Anatomical and Systematic Study of the Mature Larvae of the Nitidulidae (Coleoptera)

by Adam G. Böving ‡ and Jerome G. Rozen, Jr. ¹

At its inception under the sole direction of the first author, this study was intended to be a detailed investigation of the external anatomy, musculature, and taxonomy of the mature larvae of the beetle family Nitidulidae. It was to be similar in scope and presentation to his earlier work on anobiid larvae (Böving, 1954). At the time to his death in 1957, the research for the project had nearly been finished, but very little had been committed to paper. In the taxonomy section, most of the illustrations had been prepared but only the keys had been written. Of the numerous anatomical illutrations drawn, only those dealing with the thoracic musculature seem to have been finished, and only the anatomical description of the head capsule had been drafted.

After the first author died, the second author undertook the preparation of the manuscript. However, because of time limitations imposed by other duties, it became apparent that he could not complete the paper as originally planned. Further, to have done so would have necessitated re-doing most of the research with the result that the final interpretations and conclusions, except those already written by the first author, would have been those of the second author alone. The primary effort therefore has been to tie together the illustrations, keys, and notes of the senior author into as coherent and as useful a manuscript as possible.

This study has been based upon the nitidulid larvae in the collection of the United States National Museum. Although no field work was directly involved with the work, the ecological data included in the appended list of material studied strongly

¹ Chairman and Associate Curator, Department of Entomology, The American Museum of Natural History, New York, New York.

suggest that nitidulids have an extremely varied biology. The anatomical diversity of the larvae provide further support for this idea.

Some of the drawings for the taxonomic section were prepared by Marjorie Statham.

ANATOMY

There is little question that the external anatomy as revealed by the musculature was the first author's foremost interest in the group, as became obvious during his discussions with the second author in 1956 and 1957. The many intricate preliminary illustrations of the microscopic musculature, drawn, revised and redrawn, are graphic testimony to this fact. All unpublished anatomical illustrations are available for study at the United States National Museum, Washington, D. C.

The remaining paragraphs in this section though edited by the second author were written by the first author. The description of the head capsule presumably refers only to the Carpophilinae, Nitidulinae, and Cryptarchinae, for reasons presented in the taxonomy section. Three of the first author's illustrations (figs. 1—3) of the head are presented. Although some of the major anatomical features on these drawings were labeled by the second author, many of the muscles could not be identified with absolute certainty and as a consequence were not named. The first author's discussion follows.

The results of my anatomical investigation of the nitidulid larvae have been compared with the results of many other authors interested in the anatomy of insects. I paid particular attention to the papers by Voss (1904, 1905) and the many papers and books by Snodgrass. I learned much from my study of both famous authors and some of the muscle arrangements were very similar to what I had found in nitidulid larvae. But as a whole, the pattern of the muscles of the two orthopterans and the nitidulid larvae are so different that a comparison between them would be a waste of time in view of our insufficient knowledge of insect musculature.

However, there is a surprising similarity between the muscle arrangements of the nitidulid larvae and those of the larva of *Corydalus*, as presented by Kelsey (1954) in his very careful paper. The fact that I have been able to apply Kelsey's number

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system to the muscles of nitidulid larvae illustrates that the muscle patterns of both insect larvae are surprisingly analogous if not homologous. So far, Kelsey has published only on the head and prothorax of the *Corydalus*. However, since I have found a constant pattern of the muscle arrangement in all the coleopterous larvae I have seen (1915—1954), I am rather convinced that Kelsey's forthcoming publication on the abdominal muscles of the hellgrammite will reveal an analogy between the abdominal muscles number system can be easily applied to the abdominal muscles of the coleopterous larvae.

Kelsey's muscle terminology has been adopted with a few rather insignificant alterations resulting from the fact that the neck region of nitidulid larvae lacks jugular sclerites.

Head Capsule.

The protracted and prognathous head (fig. 1) is wider than long, and appears somewhat obliquely placed on the horizontal midplane of the thorax because its under surface is shorter than the upper surface. The narrowly oval foramen magnum is as wide or almost as wide as the greatest width of the cranium and is framed by the combined occipital arch and the postocciput between which is the postoccipital sulcus. Ventrally on each side near the sagittal midline is the posterior tentorial pit.

On the dorsal surface of the cranium (fig. 1), the frontal and clypeal areas are fused into one piece which, by abutting posteriorly upon the occiput in a straight transverse line, eliminates the epicranial (= coronal) sulcus. The clypeal region is not divided into an anteclypeus and a postclypeus. The labrum, reduced to a low transverse, sclerotized lobe with a curved free margin, is set off from the clypeal region by a faint clypeolabral sulcus. The clypeo-frontal plate is separated from the parietals on each side by an angular frontal cleavage line. Although in some larval forms the anterior end of this cleavage line reaches the outside of the antennal socket, in the majority of the larvae it stops before the socket and makes a turn encircling a small oval plate to which are attached two muscles from the base of the antenna. The lateral parts of the parietals, known as the genae, are separated on the underside of the cranium by a part of the submental region. Several ocelli with

strongly curved corneas are located behind the antennal sockets.

There is no epistomal ridge but only a small sclerite with a projection for the dorsal articulation of the mandible near the inside of each antennal socket. The pleurostomal ridge is also lacking. The ventral mandibular condyle, articulating in a cup located opposite the dorsal articulation, is found in the anterior end of a long, strong, curved hypostomal ridge which extends to the posterior tentorial pit.

The endoskeletal tentorial structures invaginate in front from each of the anterior tentorial pits at the ends of the clypeolabral sulcus¹, and in the rear from the posterior tentorial pits. Each anterior tentorial part begins as a narrow neck but enlarges gradually in the middle to a broad plate, the so-called corporotentorium, with an outward concave and an inward convex outline. In the rear of the outside of the corporotentorium the plate is raised into a short and broad spout. Behind and below the hypopharyngeal swelling, known as the inculus, at the entrance to the pharynx, the corporotentorium continues in an outward, convex, spoonlike hollowed and posteriorly pointed prolongation which supports and protects the pharynx on each side. Posteriorly the paired corporotentoria meet and form a longitudinal rodlike ridge in the sagittal midline.

The posterior section of the tentorium starts as a bridge which braces the near ends of the hypostomata. A pair of arms extends forward only a short way from the bridge. Usually they then vanish or merge into an untraceable membrane, but they reappear near the pointed ends of the prolongations from the corporotentoria. Here they are united by a transverse bar-shaped connection, which laterally sends forth a strong dorsal tentorial arm on each side. The dorsal arms fuse apically with the clypeofrontal piece. From the anterior corners of the linking bar the two tentorial rods continue to the base of the hypopharyngeal

¹ The first author's concept of the anterior tentorial structures, as described in the following paragraphs, is not clear to me. One of his pencil sketches indicates that he may have revised his ideas of these structures but did not have time to modify his manuscript before he died. This sketch depicts a narrow tapering apodeme arising in the vicinity of the anterior mandibular articulation and is labeled "tentorial pit of anterior arm?". This apodeme corresponds to what I consider to be the anterior arm of the tentorium in oedemerid larvae (Rozen, 1958). — J. G. R.



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Fig. 1. Soronia sp., head, dorsal view. Fig. 2. Glischrochilus fasciatus (Olivier), head, frontal section showing epipharynx and muscles attached to dorsal wall.

Fig. 3. Glischrochilus obtusus (Say), head, sagittal section.

inculus and appear to fuse here with the hypopharyngeal structures.

The entire posterior section of the tentorial assemblage designated with the same name ("the anterior arms of tentorium") as the anterior section, is located below the pharynx. Muscles from the maxillae are attached to the upper surface of the section and muscles from labium to its under surface.

The epipharyngeal integument (fig. 2) is a continuous membrane which forms the roof lining of the rather flat cibarium and extends from the free anterior and lateral margins of the labrum and clypeus to the entrance of pharynx. It differs in appearance corresponding to the various epipharyngeal sections. The labroepipharyngeal section of the integument covers the subtriangular space between the inner margins of the anterior tentorial plates, and is segregated by a U-shaped groove into two subdivisions. The posterior subdivision is to all appearances homologous with the crepidal area in the scarabaeid and anobiid larval types. A pair of long muscles from the frontal element of the clypeo-frontal cranial part is inserted on a tail-shaped invagination of the integument in the rear of the area. The muscles are evidently labral depressor muscles and the inner tentorial ridges are probably homologous with tormal features. Both subdivisions of the labro-epipharyngeal section bear minute bundles of extremely fine setulae distributed densely over the entire adoral surface. A few sensory pores can also be found, but there are no setae on the anterior subdivision like the acanthoparial, coronal or chaetoparial setae which occur here in larvae of other beetle families.

The clypeo-epipharyngeal section of the adoral integument lies as a sheet over the entire surface of the anterior tentorial plates and has an outline that corresponds to the margins of the plates. The section has a corrugated intima with densely set longitudinal, oblique and parallel flutes and ribs, the latter bedecked with minute granulae.

Three tiny, almost vestigial clypeal dilator muscles (figs. 2, 3) of the cibarium are inserted in the epithelium of the hindermost ribs and extend to the outer ridge of the corporotentorium where they appear to be attached to the clypeal wall above. A very small anterior dorsal dilator muscle of the pharynx, with some doubt, may be traced to the other side of the clypeo-frontal shield.

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It is attached in the vicinity of a considerably stronger retractor muscle of the hypopharyngeal suspensorial bar. The latter two muscles, although located close to the dilators of the cibarium, belong to a different category of muscles in the head, as they are found behind the frontal connective nerve. The former threelie in front.

The hypopharyngeal area occupies a median part of the lower portion of the head and rests upon the labium above the prementum. It is rather flat and short, extending from the entrance to the pharynx merely to a point situated below the posterior end of the labro-clypeal area. The width at the base is equal to the sagittal length, and the contour of the area is broadly heartshaped with a short and rounded glossa. The adoral surface is generally fleshy, fringed on each side with soft hairs from the paragnathal plot. The suspensorial bars are lodged some distance inside of the lateral margin of the hypopharynx. They are rodshaped until they reach the base of the area. There they become larger, meet, and fuse medianly creating a strong swollen and hard inculus. The inculus rests on and is fused with a plateshaped enlargement of a tough ribbon-shaped bracon. This feature extends like a boom across the cranium and connects the cups of the lower mandibular articulations. Morphologically it is an invagination from the skin between the mandibles and the maxillae. The above-mentioned retractor muscle of the angle of the pharyngeal mouth-opening arises from the enlarged base of the suspensorial bar and becomes attached to the wall of the clypeo-frontal region.

Another pair of muscles are inserted at the base of the hypopharynx. Long, horizontal and subparallel, they originate from the tentorial bridge between the rear ends of the hypostomata. The place where they are fastened anteriorly may more precisely be pointed out as lying where the ends of the premental sclerite, the ventrolateral margin of the stipes and the lateral edge of the hypopharyngeal basal sclerotization come together. The identification of the muscle-pair is uncertain. They may here be interpreted as homologous with the ones described and marked "19, muscle of hypopharynx" by Dorsey (1941).

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Thoracic Musculature.

The first author prepared figures 4 to 8 depicting diagrammatically the musculature of the thorax of nitidulid larvae. Muscles numbered on these plates were described by Kelsey (1954) for *Corydalus*. His paper (1957) on the pterothoracic muscles did not appear until after the first author died. For the most part, the list of lettered muscles presented below refers to the prothorax, although the homologous muscles on the other two tharacic segments are marked on the illustrations.

- a¹ and a² The interior and dorsolateral longitudinal muscles come from the the anterior margin of the cervical membrane laterad of the insertion places of muscles 56, 58, and 59. They run to the posterior margin of the connecting membrane between the pro- and meso-thorax where they meet above the first thoracic spiracle. Muscle a¹ is fastened anteriorly to the cervical membrane where the dorsal and lateral parts of the occipital arch meet. Muscle a² is fastened anteriorly close to the insertion place of muscle 58.
- b¹ and b³ The assemblage of exterior dorsal and dorsolateral longitudinal muscles are situated between the dorsal body wall and the interior dorsal and dorsolateral longitudinal muscles. Muscles b¹ are as long as their segment and run between the anterior and posterior tergal borders. Muscles b³ are attached posteriorly to the antecostal margin of the segment. They are inserted some distance behind the anterior margin of the preceding segment and cross the b¹ muscles.
- c and e The interior and ventral longitudinal muscles are jointly attached to one of the lateral corners of the furcasternum. They diverge forward to the anterior border of the cervical membrane. Muscle c is inserted at the corner where the ventral and lateral parts of the occipital arch meet. Muscle e is inserted with muscle 62 on the ventral part of the occipital arch.
- d This muscle is attached to the rudimentary furcal arm. It extends obliquely outward and inserts at the occipital arch between the posterior tentorial pit and the corner between the ventral and lateral parts of the arch.
- f and g These are an assemblage of exterior ventral longitudinal muscles posteriorly attached to the furcasternal region and situated between the sternal body wall and interior ventral longitudinal muscles 56, 58, and 59. Muscles f are as long as the segment and they run parallel between the furcasternal region and the ventral part of the occipital arch. Muscles g are shorter than the f muscles, and are inserted somewhat behind them.
- The posterior ray of the star-shaped assemblage of muscles extends from its attachment place on the spina obliquely outward and backward to the lateral corner of the furcasternum of the segment.



Fig. 4. Lobiopa insularis (Castelnau), dorsal muscles of thorax and first abdominal segment, ventral view. See text for identification of muscles.



Fig. 5. Prothoracic musculature of nitidulid larva, sagittal section. See text for identification of muscles.

- i The oblique ventral muscle extends back from the posterior end of muscle h, and crosses the intersegmental connecting membrane behind the prothorax in an upward direction below the first thoracic spiracle.
- j This short oblique muscle runs from the anterior margin of the coxa to the middle of the anteroventral margin of the prothorax between the episternum and the posterior spina of the cervical membrane.
- k and l These two short muscles attach closely together at the lateral corner of the furcasternum and insert in the coxa. Muscle k inserts in the middle of the coxal marginal side toward the sagittal line. Musle l inserts in the opposite side of the coxa posterior to the coxal articulation with the pleural apophysis.
- m¹ and m² The two coxal rotator muscles attach on the furcasternum near the anterior portion of the spina and insert in the coxal margin toward the sagittal line. They are possibly antagonistic to muscle j. Muscles m¹ and m² are somewhat differently arranged in the meso- and metathorax.



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Fig. 6. Prothoracic musculature of nitidulid larva, sagittal section. See text for identification of muscles.

- ^{|1|}Z A solid string, possibly a reduced muscle, extends from a ringshaped base in the lateral part of mesothoracic furcasternum to to the lateral corner on the opposite side of the metathoracic furcasternum.
- In the lateral part of metathorax to the narrow intersegmental membrane behind the first abdominal segment.

TAXONOMY

At the time of the first author's death, only the keys for this section had been written. In reviewing them, the second author became aware that the first several couplets to the main key did not work. Because of this difficulty all keys were rewritten. In revising the main key, the second author included the Cateretinae, Meligethinae, and the Cybocephalinae, both because their inclusion broadens the scope of the key and because the taxonomic catalogues generally retain the groups in the Nitidu-



Fig. 7. Lobiopa insularis (Castelnau), ventral muscles of thorax and first abdominal segment, dorsal view. See text for identification of muscles.



Fig. 8. Lobiopa insularis (Castelnau), ventral muscles of thorax and first abdominal segment, dorsal view. See text for identification of muscles.

lidae. However, it is important to point out that the first author definitely considered the Cybocephalinae to be a distinct family (Böving and Craighead, 1931, p. 37, footnote 48) and he probably regarded the other two together as another family, as did Verhoeff (1928) (see Böving and Craighead, 1931, footnote 47).

The characteristics of the family are given in key form by Böving and Craighead (1931).

Key to the Mature Larvae of the Nitidulidae.

1. Urogomphi and pregomphi virtually absent (Böving and Craighead, 1931, pls. 36, 37); mandibular apex simple (*ibid.*) 2 Sharp-pointed urogomphi present (figs. 11, 18, 49); pregomphi (figs. 11, 49) usually present; mandibular apex bi- or tri-dentate (figs. 21, 23, 41, 44, 65), rarely (in Cyllodes biplagiatus, some Pallodes silaceus, and possibly Cychramus variegatus) simple. Carpophilinae, Nitidulinae, Cryptar-2(1). Numerous body setae club-shaped (Böving and Craighead, 1931, pl. 37); eighth and ninth abdominal segments each with pair of lateral conical projections (ibid.). Cybocephalinae..... Cybocephalus prob. californicus Horn Body setae hair-like (*ibid.*, pl. 36); eighth and ninth abdo-3(2). Mandible without subapical teeth and with large adoral membranous projection between mola and apex (Böving and Craighead, 1931, pl. 36, C); frontoclypeal area broadly truncate posteriorly (*ibid.*, A). Meligethinae Meligethes aeneus (Fabricius) Mandible subapically dentate dorsally and without adoral projection between mola and apex (*ibid.*, L); frontoclypeal area pointed (Amartus tinctus, Cercometes abdominalis) or narrowly rounded (Brachypterolus pulicarius) posteriorly. Cateretinae 4 4(3). Coronal ecdysial line short but present; mandibular mola smooth; maxillary palpus two segmented Cercometes abdominalis (Erichson) Frontal ecdysial lines meeting at posterior margin of head; mandibular mola conspicuously dentate; maxillary palpus

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Figs. 9—11. Colopterus truncatus (Randall). 9. Entire larva, dorsal view, 10. Labio-epipharynx. 11. Ninth and tenth abdominal segments, lateral view.

Fig. 12 Colopterus amputatus Erichson, abdominal segments nine and ten, lateral view.

Fig. 13. Carpophilus hemipterus (Linnaeus), labio-epipharynx.

Figs. 14, 15. *Brachypeplus rubidus* Murray. 14. Mesothorax, metathorax, and first abdominal segment, dorsal view. 15. Spiracular tube of first abdominal segment, posterior view.

Figs. 16-19. *Macrostola lutea* Murray. 16. Larva, dorsal, lateral, and ventral views. 17. Right anterior leg, anterior view. 18. Abdominal segments nine and ten, lateral view. 19. Head, dorsal view.

5(4). Abdomen with pigmented paired dorsal sclerites on each segment; tibiotarsus with setae unmodified Amartus tinctus (Mannerheim) Abdomen without sclerites (Böving and Craighead, 1931, pl. 36, M, N, as Heterostomus pulicarius L = Brachypterusgravidus Illig.); tibiotarsus with elongate, fan-shaped apical setae (*ibid.*, O) Brachypterolus pulicarius (Linnaeus) 6(1). Urogomphi (fig. 66) apically three-branched and sometimes with additional basal branch (fig. 67); abdomen bearing lateral conical processes (fig. 66) that are approximately equal to or longer than typical spiracular tubes, which are themselves conspicuous; typical abdominal segment not covered with paired transversely rectangular granulated dorsal sclerites, though two species with numerous sclerotized granules, some of which may be borne on small sclerites (figs. 67, 69) Cryptarcha (See key to species, p. 290) Urogomphi usually apically simple (figs. 11, 49) or bifurcate (figs. 18, 25), but if rarely distinctly or indistinctly threebranched, then lateral tubercles of abdomen at most weakly developed (figs. 20, 28, 38) and/or typical abdominal segment covered by pair of transversely rectangular granulated sclerites (figs. 20, 28, 38) 7 7(6). Mandibles apically tridentate (Böving and Craighead, 1931, pl. 35, K); urogomphi directed posteriorly, in same plane as ninth abdominal tergum, the median section of which is produced posteriorly between urogomphi (ibid., M) Prometopia sexmaculata (Say) Mandibles apically bidentate or simple (figs. 41, 55); urogomphi rising above ninth tergum; ninth tergum not produced between urogom_Phi (figs. 27, 49)..... 8 8(7). Abdominal segments I-VII either with variable-sized sclerites (figs. 47), with dorsal tubercles or granules (fig. 43), or with both (fig. 38); legs normally long, so that tibiotarsus at least two-thirds length of femur (fig. 45).... 9 Abdominal segments I-VII without dorsal granules or tubercles (figs. 56, 73) and usually without dorsal sclerites; if rarely covered with weak sclerites (in *Macrostola*, fig. 16), then legs extremely short, the tibiotarsus being much less than one-half length of femur (fig. 17)..... 19

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Figs. 20, 21. Orthostolus prosternalis Sharp. 20. Left half of abdominal segments eight and nine, dorsal view. 21. Apex of right mandible, ventral view.

Figs. 22-24. Conotelus stenoides Murray. 22. Abdominal segments eight and nine, dorsal view. 23. Apex of right mandible, ventral view, 24. Abdominal segments nine and ten, lateral view.

Figs. 25, 26. Conotelus mexicanus Murray. 25. Abdominal segments nine and ten, lateral view. 26. Abdominal segments eight and nine, dorsal view.

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- 9(8). Head with three large, distinct, equal-sized ocelli on each side (figs. 36, 42); each typical abdominal segment bearing sclerites, from which arise more than two variable-sized tubercles or granules (figs. 37, 40)..... 10 Head with one, two, or four ocelli on each side (figs. 48, 51) or if questionably with three (i. e., *Cychramus variegatus*), dorsal sclerites absent on typical abdominal segments, though elongate sclerotized paired paramedian tubercles present (fig. 43)...... 12
- 10(9). Mesothorax, metathorax and following eight abdominal segments each with paramedian dorsal sclerites transversely rectangular and well separated medially (fig. 38); lateral abdominal tubercles scarcely noticeable, much shorter than typical spiracular tubes (fig. 38); urogomphi with numerous long setae, some of which are borne on elongate tubercles (fig. 38).....

..... Amphicrossus ciliatus (Olivier)

- - 12(9). Typical abdominal segment without dorsal sclerites but with pair of large paramedian sclerotized tubercles (fig. 43)..... Cychramus variegatus (Herbst) Typical abdominal segment usually with large or small dorsal sclerites, which may or may not bear tubercles or granules (figs. 47, 50); rarely (*Carpophilus antiquus* Melsheimer) dorsal sclerites apparently not developed

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Fig. 27. Epuraea monogama Crotch, abdominal segments seven, eight, and nine, dorsal view.

Fig. 28. Epuraea linearis Mäklin, same.

Fig. 29. Epuraea laeviuscula (Gyllenhal), same.

Fig. 30. Epuraea thoracica Tournier, seventh abdominal segment, dorsal view.

Fig. 31. Epuraea avara (Randall), same.

Fig. 32. Epuraea unicolor (Olivier), ninth abdominal segment, dorsal view.

Fig. 33. Epuraea melina Erichson, same.

Fig. 34. Haptoncus luteolus (Erichson), same.

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- 14(13). Mandible without swelling along aboral edge, i. e., normal (fig. 46); typical abdominal segment bearing smooth, nearly square, paired, paramedian, contiguous dorsal sclerites (fig. 47)..... Omosita colon (Linnaeus) Mandible with conspicuous swelling (figs. 52, 55) along aboral edge; typical abdominal segment bearing well-separated, paired, variable-shaped dorsal sclerites, which bear several small granules (fig. 50) 15
- 16(13). Ninth abdominal tergum without setiferous tubercles except for at most one laterad of each pregomphus and urogomphus (Connell, 1957, fig. 2); urogomphi simple (*ibid.*); either typical abdominal segment with pair of transversely elongate-oval dorsal sclerites each of which is bordered by more or less evenly spaced granules, or typical abdominal segment with small barely discernible asperities among which are located at most five



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Figs. 35–37. Soronia sp. 35. Larva, dorsal view. 36. Head, dorsal view. 37. Right half of eighth abdominal segment, dorsal view.

Fig. 38. Amphicrossus ciliatus (Olivier), larva, dorsal view.

Figs. 39-42. Lobiopa insularis (Castelnau). 39. Larva, dorsal view. 40. Tip of abdomen, dorsal view. 41. Left mandible, ventral view. 42. Head, dorsal view.

or six granules on each side (Connell, 1957, fig. 1)... Carpophilus, in part (C. humeralis and antiquus; for key to species, see Connell, 1957) Ninth abdominal tergum with numerous granules or setiferous tubercles (figs. 20, 22, 26, 27); urogomphi sometimes branched (fig. 25); typical abdominal segment covered dorsally with a pair of coarsely or finely granulated, transversely rectangular plates (figs. 20, 22, 26, 27) 17(16). Mandible with at least one subapical ventral tooth (fig. 21); anal hooks absent; typical abdominal segment with dorsal granules very small and arranged in indistinct rows (fig. 20); urogomphi usually more attenuate (fig. 20) Orthostolus prosternalis Sharp Mandible without subapical ventral teeth (fig. 23); anal hooks present (fig. 24); typical abdominal segments with dorsal granules large and usually arranged in distinct linear series (figs. 22, 28); urogomphi less attenuate (figs. 22, 34) 18 18(17). Typical abdominal tergum with at most one-tenth of granules bearing setae (figs. 22, 26); granules small, even-sized, and arranged in transverse as well as longitudinal series (figs. 22, 26) Conotelus (See key to species, p. 292) Typical abdominal tergum with all granules bearing setae (fig. 27); granules usually large, usually variable in size, and either appearing randomly scattered (fig. 27) or arranged in only longitudinal linear series (fig. 28) Epuraea and Haptoncus (See key to species, p. 292) 19(8). Urogomphi apically bifurcate¹ (figs. 18, 71) 20 Urogomphi apically simple (figs. 59, 63) 21 20(19). Frontoclypeal area acutely pointed posteriorly (fig. 19); legs short, so that tibiotarsus much less than one-half length of femur (fig. 17); body extremely elongate (fig. 16) Macrostola lutea Murray Macrostola sp.

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¹ One ramus of urogomphus may be small, as in *Glischrochilus vittatus* (fig. 74) and therefore easily overlooked.



Figs. 43-45. Cychramus variegatus (Herbst). 43. Larva, dorsal view. 44. Right mandible, dorsal view. 45. Right front leg, anterior view.

Figs. 46-49. *Omosita colon* (Linnaeus). 46. Right mandible, dorsal view. 47. Larva, dorsal view. 48. Head, dorsal view. 49. Ninth abdominal tergum, dorsal view.

Frontoclypeal area broadly truncate posteriorly (fig. 73); legs normally long, so that tibiotarsus approximately two-thirds length of femur (fig. 72); body normally robust (fig. 73)...... Glischrochilus (See key to species, p. 294)

- 21(19). Mesothorax and metathorax each with lateral pair of tapering conical projections that are slightly longer than spiracular tubes of abdomen (fig. 14); abdominal spiracles located ventrally near base of elongate spiracular tubes (fig. 15) Brachypeplus rubidus Murray Mesothorax and metathorax without lateral projections (fig. 9); abdominal spiracles situated at apex of spiracular tubes if spiracular tubes are developed (fig. 60) 22
- 22(21). Mandible markedly swollen at base (gibbous) and with conspicuous subapical teeth both dorsally and ventrally (figs. 57, 61) (because of torsion of mandibular apex in Cyllodes biplagiatus, fig. 57, subapical teeth are aboral and adoral in position); pregomphi indistinct, at most represented merely as vague swellings on ninth abdominal tergum (figs. 56, 60) (urogomphi simple)..... 23
 Mandibles normal, not or but slightly swollen at base, and with only dorsal subapical teeth; pregomphi, even if minute, rising sharply from ninth abdominal tergum (figs. 59, 63) (in Colopterus amputatus processes arising from base of urogomphi are pregomphi, fig. 12)... 24
- 23(22). Mandibular apex twisted nearly 90°, so that subapical teeth on adoral and aboral margins (fig. 57); prostheca reduced to small pad with indistinct series of minute denticles (fig. 57) Cyllodes biplagiatus LeConte Mandibular apex normal, so that subapical teeth on dorsal and ventral margins (fig. 61); prostheca distinct, with three stiff denticles and some ordinary setae (fig. 61).

..... Pallodes silaceus Erichson 24(22). Eighth abdominal segment with length of spiracular tubes at most one-half their diameter at base (fig. 9), but if longer (Colopterus amputatus), then pregomphus arising from basal section of urogomphus (fig. 12)...... 25 Eighth abdominal segment with length of spiracular tubes approximately equal to or longer than their diameter



Figs. 50-52. *Phenolia grossa* (Fabricius). 50. Larva, dorsal view. 51. Head, lateral view. 52. Right mandible, dorsal view.

Figs. 53—55. Aethina sp. 53. Apex of right mandible, ventral view. 54. Head, lateral view. 55. Right mandible, dorsal view.

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25(24).	at base (figs. 58, 63); pregomphi arising from ninth ab- dominal tergum (figs. 56, 63)
	(see Connell, 1957, for key to species) Labio-epipharynx with several short nearly straight se-
	tae on each side of anterior margin (fig. 10); either uro- gomphi and pregomphi very small (fig. 11) or each pre- gomphus arising from base of urogomphus (fig. 12)
	Colopterus
	(See key to species, p. 296)
26(24).	Pregomphi minute, their length being less than one-fifth
	that of urogomphi (fig. 63)
	Pregomphi moderately long, their length being more than
	one-third that of urogomphi (fig. 59)
	Stelidota geminata (Say)

Key to the Mature Larvae of Cryptarcha.

1. Typical abdominal segment with single median dorsal tubercle (figs. 64, 66, 70); urogomphus without distinct basal lateral branch (though pregomphi present) ... 2 Typical abdominal segment with eight or more dorsal small tubercles (or granules) (figs. 67-69); urogomphus with basal lateral branch (figs. 67, 69) 3 2(1). Typical abdominal segment with dorsal tubercle smaller (fig. 70) Cryptarcha sp. a Typical abdominal segment with dorsal tubercle larger (fig. 66) Cryptarcha ampla Erichson 3(1). Typical abdominal segment with all granules arising from nonsclerotized integument (fig. 67); ninth abdominal segment without tubercles anterior to pregomphi (fig. 67) Cryptarcha sp. b Typical abdominal segment with some granules arising from small sclerites (fig. 69); ninth abdominal segment with two distinct paramedian tubercles anterior to pregomphi (fig. 69)..... Cryptarcha glabra Schaeffer?

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Figs. 56, 57. Cyllodes biplagiatus LeConte. 56. Larva, dorsal view. 57. Right mandible, dorsal view.

Figs. 58, 59. Stelidota geminata (Say). 58. Larva, dorsal view. 59. Abdominal segments nine and ten, lateral view.

Figs. 60-62. Pallodes silaceus Erichson. 60. Larva, dorsal view. 61. Left mandible, ventral view. 62. Urogomphi, dorsal view.

Fig. 63. Orthopeplus quadricollis Horn?, tip of abdomen, lateral view.

Key to the Mature Larva of Conotelus.

1. Urogomphus with apical branches subequal or with posterior one slightly shorter than anterior one (fig. 24); typical abdominal segment with longitudinal linear series of granules dividing tergum into nine posterior cells (as numbered in fig. 22)..... Conotelus stenoides Murray Urogomphus with anterior branch more than twice as long as posterior one (fig. 25); typical abdominal segment with longitudinal linear series of granules dividing tergum into five posterior cells (fig. 26). Conotelus mexicanus Murray

Key to the Mature Larvae of Epuraea and Haptoncus.

1.	Typical abdominal segment with all setae sharp-pointed,
	i. e., setae setiform or lanceolate (figs. 27-30) 2
	Typical abdominal segment with some setae rounded apic-
	ally, i. e., setae obovate, spatulate, capitate, or ligulate
	(fig. 31)
2(1).	Head with frontoclypeal region without minute papillae,
	though with setiferous granules; typical abdominal tergum
	with granules very small and arranged without apparent
	order (fig. 27); urogomphi elongate (fig. 27)
	Epuraea monogama Crotch
	Head with frontoclypeal region minutely papillate in ad-
	dition to bearing setiferous granules; typical abdominal
	tergum with granules larger and arranged in obvious
	longitudinal series (figs. 28-30); urogomphi shorter (figs.
	28, 29)
3(2).	Abdominal tergum VIII minutely, continuously papillate
	between granules (fig. 29); typical abdominal tergum with
	first (paramedian) longitudinal series of granules com-
	posed of only two minute granules (fig. 29)
	Epuraea laeviuscula (Gyllenhal)
	Abdominal tergum VIII smooth or with but few indistinct $% \left({{{\left[{{{\rm{Abd}}} \right]}_{\rm{A}}}_{\rm{A}}} \right)$
	papillae between granules, except marginally (fig. 28);
	typical abdominal tergum with first longitudinal series of
	granules composed of three larger granules (figs. 28, 30) 4
4(3).	Typical abdominal tergum with third longitudinal series of
	granules composed of three granules (fig. 28)
	Epuraea linearis Mäklin



Figs. 64—66. Cryptarcha ampla Erichson. 64. Larva, dorsal view. 65. Left mandible, ventral view. 66. Abdominal segments seven, eight, and nine, dorsal view.

Figs. 67, 68. Cryptarcha sp. b. 67. Abdominal segments seven, eight, and nine, dorsal view. 68. Larva, dorsal view.

Fig. 69. Cryptarcha glabra Schaeffer?, abdominal segments seven, eight, and nine, dorsal view.

Fig. 70. Cryptarcha sp. a, same.

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	Typical abdominal tergum with third longitudinal series of
	granules composed of two granules (fig. 30)
	Epuraea thoracica Tournier
5(1).	Typical abdominal tergum with at least some papillae be-
	tween granules (fig. 31) Epuraea avara (Randall)
	Typical abdominal tergum without papillae except some-
	times marginally (as in fig. 30) 6
6(5).	Urogomphi, when viewed from above, with median branch
	visible (fig. 32); urogomphi and pregomphi elongate (fig.
	32) Epuraea unicolor (Olivier)
	Urogomphi, when viewed from above, without visible median
	branch (figs. 33, 34); urogomphi and pregomphi shorter
	(figs. 33, 34)
7(6).	Urogomphal apices parallel (fig. 34)
	Haptoncus luteolus (Erichson)
	Urogomphal apices diverging posteriorly (fig. 33)
	Epuraea melina Erichson

Key to the Mature Larvae of Glischrochilus.

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Figs. 71-73. *Glischrochilus obtusus* (Say). 71. Tip of abdomen, lateral view. 72. Right front leg, anterior view. 73. Larva, dorsal view.

Fig. 74. Glischrochilus vittatus (Say), ninth abdominal tergum, lateral view.

Fig. 75. Glischrochilus japonius (Motschulsky), same.

Fig. 76. Glischrochilus fasciatus (Olivier), same.

Key to the Mature Larvae of Colopterus.

 Pregomphi and urogomphi short (fig. 11); each pregomphus arising from ninth abdominal tergum (fig. 11)......
 Colopterus truncatus (Randall) Pregomphi and urogomphi long (fig. 12); pregomphus appearing to arise from basal section of urogomphus, especially when viewed from side (fig. 12)......
 Colopterus amputatus Erichson

Material Studied.

Cateretinae

Amartus tinctus (Mannerheim): 17 larvae, 5 adults, Fresno, Calif., in flowers of *Escholtzia*, E. A. Schwarz [presumably det. collr.].

Brachypterolus pulicarius (Linnaeus): 1 larva, Denmark, Aug. [det. as Brachypterus gravidus possibly by A. G. Böving].

Cercometes abdominalis (Erichson): 4 larvae, 11 adults, College Park, Md., V-11-40, in buds Sambucus, W. H. Anderson [adults det. E. A. Chapin]. 6 larvae, Priest Bridge, Md., V-3-41, ex terminals of Sambucus, W. H. Anderson.

Meligethinae

Meligethes aeneus (Fabricius): 1 larva, Finland, U. Saalas [presumably det. collr.].

Carpophilinae

Brachypeplus rubidus Murray: 12 larvae, 11 pupae, West Africa [quarantine interception], II-3-38, in tiger-wood (*Lovea klaineana*) under bark [det.?]. 1 larva, 1 pupa, Africa [quarantine interception], XI-15-38, *Lovea klaineana* wood.

Colopterus amputatus Erichson: 2 larvae, Marathon, Fla., III-8-19, on sap exuding from stumps of "gumbo limbo", Schwarz and Barber [presumably det. collrs.].

Colopterus truncatus (Randall): 40 larvae, 1 adult, Yuma, Calif., [adult det. E. A. Chapin]. 16 larvae, 1895, from cones of *Pinus strobus*, Chittenden. 6 larvae, 3 adults, Falls Church, Va., larvae found on bottom of red oak stick infested with ambrosia beetles; some white fungus developed and larvae feeding in it when found, R. St. George.

Conotelus mexicanus Murray: 2 larvae, 1 pupa, 1 adult, Nogales, Ariz. [quarantine interception], dried squash blossom, reared VIII-16-41—VIII-30-41, G. [or C.] F. Haller [adult det. J. G. Rozen]. 7 larvae, Guatemala, VI-13-48, in gardenia bloom.

Conotelus stenoides Murray: 6 larvae, 1 pupa, 6 adults, Pulaski, Giles Co., Tenn., VII-5-46, ear of corn (with *Carpophilus*) through G. M. Bentley [adults det. J. G. Rozen]. 25 larvae, Santa Maria, Tex., 1909, in grain of shock corn, McMillan. 1 larva, Mexico, VI-1942, green corn. 50 larvae, same except VIII-1940. 1 larva, same, II-7-38, pineapple plant. 7 larvae, Nogales, Mex. [quarantine interception], VII-5-39, green corn kernel, cob, and silk. 26 larvae, same, VI-28-40, green corn. 4 larvae, same, VII-22-35. 6 larvae, 1 adult, Izamal, Yucatan, Mex., VII-1910, bred from larvae found on leaves of *Agave*, F. G. Gaumer [adult det. J. G. Rozen]. 1 larva, 4 pupae, 30 adults, Mexico, in Irish potatoes [adults det. J. G. Rozen]. 1 larva, Osorio, Tamaulipas, Mex., I-1913, W. M. Hanson.

Macrostola lutea Murray: 50 larvae, 10 adults, Island of Monserrat, Lesser Antilles, W. I., in closed flowers of *Philodendron*, H. G. Hubbard [det. E. A. Schwarz; see Insect Life, 7: 340, 1894].

Macrostola sp.: 10 larvae, Panama, X-I4-40, Montrichardia sp. spadix [det. as Macrostola sp. (picea Sharp or straminea Murr.) by W. H. Anderson].

Orthostolus prosternalis Sharp: 13 larvae, 1 adult, Hawaiian Islands, IV-11-35, ex dead Clermontia, O. H. Sweezey [presumably det collr.].

Nitidulinae

Aethina sp.: 30 larvae, 1 adult, Guatemala, IV-8-48, in Nephthytis fruit [adult det. E. A. Chapin]. 6 larvae, 1 adult, same, V-18-48, in Monstera seed pods [adult det. E. A. Chapin].

Amphicrossus ciliatus (Olivier): 5 larvae, 8 adults, College Park, Md., VII-4-42, at sap flow on oak, W. H. Anderson [adults det. E. A. Chapin]. 2 larvae, Md., 1939, through W. Cory. 18 larvae, Selma, Ala., IX-21-1880, sap of ash.

Cychramus variegatus (Herbst): 2 larvae, Innsbruck, Austria, X-2-34, in Armillaria mellea, Karl Hofeneder [det. collr.].

Cyllodes biplagiatus LeConte: 7 larvae, Springfield, Mass., VII-1-00, reared from sporophores of the agaricid fungus *Pleurotus ostreatus* on *Populus grandidentata*, Dimmock [possibly det. collr.].

Epuraea avara (Randall): 1 larva, Auburn, Ala., fungus on *Pinus taeda*, J. A. Lintner [presumably det. A. G. Böving].

Epuraea laeviuscula (Gyllenhal): 1 larva, Suomi, Suomussalmi, Finland, VII-28-14, *Pinus silvestris (Xyloterus lineata)*, U. Saalas [presumably det. collr.].

Epuraea linearis Mäklin: 6 larvae, Sula, Mont., lodgepole pine, IX-6-28, Hopk. U. S. 19941 [det.?].

Epuraea melina Erichson: 1 larva, Ordrup, Denmark, VIII-2-06, in nest of *Bombus* (reared). E. A. Rosenberg [presumably det collr.].

Epuraea monogama Crotch: 4 larvae, North Bend, British Columbia, Canada, VI-7-92 [det.?].

Epuraea thoracica Tournier: 1 larva, Suomi, Finland, VIII-17-13, *Picea excelsa (Polygraphus)*, U. Saalas [presumably det. collr.].

Epuraea unicolor (Olivier): 1 larva, Denmark, 1880, Meinert [det. as *E. obsoleta* F. presumably by Meinert].

Haptoncus luteolus (Erichson): 7 larvae, Crest City, Fla., 1881 [det.?].

Lobiopa insularis (Castelnau): 11 larvae, 1 adult, Ponchatoula, La., V-21-53, destroying strawberry fruit, C. E. Smith [adult det. E. A. Chapin].

Lobiopa sp.: 4 larvae, 4 adults, Ft. Sherman, Canal Zone, IX-7-23, from ripe fruit of *Spondias lutea*, Zetek and I. Molino.

Omosita colon (Linnaeus): 1 larva Plummers Island, Md., V-1908, in dried chicken, H. S. Barber [presumably det. collr.]. 1 larva, Va. shore opp. Plummers Island, Md., VII-8-20, on dry carcass of coon.

Orthopeplus quadricollis Horn?: 1 larva, Bly, Ore., in fungus on Pinus ponderosa, F. P. Keen [det. A. G. Böving by elimination and locality].

Pallodes silaceus Erichson: 7 larvae, 2 adults, Falls Church, Va., pupated VIII-1-19, reared VIII-19-19, on lamella of fungus; F. C. Craighead and R. St. George [adults presumably det. St. George]. 15 larvae, 11 adults, Hopkin's farm, W. Va., in decaying mushroom — some in ground, F. C. Craighead. 12 larvae, 14 pupae, 2 adults, Plummers Island, Md., larvae and pupae in white fleshy gilled fungi on tulip poplar log IX-6-13, adults bred IX-28-13, Schwarz and Barber [adults presumably det. collrs.].

Phenolia grossa (Fabricius): 80 larvae, 16 adults, Cabin John Bridge, Md., VII-31-13, in fungus, *Laetiporus speciosus*, H. S. Barber. 11 larvae, Springfield, Mass., VII-1900, fungus. 4 larvae, 3 pupae, St. Louis, Mo. 7 larvae, 1 pupa, 6 adults, Dead Run, Va., near Potomac River, IX-28-40, in *Hyd*num(?), coll. and reared B. E. Rees [adults det. E. A. Chapin].

Prometopia sexmaculata (Say): 1 larva, 1 cast skin, Virginia, in hickory, reared, Hopk. U. S. 11876 g [det.?].

Soronia sp.: 11 larvae, Falls Church, Va., VI-26-20, in oozing sap on white oak, R. St. George. 5 larvae, same, VI-1920, F. C. Craighead [det. W. H. Anderson].

Stelidota geminata (Say): 14 larvae, 18 adults, Hyattsville, Md., VII-4-42, rotting apples, W. H. Anderson [adults det. E. A. Chapin]. 20 larvae, 2 adults, Falls Church, Va. VIII-1-27, in decaying green persimmon, Hopk. U. S. 10088 g. 3 larvae, St. Louis, Mo.

Cryptarchinae

Glischrochilus fasciatus (Olivier): 2 larvae, 2 adults, Carolina, in chestnut, Hopk. U. S. 9193 q [adults det. J. G. Rozen].

Glischrochilus japonius (Motschulsky): 2 larvae, 1 adult, 34 Route Doumer, Shanghai, China, VI-11-36, E. Suenson [adult det. E. A. Chapin].

Glischrochilus obtusus (Say): 35 larvae, Falls Church, Va., VI-1920, from sap on white oak, F. C. Craighead [det. W. H. Anderson]. 13 larvae, same, no date, in oozing sap on white oak, R. St. George. 2 larvae, Washington, D. C., V-25-22, in *Quercus* sp. from estate of Assistant Secretary of State Bliss, W. Middleton. 11 larvae, Linglestown, Pa., in oak, Hopk. U. S. 12216 k.

Glischrochilus quadrisignatus (Say): 13 larvae, 1 adult, Fielding, Ut., VI-23-47, damaging onions, H. E. Dorst [adult det. L. L. Buchanan].

Glischrochilus vittatus (Say): 2 larvae, Sula, Mont., VI-11-29, lodge-pole pine, Hopk. U. S. 19943 [adults det. E. C. van Dyke].

Cryptarcha ampla Erichson: 50 larvae, 80 adults, Falls Church, Va., V-20-20, larvae in oozing sap on Robinia pseudacacia; adults reared VI-16-20, R. St. George [presumably det. collr.]. 30 larvae, same VI-26-20, in decaying sap ... on white oak, R. St. George. 4 larvae, 1 adult, Aiken, S. C., in Chionanthus. 6 larvae, Kansas City, Mo., VI-13-24, in oak, L. A. Walmsley. 4 larvae, Lonestown, Pa. VII-5-12, in living willow, Hopk. U. S. 9741. 14 larvae, Flint, Mich., VII-14-37, poplar bark, E. Smith. 2 larvae, New Brunswick, N. J., VII-15-22, under bark on oak just above roots.

Cryptarcha glabra Schaeffer?: 1 larva, Bisbee, Ariz., IX-5-44, home orchard deciduous fruit tree, H. W. Gray [det. J. G. Rozen, based on distribution]. Böving & Rozen: Anatomical and Systematic Study ... of the Nitidulidae 299

Cryptarcha sp. a: 1 larva, Mexico, intercepted VII-17-42, in mango, A. H. Lewis.

Cryptarcha sp. b: 4 larvae, Tanavan, Batangas, P. I., IX-10-11, from injuries on larger branches of *Citrus nobilis* from which sap exudes [det. H. S. Barber].

Cybocephalinae

Cybocephalus prob. californicus Horn: 1 larva, 4 adults, Winter Haven, Dimmit Co., Tex., S. E. Jones [adults det. E. A. Chapin].

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