

A PRELIMINARY STUDY OF LARVAL STRUCTURE IN THE DRYOPIDÆ.

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I. INTRODUCTION.

(a) *Plan and scope of the work.*

Originally undertaken with a view to making a substantial contribution to our knowledge of the biology of this group, the present work is manifestly incomplete. Circumstances prevent further investigation in the immediate future however, and it is felt that the results which have been secured are such as to warrant publication at this time. The nature of the work may be briefly explained:

All larval material available in this family has been separated into a number of distinct types, which are described herewith in detail and are accompanied with figures showing all the important distinguishing structures. The possible identity of these types, in most cases, can be only inferred by reason of their association with adult forms already known, but since no attempt has been made to establish the identity of these forms beyond the genus, such inferred identifications answer quite satisfactorily the purposes of this paper. These various larval types are then discussed with reference to the adaptation of their form and structure to the environments in which they are found, and there is included an attempt at interpretation from a phylogenetic point of view. To make more clear the distinguishing characters, also to provide for ready detection by other workers of any types not here treated, a brief analytical table is appended.

The writer is of course aware that modern views associate the Heteroceridæ and Georyssidæ with the Psephenidæ, Dryopidæ and Elmidæ in the superfamily Dryopoidea, as set forth in Leng's Catalogue ('20). In the present paper, however, the family name Dryopidæ is used in its older sense, as inclusive of the three subfamilies—Psepheninæ, Dryopinæ and Elminæ. (Cf. Parnidæ of Blatchley's Catalogue, also of Zaitzev ('08, '10).

(b) *Sources of material; acknowledgments.*

All material used in the present study was taken within the boundaries of the United States. A major portion was collected by the writer in the vicinity of Ithaca, N. Y., but a considerable quantity of western material was furnished by Dr. J. G. Needham, to whom the writer desires to make acknowledgment for much helpful encouragement and advice. Thanks are also due to Dr. W. T. M. Forbes, to Dr. G. C. Embury and to Professor W. A. Clemens for various courtesies extended during the course of the work, likewise to Dr. Adam G. Boving, for the privilege of studying the unpublished manuscript of his paper "On the Classification of Beetles According to Larval Characters."*

II. PREVIOUS STUDIES.

Although a very large number of titles have to do with Dryopid Coleoptera from a *taxonomic* point of view, those papers dealing with the *biology* of the group are much less numerous, and are, for the most part, widely scattered. Hence the literature as a whole affords but scant assistance in the study of larval characters. The works of certain authors, however, have proven of considerable value and should be mentioned at this point.

Müller (1806) is apparently the first to take special note of the immature stages of these forms. He is followed by other European writers, notably Westwood ('39) and Erichson ('41, '48) who record various general facts concerning both structure and behavior. DeKay ('44) makes the unhappy blunder of describing the larva of *Psephenus lecontei* Lec. as a new species of Crustacean (*Fluvicola herricki*), the identity of which is finally set right by Le Conte ('49, '50), whose correspondence with T. W. Harris (published 1869) likewise furnishes certain interesting and valuable information. Dufour ('62), Perez ('63), Laboulbène ('70), Rolph ('74), Friedenreich ('81) and Beling ('83) treat largely of European forms while Hubbard ('80), Kellicott ('83), Leng ('94) and Lataste ('97) have contributed to our knowledge of various American types. Matheson's ('14) note on the life histories of *Psephenus lecontei* Lec. and *Stenelmis*

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bicarinatus Lec. is an important contribution. A valuable account by Boving ('26) of the immature stages of *Psephenoides gahani* Champ. may be said to complete the list of important papers on the biology of the Dryopidæ. The writer's notes on *Psephenus* and *Macronychus*, also his "Bibliography of the Drypoidea," published during the past year, may perhaps be found useful by subsequent workers.

III. DESCRIPTIONS OF LARVAL TYPES.

The larval types here treated are nine in number. In addition, a description (in English) of the larva of the European species, *Elmis aeneus* Mull. is included for sake of comparison with related American forms. For the purposes of this paper, it was deemed advisable to emphasize only those differences which may probably be regarded as of generic significance, leaving a more complete analysis until such time as the actual identity of the species in question can be known. So far as circumstantial evidence warrants, the *probable* identity of the larva is indicated in each case.

TYPE 1. *Psepheninæ* (*Psephenus*).

Form flattened, elliptical, bearing superficial resemblance to a trilobite. Larva proper concealed beneath an arched carapace, formed by extension of the pleurites of the first ten body segments. "Lateral lobes," especially in mature larvæ, closely approximated, fused on basal third, each tending to overlap slightly the lobe immediately posterior. Entire peripheral border ciliated, and capable of being closely appressed to the rocks. Lateral lobes of eleventh body segment tending to become obliterated. Caudal segment (ninth abdominal) composed of a broad, flat, rectangular dorsal sclerite, and a minute ventral one, nearly four times as broad as long. Anal opening situated between dorsal and ventral sclerites of last abdominal segment.

Head visible only in ventral view, being covered dorsally by that portion of the carapace derived from the prothorax; capable of being directed either downward or forward by means of a muscular apparatus suggesting a "ligamentum nuchæ," in position and function.

Antennæ three-segmented, elongate, the first segment about equal in length to the distance between the ocelli, the second, three-fifths the length of the first, the third minute, and composed of two small segments lying side by side, the larger of which bears distally a tiny spine. First antennal segment bearing usually six hairs along posterior margin. Ocelli in two groups of six each. Labrum broad, anterior margin straight or slightly rounded, outer corners convex, each bearing a row of rather coarse spines. Mandibles large, heavily chitinized, especially

near the tips, and bearing at about mid-point of inner margin, a brush, or tuft of bristles, evidently sensory in function. Outline of mandible usually sub-triangular, but occasionally, in last stage larvæ, elongate, and appearing as though composed of a basal and a terminal portion, the sensory brush being situated on the line of division. Maxillæ large, complex, with palpi of four segments (exclusive of the palpifer). Lacinia with papillæ-like prominences, grading off into short, thick spines. Galea more or less covered with stout hair. Stipes, first and second segment of palpus bearing respectively 1, 2, 2, stout bristles which in certain individuals appear to be branched. Labium short, broad, not heavily chitinized, and bearing a pair of three-segmented palpi. Tip of third segment, like fourth segment of maxillary palpi, beset with tiny tubercles evidently tactile in function. Basal segment of palpus bearing three branched spines. Mentum quadrangular, broad, divided by only a faint suture from the more distal portion.

Legs all similar, stout, rather thickly beset with hair, and each bearing a single strong claw with short interior spine. No tarsal segments other than the claw itself. Gills ventral, arranged in five pairs, and taking origin from the posterior margin of abdominal segments 2-6. Each gill tuft composed, on the average, of ten filaments, arranged somewhat in comb-like fashion. No anal gills present. Length of mature larva, 8.5 mm. Width, 5.75 mm.

Description drawn from several specimens of *Psephenus lecontei* Lec.

TYPE 2. *Dryopinæ* (*Helichus*).

(Plate I, Figure 7. Plate II).

The body form elliptical-ovate, flattened, similar to *Psephenus*, but differing particularly in that the lateral lobes of the carapace are not closely joined to one another. That portion of the carapace derived from the prothorax is characterized by backward-projecting posterior-lateral angles. Dorsal surface bearing many very small tubercles, scattered irregularly over the prothorax and the lateral lobes, but in the mid-dorsal region arranged in six longitudinal rows, the outer four tending to join up anteriorly in the pattern of a broken W. Lateral lobes of abdominal segment 8 developed as in the segment preceding. Junction of pleuræ with sternum not in line with base of lateral lobes, as in *Psephenus*, but at a considerable distance nearer the mid-line. Posterior abdominal segment flattened, sub-rectangular. Dorsal sclerite slightly longer than broad, ventral sclerite two-thirds as wide and nearly as long as the dorsal one. Entire margin of animal ciliate with curiously tufted hairs, ciliation tending to disappear on the anterior and posterior border of the more anterior lateral lobes.

Head large, concealed beneath the carapace, and usually directed forward; capable of partial withdrawal into a rather elaborate, surrounding collar, composed of a reflected portion of the integument of the neck. Antennæ moderately conspicuous, composed of three segments, the first stout, and barely twice as long as broad, the second somewhat

more slender and of slightly greater diameter at the middle than at either end, and the third duplicate, as in *Psephenus*, being composed of two similar members arranged side by side. Basal segment of antennæ usually bearing three, the second, one, strong spine. Labrum nearly two-thirds as long as broad; front margin regularly convex with slight anterior medial expansion; antero-lateral angles heavily ciliate with hair. Mandibles large, heavily chitinized, conspicuous, similar to those of *Psephenus*, with stout interior sensory filament covered with distally directed setæ, and surrounded at the base with a considerable mass of sensory hairs. Elongate type of mandible most common, especially in more mature specimens, but short, sub-triangular form also occurs. Maxillæ complex, rather membraneous, bearing small, four-segmented palpi, the distal segment being very minute. Hairs on stipes and basal segments of palpus noticeably branched. Galea without characteristic form, being roughly cuboidal, bearing distally about six, stout, curved spines, together with many lesser hairs, which cover a large portion of its surface. Lacinia tending to simulate a truncate sleeve, open along the free margin, and bordered distally with many, fairly stout spines. Labium membraneous, somewhat elaborate in structure, fully twice as long as broad, the mentum but doubtfully distinct from the palpi-bearing distal portion. Distal portion with heavily ciliate anterior margin, and with internal structure suggestive of differentiation into glossa and paraglossæ. Palpi of three segments in addition to the palpiger.

Legs similar to *Psephenus*, but characterized by the presence, on the ventral surface of the femur, of several modified spines (usually 6), each spine short, considerably thickened, and bearing many tiny processes. Claws each with a slender interior spine. Gills anal in position, arranged in three principal tufts and capable of extrusion between the ventral and dorsal sclerites of the posterior abdominal segment. Spiracles confined to eighth abdominal segment. Length of mature larva, 5.5 mm. Width, 3.5 mm.

Description drawn from several specimens supposedly *Helichus lithopilus* Germ. Most of the material at hand was collected from either Oneida or Tompkins Counties, New York.

TYPE 3. **Dryopinæ? (Lara?)**.

(Plate I, Figs. 2, 6. Plates II, III).

Form elongate, sub-cylindrical and tapering caudally. Body segments very distinct, each appearing as though telescoped into the one preceding. Thoracic segments especially, with tergum overhanging laterally in form of a dorsal shield. Larva, in lateral view, noticeably convex dorsally, ventral surface correspondingly concave. Dorsal ornamentation of all segments elaborate, consisting of tubercles and papillæ arranged in an irregular pattern, similar for all segments. Posterior, and in part, lateral margins of each dorsal segment bearing a variable, complex row of backward-projecting processes (papillæ)

which are in turn adorned with fine spines. Ornamentation so arranged as to give effect of four longitudinal rows of large backwardly projecting processes, extending the length of the dorsum, but more conspicuous in the abdominal region. Two of these rows are sub-dorsal, two lateral. Posterior abdominal segment cylindrical at base and tapering distally; about as long as the two preceding segments taken together. Dorsal sclerite, viewed from above, terminating in two rather conspicuous, sharp processes. Ventral sclerite sub-quadrate, and bearing two elongate posteriorly directed processes on its inner (upper) surface, hooked at their tips and with many spines on basal portion.

Head roughly orbicular, directed forward, and adorned above with many tubercles of various size. Ocelli in two groups of five each, each group arranged in two vertical rows, three in the first, two in the second. Antennæ short but fairly conspicuous and noticeably hairy. First segment one and one-half times as long as broad, second more than half the thickness of the first, and one and one-half times as long. Third segment duplicate consisting of two sub-equal members lying side by side, one of which bears an exceedingly minute terminal spine, (not seen in all specimens). Labrum three times as broad as long, very spiny, lateral margins obliquely rounded, medial portion of anterior margin concave. Mandibles sub-quadrate, with deep concavity along inner margin. Inner "sensory brush" situated one-third the distance from base to tip. Tip bidentate. Outer surface of mandible very hairy, with long waving setæ. Maxillæ complex, rather heavily chitinized; cardo with a very conspicuous, sharp hook; lacinia and galea each bearing many short, thick sensory spines. Those borne on lacinia are much more robust than those on galea. Lacinia modified in the form of a truncate sleeve, open along the free surface. Stipes, near point of origin of the four-segmented palpi, bearing a considerable mass of flexible and elongate spines. Labium sub-rectangular, twice as long as broad and bearing three-segmented palpi. Mentum not to be clearly differentiated from palpi-bearing distal portion. Palpi, especially on second segment, conspicuously setaceous. Small, circular area at tip of palpus supplied with minute papillæ, serving apparently, a special sensory function. Entire margin of distal half of labium conspicuously hirsute, the longest spines occurring in the region of the palpi.

Legs stout and similar to those of other types, each terminating in a stout claw which bears internally a tapering spine. Spines present on all segments, longest on the tibia. On both femur and tibia, spines are sometimes very short and thick, but never of the "taste-bud" form found in *Helichus*. Coxæ not particularly modified for reception of femora. Gills caudal, arranged in three principal tufts and capable of being extruded between sclerites of last abdominal segment. Spiracles easily observed, situated laterally on first eight abdominal segments. Length of mature larva, 15.5 mm. Width, 2.25 mm. (Greatest expansion of prothorax).

Description drawn from several specimens collected from Yellowstone National Park, and from San Jacinto Mts., Calif.

By reason of its size and geographical distribution, tentatively assigned to *Lara avara* Lec. It might here be mentioned that according to Grouvelle, *Lara avara* is not a true Dryopid, but might better be considered as belonging to the Helodidæ. (Zaitaev '08).

TYPE 4. **Elminæ (Stenelmis).**

(Plate I, Fig. 8. Plate III).

Larva elongate, of the form of an attenuated hemi-cylinder, i. e., with ventral surface nearly flat, but with dorsum arched, so as to appear in cross-section semi-circular. Median dorsal line but faintly indicated; not elevated into a carina of any sort. Prothorax one and one-half times the length of the succeeding segment. Seen in dorsal view, margins of all body segments except the last appear bisymmetrically rounded, the margin of the prothorax alone being very slightly sinuate. Posterior abdominal segment sub-conical; the dorsal sclerite rather abruptly narrowed posteriorly and terminating in two sharp points. Ventral sclerite occupying posterior half of segment, of the form of a quadrangle with an equilateral triangle attached posteriorly; with two elongate, slender appendages, bearing numerous spines, and recurved at the tips. Entire dorsal surface of the larva, except the head, covered with a close sprinkling of fine tubercles, each of which tends to give rise to a minute, backwardly directed spine. These tubercles tend to be replaced by spines on posterior segments. Those spines along the posterior margin of each segment are more stout and elongate, forming a ciliate border to the segment. Larva slightly broadest in the region of the first two or three abdominal segments; diminishing slightly in size both anteriorly and posteriorly from this point.

Head large, exserted, rather conspicuous, being nearly three-fourths as broad as prothorax; with conspicuous Y-shaped epicranial suture visible dorsally. Antennæ short, composed of three segments; the first rather deeply inserted and but slightly longer than broad, the second much more slender, fully twice the length of the first and, seen laterally, more expanded at distal end than at the base; the third duplicate, being composed of two small, transparent articles arranged side by side, the one gradually tapering, the other more robust and of the same diameter throughout. No terminal spine has been demonstrated on either of these articles. Ocelli situated behind the antennæ, each group composed of apparently five units. Labrum simple, with lateral margins evenly rounded; slightly emarginate anteriorly. Anterior and lateral margins, as well as entire upper surface, beset with rather stout spines. Mandibles sub-triangular, distinctly tri-dentate, and bearing a large "taste-brush" on the inner surface at about one-third the distance from base to tip. Outer surface bearing at least two branching spines. Maxillæ small, with four-segmented palpi. Stipes, near base of palpus, bearing at least one stout branching spine. Small area on distal portion of last palpal segment provided with papillæ, evidently tactile in function. Lacinia lying close upon

galea and of the usual form, i. e., resembling a truncate sleeve, or cylinder, open along the exposed surface and adorned distally with a variable number of stout spines. Galea without characteristic form, bearing distally several stout curving spines. Labium membraneous, nearly twice as long as broad, and bearing three-segmented palpi, of which the third segment is much the smallest and bears distally a small sensory area, where are located usually four tactile papillæ. Outside of, and opposite to first palpal segment may be found, on each side, a short, stubbed spine. Mentum rather clearly bounded by a suture at the base of the palpi. Distal portion of labium evenly convex and adorned with a great number of fine, tactile hairs.

Legs composed of the usual parts and adorned with a rather scanty covering of spines. Coxæ somewhat excavated anteriorly, and thus adapted for reception of femora. Distal portion of excavation cushion-like in appearance, with a mass of small closely ranged tubercles. Claw bearing on its inner surface a slender, and sometimes curving spine. Gills caudal, arranged in three principal tufts and capable of extrusion between the sclerites of the posterior abdominal segment. Spiracles situated laterally, one pair on the meso-thorax and one pair on each of the first eight abdominal segments. Length of mature larva, 6.5 mm. Greatest width (at first abdominal segment), .91 mm.

Description drawn from several specimens taken at Walnut Creek, Michigan, and assigned to *Stenelmis* since several adults of that genus were associated with them. Also the larva of *Stenelmis bicarinatus* Lec. as figured by Matheson ('14) comes closer to this type than to any other studied so far.

TYPE 5. **Elminæ** (*Stenelmis*?).

(Plate I, Fig. 9. Plate IV).

Larva elongate, of the hemi-cylindrical form described under type 4. Viewed dorsally, the thoracic segments are seen to be expanded somewhat, giving the appearance of deep notches between the segments. Prothorax about one and two-thirds times the length of the succeeding segment, somewhat narrower anteriorly and with a faintly sinuate impression parallel to, and near each lateral margin. First six body segments of approximately equal width, the last six abdominal segments becoming gradually less in size. Median dorsal line indicated by a faint elevation, conspicuous only on the last abdominal segment, where it forms a very low median carina. Posterior segment roughly conical, terminating dorsally in two very short, blunt processes (i. e., nearly truncate as compared with type 4). Ventral sclerite occupying posterior two-fifths of ventral surface of segment, of the form of a quadrangle with an equilateral triangle appended posteriorly, and bearing on its inner surface two slender, tapering, recurved appendages, rather generously provided with spines. Dorsum of larva without ornamentation save for almost uniform sprinkling of tubercles over all body segments. Most of these tubercles are in the form of exceedingly

short, blunt, spines, directed somewhat posteriorly. Those along the posterior margin of each body segment, other than the last, tend to be bidentate, giving the effect of a row of closely ranged spines bordering the segment.

Head comparatively much smaller than in type 4, usually conspicuously exerted, and with epicranial suture usually visible. Antennæ short, but fairly conspicuous, being directed forward, and composed of three segments, the first about as broad as long, the second twice the length of the first and only half as thick, the third duplicate, consisting of two, semi-transparent articles lying side by side, the length of the longer being equal to half that of the segment preceding. Basal segment bearing two or three fairly large spines. Ocelli situated behind the antennæ, each group consisting of apparently five units. Head, just below the ocelli, on either side bearing at least two very short, modified spines of the "taste-bud" type. Labrum about twice as broad as long, somewhat concave anteriorly, and with lateral angles smoothly rounded; bearing on dorsal surface and on anterior margin, many stout spines of varying length. Mandibles elongate-triangular, heavily chitinized, bidentate at the tip. Interior surface with a hemispherical concavity, of doubtful function since it collects all manner of debris. Inner "tactile brush" situated just below this concavity, and hirsute, largely, on the upper side only. External surface of mandibles bearing usually one stout spine besides a three or four branched sensory spine of curious form. Maxillæ small, compact, bearing four-segmented palpi. Cardo boat-shaped for reception of sub-galea. Stipes long and slender, bearing two, much branched spines near base of palpus. Galea without characteristic form, adorned distally with a variable number of stout, more or less curved spines. Lacinia lying close upon galea and of the form of a truncate cylinder, somewhat constricted in the middle and open along the exposed surface; bearing distally a number of stout, curving spines. Labium small, membranous, bearing three-segmented palpi of which the terminal segments possess each a number of very fine tactile setæ grouped at the very tip. Maxillary palpi have each, distally, a similar tactile structure. Labium with a pair of short, stout spines, situated, one just exterior to the basal segment of each palpus. Entire distal surface of labium beset with very minute papillæ, each bearing a minute hair.

Legs consisting of the usual number of parts, coxa somewhat modified anteriorly for reception of the femur, the shallow groove being bordered on either side by a tuberculate ridge. Floor of groove, near trochanter, covered with many fine, closely ranged tubercles, as in preceding species. Trochanter and femur each supplied with several short, thick, modified spines, of the taste-bud type. All segments more or less adorned with setæ of various size. Claw elongate and with a slender spine arising from interior surface. Gills caudal in position, arranged in three principal tufts and capable of withdrawal and extrusion between the sclerites of the posterior abdominal segment. Spiracles to the number of nine pairs, situated on the mesothorax and on each of the first eight abdominal segments. Length of mature larva, 5.3 mm. Greatest width (mesothorax), 0.8 mm.

Description drawn from several specimens most of which were also taken at Walnut Creek, Michigan. Tentatively assigned to *Stenelmis* because of the many structural features in which it is similar to Type 4.

TYPE 6. **Elminæ.**

(Plate I, Fig. 5. Plates IV, V).

Form very elongate, almost perfectly cylindrical, characteristically arched dorsally, hence ventrally concave (as seen in lateral view). Length of all abdominal segments equal to, and in the last three or four greatly exceeding their thickness. Posterior abdominal segment typically sub-conical; dorsal sclerite, as seen from above, with serrate lateral margin, terminating posteriorly in two short, pointed, lateral processes. Posterior ventral sclerite occupying distal two-fifths of ventral surface of the segment; of the form of a rectangle with a broad isosceles triangle appended posteriorly, and bearing on the inner surface the usual pair or slender, tapering appendages, recurved at the tip. Appendages more or less covered with hair, also distal portion of sclerite (interior surface). Entire dorsum of larva sprinkled with small tubercles which tend to be directed posteriorly, not a few, especially near the mid-line giving rise each to a fine spine. Tubercles arranged in an even row across posterior margin of each body segment, (except the last); each is here prolonged posteriorly in the form of a double, tooth-like spine, thus giving the appearance of a spinose border for each segment.

Head somewhat elongate, directed forward and freely movable, variously adorned with small spines; antennæ inconspicuous, being usually very closely appressed; of three segments, but appearing somewhat as though made up of four, due to the rather deep insertion of the first into an elevated antennal fossa. First true segment very slightly longer than broad, and with a scanty adornment of fairly strong spines distally, second about one and one-third times the length of the first, but only half as thick, very slightly larger in the middle than at either end, and with a few sparse hairs, distally. Third segment merely an elongate slender, tapering spine, somewhat curved and nearly as long as the second segment; in my specimens at least with no tendency to duplication! Ocelli just posterior to antennæ, with apparently five units in each group. Labrum about twice as broad as long, heavily spined, the lateral corners rounded, the anterior margin showing but a very slight tendency to concavity. Mandibles elongate-triangular, heavily chitinized, tending to become bi-dentate at the tip. Inner surface smoothly concave, but nowhere deeply excavated. Inner "sensory brush" situated at a point about one-fourth the distance from base to tip, and hirsute on its upper surface only. Maxillæ typical, with cardo concave for reception of sub-galea, palpi four-segmented, and with lacinia truncate, and open along the exposed face. Stipes, near base of palpus bearing two very stout spines, one some distance below the other. All segments of palpus bearing at least a few slender

hairs. Terminal segment bearing at the distal extremity two or three sensory papillæ. Both lacinia and galea bearing distally several very stout and somewhat curved, sensory spines. Labium more than twice as long as broad with palpi of the usual three segments. All three segments of palpi sub-equal, the distal one bearing two or three terminal papillæ. Mentum with a single large spine on each side, just below first segment of palpus. Distal end of labium covered with many small papillæ, closely and evenly arranged; each bearing a tiny sensory hair.

Legs, as compared with those of most types, rather slender, variously adorned with spines, including, on the trochanter and femur several modified into the "taste-bud" type found on *Helichus* (Type 2) and certain others. Coxæ conspicuous by reason of peculiar scaly outer surface. Anterior coxal margin deeply grooved for reception of femur, which groove is cushion-like distally, by reason of the presence of fine tubercles, and is bordered on each side by a row of heavily chitinized teeth. Gills caudal, arranged in three principal tufts and capable of extrusion and withdrawal between the sclerites of the last abdominal segment. Spiracles situated laterally, one pair on the mesothorax and one each of the first eight abdominal segments. Length of mature larva, 6.1 mm. Greatest vertical thickness (mesothorax), .45 mm.

Description drawn from specimens collected by Dr. Needham at Dark Valley, San Jacinto Mts., Calif. It is impossible to assign them to any group smaller than subfamily with the knowledge at hand. That they belong in the Elminæ is beyond question however, by reason of the many structural similarities between this and other types of the group.

TYPE 7. *Elminæ*.

(Plate I, Fig. 1. Plate V).

Form extremely elongate, almost perfectly cylindrical throughout. Thorax nearly as long as meso- and metathorax taken together. Posterior abdominal segment typically subconical, nearly as long as the two segments preceding and squarely truncate at the tip, i. e., with no pointed, backwardly directed prolongations. Ventral sclerite occupying distal two-fifths of posterior segment, sub-ovate in outline, and bearing on the inner surface the usual pair of elongate, tapering, and recurved appendages. Spinose ornamentation of sclerite and its appendages rather delicate as compared with many types. Entire dorsum of animal sprinkled with small tubercles, each terminating more or less distinctly in a very short, backwardly-directed spine, those along the posterior margin of each segment bearing larger spines which are thus arranged in a regular transverse row across the segment.

Head sub-orbicular, with many spines and hairs on the front, also surrounding the ocellar regions, mostly directed backward. Profile view of head suggesting a rhinoceros, the impression being due to a curious, carinate elevation involving principally the clypeus; very conspicuous. Entire head directed forward and freely movable.

Antennæ very short and robust, composed each of three segments, the first about as broad as long, and profusely adorned with long hair on the upper surface of its distal border, the second, one and one-half times as long as its greatest width, somewhat tapering, and bearing distally a very few, weak hairs, the third duplicate, being composed of two sub-ovate, semi-transparent papillæ. Ocelli situated behind the antennæ; apparently with five units in each group. Labrum short, broad, with anterior margin, and especially the rounded lateral angles bearing many stout, upturned spines which give the appearance of a "mouth brush" of generous proportions. Mandibles sub-triangular, with a slight protuberance on outer surface, at about one-third the distance from base to tip. This protuberance bears a small, branching tuft of spines and is opposite in position to the inner "sensory brush," which is surrounded at its base with a collar of short bristles. Tip of mandible distinctly tri-dentate. Maxillæ elaborate but typical, with cardo boat-shaped, adapted for the reception of subgalea, with palpi four-segmented, and with lacinia in the form of a truncate sleeve largest distally and open along the exposed surface. Both lacinia and galea bearing several stout, curved spines, those borne by galea being fewer in number, but slightly more elongate. Stipes, near base of palpus bearing three large, and at least two small tufts of branching spines. All segments of palpus adorned with at least a few hairs, the distal segment bearing two small terminal papillæ. Labium membranous, broadest at distal end of mentum, which is easily distinguishable from the palpi-bearing distal portion. Mentum itself five-sixths the total length of labium, and less than twice as long as broad. Palpi very short, robust, of three segments, the terminal segment bearing distally a number of sensory papillæ. Mentum bearing on each side, at some distance from base of palpus, a single stout spine. Distal end of labium covered with small tubercles, each giving rise to a minute hair.

Legs robust, elaborately adorned with spines, both single and branched. Coxæ and femora each with a variable number of "sensory buds." Inner surface of coxa slightly excavated for reception of femur; outer surface with very heavy chitinous spurs, distally. Claw tending to be constricted near the middle at which point, on the inner surface, arises a branching spine. Gills caudal, arranged in three principal tufts, capable of extrusion and withdrawal between the sclerites of the posterior abdominal segment. Spiracles of the number of nine pairs, one pair on the mesothorax and one on each of the first eight abdominal segments, all situated laterally. Length of mature larva, 9.5 mm. Greatest vertical thickness (mesothorax), .76 mm.

Description drawn from specimens collected by Dr. Needham at Taquitz Valley, San Jacinto Mts., Calif., assigned to the *Elminæ* on the basis of structural characters. This type is interesting since it represents the extreme opposite, in almost every particular, to the form possessed by *Psephenus*.

TYPE 8. **Elminæ** (*Elmis quadrinotatus* Say).

(Plate I, Fig. 3. Plates V, VI).

Form elongate, tapering, sub-cylindrical in cross-section and with the thoracic region somewhat arched, causing the head to be directed downward rather than forward. Larva bearing dorsally three longitudinal rows of very large prominences, the median dorsal row being barely perceptible on the thoracic segments, but becoming increasingly more prominent posteriorly, the largest being that borne by the eighth abdominal segment. Dorso-lateral prominences larger on the anterior than on the posterior segments. Last abdominal segment fully twice the length of the segment preceding, roughly cylindrical at the base, tapering distally. Dorsal surface of this segment, as seen in lateral view, strongly arched and finely serrate with backward-projecting spines, tooth-like in form. Dorsal sclerite truncate posteriorly, i. e., with no sharp, backwardly-directed prolongations. Ventral sclerite ovate-elliptical, occupying nearly the entire distal half of ventral surface of the segment, and bearing on the inner surface, the usual pair of slender, tapering, somewhat recurved appendages, hairy on their basal two-fifths. Tergum of prothorax, and also of succeeding segments, to a lesser degree, expanded somewhat in a lateral direction, but not to the point of suggesting a carapace. Entire dorsal surface, including the head, beset with very small tubercles more or less uniformly distributed. Posterior margin of each body segment bordered by a row of very short, stout, closely ranged spines, arising in pairs.

Head rather elongate; freely movable. Antennæ small and inconspicuous, composed of three segments, the first scarcely longer than broad, the second more than twice the length of the first, and more slender throughout, but tending to be enlarged at the tip, the third duplicate, composed of two semi-transparent articles lying side by side, the shorter and more robust bearing distally a fine spine. Labrum sub-rectangular, with lateral angles rounded; fully twice as broad as long, the anterior margin slightly concave and sparsely covered with hair. Upper surface bearing several heavy spines. Ocelli situated just back of antennæ, with apparently five units in each group. Mandibles elongate-triangular, heavily chitinized, noticeably concave interiorly, and bearing at about one-fourth the distance from base to tip the usual sensory filament, which in this form is spined above, but not below. Tip bluntly tridentate. External surface bearing at least two curved spines. Maxillæ of usual form with four-segmented palpi and lacinia in the form of a truncate cylinder open along the free surface. Stipes near base of palpus bearing two, very conspicuous, branched spines. Distal segment of palpus with a terminal area adapted for sensory function by the presence of several delicate hairs. Lacinia and galea each with a considerable number of strong recurved, distal spines. Labium two and one-half times as long as broad, chitinized basally, but with distal portion, including palpi, almost transparent. Mentum not clearly distinct structurally from palpi-bearing portion. Palpi actually three-segmented, but appearing sometimes as four-

segmented due to the conspicuous development of the palpiger. All palpal segments somewhat beset with hair, the third bearing distally a minute sensory apparatus in the form of a few papillæ-like hairs. Entire distal surface of labium beset with many very small tubercles, each bearing a very tiny spine.

Legs of the usual number of parts, strong but perhaps more slender and elongate than those of other types. Various spined, most conspicuous feature being the two rows of strong teeth bordering the concavity extending along the anterior surface of the coxæ. Distal half of this concavity, (which serves for reception of the femur) lined with a sort of cushion, composed of closely ranged tubercles of very small size. Claw elongate, bearing on the inner surface a delicate spine. Gills caudal, arranged in three principle tufts and capable of extrusion and withdrawal between the sclerites of the posterior abdominal segment. Spiracles situated laterally, a poorly developed pair on the mesothorax, and a conspicuous pair on each of the first eight abdominal segments. Length of mature larva, 4.75 mm. Greatest vertical thickness (third abdominal segment, including median dorsal prominence), 0.62 mm.

Description drawn from several specimens taken at various localities, mostly eastern. This species was collected by J. G. Needham at Coy Glen, Ithaca, N. Y., and reared by E. A. Richmond. Several specimens were subsequently identified as *Elmis quadrinotatus* Say.

TYPE 9. *Elminæ* (*Macronychus*?).

(Plate I, Fig. 4. Plate VI).

Form fairly elongate; sub-triangular in cross-section due to a tendency of the tergum to expand somewhat laterally and also to a perceptible elevation along the median dorsal line. Posterior abdominal segment nearly as long as the three preceding, sub-conical in form, the dorsal sclerite terminating posteriorly in two short, blunt processes. Entire segment (viewed laterally) nearly straight along the basal two-thirds of the ventral surface, but dorsally, arched and minutely serrate. Ventral sclerite occupying distal third of ventral surface of the segment, sub-ovate in outline, and bearing, on the inner surface, the usual pair of elongate, tapering appendages, recurved at the tip and more or less covered with spines. Entire dorsum of larva beset with small tubercles, many of which, especially in the median-dorsal region bear each a minute, backwardly directed spine, usually double. Tubercles along the posterior margin of all body segments (except the last) arranged in a regular row and bearing each a pair of sharp, posteriorly-directed teeth.

Head very closely joined to prothorax and evidently not capable of very free movement; mouth parts directed downward. Antennæ small, of three segments, the first about as broad as long and bearing at least two rather stout spines, tending to be more or less branched; the second nearly twice the length of the first and about half as thick,

tending to possess slightly greater diameter at either end than in the middle; third segment duplicate, composed of two sub-equal, transparent articles lying side by side, one of which appears distinctly spatulate. Ocelli situated posterior to the antennæ, in two groups, one on either side of the head, each composed of five units. Labrum about twice as broad as long, heavily spined, the antero-lateral angles rounded, and with a slight, but perceptible concavity to the anterior margin. Mandibles elongate-triangular, inner margin with a deep concavity, situated just above the sensory filament; sensory filament hairy on upper side only. Outer margin of mandibles bearing one or two short branching spines. Tip of mandible bluntly bi-dentate. Maxillæ of usual form; with sub-triangular cardo adapted for reception of galea, with four segmented palpus and with lacinia in the form of a truncate cylinder open along the free surface. Galea globoid in outline. Lacinia and galea each bearing distally several stout, curving spines. Stipes near base of palpus bearing two stout, elongate spines, one situated some distance below the other. Terminal segment of palpus with at least three distal papillæ. Labium large, nearly two and one-half times as long as broad. Mentum rather easily distinguishable from distal portion, and bearing on each side just below base of palpus, a single large, curving spine. Palpus three segmented, but borne on a well developed palpiger, hence appearing sometimes as though composed of four segments. Distal segment of palpus bearing usually three small transparent papillæ, confined to a small circular distal area. Entire distal end of labium covered with many small closely ranged papillæ, each giving rise to a tiny spine.

Legs rather elongate, variously adorned with spines, most conspicuous among which are the very large, blunt, bifurcate, distally directed and heavily chitinized scale-like teeth found in the coxæ. Interior (anterior) surface of coxæ broadly grooved for reception of femora, which groove is cushion-like, distally, by reason of a massing of small tubercles within a restricted circular area. Gills caudal, in three principle tufts and capable of extrusion and withdrawal between the sclerites of the last abdominal segment. Spiracles situated laterally, one pair on the mesothorax and one on each of the first eight abdominal segments. Length of mature larva, 3.75 mm. Greatest width, (prothorax), .74 mm.

Description drawn from three specimens collected in Taquitz Valley, San Jacinto Mts., Calif., but applying almost equally well to larvæ found associated with *Macronychus glabratus* Say at Ithaca. This description, until further knowledge is available, may be assumed to apply to *Macronychus parvulus* Horn, the western representative of this genus.

To my knowledge, the foregoing types cover most of the important variations in form encountered in the United States. There is a gap, however, between the type assigned to *Helichus*

and the other, sub-cylindrical or sub-triangular types, and in order to better illustrate the gradation of form within the family, I have introduced at this point a brief description of the European larva, *Elmis aeneus* Mull.

***Elmis maugei* Bedel. var. *aenea* Mull.**

Larva elongate and noticeably flattened dorso-ventrally. Thorax much larger than the rest of the body with prothorax as long as the meso- and metathorax taken together. Prothorax emarginate anteriorly for the reception of the head. All segments of thorax rounded bisymmetrically on the sides. Abdomen forming an isosceles triangle, with the base anterior; regularly attenuated and composed of nine segments which diminish gradually in size. Margins of abdominal segments expanded into thin lateral lobes, as are those of the thorax; those arising from the abdomen, however, being not rounded, but prolonged posteriorly. Last abdominal segment truncate, conical, and slightly notched posteriorly. Ventral sclerite, or operculum, small, sub-triangular, and provided at the extremity with two appendages, recurved ventrally. Border of all body segments with exception of the last is dilated, thin, semi-transparent and adorned with a ciliate fringe, rather complex in structure. Central portion of dorsum noticeably punctured, also posterior two-thirds of lateral processes.

Head small, but entirely visible, with two pale dorsal lines united into a Y posteriorly. Antennæ short, yellowish, composed of three segments; the first broad and rather deeply inserted, the second more elongate (3 x), more slender, and bearing distally the duplicate third segment, which consists of two small articles of less than half the length of the second segment, and lying side by side. The superior of these two articles is terminated by a small spine. Ocelli, of the number of five on each side, placed behind the antennæ, and arranged in two rows, the first of three, the second of two units. Mouth bordered by a transverse labrum, feebly sinuate laterally, provided with spines which are very large at the base, having the form of a jagged scale; of these there are ten altogether. Mandibles triangular, enlarged at the base and terminating in two strong bifid teeth. On the inner surface one finds an appendage in the form of a tendril, hairy along its upper surface. Maxillæ in two lobes, each of which (galea and lacinia) bear distally a stout brush of spines. Palpi two-segmented, the second terminated by two tiny appendages. Labium trapezoidal, hairy in front, bearing two small, biarticulate palpi.

Legs short, but strong and robust, composed of a coxa, trochanter, femur, tibia, and lastly a tarsus which terminates sharply in the form of a curved claw and bears on the under surface a stiff spine. Gills caudal in position, arranged in three principle tufts and capable of extrusion between the sclerites of the posterior abdominal segment. When extruded one tuft lies directly caudad, the others lateral to the first. Spiracles distributed as follows: One pair on the anterior border

of the metathorax;* one pair on each of the first eight abdominal segments. Length of mature larva, 3.5 mm. Width, (greatest lateral expansion of thorax), 1.0 mm.

Description adapted largely from Laboulbene ('70). This species may be said to share honors with *Psephenus lecontei*, in regard to popularity in the literature.

IV. DISCUSSION.

(a) *Comparison of larval types: correlations of structures with habit:*

There exists a remarkable tendency to gradation of type from the flattened, elliptical, limpet-like *Psephenus* to the elongate, nearly cylindrical forms predominating in the Elminæ. Between extreme types one finds hardly any superficial similarity, other than in the legs, which are, throughout the group almost invariably of a common pattern, always ending in a single stout claw adapted for clinging to the sub-stratum. One can hardly say that the gradation of form includes *all* the types with which we are concerned, or that we can arrange them in a single straight forward series. Such an attempt, indeed, would be contrary to our ideas regarding the evolution of most present-day forms, which appear to represent merely the tips of branches, the stems from which they have arisen being long since extinct. Even so, if we select a certain four of the known types, namely *Psephenus*, *Helichus*, *Elmis* (European) and *Stenelmis* we shall have this gradation excellently illustrated: The closely joined lateral lobes of *Psephenus* are no longer overlapped when we encounter them in *Helichus*. They are reduced to still less useful processes in *Elmis* and are entirely lacking in *Stenelmis*. Likewise the head in both *Psephenus* and *Helichus* is concealed beneath the expansion of the prothorax. It is set rather deeply into the prothorax in *Elmis*, but is nevertheless entirely visible from the dorsal surface. In the *Stenelmis* group, however, the head is freely movable in all directions. The fact of greatest importance is that perfect homology of structure may be recognized throughout the series, the form of the first three being apparently due to

*According to Erichson ('48) the first pair of spiracles occur on the mesothorax. I am inclined to think that this is correct and that Laboulbene's interpretation is erroneous.

more or less elaborate modification of a simpler plan of structure such as is found in the fourth.

The one serious obstacle in the tracing of homologies, concerns the position of the respiratory organs. This problem, though puzzling, appears to be of fundamental significance. In *Psephenus* alone, are the gills ventral, in all the others caudal. Le Conte, more than once mentions *Psephenus* as having its chief branchial filaments in the anal region, but in this he was apparently deceived. Neither Kellicott nor I have been able to find gills in this position. The very similar larva of *Psephenoides* (native to northern India) has, however, the three-tufted anal gills characteristic of *Helichus*, *Elmis*, and related genera. This feature alone would tend to indicate that *Psephenus* is of a separate line of descent, related not so closely to either *Helichus* or *Elmis* as those two are to one another. Such an assumption is further supported to some extent by the fact that in *Psephenus* the lateral lobes, with the exception of the prothoracic expansion, seem to be composed entirely of modified pleurites, while in *Helichus* and *Elmis* the tergum plays a much more important part. It is here interesting to note that the genus *Eurypalpus* (*Psephenus*) was considered an anomalous one by Le Conte, Harris and others, before the larva was ever known. Harris criticized Le Conte freely for placing it with the Parnidæ. Leading authorities now consider the genus as standing quite apart, in its capacity as type genus of the Psephenidæ.

Another very interesting feature relates to the structure of the posterior abdominal segment, which is strikingly similar in most of those larvæ which have gills caudal in position. In *Helichus* alone (of American genera) are there no appendages on the inner surface of the ventral sclerite to correspond with the two slender more or less recurved processes found in all the others. Why they should here be absent, is difficult to understand. Dufour ('62) figures the not distantly related *Potamophilus* with conspicuous appendages in this position. Correlated with the lack of appendages is the fact that the caudal segment of *Helichus* closely resembles that of *Psephenus* in being broad, flattened and definitely forming part of the carapace by which the greater portion of the larva proper is covered. But the ventral sclerite in *Psephenus* is so reduced in size that appendages are virtually impossible. In all the rest, that is in those forms in which appendages are present,

the posterior segment is subcylindrical, usually tapering posteriorly, and with the ventral sclerite attached as a sort of trap-door upon the posterior portion of the ventral surface.

Bearing in mind these fundamental differences in structure we shall now attempt to show how adaptation to environment is well illustrated by the body-form of each type studied: Both *Psephenus* and *Helichus* are principally stone dwellers, the margins of their carapaces when firmly appressed to the stone being excellent aids in clinging, no matter how swift the current. They are thus able to roam at will over exposed surfaces without danger of being swept away, and by reason of the difficulty with which they may be detached, they are not an easy prey for predators. There is no doubt that *Psephenus* greatly exceeds *Helichus* in this adaptability since the more perfectly joined seams of its carapace not only make suction more complete, but seem also to exclude all silt, whereas *Helichus* can surely have but little natural protection against the dangers of muddy waters. It has the ability, it is true, to extend and to withdraw its gills, as have all the others of the family in which the gills are caudal in position, and this is no doubt protective to a degree, but the fact that *Psephenus* is the most universally distributed, at the same time most abundant in number of individuals of any genus in the group, argues well for its superior ability to meet the vicissitudes of changing environment. In the experimental work conducted in connection with this investigation it was found practically impossible to maintain alive, those types with caudal gills, due to the unavoidable amount of silt which accumulated in the hatchery troughs; but *Psephenus*, on the other hand, survived most satisfactorily, and on one occasion, when, as a result of rising water an accumulation of one-fourth inch of mud and silt covered the stones on which the larvæ were feeding, a careful washing away of the deposit revealed the entire colony alive and apparently normal. The hairy margins of their lateral lobes serve evidently as most excellent filters, to the end, that beneath the body, where the water is made to flow past the gill-tufts by the perpetual rhythmic motion of the posterior abdominal segment, there is practically no possibility of sufficient contamination to affect harmfully the respiratory apparatus. It is conceivable that they are thus able to mine beneath a layer of silt, feeding on whatever algæ may be attached to the rock, for an indefinite period of time.

The European *Elmis*, in spite of its tendency to imitate *Helichus* in the possession of lateral lobes, is obviously not able to make as good use of them as either *Psephenus* or *Helichus*. It has, however, gotten away from the cylindrical form to a very considerable extent and is assuredly better adapted for currents than are the more elongate types. It is well suited for the head-up-stream position so commonly observed in Plecopterous and Ephemeropterid nymphs, its backwardly-directed lateral lobes in every way suggesting adaptation for this, but we cannot conceive that it would be a successful competitor of *Psephenus* on smooth rocks, in swiftly flowing water.

All the remaining types, with certain negligible exceptions, lack any development even comparable to the carapace idea, and the situations in which they are found quite naturally reflect their structure. *Macronychus*, in particular, is a dweller of wood, rather than rock. It seeks out the crevices and makes shallow burrows for its comfort and security. Various others of the Elminæ, are, it is true, collected from stones, but they always take advantage of quiet down-stream surfaces, or of niches, or of clinging vegetation to render their position secure. All have a tendency to curvature of the body, the dorsal surface being convex, the ventral concave (as seen in lateral view), and of this they take advantage, employing the abdomen as a sort of large, seventh foot to assist in maintaining their hold.

One marked advantage, may be correlated with the lack of a carapace, and that is the possession of a freely movable head. Both *Psephenus* and *Helichus* have the head concealed. In all probability they can perceive through their carapaces various intensities of light (always reacting negatively when the stimulus is strong) but for intimate knowledge of their surroundings they must rely wholly on the tactile function of antennæ and palps. The larva of *Psephenus* in fact seems to derive its nourishment simply by scraping up everything that the surface of the rock affords, passing through the intestine that which proves indigestible. It is not conceivable that the sense of vision plays any real part in food selection. *Helichus* appears to be somewhat better equipped in this particular. Besides the fact that its carapace tends frequently to be less heavily chitinized, especially over the head region, there are, on the dorsum of the abdomen four yellowish spots, which possibly

may be more sensitive to light than other portions of the carapace. In relation to the apprehension of food, we should not fail to mention the presence of several curious bud-like processes, arranged along the under surface of the femora, in this genus. It is possible that by means of these little structures, the larva tastes, or at least explores freely with its legs, and is thus able to obtain a more intimate knowledge of its surroundings. These modified spines occur also on the legs of certain Elmid types.

It has already been mentioned that *Elmis* (European) possesses a head, which, though not capable of great freedom of movement, is at least directed forward, and is perfectly visible dorsally. It therefore represents a transition between the cylindrical types with head freely movable, and those in which it is concealed beneath the expanded prothorax.

Turning now to less conspicuous features of structure, we find that the antennæ, throughout the group, tend to be of a uniform type, consisting of three segments, the third always diminutive, and in most cases duplicate. The duplicate condition was first interpreted by Erichson ('48). This author states that the larger member, usually bearing a minute spine distally, is the true third segment. The other is construed as an appendage (modified spine) of the second antennal segment, and tends to closely resemble the true third joint. Beling ('82) in his description of the larvæ of *Pomatinus substriatus* Mull. and *Parnus auriculatus* Panz (nec. Geoffr.) mentions but a single spine as constituting the third segment in these two forms. I should have been inclined to regard his descriptions as erroneous, had I not discovered an American form the antenna of which possesses but a single member in this position. (Type 6 of this paper). The identity of this larva is at present unknown to me, but it appears to be allied with the *Elminæ* rather than the *Dryopinæ*. We may therefore regard the single or double condition of the third segment as of at least no more than generic significance. It is perhaps also worthy of note that *Psephenus*, with its concealed head, has, in proportion to other structures, the most elongate antennæ in the entire group, while type 7, the most cylindrical and elongate form studied, possesses the extreme of shortened and thickened antennal segments.

These facts all tend to show that those portions of the anatomy most freely exposed, and hence most liable to be affected by environmental conditions manifest greatly divergent modifications as we pass from one type to another. It is in the mouth parts, on the other hand, that we find most strikingly illustrated that "certain air de famille," to which Perez ('63) refers.

Concerning the labrum we need say but little save that it bears almost always a considerable number of tactile setæ. The mandibles, however, are of particular interest, for here we find the most striking similarity throughout the group. In fact the greatest differences encountered in the mandibles were between individuals of the same species, rather than between types. All have mandibles subtriangular in outline, with a conspicuous condyle on the outer angle of the basal margin. Somewhere on the inner margin, usually about one-third the distance from base to tip may be found some form of brush-like organ, either a tuft of coarse spines (*Psephenus*) or, more frequently, a finger-like filament bearing many hairs or setæ, and in miniature resembling somewhat the tail of a fox. This structure is always present, and may very probably function in the selection of food. Between this tactile organ and the tip, the mandible is always more or less excavated or grooved, the pattern of the concavity being typical for each form, as shown in the figures.

It was in *Psephenus* and *Helichus* however that the most interesting fact was brought out in connection with mandibular form, namely that two types of mandibles are possible in the same species. These have already been mentioned in the foregoing descriptions. Plate II, figure 5 shows an interesting condition, illustrative of this point, which was observed in each of two individuals of the *Helichus* series. Both these larvæ were evidently about to molt. It will be seen that the more nearly triangular mandible, belonging to the younger stage, is about to be replaced by a more elongate type, which appears almost as though made up of two parts, a broad basal, and a tapering distal portion. Both these types are to be found in *Psephenus* also, where the triangular form is predominant, even in the mature larva. Kellicott ('83) however, figures the elongate mandible as typical for *Psephenus*, and merely mentions that the mandibles of younger larvæ tend to be shorter. This

would seem to hold true for *Helichus*, much better than for *Psephenus*, since all my early dissections of the former, being made of larger individuals, disclosed only elongate mandibles, and it was not until an earlier stage was examined that the condition shown in the figure was discovered. Taking into consideration the apparent absence of mandibles *intermediate* in outline, we can scarcely hope to account for these findings by assuming that the shorter mandibles represent merely elongate types that have been worn down by continual scraping against the surface of the rocks. This point, in particular, needs further study.

The maxillæ, like the mandibles, though complex and difficult of interpretation as to constituent parts, are essentially similar throughout the group. All have four-segmented palpi, the distal member of which bears at its tip a sensory apparatus, sometimes minute, sometimes consisting of definite number of fairly conspicuous papillæ, but apparently serving a similar function in all forms. Cardo, stipes, lacinia sub-galea and galea are each represented but the basal parts tend frequently to be so fused that only lacinia and galea may be recognized with certainty. These both bear distally various spines, papillæ, and other sensory apparatus. Lacinia is often curiously modified, tending usually to take the form of a truncate sleeve, open along the free margin. This tendency is most pronounced in the *Elminæ*, is not at all indicated in *Psephenus*, and may prove to be of minor importance at least, as a group character.

The labium of each type, likewise, bears a fairly close resemblance to that of every other. The only conspicuous differences are those of proportion, which of course is always to be correlated, with the shape and characteristic attitude of the head. Thus we find the labium shortest and broadest in *Psephenus*, and most elongate in the type referred to *Macronychus*, but the fundamental similarity of structure cannot be ignored. In nearly all cases the labium tends to be membranous rather than heavily chitinized. The line of demarcation between the mentum and the palpi-bearing distal portion (ligula) is rarely more than indistinctly present. The distal region itself, though tending in certain types to be differentiated into glossa and para-glossæ, in most cases appears as a more or less unified structure. The palpi are always three-segmented,

though the palpiger, (as in types 8 and 9) may appear at times very much like a basal segment.

The tips of all labial palpi studied, and the distal margins of the labia themselves are always provided with sensory papillæ, or their equivalent in the form of tiny setæ or spines.

(b) *Natural grouping within the family on basis of larval characters: interpretation from an evolutionary point of view.*

We are usually safe in asserting that group characters of primary importance tend to be found in obscure places where they have had little opportunity to be affected by the influences of environment. Thus we have found, running through this family a great similarity in the structure of mouth parts, even down to minute details, while general body form, position of head and of respiratory apparatus, show great modification along more or less diverging lines. True, the food habit is similar for all, there being none but that are vegetable feeders in aquatic situations, a fact which has probably tended to preserve the fundamental character of these structures, or, at most to modify all in somewhat similar fashion. If this were not the case, we might be at considerable loss to fasten upon characters which would show clearly the family relationship of all forms studied.

When it comes to the matter of dividing the family into minor groups on the basis of larval structure, we have but a single striking character, namely, the position of the gills. *Psephenus* alone has these ventral in position. Thus it may be assumed that whatever the ancestral family type may have been, there apparently occurred, in the phylogeny of this group, a very early split, one line developing the ventral gills, while all the rest developed (or perhaps retained) a caudal respiratory apparatus. The latter type of gills being capable of withdrawal into the body, were in a measure, protected, and but little secondary modification of body form appeared in either the Dryopid or the Elmid group. In *Psephenus*, however, the remarkable adaptation in the form of a pseudo-carapace made its appearance, serving not only to increase the ability of the animal to cling to rocks in swiftly flowing water, but also as an almost necessary protection from the silt, which must have wrought havoc with the exposed gills before they became thus protected, if, indeed, the carapace did not appear before

fixed gills replaced the spiracles. The suggestion is entirely speculative, but it is not impossible that the Psephenid stock was once equipped with caudal filaments also, such as are found in *Helichus*, and that these were not lost until conditions became favorable for more efficient use of the ventral equipment.

As for the carapace of *Psephenoides*, also the fairly pretentious lateral expansions of *Helichus* and their lesser homologues in the European *Elmis*, we can say only that this type of body form appears to be an adaptive structure developed independently in each group in response to external conditions. In all these forms it is useful in giving the larva somewhat of a limpet-like outline, a very desirable asset in itself, in manouvering beneath a strong current, but its adaptation as protection for the respiratory system is not found except in *Psephenus*.

Thus we see that our assumed "gradation of form" lacks any great significance except to show rather subtle tendencies of relationship, which may be partially elucidated as follows. In the Psepheninæ, *all* species possess the carapace-like modification in its most extreme form. In the Dryopinæ which we generally regard as lying between the Psepheninæ and the Elminæ, we find, so far as is known, the elliptical form confined to the two genera, *Psephenoides* and *Helichus*, and perhaps to only certain species of the latter. Beling ('82) has the larva of *Pomatinus substriatus* Mull., also that of *Parnus auriculatus* Panz. as cylindrical in form. But the genus *Pomatinus* is not now regarded as distinct from *Helichus* (Zaitzev, '08) and *Dryops* (*Parnus*) is certainly most intimately related to *Helichus* also. In addition, the large larva tentatively called *Lara* (type 3 of this paper) is far from resembling the *Helichus* type mentioned above, yet *Lara* has long been accepted as a close relative of both *Helichus* and *Potamophilus*. But the latter, as shown clearly by Dufour ('62) and Perez ('63) is not dissimilar from *Macronychus*, which is an Elmid genus!

Turning therefore to the Elminæ we note that the usual form is here even more cylindrical, with little or no hint of modification of the pleuræ into lobes, yet in the very genus supposed to be typical for the group, are species exhibiting a modification strongly suggesting *Helichus* (*Elmis aemeus* Mull., and *E. volkmari* Panz.). The apparent absence of similar

larvæ in America, where adults belonging to the same genus are of frequent occurrence, is assuredly of some significance in this connection. The only American *species* of which the larva is known is *Elmis quadrinotatus* Say. This larva is the sub-cylindrical, warty-backed form designated in this paper as type 8. Comparison of the descriptions will disclose little suggestive of close relationship between this larva and that of *Elmis aeneus*. Surely then, in both Dryopinæ and Elminæ, the tendency to elliptical body form cannot have more than generic significance, if indeed it has that.

Because of this nearly parallel performance of the two related subfamilies, (Dryopinæ and Elminæ), we are left without a character or combination of characters which will separate the larvæ of these two groups. This is, in a measure disappointing, but on the other hand it confirms clearly the assumption that the Psephenid stem was separate long before there existed any marked tendency for the main line to become diversified, and that there has never been a second split quite so profound as that which was responsible for the differentiation of ventral and caudal respiratory organs.*

Whatever interpretation may be placed upon the various facts brought out, it at least seems definitely assured that in *Psephenus* the greater specialization has occurred in the larva, which, by extraordinary modification of structure, has most successfully adapted itself to the environment in which it is found. Probably it is the larva alone which takes food and it is a well known fact that in the larval form only is the species able to withstand the winter. The greater portion of the life history is spent in the larval stages, and the adult is important only for the perpetuation of the species. In other words the larva has acquired, while the adult has lost, various important functions.

At the other extreme, let us consider *Macronychus*. Surely, the larva is here comparatively primitive. There are prac-

*Regarding the relationships of the Psepheninæ, Dr. Boving holds a somewhat different opinion, preferring, by reason of the ventral gills and the absence of a cloacal chamber, to derive this group from the Ptilodactylidæ. In recent correspondence Dr. Boving mentions receiving, from China, an unidentified larva, elongate-cylindrical in outline, but possessing long gills beneath the abdomen, and without a cloacal chamber. This Dr. Boving interprets as representing a connecting link between *Psephenus* and *Eurypogon* (of the Dascyloidea). The genus *Eubryanax* (hitherto listed with the Dascyloidea) should undoubtedly be transferred to the Psephenidæ as Dr. Boving suggests, since its larva is structurally very similar to that of *Psephenus*.

tically no modifications of structure to assist in clinging, other than six good legs, and it is therefore quite natural that slowly, rather than rapidly moving waters are preferred. The habit of making shallow burrows in rotten wood may be compensation for the lack of specialized body form, but at the same time the ability of the larva to move about is thereby obviously limited. In this genus it is the *adult* which is the more perfectly adapted for life on submerged surfaces. They cling tenaciously to submerged wood with their enormous claws, two to each of their six sprawling legs. These beetles live long, and are known to survive the winter. (West, '29c).

Now the general similarity between the larvæ, and also between the adults of most of the Elminæ, is strong evidence that we have here not only a single genus but indeed a whole group which is finding itself, by specialization of *adult*, rather than larval structures. These beetles, being provided with means of taking their air with them, seem to be quite unrestricted in their movements when submerged. They roam wheresoever they will, so long as the substratum is favorable for their feet. They are forsaking the aerial for the aquatic life. Dufour ('34) reports certain individuals of *Macronychus quadrituberculatus* Mull. as having but rudimentary wings, while other individuals have wings normally developed. In several dissections of *Macronychus glabratus* Say., I found only the rudimentary type present!

A further analysis of the relationships in this group must await not only added information on matters of embryology and internal anatomy, but also more detailed knowledge of life histories, that there may be established, beyond doubt, the identity of all forms under consideration. Only when this data becomes available, shall we be able to discuss satisfactorily the relationships of *genera* and *species*.

VI. ANALYTICAL KEY TO A FEW LARVAL TYPES.

(Including Six European Forms).

1. Gills ventral in position, consisting of five pairs situated on posterior margins of abdominal segments 2-6. *Psephenus* Hald.
(Type 1 of this paper, *P. lecontei* Lec.; American).
- Gills caudal in position, capable of extrusion and withdrawal between dorsal and ventral sclerites of posterior abdominal segment. 2.
2. Head not visible dorsally, being covered by an extension of the prothorax. 3.
- Head usually free, sometimes set more or less deeply into the prothorax, but always distinctly visible dorsally. 4.

3. Lobes of the carapace tightly joined except for distinct lanceolate apertures not far from the free margins. Outline broadly oval, the combined thoracic and combined abdominal segments about equal in size, forming two almost symmetrical halves.....*Psephenoides* Gahan. (*P. gahani* Champ.; Northern India).
- Lobes of the carapace distinctly separate at all points. Outline elongate-oval, the anterior segments more expanded than the posterior. Length to breadth as 5.5-3.5.....*Helichus* Er. (Type 2 of this paper, presumably *H. lithophilus* Germ.; American).
4. Tergum, in all body segments except the last, produced laterally in combination with pleuræ into conspicuous, more or less backwardly directed lateral lobes..... 5.
- Body form other than as above, in cross-section usually sub-cylindrical, rarely sub-triangular, but in no case with tergum produced laterally to form conspicuous lobes..... 6.
5. Form elongate-oval, gradually attenuated posteriorly. Color of first two abdominal segments not differing perceptibly from that of the others, *Lathelmis* Reitt. (*L. volckmari* Panz., as *Elmis volkmari*; European. Description after Rolph).
- Form more compact, usually smaller than the above type. Head set more deeply into prothorax, abdominal segments becoming more rapidly smaller posteriorly, lateral processes more sharply pointed and more strongly curved. Dorsum of first two abdominal segments lighter in color than the segments following..... *Elmis* Latr. (*E. Maugei* Bedel var. *aenea* Mull as *E. aeneus*; European. Description after Rolph).
6. Third antennal segment consisting of but a single member, usually a mere tapering spine..... 7.
- Third antennal segment duplicate, consisting of two sub-equal members arranged side by side upon distal end of second segment..... 9.
7. Prothorax usually from one-fourth to one-third longer than meso- and meta-thorax taken together..... 8.
- Prothorax scarcely equal to combined length of the two succeeding segments. (Type 6 of this paper; American).
8. Larger species, of darker coloration. Longitudinal furrows conspicuous along anterior margin of meso- and metathorax and first eight abdominal segments. Three small spines present on dorsal surface of last two segments..... *Helichus* Er. (*H. substriatus* Mull. as *Pomatinus substriatus*; European. Description after Beling).
- Smaller species, of lighter coloration. Longitudinal furrows present as in preceding species, but much weaker. Dorsum of two posterior abdominal segments lacking the three small spines..... *Dryops* Oliv. (*D. ernesti* Des Gozis, as *Parnus auriculatus* Ill.; European. Description after Beling).
9. Abdominal segments except the last (thoracic also, to a lesser degree) each bearing three very large more or less backwardly directed processes, one situated on the median dorsal line, the others dorso-lateral in position..... *Elmis* Latr. (Type 8 of this paper, *E. quadrinotatus* Say; American).
- Abdominal segments sometimes ornamented with small tubercles of spiny filaments, but never bearing large processes as above..... 10.
10. Antennæ short and thick, sub-conical in form. Second segment not exceeding in length the first. (Type 7 of this paper; American).
- Antennæ more or less elongate. Second segment always more slender than the first and usually all of twice as long..... 11.

11. Posterior abdominal segment (viewed dorsally) notched on caudal margin a distance equal to two-fifths the length of the entire segment. Mature larvæ with four distinct longitudinal dorsal carinæ. *Potamophilus* Germ. (*P. acuminatus* Fabr.; European. Description after Dufour).
Posterior abdominal segment (viewed dorsally) never notched for a distance greater than one-sixth the length of the entire segment. Not more than a single, median-dorsal, carina. 12.
12. Legs possessing a rudimentary tarsal piece at the inner juncture of the tibia and the claw, (not visible when viewed from above),
Macronychus Mull. (*M. quadrituberculatus* Mull.; European. Description after Perez).
Legs without such rudimentary tarsal piece. 13.
13. Dorsum conspicuously ornate with backwardly directed fingers or filaments, each with a covering of small spines; larger species. *Lara* Lec. (?) (Type 3 of this paper, presumed to be *L. avara* Lec.; American).
Dorsum unadorned, or at most with an even sprinkling of fine tubercles, which give a granular appearance to the surface; smaller species. 14.
14. Form elongate, suggesting a hemi-cylinder, the ventral surface being somewhat flattened, the dorsal roundly arched. No perceptible elevation of the median-dorsal line into a longitudinal carina. Head usually exerted and freely movable. 15.
Form more compact, sub-triangular in cross-section, ventral surface being rather flat, as compared with the strongly arched dorsum, which bears a low, but perceptible median carina for at least part of its length. Head closely joined to thorax and evidently not capable of great freedom of movement. *Macronychus* Mull. (?) (Type 9 of this paper, presumably *M. parvulus* Horn, also true for *M. glabratus* Say; American).
15. Posterior abdominal segment (viewed dorsally) with caudal margin distinctly notched, the lateral margins terminating in two sharp points,
Stenelmis Duf. (Type 4 of this paper, similar to *S. bicarinatus* Lec. as figured by Matheson; American).
Posterior abdominal segment (viewed dorsally) pseudo-truncate, i. e., with caudal margin but very slightly emarginate, suggesting at most, a bluntly bilobed condition. *Stenelmis* Duf. (Type 5 of this paper, very similar structurally to type 4; American).

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EXPLANATION OF PLATES.

PLATE I.

Fig. 1. Type 7, mature larva, lateral view. Fig. 2. Type 3, head of mature larva, dorsal view. Fig. 3. Type 8, (*Elmis quadrinotatus* Say), mature larva, lateral view. Fig. 4. Type 9, (*Macronychus?*), mature larva, dorsolateral view. Fig. 5. Type 6, mature larva, lateral view. Fig. 6. Type 3, (*Lara?*), mature larva, lateral view. Fig. 7. Type 2, (*Helichus lithophilus* Germ.), mature larva, dorsal view. Fig. 8. Type 4, (*Stenelmis?*), mature larva, dorsal view. Fig. 9. Type 5, (*Stenelmis?*), mature larva, dorsal view.

PLATE II.

Larval types 2 (*Helichus*) and 3 (*Lara?*).

Fig. 1. Type 2, antenna. Fig. 2. Type 2, leg. Fig. 3. Type 2, mandible, elongate type. Fig. 4. Type 2, labrum. Fig. 5. Type 2, mandibles of successive stages, showing marked change of form. Fig. 6. Type 2, mature larva, ventral view, (marginal ciliation omitted). Fig. 7. Type 2, labium. Fig. 8. Type 2, maxilla. Fig. 9. Type 3, leg (prothoracic). Fig. 10. Type 3, antenna.

PLATE III.

Larval types 3 (*Lara?*) and 4 (*Stenelmis?*).

Fig. 1. Type 3, maxilla. Fig. 2. Type 4, labium. Fig. 3. Type 4, maxilla. Fig. 4. Type 3, ventral sclerite of posterior abdominal segment, from within. Fig. 5. Type 4, labrum. Fig. 6. Type 4, ventral sclerite of posterior abdominal segment, from within. Fig. 7. Type 4, leg, (prothoracic). Fig. 8. Type 4, dorsal sclerite of posterior abdominal segment, from below. Fig. 9. Type 3, mandible. Fig. 10. Type 4, antenna. Fig. 11. Type 4, mandible. Fig. 12. Type 3, dorsal sclerite of posterior abdominal segment, from below. Fig. 13. Type 3, labium.

PLATE IV.

Larval types 5 (*Stenelmis?*) and 6.

Fig. 1. Type 5, maxilla. Fig. 2. Type 5, leg. Fig. 3. Type 5, labium. Fig. 4. Type 6, mandible. Fig. 5. Type 5, dorsal sclerite of posterior abdominal segment. Fig. 6. Type 5, ventral sclerite of posterior abdominal segment, from below. Fig. 7. Type 6, leg. Fig. 8. Type 5, labrum. Fig. 9. Type 5, mandible. Fig. 10. Type 5, mature larva, ventro-lateral view. Fig. 11. Type 5, antenna. Fig. 12. Type 6, labrum. Fig. 13. Type 6, antenna.

PLATE V.

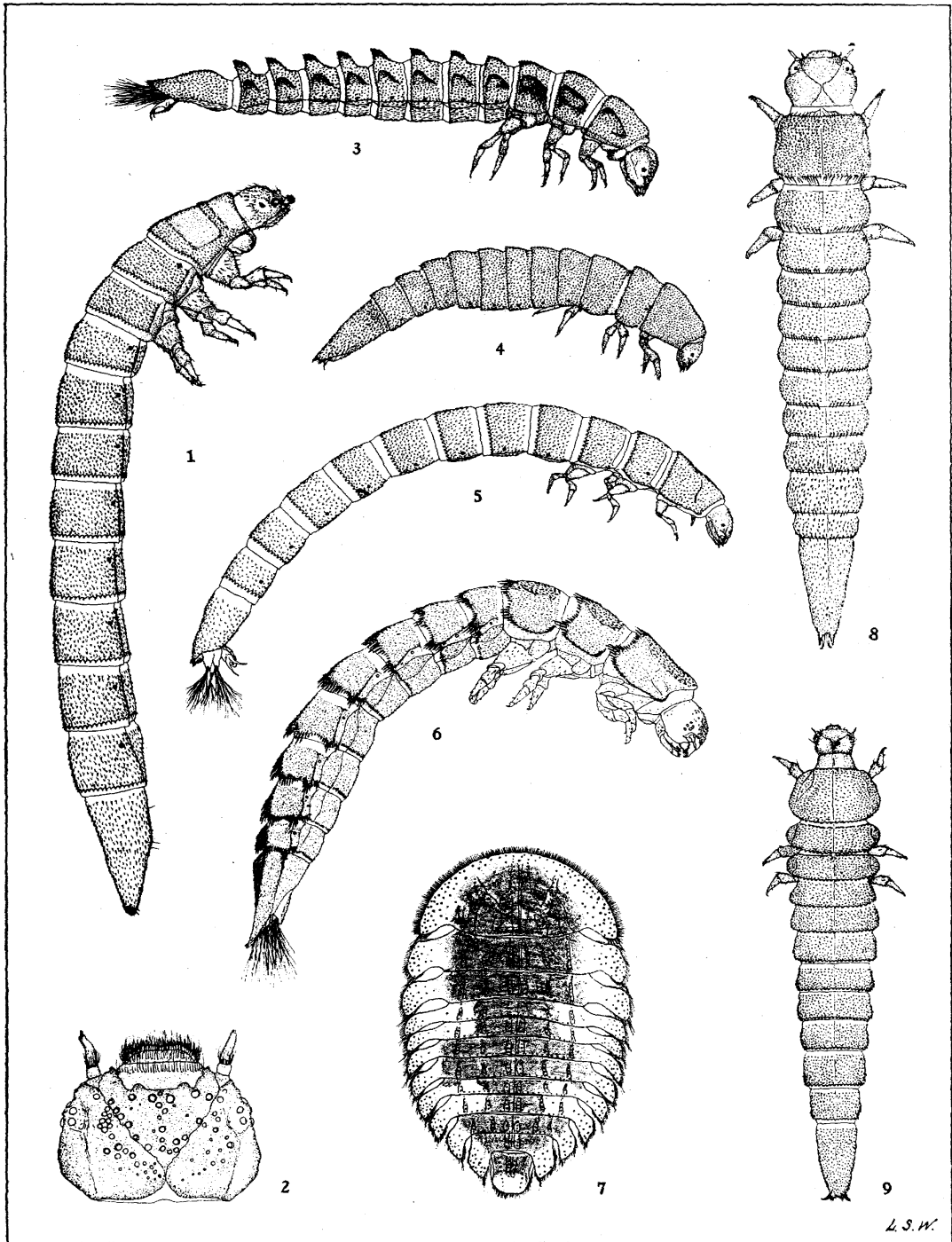
Larval types 6, 7 and 8 (*Elmis quadrinotatus* Say).

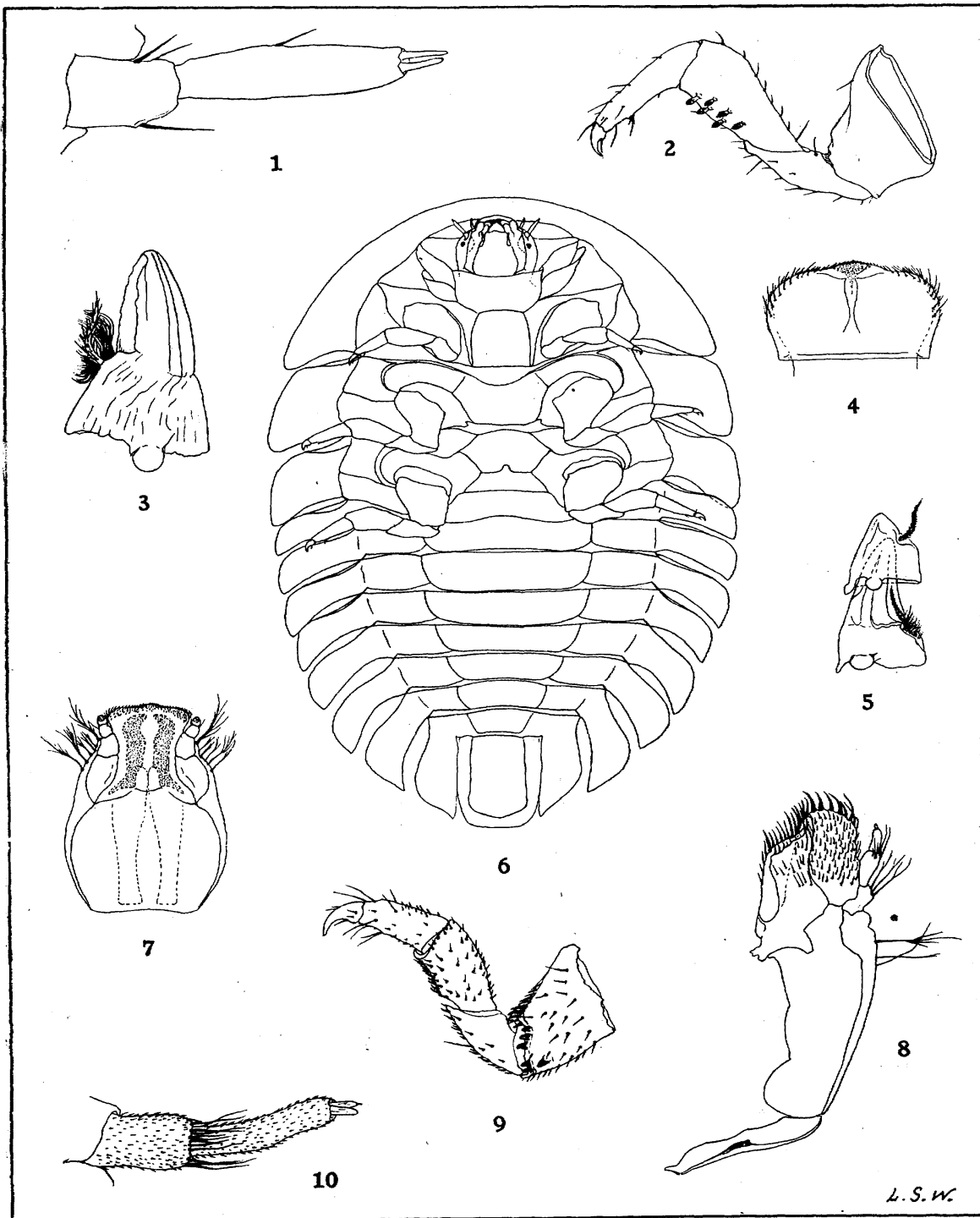
Fig. 1. Type 6, labium. Fig. 2. Type 6, ventral sclerite of posterior abdominal segment, from within. Fig. 3. Type 7, maxilla. Fig. 4. Type 7, antenna, from below. Fig. 5. Type 7, labium. Fig. 6. Type 7, leg. Fig. 7. Type 6, maxilla. Fig. 8. Type 7, ventral sclerite of posterior abdominal segment, from within. Fig. 9. Type 7, Dorsal sclerite of posterior abdominal segment, from below. Fig. 10. Type 7, mandible. Fig. 11. Type 8, antenna. Fig. 12. Type 8, leg. Fig. 13. Type 6, dorsal sclerite of posterior abdominal segment, from below.

PLATE VI.

Larval types 8 (*Elmis quadrinotatus* Say) and 9 (*Macronychus?*).

Fig. 1. Type 9, dorsal sclerite of posterior abdominal segment, lateral view. Fig. 2. Type 9, antenna. Fig. 3. Type 9, ventral sclerite of posterior abdominal segment, from within. Fig. 4. Type 8, mandible. Fig. 5. Type 9, leg. Fig. 6. Type 9, mandible. Fig. 7. Type 9, labrum. Fig. 8. Type 8, ventral sclerite of posterior abdominal segment, from within. Fig. 9. Type 8, labrum. Fig. 10. Type 8, maxilla. Fig. 11. Type 8, labium. Fig. 12. Type 9, labium. Fig. 13. Type 9, maxilla.





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