Studies on Costa Rican Odonata.

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BY

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LARVA OF CORA (ODONATA)—CALVERT.

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I—The Larva of Cora.

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(With Plates II and III)

In the course of our entomological researches in Costa Rica, a brief outline of which has already appeared in ENTOMOLOGICAL NEWS,* I collected some Odonate larvae of a form hitherto undescribed and which, it now appears, are certainly of the genus *Cora*. One of these was found at Peralta, Costa Rica, March 24, 1910, in a shallow brook in the woods west of the railroad station, clinging to a submerged stone. The altitude was about 335 meters, or 1100 feet. This larva died a few days later and was preserved in alcohol. A second is recorded in our diary, from Juan Viñas, April 27, 1910, as follows: "About half a mile farther [westward from the farther waterfall along the railroad from Juan Viñas station] is a third fall, or rather cascade, reached by a little trail through a bit of exceedingly thick damp woods full of wild ginger [*Costus* sp., Costa Rican name cañagria], heliconias,

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ferns and caladiums. The stream is extremely pretty and ought to be a favorite haunt of many forest-loving species, but the day was very dark with intervals of rain and we saw no adult dragonflies. After long hunting among the fallen leaves and stones of the brook, P. found a larva with extra gills along the sides of the abdomen. This we suspect may be the larva of *Cora*, a point still to be determined however."

The diary for April 29, 1910, also at Juan Viñas, reads: "To-day was exceedingly dark and at times with very thick mist, altho' there was no heavy rain. While A. wrote in the morning, P. collected some food for some living dragon-larvae gathered here. While so doing he found another and somewhat larger larva of the sort which we suspect to belong to the genus *Cora*. It is remarkable in having attached to each side of some of the forward abdominal segments a finger-like gill, a peculiarity possessed by no other American dragon-larva as far as known. Our chief interest in larva-raising now centres on these two individuals."

Still at Juan Viñas, the diary of May 2, 1910, records: "With a lunch, rubber poncho and umbrella, the latter two for investigating the farther waterfall, I set out for that spot, examining the ditch along the [railroad] tracks which carries the water from this fall. In going and coming, I found in all three of the supposed *Cora* larvae in this outflow. Those found last week lacked the caudal gills which, altho' forming part of the proper equipment of a whole suborder of dragonfly larvae, seem to be of indifferent use and value, for many larvae lose them by accident or by the bite of a brother or an enemy and yet pass their larval existence as tranquilly and accomplish their transformations as successfully as their brethren. * * * The three larvae found to-day have their caudal, as well as their lateral, abdominal gills, which latter have already been briefly mentioned. The three caudal gills are very odd-looking. They appear as if cut off straight across the tip, instead of tapering as usual, the straight edge [*i. e.* tip] then scalloped into three points. Each gill is much inflated and, as the gills

are each [a fifth] as long as the short 'pudgy' body, the effect is to give the larva the appearance of 'tail-heavy.' When first taken into the hand these three larvae remained motionless, 'playing 'possum' as it were for a minute or two, and then took to their legs with some speed. In spite of their double equipment of gills, the *Cora* (?) larvae found do not frequent a different abiding place from less richly 'engilled' dragons, their fellow inhabitants being larvae of *Hetaerina*, *Argia* and common types of Libellulinae." The ditch in which these larvae were found was at this time one to two feet wide and rarely as much as eight inches deep; it contained many small stones on the under sides of which the larvae were found. The waterfall whose outflow it was, was perhaps thirty feet high and was in turn fed by a stream descending in occasional cascades through forest from a height of several hundred feet higher. We took or saw imagos of *Cora chirripa* at this waterfall in different months, at previous visits, and on April 30 and May 2, 1910. The altitude at which all the *Cora* larvae from Juan Viñas were found was about 1000 meters, or 3300 feet.

On April 30, 1910, Mrs. Calvert went from Juan Viñas to our headquarters at Cartago, taking with her the *Cora* larvae of April 27 and 29, and placed them in our rearing jars. I followed on May 4 with the three larvae of May 2. At 6:50 P.M. of the same day occurred the great earthquake which destroyed Cartago. Its effect upon our larvae in rearing has been briefly described in the NEWS as quoted, but by the greatest good fortune the bottle containing the *Cora* larvae of May 2 was the single one—of all our living Odonata— that rolled out and escaped destruction from the fallen wall. Two of the larvae were alive and were carried in safety to our steamship at Port Limon. A second died May 7, and the third, with a supply of mosquito eggs to furnish food, started with us on the voyage to New York, but expired on May 14, three days before we landed. Each larva, as soon as its death was discovered, was placed in alcohol, but evidently was not in a condition for histological study. This fact must be remembered in judg-

ing of the shrunken condition of some parts, *e. g.* the tissues represented in figs. 20 and 25.

There thus have been available for the present description four larvae which may be designated as follows:

No. 1. ♂. Peralta as above, total length including antennae and caudal gills 16.5 mm.; length of body excluding the parts named 11.5 mm.

No. 2. ♀. Juan Viñas, May 2, in fragments.

No. 3. ♂. Juan Viñas, May 2, measurements as above, 20.5 and 17 mm. respectively.

No. 4. ♀. Juan Viñas, May 2, measurements the same as those of No. 3.

No. 3 has furnished dissections of internal organs. Nos. 1 and 4 have been kept almost intact.

Description of the Larvae.

Head deeply concave posteriorly (Plate III, fig. 21) for reception of the prothorax. Compound eyes and ocelli distinct. Six pale yellowish spots indistinctly visible on the upper surface of the head, two in front of the median ocellus, one anterior to and one posterior to each lateral ocellus; some of these spots wanting in some specimens.

Antennae 7-jointed, but the last joint only visible under the compound microscope (Pl. II, fig. 10); ratios of the lengths of the joints, in a detached antenna under a cover-glass, 21, 26, 17, 11, 9, 5.5, 3; joints 1 to 6 successively decreasing in thickness; joints 1 and 2 clothed with a dense pile, which is longest in larva No. 1, and consists of flattened scales as shown in fig. 5. A similar pile is found on many other parts of the body, such as the anterior margin of the nasus, the lateral margins of the head posterior to the middle of the compound eyes, margins and ridges of the thoracic and abdominal segments, of legs and of wing-pads, a transverse ante-apical line on abdominal segments 1-10 for the entire width of the dorsum, much of the surfaces of the caudal gills, etc. This pile is longer and more conspicuous on larva No. 1 than on the other three. Joints 3-7 of the antennae have a decreasingly smaller amount of pile.

Mandibles stout two-branched, external branch larger, its apex with five teeth, first two teeth, counting from the dorsal margin, less distinct from each other than are the other three, fourth tooth longest. Internal branch in larvae Nos. 1, 3 and 4 larger on the *left* mandible than on the right mandible (right mandible lacking in larva No. 2) and on the left mandible its apex is truncated and with seven teeth or crenations, dorsal-most largest (Plate II, fig. 16). On the right mandible the apex of the internal branch is pointed and has only two teeth.

Maxillae with the inner lobe attenuate at tip, which bears three short internal teeth, and three long, slender, curved, internal processes and a row of strong setae. (Pl. III, figs. 29, 31). *Labium*, when folded at rest, reaching back to the bases of the prothoracic legs but not as far as the hind ventral prothoracic margin; median (mental) lobe but very slightly produced distad in the middle and with a very slight median cleft, distal margin crenulate with a very short seta between each crenulation and its neighbor; just within the crenulations a short distance on each side of the median cleft is a small pointed tooth (fig. 28, *t**) on the dorsal surface; mental setae few (2-4 on each side of the median line both on dorsal and ventral surfaces) and short; lateral lobes with a long curved tapering terminal spine and three distal teeth of which the most internal (mesial) is shortest and is truncate while the other two are pointed. (Pl. III, figs. 27, 28, 30).

Prothorax with three lateral tubercles, a dorso-lateral (*a*) which is dorsal to an antero-lateral (*b*) and, posterior to (*b*), a postero-lateral (*c*). On the mesothorax the place of *a* of the prothorax is occupied by the spiracle, *b* is present while *c* is represented by a double tubercle. None of these tubercles are represented on the metathorax which has an indistinct spiracle on its lateral surface (Pl. II, 14, *msp*). Front wing pads reach to the hind end of abdominal segment 6 in larva No. 1, to the hind end of segment 4 in larvae Nos. 3 and 4. Hind wing-pads reach almost to the mid-length of segment 7 in larva No. 1, to mid-length of segment 5 in Nos. 3 and 4. (In Pl. II, fig. 14, the wing-pads have been divaricated and are not in exactly normal positions, hence the difference between the preceding sentence and the figure). Legs not of a burrowing type, tarsi 3-jointed with an empodium-like structure (Pl. II, figs. 6, 12).

Abdomen triangular in cross-section, of ten complete segments, which decrease slightly in width from 1 to 8; 9 and 10 distinctly narrower owing to their lateral margins not being produced laterad as far as on the segments preceding (Pl. II, fig. 15). A curved, caudad-directed, mid-dorsal hook on segments 2-9 (larva No. 1) or 1-9 (larvae Nos. 3 and 4), hooks increasing in length from segment 1 or 2 to segment 7 or 8, that of 9 slightly shorter than that of 8. (Pl. II, fig. 14). Hind dorsal margin of segment 10 with a wide median notch whose depth is half, or less than half, the length of the segment. (Pl. II, fig. 8). Segments 2-7 each with a pair of tapering, finger-like ventral gills. Rudiments of ♂ genitalia on the ventral side of segment 2 indistinct in larva No. 1; in larva No. 3 they consist of two distinct black lines reaching from the intersegmental groove of 1-2 to behind the hind end of the sternite of 2. Rudiments of ♂ gonapophyses are present on segment 9 of larvae Nos. 1 and 3 (Pl. II, fig. 18). Rudiments of ♀ gonapophyses are shown in Pl. II, figs. 7, 8, 14, 15.

The three caudal gills together are much wider than the abdomen at its widest part. Each one is petiolate at base and much enlarged in all diameters beyond the petiole. *Median gill* approximately equal in length to that of segments 8+9+10, much enlarged dorso-ventrally and less so laterally immediately after the petiole, thence increasing in height gradually and slightly to the apex which is triangulate in profile view, the ventral angle most obtuse, the median angle most acute, the dorsal angle projecting not as far caudad as the other two. At a little less than half length from the base there is an angular protuberance on each side at about one-fourth height of the gill from the dorsal crest, so that there are in all five angular projections on this gill. Most of the chitin of this gill is brown and opaque, or at most only translucent, and is covered with scales, but on each of the two lateral faces there is an area of colorless transparent chitin occupying the ventral two-fifths of the height and about four-fifths of the length from the base caudad (Pl. II, fig. 14) lacking scales.

Each lateral caudal gill is somewhat longer than the median gill, roughly triangular in cross-section, one surface being convex, the other two approximately plane. These latter two are ventral and internal (mesial) respectively, the convex surface is lateral (external) and dorsal and greater in extent than either of the other two. There are four angular protuberances: one at half-length, or a little less than half-length, of the gill on the middle of the convex dorso-external surface; one at three-fourths of the length of the gill on the convex surface close to the margin of the mesial surface; one at seven-eighths of the length of the gill on the middle of the convex surface; and one, the most obtuse, forming the apex of the gill. The convex dorso-external surface of the gill is of brown chitin and scale-covered, the ventral and mesial surfaces chiefly of colorless, transparent chitin and lacking scales, except along the margins where each meets the dorso-external surface respectively. (Pl. II, figs. 3, 4, 9, 14, 15).

Between the bases of the three caudal gills are the rudiments of the superior appendages or 'cercoids' of the imago (Pl. II, figs. 7, 8, *sa*) and the supra-anal (*spl*) and sub-anal (*sbl*) laminae. The rudiments of the 'cercoids' are simple, cylindrical or conical, with rounded apices, and vary in length, in the four larvae, from about one-third to more than one-half of the length of abdominal segment 10. The sub-anal plates reach to about mid-length of the 'cercoids'; each one is depressed, its apex squarely truncate but produced apparently into a short spine at its mesial angle when viewed dorsally or ventrally; this apparent spine is the end view of a vertical lamina.

The main abdominal *tracheal* trunks and their branches are shown in Pl. III, figs. 22, 20; Pl. II, figs. 9, 17, 19. The ventral gills of abdominal segments 2-7 receive each two tracheae from two separate

branches of the main lateral trachea and the gill tracheae divide and redivide inside each gill (Pl. III, figs. 20, 25, 26). Owing to the opacity of the chitin, the thickness of the gills and the obstacles met in clearing them, I have not been able to make out more than the main branches of the tracheae supplying the caudal gills (Pl. II, fig. 9). The stomach is supplied from two anterior and two posterior tracheae, one anterior and one posterior on its right side and similarly on its left side. The right and left anterior gastric tracheae lie parallel and close together on the dorsal surface of the oesophagus and crop; each is probably a derivative from the main dorsal trunk of its own side of the body, but this was not definitely ascertained. At the anterior end of the stomach each anterior gastric trachea divides into a set of (two) dorsal and a set of (four) lateral branches as shown in Pl. II, figs. 13 and 17. The fourth, or ventralmost, lateral branch apparently forms an anastomosis with the corresponding branch of the

were made, the alimentary canal was slit open lengthwise, stained, dehydrated, cleared and mounted in balsam. No definite indications of rectal tracheal gills were found and the rectal walls appear much less richly tracheated than those of the stomach. The rectal epithelium appears to form three (glandular?) areas. The gastric epithelium was disintegrated. No food was found in the alimentary canal.

The three thoracic pairs of ganglia are clearly distinct from each other. Posteriorly are seven pairs of smaller ganglia, located as follows: 1 in metathorax, 2 in anterior part of abdominal segment 2, 3 in hind part of segment 3, 4 at the articulation of segments 4 and 5, 5 in anterior end of segment 6, 6 in anterior end of segment 7, 7 in the middle of segment 8. The nerve cord in the male larva dissected (No. 3) passed to the right of the distinct rudiments of the genitalia projecting dorsad into the cavity of segments 1 and 2.

Discussion of the More Interesting Features of Cora Larva.

In current classifications *Cora* is placed in the Calopterygine or Calopterygidae (= Agrioninae of the catalogues of Kirby, Muttkowski, etc.). Most of the Calopterygine larvae

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Line 20 from top of page 55 should read

stomach (Pl. II, figs. 17, 19. *lpgt*). The rectum has four tracheae, two

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The hind-gut or intestine is likewise supplied by branches from the main dorsal tracheal trunks. The trachea which passes to the ileum also furnishes the posterior gastric trachea for the same side of the stomach. The rectal epithelium appears to form three (glandular?) dorsals and two laterals. (Fig. 19, *rdrt, ldrt, rlrt, llrt*). After the drawings forming figures 13, 17 and 19 were made, the alimentary canal was slit open lengthwise, stained, dehydrated, cleared and mounted in balsam. No definite indications of rectal tracheal gills were found and the rectal walls appear much less richly tracheated than those of the stomach. The rectal epithelium appears to form three (glandular?) areas. The gastric epithelium was disintegrated. No food was found in the alimentary canal.

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hitherto described (Cf. Karsch, 1893, pp. 42, 48; Needham, 1903*b*, p. 220) have the first antennal joint very long, as long as all the other, or as several of the other, joints added together. *Cora* larva has the first antennal joint shorter than the second and in this respect, as in others mentioned below, shows a resemblance to the Old World larvae described by Hagen (1880, p. lxv) as pertaining to the legion Euphaea* of de Selys, and to a Mexican fragment doubtfully referred to *Cora* (*l. c.*, p. lxvi).

The scales forming a more or less dense pile on different parts of the body of *Cora* larvae are structures which have met little or no notice in the literature on the Odonata. They occur in shapes varying from almost hair-like to that in which the width is at least more than half the length (Cf. Pl. II, figs. 4, 5, 11, 3 in the order named). The central and more or less arborescently-branched portion of each scale is thicker than the often hardly discernible marginal areas.

Biramous mandibles hitherto have been noted only in *Euphaea* larvae of all the Odonata, and that very briefly (Needham, 1903*a*, p. 743). I am not able at present to determine whether the two-branched condition there is the same as that here described for the larvae of *Cora* or not. The remarkable features of these mandibles is the possibility of independent movement of the inner branch along the dotted line shown in Pl. II, fig. 16, and the difference in the form of this branch in the right and left mandibles of the same individual noted above. Heymons (1896 *b*, taf. II, fig. 29) has figured the mandibles in a young larva of *Ephemera vulgata* which are also two-branched but, in contrast to the larval mandible of *Cora*, the inner branch is larger than the outer.

The very shallow median cleft of the median lobe of the labium was hardly to be expected in larvae so apparently primitive in other features as our *Cora* larvae are. In this respect also it agrees with *Euphaea* larvae, as far as can be judged from Hagen's description (1880, p. xlv). If Miss Butler's theory (1904, pp. 114, 119) of the homologies of the labium be correct, then the small, pointed teeth (Pl. III, fig. 28 *t**) near the middle of the distal margin, would represent the apices of the original laciniae. The interpretation of Börner (1909, p. 113) is different and is essentially that of Gerstäcker, Heymons and others.

* The name of the type genus of this legion, *Euphaea*, is now replaced by *Pseudophaea* Kirby.

Hagen (1880, p. lxv) noted the existence of "une *plantula* entre les onglets" of *Euphaea* larvae and remarked (p. lxvii) "La présence d'une *plantula* entre les onglets est aussi un caractére unique chez les Odonates." The empodium-like structure mentioned above for *Cora* and shown in Pl. II, fig. 12, appears to be an homologous part.

The existence of tracheal gills on abdominal segments 2-7 is the most interesting feature of *Cora* larvae. The only Odonata previously known to possess such structures are the larvae referred to *Euphaea* and *Anisopleura* in the very brief description of Hagen (1880). One of these larvae was figured by Folsom in Packard (1898, p. 469). Hagen stated that there were gills on abdominal segments 1-8, Folsom found them on 2-8 only. There are, therefore, one pair less in *Cora* larvae. Hagen compared these gills of *Euphaea* and *Anisopleura* to those of *Sialis*, but makes no mention of Ephemerid larvae in this connection. Heymons (1896 *a*, pp. 88-90) compared the abdominal gills of Ephemerid and *Sialis* larvae, regarded them in both cases as derived from abdominal appendages and noted the agreement in the pointed form of the gills of the early larval stages of both groups. The gills of the second to seventh abdominal segments of *Cora* larva furnish an addition to this parallel. That the lateral gills of Ephemerid larvae are homologous with the thoracic legs is not universally accepted, however. Dürken (1907, 1909) and Börner (1909 *a*) are the latest representatives of the two views which look upon the Ephemerid lateral gills as dorsal and not homologous with legs and as ventral and homologous, respectively. We may not compare the lateral gills of *Euphaea*,

Anisopleura and *Cora* larvae with those of the Ephemerid larvae until much fuller data are at hand regarding the detailed structure, position, musculature and tracheation of each. The present study of *Cora* larvae supplies much fuller information than exists for either of the other two Odonate genera mentioned. The markedly ventral position of the gills in question in *Cora* is in itself some evidence against homologizing these structures with those of the Ephemeridae and in favor of their own serial homology with thoracic legs. No traces of these gills are present on the exterior of the abdomen of imagos of *Cora* preserved in alcohol immediately after capture.

The caudal tracheal gills of *Cora* larvae are very different in shape from the similarly situated gills of all other Odonate larvae yet described, including those of *Euphaea* (cf. Folsom's figure, *l. c.*) and *Anisopleura*, of which latter I possess a photograph from Hagen's specimen, taken and given to me by Prof. J. G. Needham. In both of these latter two genera the caudal gills taper posteriorly to an acute apex.

As related in the opening pages of this paper, the attempt to rear these larvae to transformation was unsuccessful. That they are the larvae of *Cora* and, so far as the Juan Viñas specimens at least are concerned, the larvae of *Cora chirripa* Calvert (1907, p. 348) is rendered practically certain from a comparison of the wing-rudiments of larva No. 4 with those of an imago of this species taken at the same ditch April 30, 1910. The left hind wing-pad of larva No. 4 was slit open, the wing rudiment removed from within and examined in alcohol under the compound microscope. The inner and outer surfaces of the rudiment gave the views represented in Pl. III, figs. 23 and 24 respectively. The veins shown in these figures are bands of reddish-brown pigment granules in the rudiment itself. The left hind wing of the imago mentioned was compared with camera drawings of the two surfaces of the wing-rudiment of the larva. At first the identification of the larval wing veins proceeded slowly until it occurred to me that perhaps the two surfaces of the wing rudiment might present only convex and concave veins respectively. Turning then to the imaginal wing the following lists were made proceeding in every case from the anterior toward the posterior wing margin. Convex veins: proximal half of the wing, C, R1, *Rs*, M4, A and Cu2; distal half, C, R1, M1*a*, two supplementary sectors, *Rs*, three supplementary sectors, M4, Cu2*a*, Cu2*b*.

Concave veins: proximal half of wing, Sc, M1, M3, Cu1; distal half, M1, two supplementary sectors, M2, one supplementary sector, M3, two supplementary sectors, Cu1, one supplementary sector between Cu2*a* and Cu2*b*.

As is well known the inner surface of the wing-pad and wing-rudiment of an Odonate larva corresponds to the upper surface of the imaginal wing, and the outer surface in the larva to the under surface in the imago. On comparing the list of convex veins with the drawing of the inner surface of the wing-rudiment and the list of concave veins with that of the outer surface of the wing-rudiment, it was seen that a close correspondence existed with these exceptions: that C (costa) showed on both surfaces, as also did a thickening all along the posterior margin and to greater or less extents Sc (sub-costa), R1 (first branch of radius), M1 (first branch of media), A (anal), Cu2*b* and the supplementary sector between Cu2*a* and Cu2*b*. The wing-rudiment was then cleared in cedar oil and examined in strong transmitted sunlight, when the vein-rudiments of both inner and outer surfaces could be seen from either surface by proper focussing, whereas before clearing only those of the surface turned up toward the lens could be discerned. All the vein-rudiments now appeared in their proper sequence giving the alternation of convex and concave veins so easily seen in an imaginal wing. Careful focussing also revealed the fact that at this stage the veins are developed only upon one surface of the wing-rudiment, either inner or outer, except in the case of the costa and of the thickening along the hind margin. The other exceptions noted above are all veins near the margins where the wing-rudiment is thinner

and where they can be seen through it. Even in these exceptions the veins appear fainter and narrower on one surface than the other and are stronger and wider on their proper surface, *e. g.* Sc and M1, concave veins, on the outer surface; R1, A and Cu2*b*, convex veins, on the inner surface.

Another fact shown by these comparisons and the figures is that the cross-veins only appear continuous from one longitudinal vein to another when the two longitudinal veins so connected are two, one of which immediately follows the other in the imaginal wing. (Cf. the cross-veins between R1 and M1 and between M1 and M2 in Pl. III, fig. 24.)

It would thus appear that each longitudinal vein develops on one surface of the wing-rudiment before it appears on the other surface. Before transformation is reached each vein has formed on both surfaces of the future wing but not necessarily equally on both surfaces, as may be seen from Hagen's figures (1889) from photographs of wings split into their two laminae immediately after transformation and expansion.

These facts of the development of the veins on one surface of the wing-rudiment before the other have a practical value in identifying Odonate larvae by this method and do not seem to be included in Prof. Needham's (1904, p. 687) suggestions on this point.

In the larva of *Cora* there exist the following generalized features: antennae with no hypertrophied joint, biramous mandibles, paired ventral tracheal gills (if they be morphologically equivalent to legs), and perhaps the empodium-like part, side by side with specialized features in the form of cuticular scales, almost completely fused halves of the labium and thickened, shortened caudal gills. If to these generalized parts of the larva we add the generalized features of the imaginal venation pointed out or implied by Prof. Needham (1903*a*, pp. 731, 746), we have good grounds for looking on *Cora* and its allies as being in many respects the most primitive of living Odonata.

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Explanation of Plates II and III.

Larva of *Cora*.

Fig. 1. Left latero-ventral view of larva No. 4 ♀.

Fig. 2. Dorsal view of larva No. 3 ♂. Right caudal gill lacking.

Figs. 1 and 2 from photographs of alcoholic specimens. × 2.6.

Fig. 3. Small fragment of surface of left caudal tracheal gill, larva No. 3, showing two scales and four articular pits for others. × 210.

Fig. 4. Scale from same gill as fig. 3. × 210.

Fig. 5. Scale from first antennal joint shown in fig. 10. × 210.

Fig. 6. First left tibia and tarsus of larva No. 4. × 8.5.

Fig. 7. End view, hind end of abdomen of larva No. 2 ♀, caudal gills removed. × 8.5.

Fig. 8. Dorsal view, hind end of abdomen of larva No. 2 ♀, caudal gills removed. × 8.5.

Fig. 9. Left caudal gill, ventro-mesial view, combined from drawings from larvae Nos. 1, 2, 3, to show tracheation. The dotted line indicates the boundary between a central, clearer, unscaled area and an opaque, scaled margin. × 5.8.

Fig. 10. Right antenna, dorsal view, larva No. 3, ♂. × 16.5.

Fig. 11. Scale from tibia or tarsus of fig. 6. × 210.

Fig. 12. Ventral surface of distal end of tarsus. × 8.5.

Fig. 13. Dorsal view of branches of left anterior gastric trachea shown in fig. 17. × about 12.5.

Fig. 14. Right lateral view of metathorax and abdomen of larva No. 4, ♀. × 5.5.

Fig. 15. Ventral view of same. × 5.5.

Fig. 16. Left mandible, mesial surface, larva No. 2, ♀. × 21. The dotted line shows the line of flexure of the internal branch.

Fig. 17. Left side of stomach to show tracheation, larva No. 3, ♂. × about 12.5.

Fig. 18. Ninth abdominal segment to show gonapophyses, larva No. 3, ♂. × 5.5.

Fig. 19. Left latero-dorsal view of intestine to show tracheal supply, larva No. 3, ♂; Malpighian tubules omitted. × about 12.5.

Fig. 20. Right gill of fifth abdominal segment, larva No. 3, ♂. The gill has been left untouched, the viscera of the segment removed with the exception of the tracheae supplying the gill. To the left of *chr* a portion of the chitinous ventral wall of the segment is shown, to the right of *chr* is a portion of the tergite which has been turned outward (laterad) to show the structures within the segment. The portions of the two main tracheal trunks *rdt* and *rlt* have been turned outward to give a clearer view of the branches to the gill. Compare with the fifth abdominal segment in fig. 22. × about 23.

Fig. 21. Dorsal view of head, larva No. 4, ♀. The dotted lines show the outlines of pale marks. × 7.8.

Fig. 22. Dorsal view of chief thoracic and abdominal viscera, larva No. 3, ♂. The body has been opened along the mid-dorsal line. The ganglion has been omitted from second abdominal segment, the wing-pads from left side, the dorsal longitudinal abdominal muscles from the right; not all of these muscles (*dlm*) are shown even on the left side. × 7.8.

Fig. 23. Inner surface of left hind wing-rudiment (= upper surface of imaginal wing) with the outline of its enveloping wing pad, *wp*, larva No. 4, ♀. × 12.4.

Fig. 24. Outer surface of the same (= under surface of imaginal wing). × 12.4.

Fig. 25. Transverse section of right gill of sixth abdominal segment of larva No. 3, ♂. × 55.5.

Fig. 26. Transverse section of chief tracheal trunk of same gill in section immediately following that shown in fig. 25. × 55.5.

Fig. 27. Distal end of lateral lobe from fig. 30. × 28.

Fig. 28. Inner (dorsal) surface of distal end of median lobe from fig. 30. × 28.

Fig. 29. Distal end of left maxilla from fig. 31. × 25.

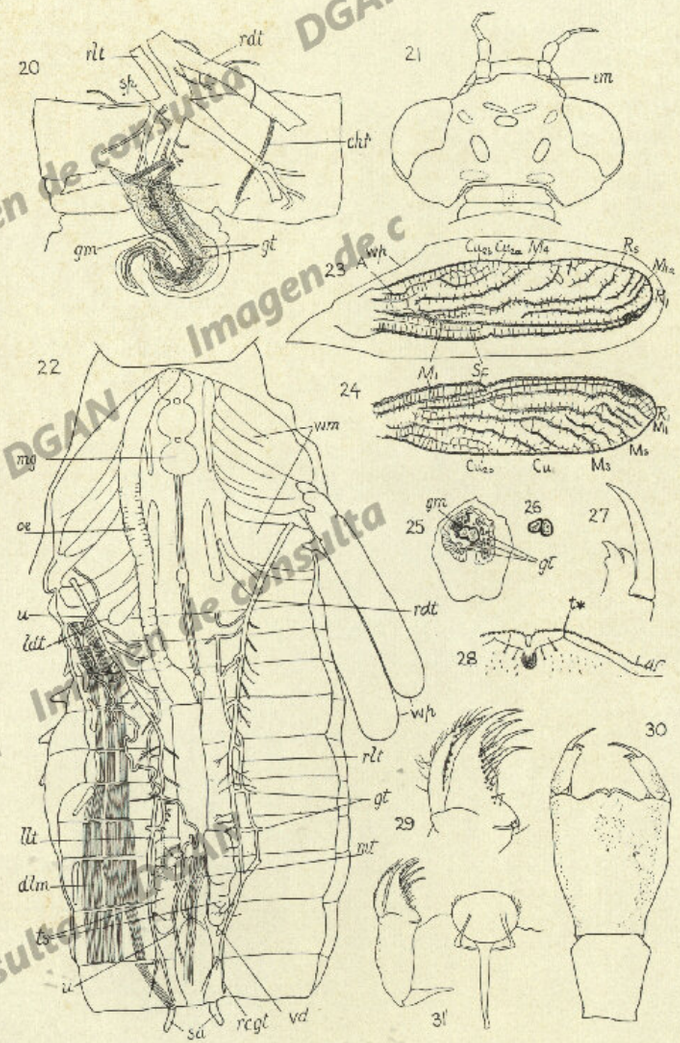
Fig. 30. Ventral (outer) surface of labium, larva No. 2, ♀. × 8.

Fig. 31. Left maxilla and hypopharynx, ventral view, larva No. 2, ♀. × 13.

Abbreviations Used in the Plates.

A, Anal vein (= proximal part of second sector of triangle of Selys).
chr, Chitinous ridge forming lateral margin of an abdominal segment.
Cu1, Cu2, First and second branches of cubitus vein (= first and distal part of second sectors of triangle of de Selys).
d, *d1*, *d2*, Dorsal branches of *lagt*.
dlm, Dorsal longitudinal muscles.
gm, Gill muscle fibres.
gp, Gonapophyses.
gt, Gill trachea.
im, Interarticular membrane between first antennal joint and head.
IX, Ninth abdominal segment.
l, *l1*-*l4*, Lateral branches of *lagt*.
lagt, Left anterior gastric trachea.
lcg, Point of attachment of left caudal gill.
ldt, Left dorsal trachea.
ldrt, Left dorsal rectal trachea.
llt, Left lateral trachea.
lrt, Left lateral rectal trachea.
lpgt, Left posterior gastric trachea.
M1, *M2*, *M3*, *M4*, Branches of media vein (= principal, nodal, median and short sectors of de Selys respectively).
M1a, Branch of *M1* (=ultra-nodal sector of de Selys).
mcg, Median caudal gill.

mg, Metathoracic (+ first abdominal?) ganglion.
msp, Metathoracic spiracle.
mt, Malpighian tubes.
oe, Oesophagus.
*R*1, First branch of radius vein (= median vein of de Selys).
*r*4, Fourth lateral branch of right anterior gastric trachea.
rcg, Point of attachment of right caudal gill.
rcgt, Right caudal gill trachea.
rdrt, Right dorsal rectal trachea.
rdt, Right dorsal trachea.
rlrt, Right lateral rectal trachea.
rlt, Right lateral trachea.
Rs, Radial sector (= sub-nodal sector of de Selys).
sa, Superior appendages of imago ('Cercoids').
Sc, Subcosta vein.
sbl, Sub-anal lamina.
sp, Site of future spiracle.
spl, Supra-anal lamina.
tab, Tendon of abductor mandibulae.
tad, Tendon of adductor mandibulae.
ts, Testes.
*t**, Tooth on median labial lobe.
u, Undetermined tube.
vd, Vas deferens (beginning of).
wm, Wing muscle.
wp, Outline of wing-pad.
X, Tenth abdominal segment.



LARVA OF CORA (ODONATA)—CALVERT.

Prof. J. Fidel Tristán
with the kind regards
of P. P. Calvert.

Studies on Costa Rican Odonata.

I—The Larva of Cora.

BY

PHILIP P. CALVERT, PH.D.

Reprint from Entomological News, Volume XXII, No. 2, 1911.

LARVA OF CORA (ODONATA)—CALVERT.

Studies on Costa Rican Odonata.

I—The Larva of Cora.

By PHILIP P. CALVERT, PH. D.
University of Pennsylvania, Philadelphia, Pa.

(With Plates II and III)

In the course of our entomological researches in Costa Rica, a brief outline of which has already appeared in ENTOMOLOGICAL NEWS,* I collected some Odonate larvae of a form hitherto undescribed and which, it now appears, are certainly of the genus *Cora*. One of these was found at Peralta, Costa Rica, March 24, 1910, in a shallow brook in the woods west of the railroad station, clinging to a submerged stone. The altitude was about 335 meters, or 1100 feet. This larva died a few days later and was preserved in alcohol. A second is recorded in our diary, from Juan Viñas, April 27, 1910, as follows: "About half a mile farther [westward from the farther waterfall along the railroad from Juan Viñas station] is a third fall, or rather cascade, reached by a little trail through a bit of exceedingly thick damp woods full of wild ginger [*Costus* sp., Costa Rican name cañagria], heliconias,

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ferns and caladiums. The stream is extremely pretty and ought to be a favorite haunt of many forest-loving species, but the day was very dark with intervals of rain and we saw no adult dragonflies. After long hunting among the fallen leaves and stones of the brook, P. found a larva with extra gills along the sides of the abdomen. This we suspect may be the larva of *Cora*, a point still to be determined however."

The diary for April 29, 1910, also at Juan Viñas, reads: "To-day was exceedingly dark and at times with very thick mist, altho' there was no heavy rain. While A. wrote in the morning, P. collected some food for some living dragon-larvae gathered here. While so doing he found another and somewhat larger larva of the sort which we suspect to belong to the genus *Cora*. It is remarkable in having attached to each side of some of the forward abdominal segments a finger-like gill, a peculiarity possessed by no other American dragon-larva as far as known. Our chief interest in larva-raising now centres on these two individuals."

Still at Juan Viñas, the diary of May 2, 1910, records: "With a lunch, rubber poncho and umbrella, the latter two for investigating the farther waterfall, I set out for that spot, examining the ditch along the [railroad] tracks which carries the water from this fall. In going and coming, I found in all three of the supposed *Cora* larvae in this outflow. Those found last week lacked the caudal gills which, altho' forming part of the proper equipment of a whole suborder of dragonfly larvae, seem to be of indifferent use and value, for many larvae lose them by accident or by the bite of a brother or an enemy and yet pass their larval existence as tranquilly and accomplish their transformations as successfully as their brethren. * * * The three larvae found to-day have their caudal, as well as their lateral, abdominal gills, which latter have already been briefly mentioned. The three caudal gills are very odd-looking. They appear as if cut off straight across the tip, instead of tapering as usual, the straight edge [*i. e.* tip] then scalloped into three points. Each gill is much inflated and, as the gills

are each [a fifth] as long as the short 'pudgy' body, the effect is to give the larva the appearance of 'tail-heavy.' When first taken into the hand these three larvae remained motionless, 'playing 'possum' as it were for a minute or two, and then took to their legs with some speed. In spite of their double equipment of gills, the *Cora* (?) larvae found do not frequent a different abiding place from less richly 'engilled' dragons, their fellow inhabitants being larvae of *Hetaerina*, *Argia* and common types of Libellulinae." The ditch in which these larvae were found was at this time one to two feet wide and rarely as much as eight inches deep; it contained many small stones on the under sides of which the larvae were found. The waterfall, whose outflow it was, was perhaps thirty feet high and was in turn fed by a stream descending in occasional cascades through forest from a height of several hundred feet higher. We took or saw imagos of *Cora chirripa* at this waterfall in different months, at previous visits, and on April 30 and May 2, 1910. The altitude at which all the *Cora* larvae from Juan Viñas were found was about 1000 meters, or 3300 feet.

On April 30, 1910, Mrs. Calvert went from Juan Viñas to our headquarters at Cartago, taking with her the *Cora* larvae of April 27 and 29, and placed them in our rearing jars. I followed on May 4 with the three larvae of May 2. At 6:50 P. M. of the same day occurred the great earthquake which destroyed Cartago. Its effect upon our larvae in rearing has been briefly described in the NEWS as quoted, but by the greatest good fortune the bottle containing the *Cora* larvae of May 2 was the single one—of all our living Odonata— that rolled out and escaped destruction from the fallen wall. Two of the larvae were alive and were carried in safety to our steamship at Port Limon. A second died May 7, and the third, with a supply of mosquito eggs to furnish food, started with us on the voyage to New York, but expired on May 14, three days before we landed. Each larva, as soon as its death was discovered, was placed in alcohol, but evidently was not in a condition for histological study. This fact must be remembered in judg-

ing of the shrunken condition of some parts, *e. g.* the tissues represented in figs. 20 and 25.

There thus have been available for the present description four larvae which may be designated as follows:

No. 1. ♂. Peralta as above, total length including antennae and caudal gills 16.5 mm.; length of body excluding the parts named 11.5 mm.

No. 2. ♀. Juan Viñas, May 2, in fragments.

No. 3. ♂. Juan Viñas, May 2, measurements as above, 20.5 and 17 mm. respectively.

No. 4. ♀. Juan Viñas, May 2, measurements the same as those of No. 3.

No. 3 has furnished dissections of internal organs. Nos. 1 and 4 have been kept almost intact.

Description of the Larvae.

Head deeply concave posteriorly (Plate III, fig. 21) for reception of the prothorax. Compound eyes and ocelli distinct. Six pale yellowish spots indistinctly visible on the upper surface of the head, two in front of the median ocellus, one anterior to and one posterior to each lateral ocellus; some of these spots wanting in some specimens.

Antennae 7-jointed, but the last joint only visible under the compound microscope (Pl. II, fig. 10); ratios of the lengths of the joints, in a detached antenna under a cover-glass, 21, 26, 17, 11, 9, 5.5, 3; joints 1 to 6 successively decreasing in thickness; joints 1 and 2 clothed with a dense pile, which is longest in larva No. 1, and consists of flattened scales as shown in fig. 5. A similar pile is found on many other parts of the body, such as the anterior margin of the nasus, the lateral margins of the head posterior to the middle of the compound eyes, margins and ridges of the thoracic and abdominal segments, of legs and of wing-pads, a transverse ante-apical line on abdominal segments 1-10 for the entire width of the dorsum, much of the surfaces of the caudal gills, etc. This pile is longer and more conspicuous on larva No. 1 than on the other three. Joints 3-7 of the antennae have a decreasingly smaller amount of pile.

Mandibles stout two-branched, external branch larger, its apex with five teeth, first two teeth, counting from the dorsal margin, less distinct from each other than are the other three, fourth tooth longest. Internal branch in larvae Nos. 1, 3 and 4 larger on the *left* mandible than on the right mandible (right mandible lacking in larva No. 2) and on the left mandible its apex is truncated and with seven teeth or crenations, dorsal-most largest (Plate II, fig. 16). On the right mandible the apex of the internal branch is pointed and has only two teeth.

Maxillae with the inner lobe attenuate at tip, which bears three short internal teeth, and three long, slender, curved, internal processes and a row of strong setae. (Pl. III, figs. 29, 31). *Labium*, when folded at rest, reaching back to the bases of the prothoracic legs but not as far as the hind ventral prothoracic margin; median (mental) lobe but very slightly produced distad in the middle and with a very slight median cleft, distal margin crenulate with a very short seta between each crenulation and its neighbor; just within the crenulations a short distance on each side of the median cleft is a small pointed tooth (fig. 28, *t**) on the dorsal surface; mental setae few (2-4 on each side of the median line both on dorsal and ventral surfaces) and short; lateral lobes with a long curved tapering terminal spine and three distal teeth of which the most internal (mesial) is shortest and is truncate while the other two are pointed. (Pl. III, figs. 27, 28, 30).

Prothorax with three lateral tubercles, a dorso-lateral (*a*) which is dorsal to an antero-lateral (*b*) and, posterior to (*b*), a postero-lateral (*c*). On the mesothorax the place of *a* of the prothorax is occupied by the spiracle, *b* is present while *c* is represented by a double tubercle. None of these tubercles are represented on the metathorax which has an indistinct spiracle on its lateral surface (Pl. II, 14, *msp*). Front wing pads reach to the hind end of abdominal segment 6 in larva No. 1, to the hind end of segment 4 in larvae Nos. 3 and 4. Hind wing-pads reach almost to the mid-length of segment 7 in larva No. 1, to mid-length of segment 5 in Nos. 3 and 4. (In Pl. II, fig. 14, the wing-pads have been divaricated and are not in exactly normal positions, hence the difference between the preceding sentence and the figure). Legs not of a burrowing type, tarsi 3-jointed with an empodium-like structure (Pl. II, figs. 6, 12).

Abdomen triangular in cross-section, of ten complete segments, which decrease slightly in width from 1 to 8; 9 and 10 distinctly narrower owing to their lateral margins not being produced laterad as far as on the segments preceding (Pl. II, fig. 15). A curved, caudad-directed, mid-dorsal hook on segments 2-9 (larva No. 1) or 1-9 (larvae Nos. 3 and 4), hooks increasing in length from segment 1 or 2 to segment 7 or 8, that of 9 slightly shorter than that of 8. (Pl. II, fig. 14). Hind dorsal margin of segment 10 with a wide median notch whose depth is half, or less than half, the length of the segment. (Pl. II, fig. 8). Segments 2-7 each with a pair of tapering, finger-like ventral gills. Rudiments of ♂ genitalia on the ventral side of segment 2 indistinct in larva No. 1; in larva No. 3 they consist of two distinct black lines reaching from the intersegmental groove of 1-2 to behind the hind end of the sternite of 2. Rudiments of ♂ gonapophyses are present on segment 9 of larvae Nos. 1 and 3 (Pl. II, fig. 18). Rudiments of ♀ gonapophyses are shown in Pl. II, figs. 7, 8, 14, 15.

The three caudal gills together are much wider than the abdomen at its widest part. Each one is petiolate at base and much enlarged in all diameters beyond the petiole. *Median gill* approximately equal in length to that of segments 8+9+10, much enlarged dorso-ventrally and less so laterally immediately after the petiole, thence increasing in height gradually and slightly to the apex which is triangulate in profile view, the ventral angle most obtuse, the median angle most acute, the dorsal angle projecting not as far caudad as the other two. At a little less than half length from the base there is an angular protuberance on each side at about one-fourth height of the gill from the dorsal crest, so that there are in all five angular projections on this gill. Most of the chitin of this gill is brown and opaque, or at most only translucent, and is covered with scales, but on each of the two lateral faces there is an area of colorless transparent chitin occupying the ventral two-fifths of the height and about four-fifths of the length from the base caudad (Pl. II, fig. 14) lacking scales.

Each lateral caudal gill is somewhat longer than the median gill, roughly triangular in cross-section, one surface being convex, the other two approximately plane. These latter two are ventral and internal (mesial) respectively, the convex surface is lateral (external) and dorsal and greater in extent than either of the other two. There are four angular protuberances: one at half-length, or a little less than half-length, of the gill on the middle of the convex dorso-external surface; one at three-fourths of the length of the gill on the convex surface close to the margin of the mesial surface; one at seven-eighths of the length of the gill on the middle of the convex surface; and one, the most obtuse, forming the apex of the gill. The convex dorso-external surface of the gill is of brown chitin and scale-covered, the ventral and mesial surfaces chiefly of colorless, transparent chitin and lacking scales, except along the margins where each meets the dorso-external surface respectively. (Pl. II, figs. 3, 4, 9, 14, 15).

Between the bases of the three caudal gills are the rudiments of the superior appendages or 'cercoids' of the imago (Pl. II, figs. 7, 8, *sa*) and the supra-anal (*spl*) and sub-anal (*sbl*) laminae. The rudiments of the 'cercoids' are simple, cylindrical or conical, with rounded apices, and vary in length, in the four larvae, from about one-third to more than one-half of the length of abdominal segment 10. The sub-anal plates reach to about mid-length of the 'cercoids'; each one is depressed, its apex squarely truncate but produced apparently into a short spine at its mesial angle when viewed dorsally or ventrally; this apparent spine is the end view of a vertical lamina.

The main abdominal *tracheal* trunks and their branches are shown in Pl. III, figs. 22, 20; Pl. II, figs. 9, 17, 19. The ventral gills of abdominal segments 2-7 receive each two tracheae from two separate

branches of the main lateral trachea and the gill tracheae divide and redivide inside each gill (Pl. III, figs. 20, 25, 26). Owing to the opacity of the chitin, the thickness of the gills and the obstacles met in clearing them, I have not been able to make out more than the main branches of the tracheae supplying the caudal gills (Pl. II, fig. 9). The stomach is supplied from two anterior and two posterior tracheae, one anterior and one posterior on its right side and similarly on its left side. The right and left anterior gastric tracheae lie parallel and close together on the dorsal surface of the oesophagus and crop; each is probably a derivative from the main dorsal trunk of its own side of the body, but this was not definitely ascertained. At the anterior end of the stomach each anterior gastric trachea divides into a set of (two) dorsal and a set of (four) lateral branches as shown in Pl. II, figs. 13 and 17. The fourth, or ventralmost, lateral branch apparently forms an anastomosis with the corresponding branch of the opposite side of the stomach.

balsam. No definite indications of rectal tracheal gills were found and the rectal walls appear much less richly tracheated than those of the stomach. The rectal epithelium appears to form three (glandular?) areas. The gastric epithelium was disintegrated. No food was found in the alimentary canal.

The three thoracic pairs of ganglia are clearly distinct from each other. Posteriorly are seven pairs of smaller ganglia, located as follows: 1 in metathorax, 2 in anterior part of abdominal segment 2, 3 in hind part of segment 3, 4 at the articulation of segments 4 and 5, 5 in anterior end of segment 6, 6 in anterior end of segment 7, 7 in the middle of segment 8. The nerve cord in the male larva dissected (No. 3) passed to the right of the distinct rudiments of the genitalia projecting dorsad into the cavity of segments 1 and 2.

Discussion of the More Interesting Features of Cora Larva.

In current classifications *Cora* is placed in the Calopteryginae or Calopterygidae (= Agrioninae of the catalogues of Kirby, Muttkowski, etc.). Most of the Calopterygine larvae

The three caudal gills together are much wider than the abdomen at its widest part. Each one is petiolate at base and much enlarged in all diameters beyond the petiole. *Median gill* approximately equal in length to that of segments 8+9+10, much enlarged dorso-ventrally and less so laterally immediately after the petiole, thence increasing in height gradually and slightly to the apex which is triangulate in profile view, the ventral angle most obtuse, the median angle most acute, the dorsal angle projecting not as far caudad as the other two. At a little less than half length from the base there is an angular protuberance on each side at about one-fourth height of the gill from the dorsal crest, so that there are in all five angular projections on this gill. Most of the chitin of this gill is brown and opaque, or at most only translucent, and is covered with scales, but on each of the two lateral faces there is an area of colorless transparent chitin occupying the ventral two-fifths of the height and about four-fifths of the length from the base caudad (Pl. II, fig. 14) lacking scales.

Line 20 from top of page 55 should read

stomach (Pl. II, figs. 17, 19, *lpgt*). The rectum has four tracheae, two

half-length, of the gill on the middle of the convex dorso-external surface; one at three-fourths of the length of the gill on the convex surface close to the margin of the mesial surface; one at seven-eighths of the length of the gill on the middle of the convex surface; and one, the most obtuse, forming the apex of the gill. The convex dorso-external surface of the gill is of brown chitin and scale-covered, the ventral and mesial surfaces chiefly of colorless, transparent chitin and lacking scales, except along the margins where each meets the dorso-external surface respectively. (Pl. II, figs. 3, 4, 9, 14, 15).

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The hind-gut or intestine is likewise supplied by branches from the main dorsal tracheal trunks. The trachea which passes to the ileum also furnishes the posterior gastric trachea for the same side of the stomach. The rectal epithelium appears to form three (glandular?) dorsals and two laterals. (Fig. 19, *rdrt, ldrt, rlrt, llrt*). After the drawings forming figures 13, 17 and 19 were made, the alimentary canal was slit open lengthwise, stained, dehydrated, cleared and mounted in balsam. No definite indications of rectal tracheal gills were found and the rectal walls appear much less richly tracheated than those of the stomach. The rectal epithelium appears to form three (glandular?) areas. The gastric epithelium was disintegrated. No food was found in the alimentary canal.

The three thoracic pairs of ganglia are clearly distinct from each other. Posteriorly are seven pairs of smaller ganglia, located as follows: 1 in metathorax, 2 in anterior part of abdominal segment 2, 3 in hind part of segment 3, 4 at the articulation of segments 4 and 5, 5 in anterior end of segment 6, 6 in anterior end of segment 7, 7 in the middle of segment 8. The nerve cord in the male larva dissected (No. 3) passed to the right of the distinct rudiments of the genitalia projecting dorsad into the cavity of segments 1 and 2.

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hitherto described (Cf. Karsch, 1893, pp. 42, 48; Needham, 1903*b*, p. 220) have the first antennal joint very long, as long as all the other, or as several of the other, joints added together. *Cora* larva has the first antennal joint shorter than the second and in this respect, as in others mentioned below, shows a resemblance to the Old World larvae described by Hagen (1880, p. lxv) as pertaining to the legion Euphaea* of de Selys, and to a Mexican fragment doubtfully referred to *Cora* (*l. c.*, p. lxvi).

The scales forming a more or less dense pile on different parts of the body of *Cora* larvae are structures which have met little or no notice in the literature on the Odonata. They occur in shapes varying from almost hair-like to that in which the width is at least more than half the length (Cf. Pl. II, figs. 4, 5, 11, 3 in the order named). The central and more or less arborescently-branched portion of each scale is thicker than the often hardly discernible marginal areas.

Biramous mandibles hitherto have been noted only in *Euphaea* larvae of all the Odonata, and that very briefly (Needham, 1903*a*, p. 743). I am not able at present to determine whether the two-branched condition there is the same as that here described for the larvae of *Cora* or not. The remarkable features of these mandibles is the possibility of independent movement of the inner branch along the dotted line shown in Pl. II, fig. 16, and the difference in the form of this branch in the right and left mandibles of the same individual noted above. Heymons (1896 *b*, taf. II, fig. 29) has figured the mandibles in a young larva of *Ephemera vulgata* which are also two-branched but, in contrast to the larval mandible of *Cora*, the inner branch is larger than the outer.

The very shallow median cleft of the median lobe of the labium was hardly to be expected in larvae so apparently primitive in other features as our *Cora* larvae are. In this respect also it agrees with *Euphaea* larvae, as far as can be

* The name of the type genus of this legion, *Euphaea*, is now replaced by *Pseudophaea* Kirby.

judged from Hagen's description (1880, p. xlv). If Miss Butler's theory (1904, pp. 114, 119) of the homologies of the labium be correct, then the small, pointed teeth (Pl. III, fig. 28 *t**) near the middle of the distal margin, would represent the apices of the original laciniae. The interpretation of Börner (1909, p. 113) is different and is essentially that of Gerstäcker, Heymons and others.

Hagen (1880, p. lxv) noted the existence of "une *plantula* entre les onglets" of *Euphaea* larvae and remarked (p. lxvii) "La présence d'une *plantula* entre les onglets est aussi un caractére unique chez les Odonates." The empodium-like structure mentioned above for *Cora* and shown in Pl. II, fig. 12, appears to be an homologous part.

The existence of tracheal gills on abdominal segments 2-7 is the most interesting feature of *Cora* larvae. The only Odonata previously known to possess such structures are the larvae referred to *Euphaea* and *Anisopleura* in the very brief description of Hagen (1880). One of these larvae was figured by Folsom in Packard (1898, p. 469). Hagen stated that there were gills on abdominal segments 1-8, Folsom found them on 2-8 only. There are, therefore, one pair less in *Cora* larvae. Hagen compared these gills of *Euphaea* and *Anisopleura* to those of *Sialis*, but makes no mention of Ephemerid larvae in this connection. Heymons (1896 *a*, pp. 88-90) compared the abdominal gills of Ephemerid and *Sialis* larvae, regarded them in both cases as derived from abdominal appendages and noted the agreement in the pointed form of the gills of the early larval stages of both groups. The gills of the second to seventh abdominal segments of *Cora* larva furnish an addition to this parallel. That the lateral gills of Ephemerid larvae are homologous with the thoracic legs is not universally accepted, however. Dürken (1907, 1909) and Börner (1909 *a*) are the latest representatives of the two views which look upon the Ephemerid lateral gills as dorsal and not homologous with legs and as ventral and homologous, respectively. We may not compare the lateral gills of *Euphaea*,

Anisopleura and *Cora* larvae with those of the Ephemerid larvae until much fuller data are at hand regarding the detailed structure, position, musculature and tracheation of each. The present study of *Cora* larvae supplies much fuller information than exists for either of the other two Odonate genera mentioned. The markedly ventral position of the gills in question in *Cora* is in itself some evidence against homologizing these structures with those of the Ephemeridae and in favor of their own serial homology with thoracic legs. No traces of these gills are present on the exterior of the abdomen of imagos of *Cora* preserved in alcohol immediately after capture.

The caudal tracheal gills of *Cora* larvae are very different in shape from the similarly situated gills of all other Odonate larvae yet described, including those of *Euphaea* (cf. Folsom's figure, *l. c.*) and *Anisopleura*, of which latter I possess a photograph from Hagen's specimen, taken and given to me by Prof. J. G. Needham. In both of these latter two genera the caudal gills taper posteriorly to an acute apex.

As related in the opening pages of this paper, the attempt to rear these larvae to transformation was unsuccessful. That they are the larvae of *Cora* and, so far as the Juan Viñas specimens at least are concerned, the larvae of *Cora chirripa* Calvert (1907, p. 348) is rendered practically certain from a comparison of the wing-rudiments of larva No. 4 with those of an imago of this species taken at the same ditch April 30, 1910. The left hind wing-pad of larva No. 4 was slit open, the wing rudiment removed from within and examined in alcohol under the compound microscope. The inner and outer surfaces of the rudiment gave the views represented in Pl. III, figs. 23 and 24 respectively. The veins shown in these figures are bands of reddish-brown pigment granules in the rudiment itself. The left hind wing of the imago mentioned was compared with camera drawings of the two surfaces of the wing-rudiment of the larva. At first the identification of the larval wing veins proceeded slowly until it occurred to me that perhaps the two surfaces of the wing rudiment might present only convex and concave veins respectively. Turning then to the imaginal wing the following lists were made proceeding in every case from the anterior toward the posterior wing margin. Convex veins: proximal half of the wing, C, R1, R*s*, M4, A and Cu2; distal half, C, R1, M1*a*, two supplementary sectors, R*s*, three supplementary sectors, M4, Cu2*a*, Cu2*b*.

Concave veins: proximal half of wing, Sc, M1, M3, Cu1; distal half, M1, two supplementary sectors, M2, one supplementary sector, M3, two supplementary sectors, Cu1, one supplementary sector between Cu2*a* and Cu2*b*.

As is well known the inner surface of the wing-pad and wing-rudiment of an Odonate larva corresponds to the upper surface of the imaginal wing, and the outer surface in the larva to the under surface in the imago. On comparing the list of convex veins with the drawing of the inner surface of the wing-rudiment and the list of concave veins with that of the outer surface of the wing-rudiment, it was seen that a close correspondence existed with these exceptions: that C (costa) showed on both surfaces, as also did a thickening all along the posterior margin and to greater or less extents Sc (sub-costa), R1 (first branch of radius), M1 (first branch of media), A (anal), Cu2*b* and the supplementary sector between Cu2*a* and Cu2*b*. The wing-rudiment was then cleared in cedar oil and examined in strong transmitted sunlight, when the vein-rudiments of both inner and outer surfaces could be seen from either surface by proper focussing, whereas before clearing only those of the surface turned up toward the lens could be discerned. All the vein-rudiments now appeared in their proper sequence giving the alternation of convex and concave veins so easily seen in an imaginal wing. Careful focussing also revealed the fact that at this stage the veins are developed only upon one surface of the wing-rudiment, either inner or outer, except in the case of the costa and of the thickening along the hind margin. The other exceptions noted above are all veins near the margins where the wing-rudiment is thinner

and where they can be seen through it. Even in these exceptions the veins appear fainter and narrower on one surface than the other and are stronger and wider on their proper surface, *e. g.* Sc and M1, concave veins, on the outer surface; R1, A and Cu2*b*, convex veins, on the inner surface.

Another fact shown by these comparisons and the figures is that the cross-veins only appear continuous from one longitudinal vein to another when the two longitudinal veins so connected are two, one of which immediately follows the other in the imaginal wing. (Cf. the cross-veins between R1 and M1 and between M1 and M2 in Pl. III, fig. 24.)

It would thus appear that each longitudinal vein develops on one surface of the wing-rudiment before it appears on the other surface. Before transformation is reached each vein has formed on both surfaces of the future wing but not necessarily equally on both surfaces, as may be seen from Hagen's figures (1889) from photographs of wings split into their two laminae immediately after transformation and expansion.

These facts of the development of the veins on one surface of the wing-rudiment before the other have a practical value in identifying Odonate larvae by this method and do not seem to be included in Prof. Needham's (1904, p. 687) suggestions on this point.

In the larva of *Cora* there exist the following generalized features: antennae with no hypertrophied joint, biramous mandibles, paired ventral tracheal gills (if they be morphologically equivalent to legs), and perhaps the empodium-like part, side by side with specialized features in the form of cuticular scales, almost completely fused halves of the labium and thickened, shortened caudal gills. If to these generalized parts of the larva we add the generalized features of the imaginal venation pointed out or implied by Prof. Needham (1903*a*, pp. 731, 746), we have good grounds for looking on *Cora* and its allies as being in many respects the most primitive of living Odonata.

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Explanation of Plates II and III.

Larva of *Cora*.

Fig. 1. Left latero-ventral view of larva No. 4 ♀.

Fig. 2. Dorsal view of larva No. 3 ♂. Right caudal gill lacking.

Figs. 1 and 2 from photographs of alcoholic specimens. × 2.6.

Fig. 3. Small fragment of surface of left caudal tracheal gill, larva No. 3, showing two scales and four articular pits for others. × 210.

Fig. 4. Scale from same gill as fig. 3. × 210.

Fig. 5. Scale from first antennal joint shown in fig. 10. × 210.

Fig. 6. First left tibia and tarsus of larva No. 4. × 8.5.

Fig. 7. End view, hind end of abdomen of larva No. 2 ♀, caudal gills removed. × 8.5.

Fig. 8. Dorsal view, hind end of abdomen of larva No. 2 ♀, caudal gills removed. × 8.5.

Fig. 9. Left caudal gill, ventro-mesial view, combined from drawings from larvae Nos. 1, 2, 3, to show tracheation. The dotted line indicates the boundary between a central, clearer, unscaled area and an opaque, scaled margin. × 5.8.

Fig. 10. Right antenna, dorsal view, larva No. 3, ♂. × 16.5.

Fig. 11. Scale from tibia or tarsus of fig. 6. × 210.

Fig. 12. Ventral surface of distal end of tarsus. × 8.5.

Fig. 13. Dorsal view of branches of left anterior gastric trachea shown in fig. 17. × about 12.5.

Fig. 14. Right lateral view of metathorax and abdomen of larva No. 4, ♀. × 5.5.

Fig. 15. Ventral view of same. × 5.5.

Fig. 16. Left mandible, mesial surface, larva No. 2, ♀. × 21. The dotted line shows the line of flexure of the internal branch.

Fig. 17. Left side of stomach to show tracheation, larva No. 3, ♂, × about 12.5.

Fig. 18. Ninth abdominal segment to show gonapophyses, larva No. 3, ♂. × 5.5.

Fig. 19. Left latero-dorsal view of intestine to show tracheal supply, larva No. 3, ♂; Malpighian tubules omitted. × about 12.5.

Fig. 20. Right gill of fifth abdominal segment, larva No. 3, ♂. The gill has been left untouched, the viscera of the segment removed with the exception of the tracheae supplying the gill. To the left of *chr* a portion of the chitinous ventral wall of the segment is shown, to the right of *chr* is a portion of the tergite which has been turned outward (laterad) to show the structures within the segment. The portions of the two main tracheal trunks *rdt* and *rlt* have been turned outward to give a clearer view of the branches to the gill. Compare with the fifth abdominal segment in fig. 22. × about 23.

Fig. 21. Dorsal view of head, larva No. 4, ♀. The dotted lines show the outlines of pale marks. × 7.8.

Fig. 22. Dorsal view of chief thoracic and abdominal viscera, larva No. 3, ♂. The body has been opened along the mid-dorsal line. The ganglion has been omitted from second abdominal segment, the

wing-pads from left side, the dorsal longitudinal abdominal muscles from the right; not all of these muscles (*dlm*) are shown even on the left side. × 7.8.

Fig. 23. Inner surface of left hind wing-rudiment (= upper surface of imaginal wing) with the outline of its enveloping wing-pad, *wp*, larva No. 4, ♀. × 12.4.

Fig. 24. Outer surface of the same (= under surface of imaginal wing). × 12.4.

Fig. 25. Transverse section of right gill of sixth abdominal segment of larva No. 3, ♂. × 55.5.

Fig. 26. Transverse section of chief tracheal trunk of same gill in section immediately following that shown in fig. 25. × 55.5.

Fig. 27. Distal end of lateral lobe from fig. 30. × 28.

Fig. 28. Inner (dorsal) surface of distal end of median lobe from fig. 30. × 28.

Fig. 29. Distal end of left maxilla from fig. 31. × 25.

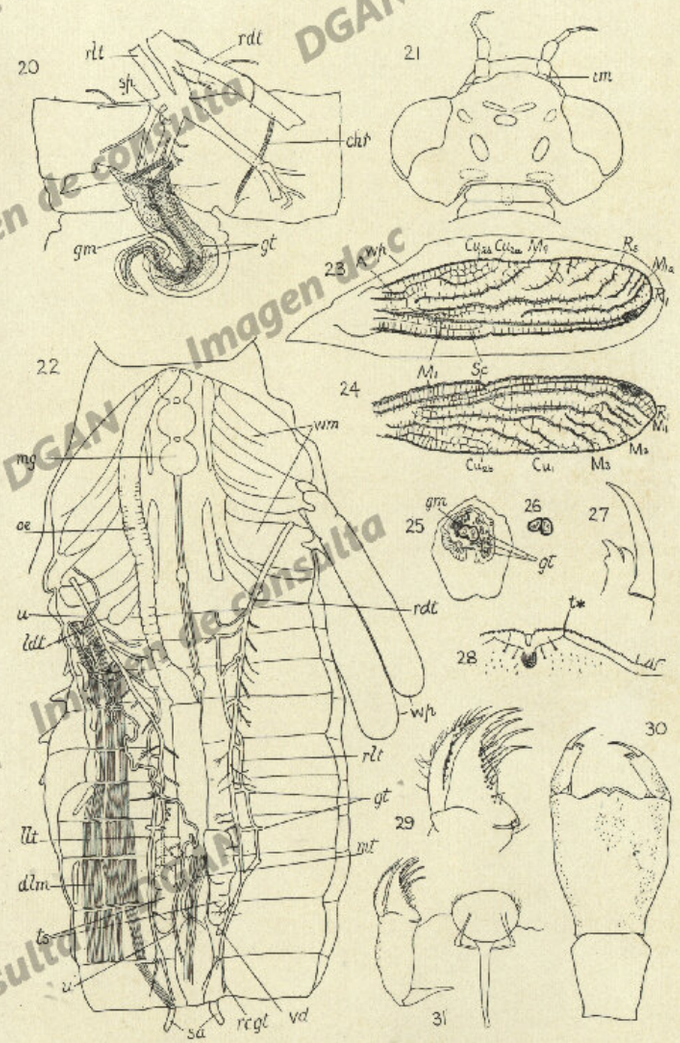
Fig. 30. Ventral (outer) surface of labium, larva No. 2, ♀. × 8.

Fig. 31. Left maxilla and hypopharynx, ventral view, larva No. 2, ♀. × 13.

Abbreviations Used in the Plates.

A, Anal vein (= proximal part of second sector of triangle of Selys).
chr, Chitinous ridge forming lateral margin of an abdominal segment.
Cu1, Cu2, First and second branches of cubitus vein (= first and distal part of second sectors of triangle of de Selys).
d, *d*1, *d*2, Dorsal branches of *lagt*.
dlm, Dorsal longitudinal muscles.
gm, Gill muscle fibres.
gp, Gonapophyses.
gt, Gill trachea.
im, Interarticular membrane between first antennal joint and head.
IX, Ninth abdominal segment.
l, *l*1-*l*4, Lateral branches of *lagt*.
lagt, Left anterior gastric trachea.
lcg, Point of attachment of left caudal gill.
ldt, Left dorsal trachea.
ldrt, Left dorsal rectal trachea.
llt, Left lateral trachea.
lrt, Left lateral rectal trachea.
lpgt, Left posterior gastric trachea.
*M*1, *M*2, *M*3, *M*4, Branches of media vein (= principal, nodal, median and short sectors of de Selys respectively).
*M*1*a*, Branch of *M*1 (=ultra-nodal sector of de Selys).
mcg, Median caudal gill.

mg, Metathoracic (+ first abdominal?) ganglion.
msp, Metathoracic spiracle.
mt, Malpighian tubes.
oe, Oesophagus.
*R*1, First branch of radius vein (= median vein of de Selys).
*r*4, Fourth lateral branch of right anterior gastric trachea.
rcg, Point of attachment of right caudal gill.
rcgt, Right caudal gill trachea.
rdrt, Right dorsal rectal trachea.
rdt, Right dorsal trachea.
rlrt, Right lateral rectal trachea.
rlt, Right lateral trachea.
Rs, Radial sector (= sub-nodal sector of de Selys).
sa, Superior appendages of imago ('Cercoids').
Sc, Subcosta vein.
sbl, Sub-anal lamina.
sp, Site of future spiracle.
spl, Supra-anal lamina.
tab, Tendon of abductor mandibulae.
tad, Tendon of adductor mandibulae.
ts, Testes.
*t**, Tooth on median labial lobe.
u, Undetermined tube.
vd, Vas deferens (beginning of).
wm, Wing muscle.
wp, Outline of wing-pad.
X, Tenth abdominal segment.



LARVA OF CORA (ODONATA)—CALVERT.