

## THE TRIBE OPISTHIINI (COLEOPTERA: CARABIDAE): DESCRIPTION OF THE LARVAE, NOTE ON HABITAT, AND BRIEF DISCUSSION ON ITS RELATIONSHIPS

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**Abstract.**—All instar larvae of *Opisthius richardsoni* Kirby, 1837 and the first and second instar larvae of *Paropisthius indicus* (Chaudoir, 1863) are described and the character states of the tribe Opisthiini are highlighted. The two species differ mainly by the shape of the nasale, length of the antennae, shape of the seta TE<sub>10</sub> on tergites VII and VIII, and the presence or absence of secondary setae on the tarsi. The adults of *O. richardsoni* are strictly riparian, occurring mainly on sandy or clayish-sandy banks of rivers. Those of *P. indicus* occur at high elevations (3,000–3,900 m) on well-drained substrate in open habitats, away from water. The larvae of both species can jump vigorously when disturbed. The analysis of the character states of the known larvae of Nebriitae does not support the accepted classification of the group based on the character states of the adults.

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The Opisthiini form a small tribe of primitive carabids. The adults look superficially like members of the genus *Elaphrus* Fabricius, because of their elytral sculpture, and the tribe has been classified near the Elaphrini by some 19th century authors. Many character states, however, clearly show that the Opisthiini belong to the nebrioid complex. Only five species of Opisthiini have been described to date: *Opisthius richardsoni* Kirby, 1837 which occurs in western North America, from the Prairies to the Pacific Coast (Lindroth, 1961), and four species of *Paropisthius* Casey, namely *P. indicus* (Chaudoir, 1863) from the Himalaya, *P. unctulus* Andrewes, 1932 from North Kumaon in the Indian state of Uttar Pradesh, *P. davidis* (Fairmaire, 1887) from the Chinese province of Yunnan, and *P. masuzoi* Kasahara, 1989 from Taiwan.

Until fairly recently, opisthiine larvae were unknown. Gardner (1954), Lindroth (1960) and Thompson (1979) described those of *O. richardsoni*, based on specimens collected in the field. The purpose of this paper is to describe the larvae of both genera of Opisthiini, add information on the bionomics of these species, and briefly discuss the relationships of the tribe.

### MATERIALS AND METHODS

The description of *Opisthius richardsoni* is based on 18 larvae (12L<sub>1</sub>, 4L<sub>2</sub>, 2L<sub>3</sub>) reared *ex ovo* from adults collected at Edmonton, Alberta, Canada; that of *Paropisthius indicus* is based on 10 larvae (8L<sub>1</sub>, 2L<sub>2</sub>) reared *ex ovo* from adults collected by the junior author above Syabru (3,700–3,900 m), Rasuwa District, Nepal. Larvae are deposited in the Canadian National Collection, Ottawa.

About half of these specimens have been cleared in hot 10% KOH, impregnated with glycerine (see Goulet, 1977), and studied with an interference contrast microscope at 100–400×. The remaining specimens were studied superficially in ethanol using a stereoscopic microscope at 40–80×.



Terms used for structures have been explained previously (Bousquet, 1985; Bousquet and Smetana, 1986). The notation of primary setae and pores follows that of Bousquet and Goulet (1984).

In addition to larvae of Opisthiini, those of a few species of *Nebria* Latreille, *Leistus* Frölich, and *Notiophilus* Duméril were also studied. Information on larvae of *Peilophila* Dejean was taken from Andersen (1970) and Luff (1972).

#### TRIBE OPISTHIINI

**Diagnosis.** The larvae of Opisthiini differ from those of most other carabid groups by the combination of the following character states: head not constricted; antennomere III with numerous setae; urogomphi long, articulated to tergite IX; and leg with 2 unequal claws.

**Description.** First instar: *Microsculpture*. Parietale dorsolaterally with meshed microsculpture, sculpticells somewhat scalelike. Discal area of pronotum with meshed microsculpture, sculpticells scalelike. Discal area of mesonotum and metanotum mostly with multipointed microsculpture. Discal area of tergites I–IX with pointed and multipointed microsculpture. Urogomphi with strong pointed microsculpture. Pygidium with pointed microsculpture.

**Chaetotaxy.** Setae FR<sub>1</sub>, FR<sub>3</sub>, FR<sub>4</sub> and FR<sub>6</sub> on frontale moderately long, about 0.5 length of seta FR<sub>2</sub>; seta FR<sub>1</sub> located in front of FR<sub>2</sub>. Setae PA<sub>4</sub> and PA<sub>8</sub> on parietale moderately long, clearly longer than PA<sub>1</sub>–PA<sub>3</sub>; seta PA<sub>5</sub> small, about same size as PA<sub>3</sub>; seta PA<sub>8</sub> anterior to level of seta PA<sub>9</sub>; seta PA<sub>6</sub> close to posterior row of stemmata. Antennomere III with numerous additional setae (Fig. 4). Setal group gMX of maxilla with about 30 setae (Fig. 6); seta MX<sub>2</sub> located on anterior half, shorter than MX<sub>3</sub>; seta MX<sub>6</sub> on lacinia very small, laterad; maxillary palpomere III with 4 setae (including MX<sub>11</sub> and MX<sub>12</sub>). Seta LA<sub>4</sub> on prementum absent. Setae PR<sub>2</sub>, PR<sub>3</sub>, PR<sub>6</sub>, PR<sub>9</sub>, PR<sub>10</sub>, PR<sub>11</sub>, PR<sub>12</sub> and PR<sub>14</sub> on pronotum moderately long, more or less subequal in length; seta PR<sub>8</sub> indistinct. Setae ME<sub>1</sub>, ME<sub>8</sub>\*, ME<sub>9</sub>, ME<sub>11</sub>, ME<sub>12</sub> and ME<sub>13</sub> on mesonotum and metanotum moderately long, more or less subequal in length; seta ME<sub>2</sub>\* indistinct. Setae TE<sub>1</sub>, TE<sub>7</sub>, TE<sub>9</sub> and TE<sub>10</sub> on tergites I–VIII moderately long, more or less subequal in length (except TE<sub>10</sub> on tergites VII and VIII in *Paropisthius*); seta TE<sub>6</sub> indistinct. Seta UR<sub>2</sub> on tergite IX moderately long; seta UR<sub>3</sub> very small, porelike; setae UR<sub>4</sub>–UR<sub>8</sub> on urogomphi moderately long; seta UR<sub>4</sub> located near middle of urogomphus. Seta FE<sub>6</sub> spiniform as FE<sub>2</sub>–FE<sub>5</sub>; setae UN<sub>1</sub> and UN<sub>2</sub> on claws very small.

**Head.** Cephalic capsule (Fig. 4) subquadrate or transverse. Egg-bursters consisting of longitudinal carina at each side of frontale, extending from base to level of FR<sub>1</sub>; nasale (Figs. 2, 3) not prominent, with 4 toothlike processes; adnasale not prominent; frontal suture V-shaped; coronal suture relatively long, its length at least 0.7 × that of antennomere I. Parietale with 6 stemmata, in two rows of 3, on each side; cervical and ocular grooves absent. Antenna (Fig. 4) same length or longer than mandible; sensorial appendage on antennomere III rather small, located ventrally at apex. Mandible (Fig. 4) moderately curved; terebra with medial margin smooth; retinaculum well-developed, located just behind middle, its posterior margin smooth; penicillum present, consisting of many setae. Stipes (Fig. 6) elongated, about 2.2 × as long as wide, with narrow membranous notch on lateral half of ventral side; lacinia present, strongly acuminate apically; galea 2-segmented, both segments subequal



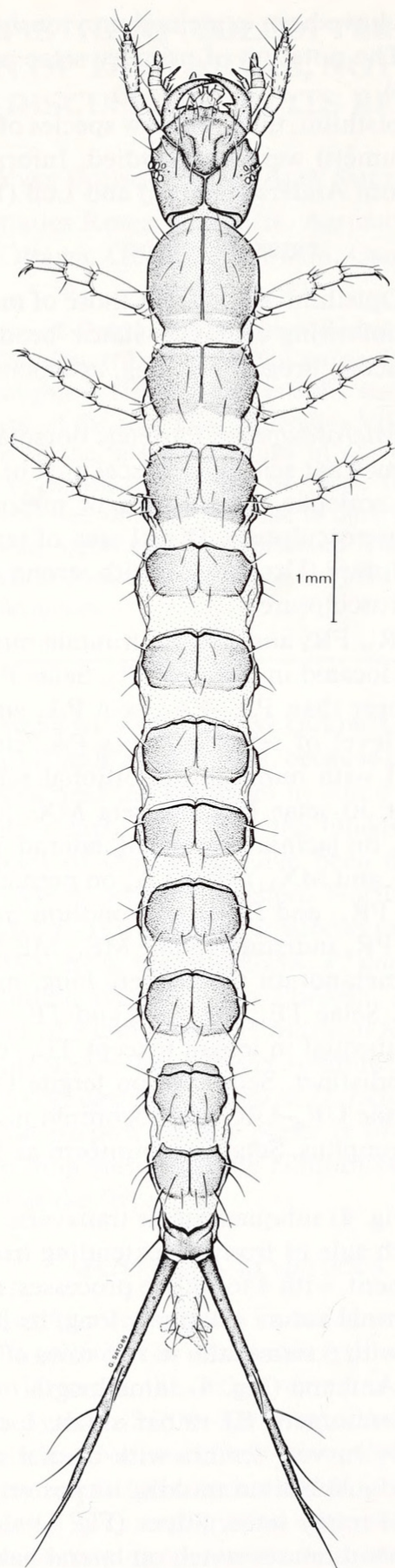


Fig. 1. Larva of *Paropisthius indicus* Chaudoir, L<sub>1</sub>.



in length; palpomeres I, II and III short, subequal in length, palpomere IV about  $3\times$  longer than other palpomeres. Prementum (Fig. 5) subquadrate; ligula present, wide, as long as palpomere I, with apical margin slightly notched medially; palpomere I shorter than palpomere II.

*Thorax.* Notal carina indistinct.

*Abdomen.* Tergal carina indistinct on all segments. Urogomphi (Fig. 7) long,  $7-9\times$  as long as tergite IX, thin, articulated, usually slightly divergent posteriorly, not segmented but with small, narrow unsclerotized bands under levels of setae UR<sub>4</sub>, UR<sub>5</sub>, UR<sub>6</sub> and UR<sub>7</sub>. Pygidium elongated, with tergum and sternum distinct. Pleura of segment I with small invaginated structure (distinct only under compound microscope) near hypopleurite. Epipleurites distinct on segments I-IX; hypopleurite small, poorly pigmented (especially in *Opisthius*) and often more or less distinct.

*Legs.* Legs rather long; tibia shorter than femur; tarsus subequal to femur; claws unequal, anterior one longer and about  $0.6\times$  length of tarsus.

Second instar: *Microsculpture.* Discal area of tergites I-VIII with mainly multipointed microsculpture. Urogomphi with strong, pointed microsculpture all over. Pygidium with multipointed microsculpture all over.

*Chaetotaxy.* Antennomere I with 1 medial seta, antennomere II with 3 apical setae; antennomere III with numerous setae; antennomere IV without secondary setae. Mandible with 1 small secondary seta posterior to MN<sub>1</sub>. Stipes without secondary setae laterally; seta MX<sub>2</sub> located on anterior half; gMX with about 40 setae, most setae of gMX on anterior half bigger than remaining ones; seta MX<sub>6</sub> on lacinia very small; galeomeres and palpomeres I, II and IV without secondary setae; palpomere III with 4-5 setae apically. Prementum with 2-4 secondary setae on each side; seta LA<sub>4</sub>, absent; labial palpomeres without setae. Pronotum, mesonotum and metanotum with few (less than 10), small, secondary setae on each side. Tergites I-VIII with 1-4 small secondary setae on each side; setae TE<sub>1</sub>, TE<sub>7</sub> and TE<sub>9</sub> moderately long, subequal in length; seta TE<sub>6</sub> very small, about same size as TE<sub>4</sub>. Tergite IX with 1-3 secondary setae each side near base of urogomphi; seta UR<sub>2</sub> on tergite IX about same size as secondary setae on urogomphi; seta UR<sub>3</sub> very small. Urogomphus with 20-25 secondary setae, most of them on basal half; most secondary setae smaller than primary setae UR<sub>4</sub>-UR<sub>8</sub>. Epipleurite with 4-6 small, secondary setae; hypopleurite with 2-4 small, secondary setae. Pygidium with about 20 small, secondary setae on sternite. Femur with about 10 small, secondary setae; tibia with 0-3 small, secondary setae.

*Head.* Cephalic capsule transverse. Nasale not prominent, with 4 toothlike processes; adnasale not prominent; frontal suture V-shaped; coronal suture distinct, its length  $0.6-0.8\times$  that of antennomere I. Parietale with 6 stemmata, in two rows of 3, on each side; cervical and ocular grooves absent. Antenna subequal or longer than mandible; sensorial appendage on antennomere III rather small, located ventrally at apex. Mandible moderately curved; terebra with medial margin smooth; retinaculum well-developed, located just behind middle, its posterior margin smooth; penicillum present, consisting of many setae. Stipes elongated, about  $2.2\times$  as long as wide, with narrow membranous notch on lateral half of ventral side; lacinia present, strongly acuminate apically; galea 2-segmented, segments subequal in length; palpomeres I, II and III short, subequal in length, palpomere IV  $2.5-3.0\times$  longer than other palpomeres. Prementum subquadrate; ligula present, wide, nearly as long as palpomere







I, with apical margin notched medially; palpomere I slightly shorter than palpomere II.

*Thorax.* Notal carina distinct or indistinct.

*Abdomen.* Tergal carina indistinct on all segments. Urogomphi (Fig. 8) long, 6–9 × as long as tergite IX, thin, articulated, usually divergent posteriorly, not segmented but with 4–5 small, narrow, unsclerotized bands on posterior half. Pygidium elongated; apical folds without conspicuous crochets.

*Legs.* Legs rather long; tibia shorter than femur; tarsus subequal in length to femur; claws unequal, anterior one longer and about 0.6 × length of tarsus.

Third instar<sup>1</sup>: Same as second instar except for the following character states.

*Chaetotaxy.* Antennomere I with 2 medial setae; antennomere II with 4–5 apical setae. gMX on stipes with more than 40 setae. Pronotum with about 20 distinct secondary setae (at 40 × under stereo microscope); mesonotum and metanotum with about 10 distinct secondary setae (at 40 × under stereo microscope). Tergite I–VIII with 5–7 distinct secondary setae (at 40 × under stereo microscope); seta TE<sub>6</sub> moderately long, longer than TE<sub>4</sub>.

*Head.* Length of coronal suture 0.4–0.5 × that of antennomere I. Antenna subequal in length to mandible. Stipes about 2.4 × as long as wide. Maxillary palpomere IV about 2.0 × longer than palpomere III. Labial palpomeres subequal in length.

*Thorax.* Notal carina indistinct.

*Abdomen.* Urogomphi about 5 × as long as tergite IX.

#### *Paropisthius indicus* Chaudoir, 1863

**Diagnosis.** The larvae of this species are easily distinguished from those of *Opisthius richardsoni* by having the lateral toothlike processes of the nasale in contact with the medial ones (Fig. 2), the antennae distinctly longer than the mandibles (Fig. 4), and setae TE<sub>10</sub> on tergites VII and VIII thin and spatulate apically (Fig. 9b). In the second instar, the species is also recognized by the presence of secondary setae on the tarsi.

The third instar is unknown, but it will likely differ from the third instar of *O. richardsoni* by the same diagnostic character states as those mentioned for the first and second instars.

**Description.** First instar: *Chaetotaxy.* Length of seta PR<sub>13</sub> on pronotum 0.2–0.3 × that of PR<sub>12</sub>. Seta TE<sub>10</sub> on tergites VII and VIII thin, spatulate apically (as in Fig. 9b). *Head.* Cephalic capsule subquadrate (length/width ratio about 1). Nasale with lateral toothlike processes in contact with medial ones (Fig. 2). Length of coronal suture about 1.2 × that of antennomere I. Antenna longer than mandible (Fig. 4); length of antennomere I about 1.1 × that of antennomere II, about 0.4 × that of antennomere III, and about 1.6 × that of antennomere IV. Apical margin of ligula

<sup>1</sup> The description is based on the examination of *Opisthius* larvae only.

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Figs. 2–9. Larva of *P. indicus* (except Figs. 3 and 9a). 2. nasale, L<sub>1</sub>; 3. nasale of *Opisthius richardsoni*, L<sub>1</sub>; 4. Cephalic capsule, left antenna, and right mandible, L<sub>1</sub>; 5. prementum (dorsal view), L<sub>1</sub>; 6. maxilla (dorsal view), L<sub>1</sub>; 7. urogomphi and ninth tergite, L<sub>1</sub>; 8. urogomphi and ninth tergite, L<sub>2</sub>; 9. Tergite VIII of *O. richardsoni* (a) and *P. indicus* (b), L<sub>2</sub>.



slightly notched medially (Fig. 5). *Abdomen*. Length of urogomphi about  $9\times$  that of tergite IX (Fig. 7).

Second instar: *Microsculpture*. Microsculpture on frontale poorly impressed. *Chaetotaxy*. Frontale without distinct secondary setae (at  $40\times$  under stereo microscope). Seta  $TE_{10}$  on tergites VII and VIII thin, spatulate apically, distinctly smaller than  $TE_9$  (Fig. 9b). Tarsus with about 10 secondary setae. *Head*. Cephalic capsule slightly transverse, (length/width ratio about 0.9). Nasale with lateral toothlike processes in contact with medial ones (as in Fig. 2). Length of coronal suture about  $0.8\times$  that of antennomere I. Antenna distinctly longer than mandible; antennomere I subequal to antennomere II, about  $0.5\times$  length of antennomere III; antennomere III about  $5.5\times$  length of antennomere IV. Apical margin of ligula slightly notched medially (as in Fig. 5). *Thorax*. Notal carina distinct. *Abdomen*. Urogomphi longer, length about  $8-9\times$  that of tergite IX (Fig. 8). *Legs*. Legs proportionally longer.

Third instar: Unknown.

*Measurements*. Head width: 0.69–0.75 mm ( $L_1$ ;  $n = 8$ ); 0.91 mm ( $L_2$ ;  $n = 2$ ).

*Opisthius richardsoni* Kirby, 1837

*Diagnosis*. The larvae of this species differ from those of *Paropisthius indicus* mainly by the separated and equidistant toothlike processes of the nasale (Fig. 3), the antennae subequal in length to the mandibles, and the unmodified (i.e., not spatulate at apex) setae  $TE_{10}$  on tergites VII and VIII (Fig. 9a). In the second instar, the species is also distinguished by the absence of secondary setae on the tarsi.

*Description*. First instar: *Chaetotaxy*. Length of seta  $PR_{13}$  on pronotum about  $0.6\times$  that of  $PR_{12}$ . Seta  $TE_{10}$  on tergites VII and VIII unmodified, spiniform (as in Fig. 9a). *Head*. Cephalic capsule transverse (length/width ratio about 0.85). Nasale with toothlike processes separated, equidistant (Fig. 3). Length of coronal suture about  $0.8\times$  that of antennomere I. Antenna subequal in length to mandible; length of antennomere I about  $1.4\times$  that of antennomere II, about  $0.6\times$  that of antennomere III, and about  $1.3\times$  that of antennomere IV. Apical margin of ligula deeply notched medially. *Abdomen*. Length of urogomphi about  $7\times$  that of tergite IX.

Second instar: *Microsculpture*. Microsculpture on frontale distinctly impressed. *Chaetotaxy*. Frontale with distinct secondary setae (at  $40\times$  under stereo microscope). Seta  $TE_{10}$  on tergites VII and VIII thick, spiniform, slightly shorter than  $TE_9$  (Fig. 9a). Tarsus without secondary setae. *Head*. Cephalic capsule distinctly transverse, (length/width ratio about 0.8). Nasale with toothlike processes separated, equidistant (as in Fig. 3). Length of coronal suture about  $0.6\times$  that of antennomere I. Antenna subequal in length to mandible; antennomere I about  $1.4\times$  length of antennomere II, about  $0.7\times$  that of antennomere III; antennomere III about  $2.5\times$  length of antennomere IV. Apical margin of ligula deeply notched medially. *Thorax*. Notal carina indistinct. *Abdomen*. Urogomphi smaller, length about  $6-7\times$  that of tergite IX. *Legs*. Legs proportionally shorter.

Third instar: Same character states as second instar except for the following. *Head*. Length of coronal suture  $0.4-0.5\times$  that of antennomere I. Antennomere III about  $4\times$  length of antennomere IV. *Abdomen*. Urogomphi about  $5\times$  length of tergite IX.

*Measurements*. Head width: 0.63–0.67 mm ( $L_1$ ;  $n = 10$ ); 0.80–0.84 mm ( $L_2$ ;  $n = 4$ ); 1.06–1.09 mm ( $L_3$ ;  $n = 2$ ).



## BIONOMICS

Adults of *Opisthius richardsoni* are strictly riparian. They occur on sandy and gravel banks of large creeks and rivers. According to Lindroth (1960), they prefer habitats close to water "where the soil consists of sand with more or less pronounced mixture of clay and is devoid of higher vegetation." This information concurs with our own observations. However, the association of *Opisthius* with species of the staphylinid genus *Bledius* Mannerheim does not seem to be as constant as postulated by Lindroth (1960). The larvae live in the same habitat as the adults, buried in the soil at least during the daytime; when disturbed, "they perform a most vivid jumping, reminding of that produced by *Piophilus* maggots" (Lindroth 1960).

Adults of *Paropisthius indicus* occur away from water. In the Nepal Himalaya, they were collected at high elevations, about 3,000–3,900 m, from the upper zone of the forest to the subalpine zone. They prefer well-drained substrate consisting of sandy soil intermixed with rock debris and sometimes also clay, with little vegetation. Most specimens were collected in open habitats, such as meadowlike pastures, sometimes disturbed by grazing, surrounded by forest (Fig. 10) or on disturbed, dry ground along hiking trails, or in the subalpine zone (Fig. 11) under similar conditions. Adults were frequently observed running on the ground during daytime, especially when the sun was shining. The larvae of *P. indicus* were not found in the field. However, when reared in the laboratory, they displayed behavior similar to that of *O. richardsoni* larvae, jumping vividly up to 10 cm when disturbed. It is assumed that the jumping ability of the larvae of Opisthiini was developed as a defensive mechanism against predators.

According to Kasahara (1989), adults of *Paropisthius masuzoi* are hygrophilous, occurring in very wet places, such as under stones half-immersed in water under small cascades. Nothing is known about the bionomics of *Paropisthius unctulus* and *P. davidis*.

## DISCUSSION

The tribe Opisthiini belongs to the supertribe Nebriitae which includes, besides the opisthiines, the tribes Nebriini, Notiokasiini and Notiophilini (Kavanaugh and Nègre, 1982). Erwin (1984, 1985) considered the Cicindisini as belonging to the Nebriitae. However, very little is known about the Cicindisini, which include two rarely collected species—one from the Persian Gulf and the other one from Argentina—and their phylogenetic relationships are still not clearly understood. There seems to be no solid evidence that the Cicindisini are related to the Nebriitae, and for that reason they are not considered further in this discussion.

The Nebriitae (sensu Kavanaugh and Nègre, 1982) is a group represented mainly in the Northern Hemisphere. Notiokasiini—with its single species *Notiokasis chaudierei* Kavanaugh and Nègre, 1982—is the only lineage represented in the Southern Hemisphere, namely in southeastern South America. Is the supertribe a monophyletic group? Adults Nebriitae share several character states, but, as pointed out by Kavanaugh and Nègre (1982), only one of them—the loss of setae on the parameres—appears apotypic for Carabidae. The character state is of low phyletic weight since it occurs in other unrelated carabid lineages. Two character states shared by larvae of Nebriitae are worth mentioning: the nasale consists of 4 toothlike processes (the





Figs. 10–11. Habitats of *Paropisthius indicus*. 10. Nepal Himalaya, Khandbari Distr., “Bakan” west of Tashigaon, about 3,200 m. Associated carabids include *Carabus pseudoharmandi* Mandl and *Nirmala odelli* Andrewes. Photo A. Smetana, 3 April 1982. 11. Nepal Himalaya, Rasuwa Distr., north slope above Syabru, about 3,800 m. Associated carabids include *Carabus tuberculipennis* Mandl, *Pterostichus yunnanus* Fairmaire, and *Amara elegantula* Tschitschérine. Photo A. Smetana, 20 April 1985.



size and relative position of which vary extensively), and the urogomphi are articulated at the base of the ninth tergite except in the first instar of *Pelophila*. These two character states, although probably apotypic for carabids, still do not strongly support the hypothesis that the Nebriitae is a monophyletic lineage since they occur in other unrelated carabid groups.

Kavanaugh and Nègre (1982) have hypothesized that Opisthiini, based on the presence of two pairs of supraorbital setae in the adults, represent the sister group of the remaining Nebriitae. Larval characters do not support nor do they contradict such an hypothesis. No synapomorphies in the morphology of the larvae have yet been discovered to support the hypothesis that the Nebriini and Notiophilini (the larvae of Notiokasiini are still unknown) form a monophyletic group. However, larvae of Notiophilini and Nebriini, without *Pelophila*, share several apotypic features, such as presence of a well-defined neck, distinctly elongated mandible and retinaculum, and absence of penicillus. Furthermore, larvae of *Leistus* (tribe Nebriini) and Notiophilini have lost the lacinia, another apotypic state within the Carabidae. Immatures of Opisthiini and *Pelophila* (tribe Nebriini) are structurally similar but, as far as we know, do not share any apotypic character states.

Larvae of Nebriitae are little known. Those of Notiokasiini are still unknown and although immatures of most genera (sens. lat.) of Nebriini and Notiophilini have been described, few species in each genus are known. Therefore, any phylogenetic hypothesis concerning the relationships of the groups within the Nebriitae based on larval characters should be evaluated with such limitations in mind. Nevertheless, it is quite clear at this time that the larval characters generally do not support the current classification of the Nebriitae based on adult characters. In fact, the immatures suggest that the Opisthiini and *Pelophila* are both primitive groups that do not share apotypic features, and that the Notiophilini and remaining Nebriini form a monophyletic lineage.

We concur with Kavanaugh and Nègre (1982) that "a significant realignment of tribes and genera will undoubtedly be required when phylogenetic relationships within the supertribe are better understood."

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