather affected the behaviour of the larvae to some extent. At first they lay in their cells against the glass, but when a cold spell set in, they retired deeper into the sawdust, pushing sawdust between themselves and the glass, so that they were no longer visible through the sides of the vessel. They reappeared against the glass more than once in milder weather, but finally both disappeared within the sawdust for the greater part of the winter.

One larva was seen moving about in its cell from the time it excavated the latter (Aug. 9) till Aug. 13. After that it went further into the sawdust and reappeared several times, and was observed lying in several different positions. Sept. 5–11, it was in a nearly vertical position, and hind end upmost during part, if not all, of the time. Sept. 13, it had pushed the sawdust away and opened a wide cell against the glass again, and was lying therein head upwards, at an angle of about 45°. When last seen (Sept. 23) it was lying on its side, nearer the horizontal. Sept. 26,

half the cell was filled with sawdust, into which it had retired, and no more was seen of the insect till May 23, 1919, when the contents of the vessel were turned out. The insect then ran out actively as an adult male, dragging at the hind end of its body an exuvium, which proved, on being mounted in balsam, to be the cast skin of the larva, not of the pupa. I cannot say, therefore, at what date this larva pupated.

The other larva allowed more of its history to be followed. It, too, was moving about in its cell from the time when it excavated the latter (Aug. 9) till Aug. 14. Aug. 16, larva much contracted, lying on its ventral surface. Aug. 18–31, larva turning about, sometimes on its back, sometimes on its ventral surface. Sept. 2, sawdust pushed over glass, larva invisible. Sept. 6, larva visible again, contracted, lying on its back in a horizontal position. Sept. 10, moving actively about in its cell. Sept. 11 and 13, lying straight out on its ventral surface (weather very cold). Sept. 17 and 20, larva lying on its side. Sept. 23, larva lying on its back on the glass bottom of the vessel. Sept. 26 and 30, larva retired into sawdust and was hardly visible. Oct. 8, lying on its back. At the beginning of November it had withdrawn so far into the sawdust that it was not clearly visible through the glass, and after Nov. 15 it was not visible at all till Jan. 15, 1919, during a mild spell, when it was on its ventral side with head towards the glass, having turned completely round since the time when it was last clearly visible in the autumn. At this time (Jan. 15) it was quite clearly seen to be still a larva. The insect was then visible no more till May 10, when (after several warm days) it was seen to be a *pupa*, quite pale, with no dark pigment in its eyes or in any other part. The pupa was observed nearly every day, and moved convulsively when the vessel was placed in a strong light. May 14, pupa lying on ventral surface, eyes darkening. May 15, lying on its back. May 19, pupa on its back, eyes quite black, general colour yellowish. May 22, morning, the adult (a female) had emerged and was lying in its cell. On the evening of May 23 the contents of the vessel were turned out, and the beetle ran out actively, with its dark coloration well developed. Assuming, therefore, that the transformation from a larva had only recently taken place when the pupa was first seen on May 10, the pupal stage lasted 12 days at least, perhaps rather longer.

Occurrence of Antherophagus in bees' nests.—The occurrence of several species of *Antherophagus* in humble-bees' nests is well known. This is not only the case with the European forms, for Grouvelle (14) has described from

Java a species, *A. ludekingi*, 5 males and a larva of which were found in the nest of a bee determined as *Bombus eximius* F. Smith. There is reason to believe that the flower-haunting adults are transported to the nests by clinging to humble-bees. Perris (**19**, p. 75) recorded the capture, in the Pyrenees, of an example of *A. nigricornis* clinging to the antenna of a *Bombus montanus*; and more recently Trautmann has published (**21**) a note (which I have been unable to see) on "an extremely rare find: *Antherophagus nigricornis* Fabr. on a living humble-bee."

I did not obtain from observation any information as to the exact part played by *Antherophagus* in the economy of the nest. Perris (**19**, p. 76) considered that the larvae are scavengers, playing the same rôle in nests of *Bombus* that those of *Cryptophagus* spp. play in wasps' nests. Cottam (**7**) records three cases of the finding of *A. pallens* in nests of *Bombus muscorum* in Derbyshire, Cheshire, and Lancashire respectively; in one of these nests larvae as well as adults were discovered, and it is noted that the larvae were in old, empty, cells of the comb. Two of these finds were made in the month of August; the third, in which only adult beetles were discovered, was in May.

Descriptions of larvae of Antherophagus.—No description is given here of the larva of *A. pallens*, of which I was only able to preserve one example. The larva has been described and figured by Gernet (**13**, p. 7), who found larvae of this species in the middle of August 1860, in numbers in cells of *Bombus muscorum*; but with them no pupae and only one adult. Perris (**19**) describes the larva of *A. silaceus* Herbst; he found adults of that species, and larvae which he referred to it without hesitation, in a nest of *Bombus sylvarum*, 23, viii, 1875. The larva of the Javanese *A. ludekingi* is described by Grouvelle (**14**).

Annual cycle of Antherophagus.—Summarising all these records, it is seen that adults have been taken in a bees' nest in May, and that adults and larvae have been found in a number of nests in August. In none of these cases have pupae been found; probably pupation occurs in the soil near the nest. The behaviour of my insects, which wintered as resting larvae and underwent a brief pupal stage in early summer, may well indicate the normal cycle of the genus in temperate countries. Presumably these beetles are double-brooded, with a short summer generation intervening between the emergence of the adults

in May and the assumption of the resting condition by the larvae in autumn.

V. **Epuraea depressa** Illiger (= **aestiva** Linn.).*

Biological observations.—About 22 larvae of this Nitidulid beetle, of various sizes, were found in the nest, but no pupae or adults. A number of examples were preserved; the rest excavated cells and pupated in them before the middle of August. Several pupae were also killed and preserved. As far as I could discover, the pupa does not have the hind end of its body clothed in the cast larval skin, a feature the presence or absence of which Ganglbauer frequently mentions in his definitions of families (**12**). In two specimens which were isolated and closely watched, the pupal period lasted 8–10 days, and the adults remained in the pupal cells 11 or 12 days after the final moult, emerging from their cells at the beginning of September.

Fowler (**11**, p. 228) records a case of the rearing of this species which reads as though the adults did not emerge till the following spring: a nest of *Bombus lucorum* containing many larvae of *E. depressa* was placed in a tin, and a large number of the adult beetles were reared "in the following spring." My specimens, however, emerged the same season, and I do not think this was due to artificial "forcing," since the larvae of *Antherophagus pallens* discussed above were kept under exactly the same conditions, and did not pupate till the following spring. Possibly, in the case recorded by Fowler, the beetles really emerged in late summer or autumn, and lay dormant in their cells till the next year. The adults are commonly taken on flowers in spring, and on several occasions numbers of them have been found in humble-bees' nests of the season. Perhaps the insect is double-brooded, the second generation passing the winter as dormant adults.

Detailed observations of pupation.—Some of the larvae were left in a large vessel containing some earth, and on Aug. 9 it was observed that certain of them were excavating cells in which to

* In the nomenclature of this species Grouvelle is followed (**15**, p. 111). Among British Coleopterists it is probably best known as *E. aestiva*; see Fowler (**11**, p. 228). Ganglbauer (**12**, p. 477) refers to it as *E. ochracea* Erichson.

pupate. Others were isolated in lightly covered glass vessels containing some litter from the nest and moist sawdust. Three of these excavated cells in the sawdust, in the angle formed by the sides and bottom of the vessel, so that they could be seen through the glass. The cells were not lined with any secretion.* Aug. 6, these three larvae were lying, slightly curved, on their backs in their cells. Aug. 7, larvae on their sides or on the ventral surface. Aug. 8, one had pupated: this pupa was killed and preserved. Of the other two larvae, one pupated during the night Aug. 9–10, the other between Aug. 10 and 12. The pupae lay at first on the ventral surface, but on Aug. 13 one, which had the dark pigment of the eyes already showing, had moved on to its side. I was absent from London from Aug. 17 to Sept. 1, during which time Mr. K. G. Blair kindly took charge of the pupae, and noted as follows:—both had the wings and jaws dark on Aug. 19; the beetles had emerged on Aug. 20 and 21 respectively, but were still in their pupal cells up to Aug. 31. On my return on Sept. 2 I found them out of their cells, walking about and readily "feigning death." They are both female.

Other records of occurrence in humble-bees' nests.—The record of many larvae being found in a nest of *Bombus lucorum* has been already mentioned (**11**). Sladen (**20**, p. 78, footnote) includes the species among the beetles found by him in nests of humble-bees. Tuck (**22**, 1896, p. 154) records it from nests of *Bombus agrorum*, *B. sylvarum*, and *B. latreillelus*, stating that he once took over 60 examples of the adult in a nest of the last.

Biological notes on other species of Epuraea.—*E. depressa* is not the only member of the genus taken from nests of Hymenoptera. Tuck (**22**) records *E. obsoleta* † from nests of *Vespa vulgaris*. Perris (**18**) states that the larvae of *E. obsoleta* Fabr., live in fermenting sap under the bark of pine and oak stumps, and that the majority pupate in the soil, but a few in the less sappy places under the bark. Perris and Tuck refer to the subjects of their respective observations by the same name. If their determinations

* The larvae of *Antherophagus* also made unlined cells in a similar situation. The angle of the glass was a favourite place for pupation with some larvae of *Necrobia ruficollis* which I had under observation; but their cells are lined. See Ann. Applied Biology, vi, pp. 101–115, 1919.

† *E. obsoleta* is considered by Grouvelle (**15**, p. 126) to be a synonym of *E. unicolor*, Oliv.

are correct, this species (*E. obsoleta*) occurs in very different habitats. Bagnall (2) found adults of *E. angustula* Er., frequently in the burrows of the Scolytid (Ipid) *Trypodendron* (*Xyloterus*) *domesticum*, and considers that the *Epuraea* preys on the bark-beetle. Bagnall also found (1) larvae pupae and adults of *E. parvula* Er. * in the fungus *Daldinia concentrica* on dead wood. Field coleopterists are of course familiar with the situations in which the members of this genus are to be found, but the precise facts of their natural history are not well known.

Food of the larvae of Epuraea depressa.—The only evidence as to the rôle played by the larvae in the nests of the bees is afforded by the remains of food in their alimentary canals. Such remains are visible in three larvae cleared by boiling in 5 % potash solution and mounted in balsam. Two have closely-packed masses of food in the hind part of the gut, the third has a mass between its mandibles. The bulk of these remains consists of mineral particles, frequently colourless. There are also many vegetable fragments, pronounced by an expert mycologist, Mr. F. T. Brooks, without doubt to be hyphae of fungi, perhaps of more than one kind : and numerous brown bodies which are almost certainly fungal spores. These objects indicate that the larvae play the part of scavengers. [Compare the view that the *adults* of *Epuraea angustula* are probably predaceous; see above.]

VI. *Larva of* Epuraea depressa. (Figs. 1–7.)

The larvae are in various stages of growth, and measure from about 3 to about 6 mm. long. The general colour is pale yellowish. In most respects the larvae agree with that of *E. obsoleta* as described by Perris (18), being characterised specially by the presence of numerous tubercles bearing flattened, spatulate, hairs, on the dorsal surface, and by having the spiracles situated at the summit of tubercular prominences. The following details are from the full-grown larva, though I have observed no structural differences between partly and fully grown examples.

Head (Fig. 2).—Dorsal surface presenting a closely dotted appearance under a high power; under a $\frac{1}{6}$-in. objective the dots, which are not indicated in fig. 2 A, are

* *E. parvula* is regarded by Grouvelle (15, p. 123) as a synonym of *E. rufomarginata*, Steph.

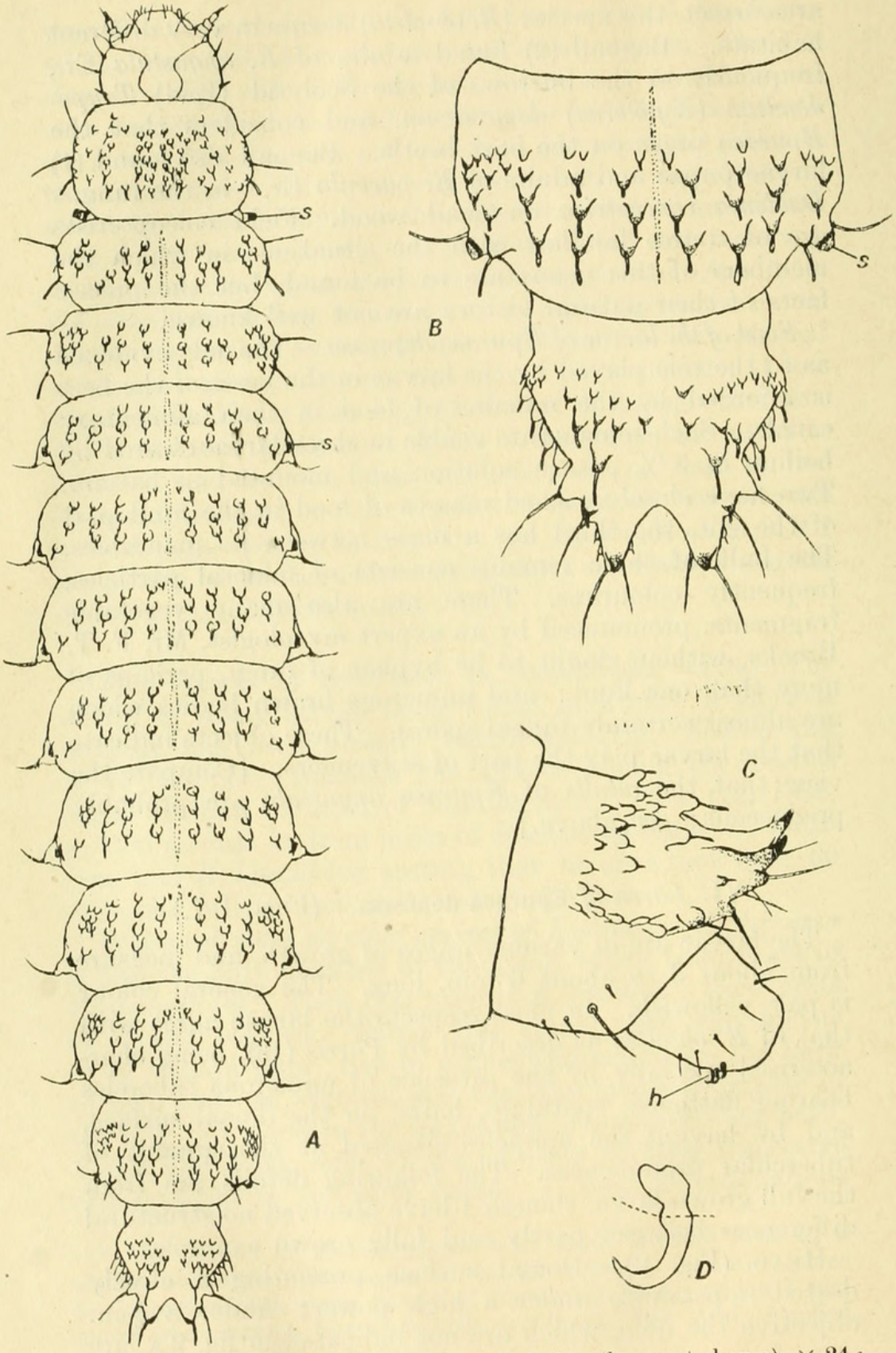

Fig. 1.—*E. depressa*, larva. **A**, dorsal view (legs not shown), × 24: *s.*, spiracles (only the thoracic and first abdominal are lettered). **B**, dorsal view of abdominal segments 8 and 9, × 56: *s.*, spiracle. **C**, 9th and 10th (anal) abdominal segments, lateral view, slightly tilted towards the observer, × 56: *h.*, pre-anal hooks. **D**, one of the pre-anal hooks, × 350. **A** and **B** are drawn from a specimen not cleared, but lying in spirit and viewed as an opaque object; **C** and **D** from a specimen cleared by treatment with caustic potash and mounted in balsam.

seen to be minute elevations in the chitin. On the front margin of the clypeus are 4 setae, the middle two shorter than the outer: just behind the front margin is a transverse series of 6 setae, the middle two shorter than the rest. The suture between clypeus and frons is very faintly indicated laterally, but obsolete in the middle.

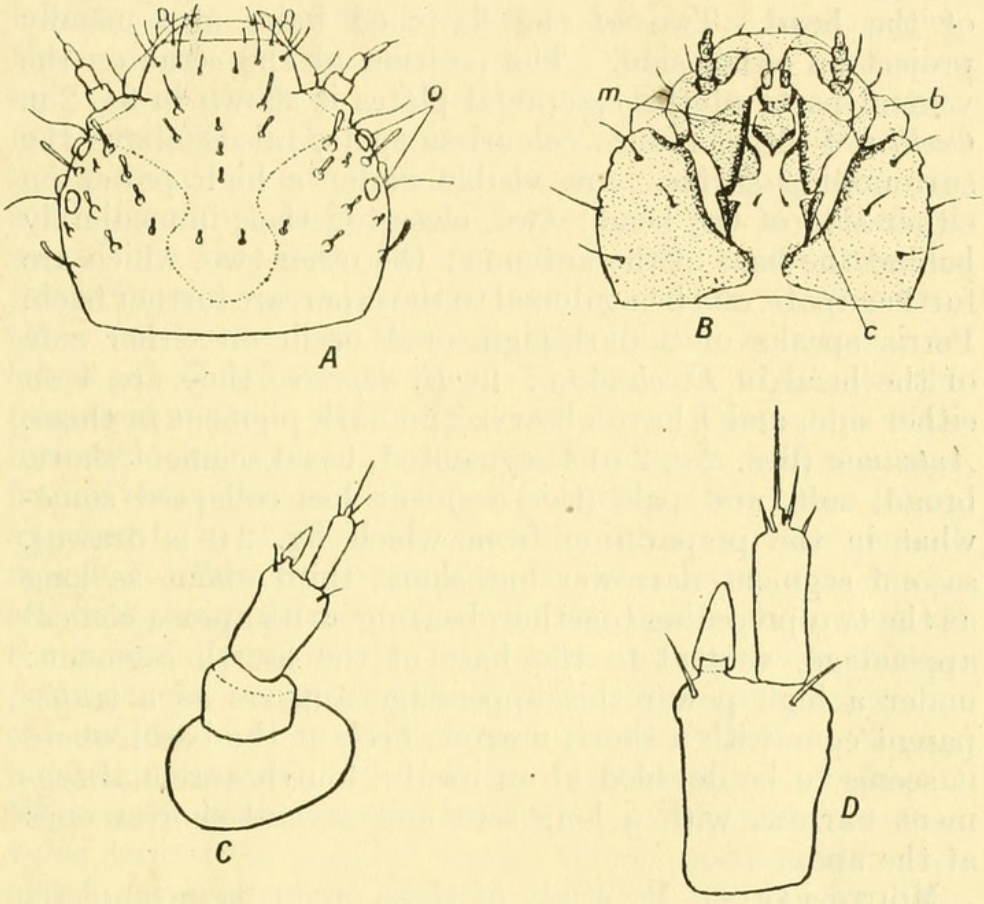

FIG. 2.—*E. depressa*, larva. **A**, dorsal view of head, × 56: *o.*, ocelli. **B**, ventral view of head, × 56: the more chitinised parts indicated by shading: *b.*, base of antenna; *c.*, cardo of maxilla; *m.*, mentum (?). **C**, whole antenna, × 170: basal segment somewhat collapsed in mounting. **D**, antenna, segments 3 and 4, and conical appendage on 3rd, × 350. **A** and **B** are drawn from a specimen not cleared, but lying in spirit and viewed as an opaque object; **C** and **D** from a specimen cleared with caustic potash and mounted in balsam.

There are several setae, near the middle line, in the frontal region. The epicranial suture is indicated in fig. 2 A by a finely dotted line. The vertex bears on either side a series of about 4 setae, commencing just behind the base of the antenna, and extending obliquely inwards and backwards: and a less regular series of about 3 just behind this. Most of these setae, especially on the posterior part

of the head, are flattened and spatulate, like those of the thoracic and abdominal segments, only narrower in proportion to their length. They require a high power for their exact discernment. Two long fine setae (not spatulate) project on either side from the outline of the head, one just behind the base of the antenna, the other further back; they arise from the lateral or ventro-lateral regions of the head. Two of the flattened hairs also usually project on either side. The position of the setae on the ventral parts of the epicranial plates is shown in fig. 2 B. *Ocelli*: 4 clear, round, colourless spots, raised above the surrounding surface, are visible under a high power on either side of the head; two, close together, immediately behind the base of the antenna; the other two, which are further apart, one being dorsal to the other, are further back. Perris speaks of 2 dark-pigmented ocelli on either side of the head in *E. obsoleta*: in *E. depressa* they are 4 on either side, and I have observed no dark pigment in them. *Antennae* (figs. 2 C, 2 D) 4-segmented, basal segment short, broad, soft, and pale (this segment has collapsed somewhat in the preparation from which fig. 2 C is drawn), second segment narrower but short, third about as long as the two preceding together, bearing at its apex a conical appendage, ventral to the base of the fourth segment: under a high power this appendage appears as a transparent cone with a short, narrow, neck at the base, where it seems to be doubled in on itself: fourth antennal segment narrow, with a long seta and several shorter ones at the apex.

Mouth-parts.—My study of these organs is incomplete, as I have been unable to devote sufficient time and material to elucidate fully the form of the hypopharynx and certain other points; nor is any attempt made to explain the homologies of all the structures described. Balsam-preparations of the whole head of three full-grown larvae have been examined, and in a fourth case the parts have been dissected and separately mounted. I have not dissected the mouth-parts of the youngest larvae, but from an examination of the underside of the head viewed as an opaque object, no structural difference from that of the full-grown larva is visible.

No structural *asymmetry* has been observed in the head or mouth-parts. Such asymmetry as appears in figs. 3 A, 5 A, and 5 B, is due to uneven pressure, or to the specimen

having moved into an oblique position with the drying of the balsam. This complete symmetry is in contrast to the condition existing in some beetle-larvae (e. g. *Dascillus* : see Carpenter and MacDowell, **5**, p. 381, etc.).

Labrum and epipharynx (Fig. 3 A).—The labrum is clearly separated from the head-capsule, the suture being represented in fig. 3 A by a sinuate, dotted line. Dorsally the labrum bears a rather long seta near either front angle : these setae are not shown in fig. 3 A, which represents only the ventral view. The front margin is nearly straight, and set with 4 short spines; between the median and outer spine on either side is a clear, circular, area, resembling a follicle from which the spine has been broken away, but this does not seem to be the explanation, as precisely the same arrangement has been observed in three specimens. At the sides the labrum is raised into lobes (cf. *Helodes* : see **5**, pl. 35, fig. 10), which (in the preparation from which fig. 3 A is drawn) project a little in front of the general outline of the margin, and the large lateral setae rise from behind (*i. e.* dorsal to) these lobes, apparently in the fold between the lobes and the general margin.* The inner margins of these lobes are closely set with hairs directed towards the middle line, and all the median part of the labrum is covered with minute prominences, some (or all) of which bear erect hairs : in the middle are 4 much larger round follicles. A pigmented, thickened, chitinous band, rather like a misshapen **W**, lies across the labrum, its median part bearing a transverse series of 4 rounded teeth; this is, presumably, part of the epipharynx (cf. *Helodes* : see **5**, pl. 35, fig. 10). No attempt is made to interpret the pigmented, thickened, chitinous parts (shaded in fig. 3 A) at the sides of the labrum near its base; nor the two curiously shaped pieces (fig. 3 A, *p.*) meeting in the middle line, and the greater part of which lies against the head-capsule behind the suture (fig. 3 A, *su.*) separating labrum from clypeus.

Mandibles (Fig. 3 B).—The upper *articulation* of the mandible is at a point on a level with the base of the antenna, but nearer the middle line, and is effected by a prominence of the head-capsule fitting into a hollow in the upper edge of the base of the mandible : this articu-

* Fig. 3 A shows 2 large setae on one side, 1 on the other. This asymmetry is accidental, or due to individual variation. A second specimen examined has 2 on either side.

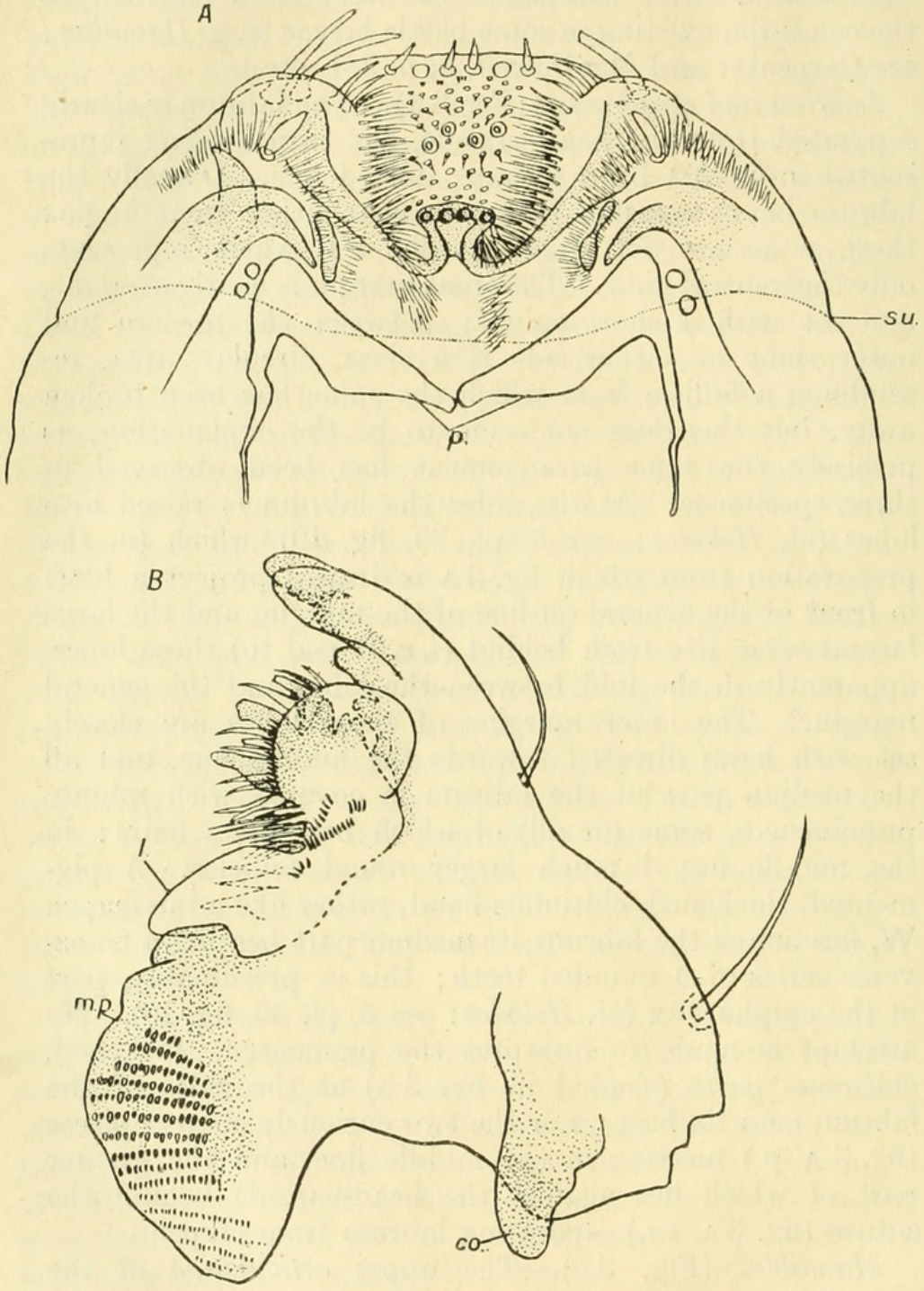

Fig. 3.—*E. depressa*, larva. **A**, labrum, epipharynx, and part of head-capsule from beneath, × 354: *su.*, dotted line indicating suture between labrum and clypeus; *p.*, chitinous pieces (see text). **B**, left mandible, ventral aspect, × 354: *co.*, condyle; *l.*, lanceolate portion of transparent lamina; *m.p.*, molar portion of mandible. Each is drawn from an example dissected out of a larva cleared with potash, and mounted in balsam.

lation is not seen in fig. 3 B. The lower articulation is brought about by the large condyle (fig. 3 B, *co.*) fitting with a point on the margin of the epicranial plate (postgena ? : see fig. 2 B).*

The *apex* of the mandible is divided into 2 teeth, and there is also, along the upper (dorsal) edge of the apical portion, a series of 4 other teeth, that furthest from the apex being very small. *Molar portion* of the mandible large (fig. 3 B, *m.p.*), its inner surface (*i. e.* towards the middle line) raised into three blunt teeth (indicated in fig. 3 B, but in mandibles remaining *in situ* in the head, which lie in a slightly different plane, they appear much more marked). The molar part also bears a number of transverse series of very minute elevations; in fig. 3 B they are only shown on its ventral surface, but actually they extend round on to the dorsal side.

Between the apical and molar parts is a complicated set of structures, difficult to represent in fig. 3 B, as they lie one behind the other in several focal planes. Viewed from the ventral side there is towards the apex a thin transparent lamina with rounded outline, its margin set with long, sharp, prominences; this lamina is extended into another thin, transparent, broadly lanceolate part (fig. 3 B, *l.*) lying just in front of the molar portion of the mandible. Dorsal to the rounded lamina (seen partly through and behind it in fig. 3 B) is a number of stout, pigmented, finger-like processes, which appear to be grouped in several series, each at right angles to the plane of the figure. Below these, and between the rounded and lanceolate laminae, is a dense group of spines and bristles of differing length and thickness, and seen through the transparent lanceolate lamina is a series of sharp-pointed structures resembling long saw-teeth. The dotted line between the transparent laminae and the main body of the mandible in fig. 3 B represents the fairly clearly defined line at which the chitin becomes very thin and colourless. Possibly the whole of this complex structure corresponds to those parts or appendages, of very different forms, which have been described in the mandibles of a

* The words " upper " and " lower " are used here with reference to the actual position of these points in the larva. According to Comstock and Kochi (**6**, pp. 14, 37) the upper articulation is, from a strictly morphological point of view, really ventral, and the lower really pleural.

number of other Coleopterous larvae: *e.g.* the slender, movably articulated, tooth ("prostheca") in the mandible of *Dascillus cervinus* (5, p. 382, pl. 36); the articulated comb-like process in that of *Helodes minuta* (5, p. 378, pl. 35); the "lacinia mobilis" in that of *Ochthebius* and *Hydroscapha* (3, pl. 18, figs. 9–12); the broad, thin, perlucid "retinaculum" in the mandible of the Coccinellid *Hyperaspis binotata* (4, p. 624, pl. 118, fig. 6); other examples doubtless could be cited.

Maxillae (Figs. 2 B, 4).—The lower parts of the maxillae and labium are so imbedded in, and continuous with, a transparent membrane, that it is not easy to delimit the parts exactly, and the boundaries are therefore sometimes represented in the figures by dotted lines.

The *cardo* (figs. 2 B, 4, *c.*) appears detached from the stipes in the figure, owing to the stretching of the membrane. On the inner side the limits between pigmented chitin and colourless membrane are not clearly marked. There is a longitudinal fold or thickening, and the posterior extremity apparently articulates with the tentorium (in fig. 2 B it appears to meet the margin of the epicranium, but is really at a deeper level, and is viewed through membrane).

The *stipes* is a large piece, passing gradually into membrane on the outer side; on the inner side there is at the base a projecting flange (fig. 4, *f.*), the flanges of the two maxillae nearly meeting in the middle line. The apical part of the stipes, from which the lobes and palp arise, is membranous (fig. 4, *me.*) and transparent, and this part is sharply demarcated from the chitinised part, as shown in the figure; the membrane below the base of the palp is somewhat torn in the figured example, as is indicated by the dotted line. The dorsal surface of the stipes, between the bases of the lobes and the palp, bears spines and hairs, which, excepting those projecting beyond the outline between galea and palp, are not indicated in fig. 4. The apex of the larger lobe (*galea*) is set with ranks of processes, one behind the other, their apices blunt, bifid, and slightly curved over. The smaller lobe (*lacinia*) is presumably represented by the darker-pigmented, 3-fingered process (fig. 4, *la.*), which appears to be slightly curved round the lower edge of the galea. Its representation in fig. 4 is complicated by the presence of a number of spines (one of which is blunt and almost spatulate) on the dorsal side of

the galea. The *maxillary palp* is clearly 4-segmented, both in the full-grown and in the smallest larvae :—unless the

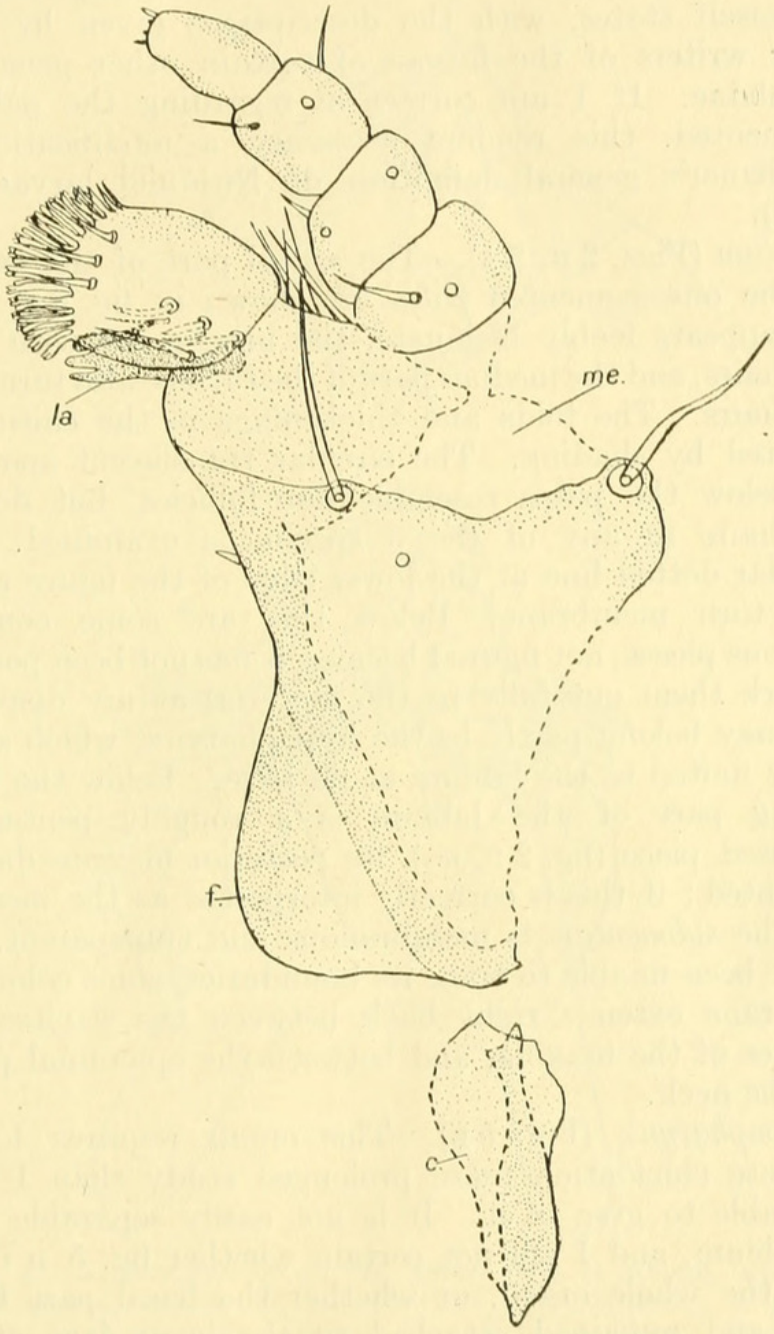

Fig. 4.—*E. depressa*, larva. Left maxilla, ventral aspect, × 354 : *c.*, cardo; *f.*, projecting flange of stipes; *la.*, lacinia; *me.*, membranous part of stipes. Drawn from an example dissected out of a larva cleared with potash, and mounted in balsam.

part which I take to be the basal segment is really to be regarded as the palpiger, but it appears to have the character of a true palpal segment, while the palpiger may be repre-

sented by the membranous part, indicated as torn in fig. 4, beneath the palp. Perris (**18,** pp. 469, 471–2) regarded the palp as 3-segmented, therein disagreeing, as he himself states, with the descriptions given by some earlier writers of the larvae of certain other genera of Nitidulidae. If I am correct in regarding the palp as 4-segmented, this renders necessary a modification of Ganglbauer's general definition of Nitidulid larvae (**12,** p. 443).

Labium (Figs. 2 B, 5 A).—The apical part of the labium and the one-segmented *palpi* are shown in fig. 5 A. The apex appears feebly bisinuate, the margin set with very short hairs, and the median part of the surface also furnished with hairs. The folds and thickenings in the chitin are indicated by shading. The circular translucent spots on and below the palps resemble hair-follicles, but do not bear hairs in any of the 3 specimens examined. The irregular dotted line at the lower edge of the figure represents torn membrane. Below this are some complex chitinous pieces, not figured because it has not been possible to work them out fully in the material at my disposal: they may belong partly to the hypopharynx, which seems closely united to the labium at its base. Below the palp-bearing part of the labium is a roughly pentagonal chitinised piece (fig. 2 B, *m.*), its posterior margins darker-pigmented: if this is correctly interpreted as the *mentum*, then the *submentum* is membranous and transparent, and I have been unable to trace its boundaries, since colourless membrane extends right back between the stipites and cardines of the maxilla, and between the epicranial plates into the neck.

Hypopharynx (Fig. 5 B).—This organ requires for its complete elucidation more prolonged study than I have been able to give to it. It is not easily separable from the labium, and I am not certain whether fig. 5 B represents the whole organ, or whether the basal part broke away and remained attached to the inner face of the labium. The most conspicuous feature is the truncated, pigmented, chitinous tooth (fig. 5 B, *t.*), which, in balsam-preparations of the head with mouth-parts *in situ*, is seen projecting forward between the molar parts of the mandibles, reaching nearly as far as the front of these molar parts. Apparently the apex of the hypopharynx diverges considerably from the labium, so that the chitin-

ous tooth lies in a different focal plane, slightly *dorsal* to the molar parts of the mandibles; but possibly the latter come very close to it, or even work against it to some

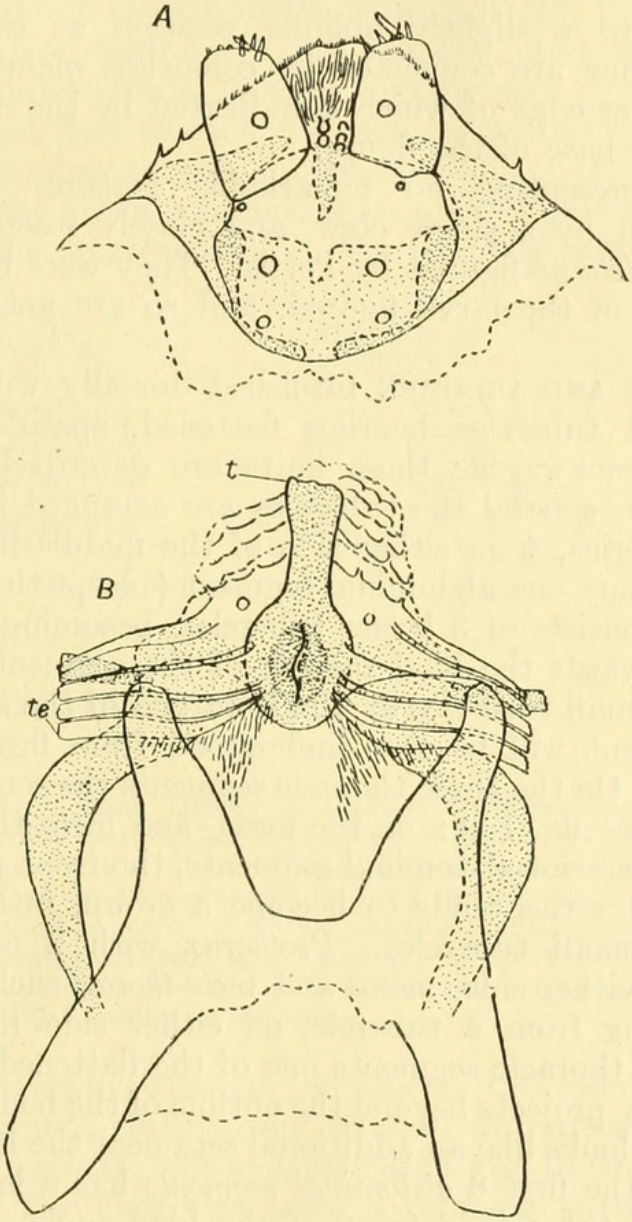

FIG. 5.—*E. depressa*, larva. **A**, apical part of labium, and palpi, ventral aspect, × 354. **B**, hypopharynx (? incomplete), × 354: *t.*, chitinous tooth projecting forward; *te.*, ends of 5 tendons. Each figure is drawn from an example dissected out of a larva cleared with potash, and mounted in balsam.

extent, when the mandibles are closed. Round this tooth is clinging some transparent membrane with torn edges and with a shagreened or scaley appearance. At the base of the tooth is a central chitinous body, oval in outline, from which arise on either side 5 tendons (fig. 5 B,

te.). The form of the chitinous pieces in the lower part of the hypopharynx is best seen from the figure, in which the more definitely pigmented parts are indicated by shading; their asymmetry is due to the organ having moved into a slightly oblique position as the balsam dried. They are connected by colourless membrane, the (torn) lower edge of which is indicated by the dotted line across the base of the figure.

Legs presenting no remarkable feature. They are terminated by a single claw, and closely resemble those of *E. obsoleta* as figured by Perris. They were bent under the body of the larva figured, and so are not shown in fig. 1 A.

Thorax and abdomen furnished dorsally with numerous small tubercles bearing flattened, spatulate, hairs, directed backwards: these hairs are described in detail below. In general the tubercles are arranged in 8 longitudinal series, 4 on either side of the middle line. Each series on any one abdominal segment (except the two last) usually consists of 3 larger tubercles, becoming gradually larger towards the hind margin of the segment, and one or more small tubercles at the front end of the series; the arrangement will be best understood from figs. 1 A, 1 B, and 7 A. On the three thoracic segments the series are less regular (see fig. 1 A): on the meso- and meta-thorax, and on the posterior abdominal segments, the front part of the outermost series tends to become a group, rather than a line, of small tubercles. *Prothorax* with 2 conspicuous setae on either side, *meso-* and *meta-thorax* each with one seta, rising from a tubercle, on either side (in each of the three thoracic segments one of the flattened hairs also frequently projects beyond the outline of the body on either side, and looks like an additional seta near the hind angle). Each of the first 8 *abdominal segments* has a large lateral setigerous tubercle in front of the hind angle. The form of the *9th abdominal segment* is best explained by fig. 1 A–C. *Anal segment* not normally visible from above, hidden under the 9th (shown in profile in fig. 1 C), bearing a transverse series of widely spaced setae, and a transverse row of about 5 *chitinous hooks*, directed forwards, immediately in front of the anus (fig. 1 C, D).

Spiracles (Figs. 1 A, 1 B, *s.*; 6 A, B) remarkable for being situated on raised tubercles, as described by Perris in the larva of *E. obsoleta.* The first pair larger than the others

and on longer tubercles, between the pro- and meso-thorax; the other pairs, on the first 8 abdominal segments, near the hind angles, just dorsal to the lateral setigerous tubercles. Pedunculate spiracles are also found in the larvae of certain other Nitidulids (**12,** p. 472) and in that of *Nosodendron* (**12,** pp. 445, 469, etc.), which, like many Nitidulid larvae, lives in running sap.

The apical part of each peduncle is chitinised and pigmented, forming a dark brown ring (fig. 6 A, B), within which, on the actual summit, is an area of pale membrane enclosing the spiracle itself. The latter is biforous, con-

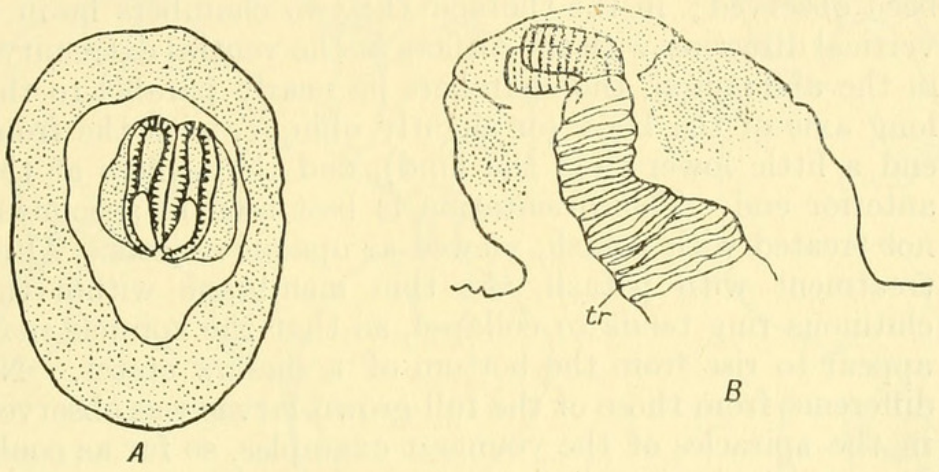

FIG. 6.—*E. depressa*, larva. **A**, spiracle between pro- and meso-thorax, in surface view, × 530 : the outer shaded ring is the pigmented part of the apex of the tubercle; the unshaded area within this represents colourless membrane surrounding the spiracle itself. **B**, spiracle on 1st abdominal segment, × 530 : shown in profile, partly in optical section, the pigmented band round the apex of the tubercle being left incomplete in front; *tr.*, trachea. Both are drawn from a larva cleared with potash and mounted in balsam.

sisting of two contiguous chambers, the side walls of which present a transversely striated appearance, clearly seen in profile (fig. 6 B) and indicated also in surface-view (fig. 6 A). The chambers have a common partition wall, though in the position from which fig. 6 B is drawn (oblique profile) they seem to some extent separate. Their tops appear at first sight to be open as two long narrow slits, but on closer examination it is seen that the aperture is only at one end, and occupies less than half the length of the chamber, the rest of which has a thin unstriated roof. The two openings appear as though united at their bases into a single U-shaped orifice : but this union is only apparent, due to a sudden break or thinning in the chitin

of the chamber walls, the space being occupied by a narrow neck of thin membrane separating the two openings, as indicated in fig. 6 A. There is also a break in the thicker chitin of the rim of each chamber at the end remote from the aperture. The trachea is united to the chambers at the end beneath the orifices. No definite atrium has been discerned, the spiral thickening coming very close, if not right up, to the point of union with the two chambers. The thoracic spiracles are considerably larger than the abdominal, and differently orientated, though in their structure no difference from the abdominal spiracles has been observed; in the thoracic the two chambers lie in a vertical direction with the orifices at the ventral extremity; in the abdominal, the chambers lie nearly parallel to the long axis of the body (or slightly oblique, with the front end a little lower than the hind), and the orifices at the anterior end. This orientation is best seen in specimens not treated with potash, viewed as opaque objects. After treatment with potash, the thin membrane within the chitinous ring tends to collapse, so that the spiracle may appear to rise from the bottom of a shallow crater. No difference from those of the full-grown larvae was observed in the spiracles of the youngest examples, so far as could be seen by viewing the latter as opaque objects.

The spatulate hairs (Figs. 1 A–C; 7 A, B). General arrangement described above. In preparations in Canada balsam, under a $\frac{1}{6}$-in. objective, the hairs borne by the dorsal tubercles are seen to be flattened, transparent, spatulate, and of varying size and length. Fig. 7 A shows them in dorsal view. Fig. 7 B shows a series of the dorsal tubercles in profile; in optical section the cuticle appears much thickened in the region of the tubercles, which seem to be formed by the throwing of the cuticle into convolutions; the minute erect processes (fig. 7B, *pr.*) spring from the general surface of the cuticle. Even the long slender setae projecting from the sides of the head and body appear, under a $\frac{1}{6}$-in. objective, more or less flattened, so that the difference between them and the spatulate hairs seems to be one of degree only, not of kind. The spatulate hairs recall similar structures figured and described by Bøving (3) as occurring on the hind margins of the segments in the aquatic larva of *Hydroscapha.*

The occurrence of these numerous tubercles and spatulate hairs can hardly be connected with life in bees' nests,

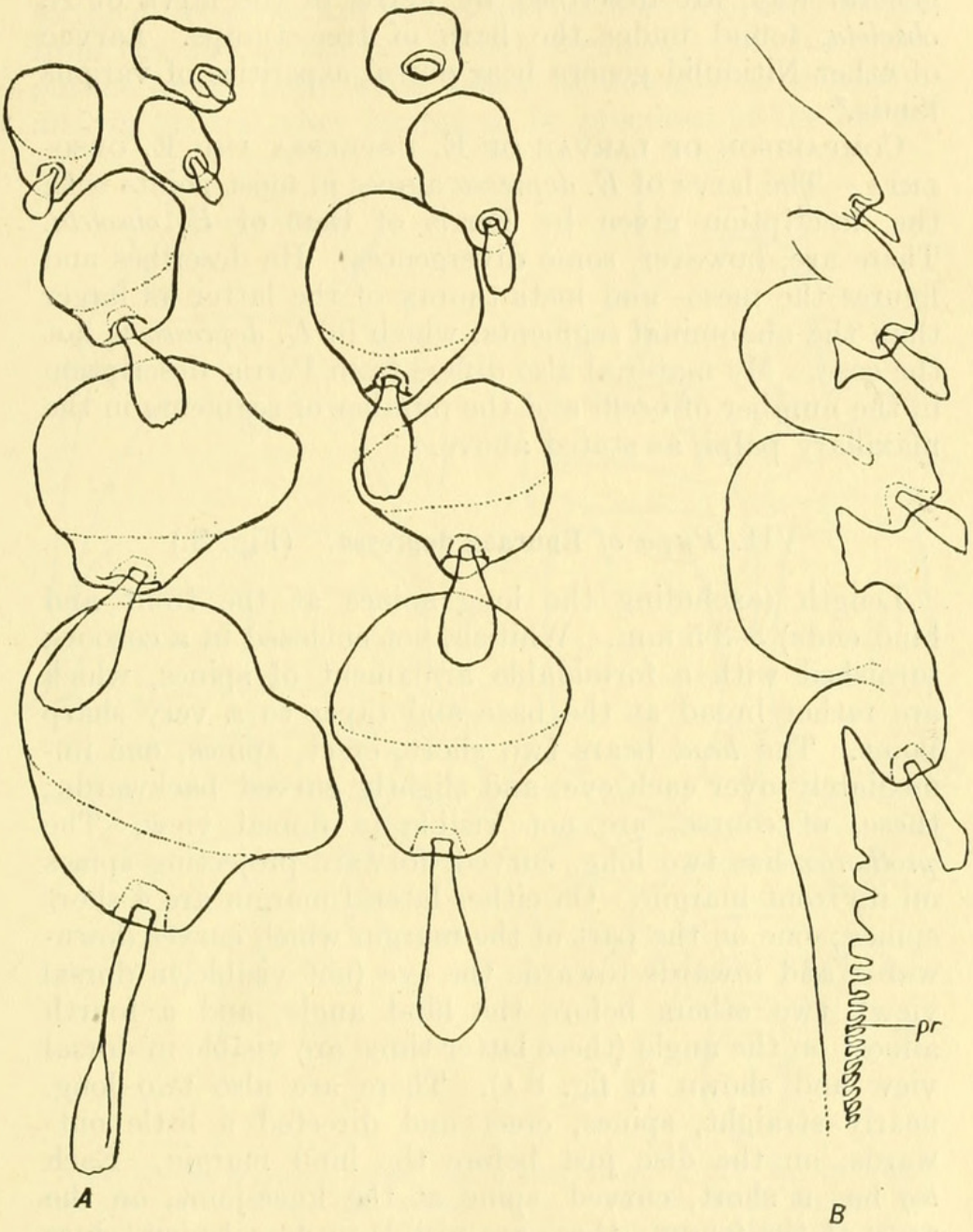

FIG. 7.—*E. depressa*, larva. **A**, two of the longitudinal series of tubercles and spatulate hairs on the 8th abdominal segment, dorsal view, × 350; the right-hand series in the figure is that immediately on the left of the middle line of the segment, and the two series are drawn exactly as they lie in relation one to the other: anterior end of series at top of figure. **B**, one of the longitudinal series on the 6th abdominal segment in profile, in optical section, × 350: anterior end at top of figure: *pr.*, minute erect processes of general surface of cuticle towards hind end of segment. **A** and **B** are drawn from two larvae cleared with potash and mounted in balsam.

since exactly the same structures, arranged in the same general way, are described by Perris in the larva of *E. obsoleta*, found under the bark of tree-stumps. Larvae of other Nitidulid genera bear dorsal asperities of various kinds.*

Comparison of larvae of E. depressa and E. obsoleta.—The larva of *E. depressa* agrees in most points with the description given by Perris of that of *E. obsoleta*. There are, however, some divergences. He describes and figures the meso- and meta-thorax of the latter as larger than the abdominal segments, which in *E. depressa* is not the case. My material also differs from Perris' description in the number of ocelli and the number of segments in the maxillary palpi, as stated above.

VII. *Pupa of* **Epuraea depressa.** (Fig. 8.)

Length (excluding the long spines at the front and hind ends) 3–3·5 mm. Whitish, not enclosed in a cocoon; furnished with a formidable armament of spines, which are rather broad at the base and taper to a very sharp point. The *head* bears two short, erect, spines, one immediately over each eye, and slightly curved backwards; these, of course, are not visible in dorsal view. The *prothorax* has two long, curved, forward-projecting spines on its front margin. On either lateral margin are 4 short spines; one on the part of the margin which curves downwards and inwards towards the eye (not visible in dorsal view), two others before the hind angle, and a fourth almost on the angle (these latter three are visible in dorsal view and shown in fig. 8 A). There are also two long, nearly straight, spines, erect and directed a little outwards, on the disc just before the hind margin. Each *leg* has a short, curved, spine at the knee-joint, on the apex of the femur; these are visible in dorsal view, since the femoro-tibial joints project beyond the outline of the body. *Abdomen*: the arrangement of spines is best shown in dorsal view. The basal segment bears none. Segments 2–8 have each two spines on either side, these

* The larva of *Pocadius ferrugineus*—the only other Nitidulid larva to hand for comparison—has 6 dorsal longitudinal series of setae, as well as setae on the lateral margins. Those of the two mid-dorsal series are borne in groups of three on tubercles. There is no modification of setae into flattened or spatulate hairs.

forming an inner and an outer longitudinal series; those of the outer series are larger, and become gradually longer from the 2nd to the 5th or 6th segment; they form the outline of the body when looked at dorsally or ventrally, and in ventral view appear to be processes of the lateral

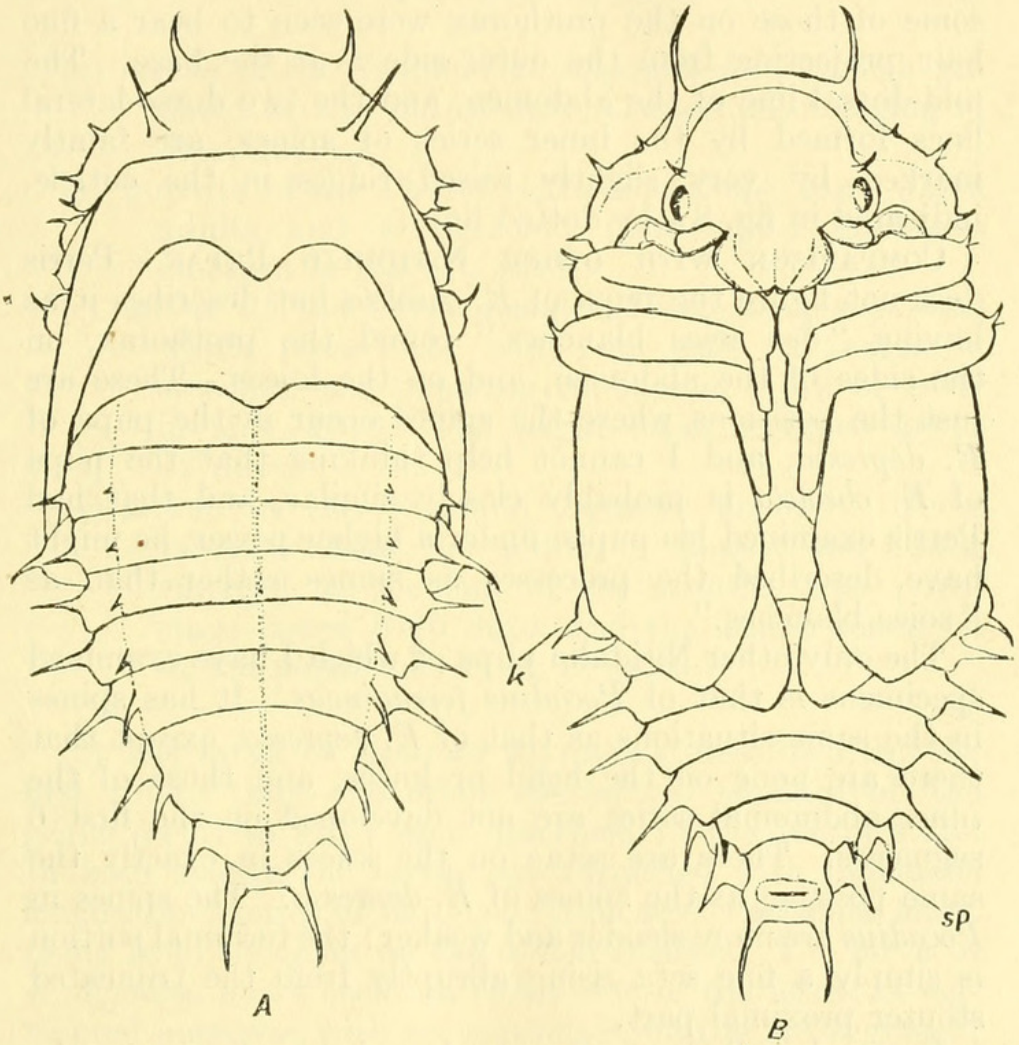

Fig. 8.—*E. depressa*, pupa. **A**, dorsal view, × 24: *k.*, knee-joint and spur of hind leg. **B**, ventral view, × 24: *k.*, as in **A**; *sp.*, 7th spine of the outer series, ventral in position and not visible from above. **A** and **B** are drawn from a single pupa, not cleared, but lying in spirit and viewed as an opaque object: the slight curvature of the pupa has caused it to appear a little longer in ventral view.

margins of the sternites; the seventh pair (*i. e.* that on the 8th segment) of this outer series is not visible in dorsal view, being ventral in position (fig. 8 B, *sp.*), and hidden by the overlapping of the spines of the inner series. The latter are very minute on the 2nd and 3rd segments, but become gradually longer on the posterior segments; they

are dorso-lateral in position until the 7th and 8th segments, where they form the lateral outline of the body viewed from above, and on the 8th segment conceal the spines of the outer series from dorsal view. In addition to these two series, there is a pair of long, curved, anal spines. Under a high power the spines on the knees and some of those on the prothorax were seen to bear a fine hair projecting from the outer side near the base. The mid-dorsal line of the abdomen, and the two dorso-lateral lines formed by the inner series of spines, are faintly marked by very slightly raised ridges in the cuticle, indicated in fig. 8 A by dotted lines.

Comparison with other Nitidulid Pupae.—Perris does not figure the pupa of *E. obsoleta* but describes it as having "des soies blanches" round the prothorax, on the sides of the abdomen, and on the knees. These are just the positions where the spines occur in the pupa of *E. depressa*, and I cannot help thinking that the pupa of *E. obsoleta* is probably closely similar, and that had Perris examined his pupae under a higher power, he might have described the processes as spines rather than as "soies blanches."

The only other Nitidulid pupa of which I have examined specimens is that of *Pocadius ferrugineus*. It has spines in the same situations as that of *E. depressa*, except that there are none on the head or knees, and those of the *inner* abdominal series are not developed on the first 6 segments. There are setae on the knees in exactly the same position as the spines of *E. depressa*. The spines in *Pocadius* are more slender and weaker: the terminal portion is simply a fine seta rising abruptly from the truncated stouter proximal part.

Perris also alludes to the cast larval skin clinging to the hind end of the abdomen of the pupa of *E. obsoleta*. As stated above (p. 105), this is not the case with any of my four pupae of *E. depressa* now, nor do I remember the larval exuvium being present when I placed them in spirit. Neither have I observed it attached to the pupae of *Pocadius*. Ganglbauer (12) gives the retention of this exuvium round the hind end of the pupa, or its absence, a rather prominent place in his definitions of certain of the Clavicorn families.

VIII. General Summary.

(1) In a nest of *Bombus derhamellus* received from Kent in July 1918 were the following insects :—

(*a*) larvae of the Tachinid *Brachycoma devia*, which pupated at the end of July, the adults emerging in May, 1919.

(*b*) puparia of the Phorid *Aphiochaeta rata*, from which adults and a Braconid (*Orthostigma pumilum*) emerged in August, 1918.

(*c*) larvae of the Cryptophagid *Antherophagus pallens*, which passed the winter in cells excavated in sawdust, not pupating till late in April or early in May, 1919. The pupal stage occupied about 12 days.

(*d*) larvae of the Nitidulid *Epuraea depressa*. These pupated about the middle of August and adults emerged at the end of the month. The pupal stage lasted 8–10 days, and the adults remained in the pupal cells 11 or 12 days.

(2) The larva of *Epuraea depressa* is described for the first time. Only one other species (*E. obsoleta*) of the genus seems to have been described in the larval state. In both species the larvae are furnished with numerous longitudinal series of flattened, truncated, spatulate hairs, rising from tubercles on the dorsal surface. The larva of *E. depressa* has 4 ocelli on either side of the head; 4-segmented antennae with an appendage on the 3rd segment; mandibles furnished with a remarkable group of processes; maxillary palpi 4-segmented; labial palpi 1-segmented; spiracles pedunculate and biforous, one pair between pro- and meso-thorax, and 8 other pairs on abdominal segments 1–8 respectively.

(3) Larvae of *E. depressa*, after treatment with caustic potash, were found to have in the gut mineral particles, spores, and fragments of fungus-hyphae.

(4) The pupa of *E. depressa* is armed with spines situated on the head and prothorax, at the femoro-tibial joints of all the legs, and arranged in two longitudinal series along either side of the abdomen.

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The following is not intended to be an exhaustive bibliography of any of the matters dealt with, but merely a list of works to which it has been necessary to refer. Concerning the biology of *Epuraea* and *Antherophagus*, some of the references given below and certain others not included here will be found in M. Rupertsberger, "Biologie der Käfer Europas" (1880), pp. 128, 134; and in the same writer's "Die biologische Literatur über die Käfer Europas von 1880 an" (1894), p. 134.

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