Research Article

Pimachrysa (Neuroptera: Chrysopidae: Nothochrysinae): Larval Description and Support for Generic Relationships

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We describe the previously unknown larval characteristics of *Pimachrysa* (second and third instars), and we provide new comparative data on the *Nothochrysa californica* Banks larvae that were described earlier. The *Pimachrysa* larvae (identified as *Pimachrysa fusca* Adams) express the numerous features that characterize the chrysopid subfamily Nothochrysinae. They resemble *Hypochrysa* larvae in many respects, but several differences support retaining the two genera as separate. It now appears that the reputedly more archaic, small bodied, nothochrysine genera (e.g., *Dictyochrysa*, *Hypochrysa*, and *Pimachrysa*) have naked larvae that differ distinctly from the larvae of *Nothochrysa* species, all of which are debris-carriers. In addition, the pattern of variability in *Nothochrysa* larval features supports the proposal that this genus has a closer relationship with the other chrysopid subfamilies than do the small-bodied nothochrysine genera. The findings are consistent with the hypothesis that larval nakedness (as opposed to debris-carrying) was the ancestral life style for the extant chrysopid clade.

1. Introduction

Considerable effort has focused on elucidating the evolutionary history of the neuropteran family Chrysopidae, and yet significant challenges remain. The subfamily Nothochrysinae is of particular interest, largely because of its position at or very near the base of the chrysopid phylogenetic tree and also because of its substantial and ancient fossil record. Members of this subfamily have primitive patterns of wing venation and unique features in their larval morphology that have been used to explore evolutionary trends within the subfamily [1–6]. However, generic relationships among the extant taxa remain ambiguous. On-going molecular studies [4, 7, 8] thus far have yielded some interesting, but contradictory results concerning the origin of the subfamily, and they have not yet resolved the relationships among its constituent genera.

Ideally, the above issues would be met with systematic comparisons among all included taxa using a broad range of

approaches (adult morphology, larval morphology, comparative biology, and molecular sequencing). In reality, a large barrier prevents such an analysis, that is, the rarity of specimens from relevant taxa. For example, except for a few species, specimens of Nothochrysinae and other basal chrysopid taxa are seldom encountered in the field; as a result the range of taxonomic coverage has been relatively narrow.

To continue efforts in overcoming this barrier, we describe the hitherto unknown larva (Semaphoront B) of the nothochrysine genus, *Pimachrysa*. Along with *Nothochrysa*, *Dictyochrysa*, and *Hypochrysa*, whose larvae were described earlier (Box 1), *Pimachrysa* is now the fourth genus of Nothochrysinae for which larvae are known. Also, we provide new data on the larva of *Nothochrysa californica* Banks that document a broader range of larval variation than previously reported for the genus. Finally, we discuss the pattern of variation among known nothochrysine larvae in relation to

the current understanding of generic relationships and the phylogeny of the subfamily.

2. Materials and Methods

2.1. Larval Material and Procedures. Our study is based on four specimens of *Pimachrysa fusca* Adams collected in late February and late April at Lower Covington Flat, Joshua Tree National Park (previously a national monument), Riverside Co., CA. Three of the specimens (two third instars and the single second instar) were used for morphological study, and one third instar was reared to confirm the specific identity of our larval specimens. The three specimens were treated in KAAD solution [9] for 24 hours and then transferred to 95% ethyl alcohol. In the laboratory the specimens were photographed, and the external gross features were described. Subsequently, one specimen from each instar was cleared in KOH and transferred to glycerin for examination of fine structures and setation. The second instar died soon after it was collected. We noted a globule of apparently sticky material on the labrum and base of the left mandible; presumably the material was exudate from aphids that we supplied the larva while we were in the field. We were able to remove the exudate from the preserved specimen without damage.

All voucher specimens are now in the Tauber Research Collection (Lot 2015: 01); a leg from one of the third instars was given to Shaun Winterton, California Department of Food and Agriculture, Sacramento, for DNA analysis.

To rear one of the third instars to the adult stage, we held it in a glass vial provided with frozen eggs of *Ephestia kuehniella* (Zeller), the Mediterranean flour moth. It was maintained at room temperature on a long-day light: dark cycle (~LD 16:8).

2.2. Terminology and Comparisons. The chrysopid larval stage typically includes three instars, the first of which (L1, Semaphoront A) differs markedly from the latter two (L2, L3), which, in turn, usually resemble each other (Semaphoront B). The main differences between second and third instars are in size, markings, and the number of thoracic and abdominal setae. In this paper, both instars of Semaphoront B are considered.

With minor exceptions, morphological terminology and chaetotaxy followed the usage of Rousset [10], Tsukaguchi [11], Tauber et al. [12], and Monserrat and Díaz-Aranda [13]. In one case there is a discrepancy. Some abdominal segments of *Nothochrysa* have a pair of laterodorsal tubercles (LDTs); in papers by Tauber and coauthors, the term tubercle refers to a protuberance bearing more than one seta. In *Nothochrysa californica* Banks, each LDT bears one long, filiform seta and one shorter seta. Thus, the tubercles of *N. californica* are consistent with those of other chrysopids. However, third instars of the two European species of *Nothochrysa* also were reported to have laterodorsal “tubercles” on abdominal segments A5 to A7; but in these species, the “tubercles” were reported to have only one, relatively long, seta [13]. If such a situation pertains (and no small seta is found on these “tubercles”), the homology of the structures should be examined

and the usage of the term “tubercle” clarified. For convenience, in this paper, we refer to the structures reported for the European species as laterodorsal tubercles (LDTs).

For our comparisons, we used specimens of *Nothochrysa californica* Banks (all instars from Alameda and Marin Counties, California) and *Hypochrysa africana* Kimmins (second instar from South Africa, see [6]), as well as earlier descriptions in the literature, as follows: *Dictyochrysa fulva* Esben-Petersen (first instar) [14], *Hypochrysa africana* (Kimmins) (second instar) [6], *Hypochrysa elegans* (Burmeister) (first and third instars) [13, 15], *N. californica* (all instars) [16], *Nothochrysa capitata* (Fabricius) (third instar) [13, 17], and *Nothochrysa fulviceps* (Stephens) (first and third instars) [13, 17]. Our comparisons are summarized in Box 2.

3. Background

3.1. Habitat. The collection site (northwestern corner of Joshua Tree National Park) is in a high elevation portion of the Mohave Desert (elevation: ~4670 ft). The area is open and arid, with scattered, low-growing trees and bushes amongst rocky outcroppings. Vegetation at the site includes *Quercus cornelius-mulleri* (Muller oak), *Juniperus californica* (California juniper), *Pinus monophylla* (single-leaf pinyon pine), *Larrea tridentata* (creosote bush), *Bebbia juncea* (Bebbia), *Yucca brevifolia* (Joshua tree), and *Yucca schidigera* (Mohave yucca). Our specimens were beaten from oak bushes, *Q. cornelius-mulleri*. The collections occurred on two days: the first (a single second instar, L2) on 26-2-2015 (cool and sunny), and the second (three third instars, L3) on 28-4-2015 (warm and sunny).

3.2. Larval Behavior. The specimens did not carry debris and they gave the overall impression of a *Chrysoperla* larva, but their bodies appeared thicker and more rounded (Figures 1(a)–1(c)). They remained motionless during much of the time we observed them; occasionally they moved quickly. The third instars, in the laboratory, fed readily on eggs of *E. kuehniella*; one specimen spun a delicate, oval shaped cocoon on the side of its vial 5-6 days after captivity; small pieces of debris were incorporated into the outer layers of the cocoon. The larva (within the cocoon) remained in diapause for 4 to 5 months, pupated ~155 days after spinning, and emerged as an adult 15 days later. The pharate adult exited the cocoon via a circular opening that it cut at the head end of the cocoon.

3.3. Generic Diagnosis. Our *P. fusca* larvae have the three diagnostic features that typify nothochrysine larvae. (i) The flagellum is very short relative to the pedicel (~1/14th the length of the pedicel) (Figure 1(d)). (ii) The terminus of the flagellum has a group of short apical setae. (iii) More than three lateral sensilla are present on the terminal segment of the labial palps (L2 = 5, L3 = 4-5) (Figure 1(e)).

Among the Nothochrysinæ with known larvae, *Pimachrysa* (*P. fusca*) closely resembles *Hypochrysa* (two species) (Box 2). That is, the larvae (second and third instars) from both genera have elongate, naked bodies; the thorax and abdomen lack lateral tubercles; the abdomen has no laterodorsal tubercles. In addition, none of the setae are

FIGURE 1: *Pimachrysa fusca* Adams, Joshua Tree National Park, Riverside Co., CA. (a, b, and c) Body, dorsal, illustrating the variation in the dorsal body markings among three third-instar specimens collected at the same locality on the same day. (d) Antenna (second instar), lateral, showing foreshortened flagellum typical of nothochrysine larvae. (e) Labial palps (second instar), lateral, showing row of five sensilla on terminal segment.

hooked, and the primary cephalic setae of the *Pimachrysa* larvae are slightly blunt and thus similar to those of *Hypochrysa*. Finally, the *Pimachrysa* head and body markings resemble those of *H. elegans*; that is, larvae of both species have dark brown, elongate, dorsal head markings, and dark brown, sublateral stripes on the thorax, and abdomen (most noticeable on the L3; see Figures 1(a), 1(c), 2(a), 2(b), and 6).

However, a number of distinguishing features differentiate the larvae of the two genera. First, other than the cephalic setae, all other setae on the *Pimachrysa* larvae, especially the abdominal submedian setae (SMS), are short and acutely tipped, whereas on *Hypochrysa* they are short and blunt or clavate. Second, the jaws of *Hypochrysa* are longer than those of the *Pimachrysa* (*Hypochrysa*: 1.7–1.8x head length; *Pimachrysa* 1.4–1.6x head length). Third, the white-to-tan body coloration of the *Pimachrysa* larvae differs markedly from the green-to-bright green coloration of both *H. elegans* and *H. africana*. In our opinion, the above differences offer significant supporting evidence for the separate identity of the two genera.

4. Description of *Pimachrysa fusca* Adams

4.1. Second Instar

4.1.1. Body (Figures 2(a)–2(c)). Length ~5.5 mm (measured in lateral view through spiracles), height ~0.94 mm (thickest

section of abdomen). Cream-colored-to-white with dark brown dorsolateral and lateral markings on each segment; lateral surface with brown dorsal band above lateral band of white and lower narrow band of dark brown; pronotal sclerites brown. All setae short, smooth, pale, of two types: “simple” = with acute tip (most setae) or “slightly blunt” = with slightly rounded tip (some primary cranial setae). Thoracic, abdominal setae often with swollen, lightly sclerotized setal bases (Figures 3(a) and 3(c)), these setal bases becoming increasingly larger and more sclerotized posteriorly.

4.1.2. Head (Figures 2(a)–2(c), 4(a), and 4(b)). Dorsum white, with dark brown markings as in figures; frontal marking elongate, without lateral arms; mesal epicranial and/or postfrontal markings reduced to pair of posterior spots below frontal marking; lateral epicranial marking elongate, extending to lateral side of antennal base; eyes with stemmata clear, integument between stemmata, surrounding all stemmata dark brown to black; cranium roughly triangular, with posterior margin (dorsal) rounded, ventral margin elongate; width (across eyes) ~0.79 mm, length (dorsum) ~0.64 mm, depth (midregion to top of eye) ~0.20 mm; base mostly exposed. Clypeolabral area elongated distally, extending over basal segment of labial palps; with large brown mark mesally. All dorsal primary cephalic setae present except S10 and S12; S11 long, S3 short and shifted mesally, others of medium length, most slightly blunt apically; Vx setae obscured by cervix, probably

FIGURE 2: *Pimachrysa fusca* Adams, second instar (Joshua Tree National Park, Riverside Co., CA). (a) Body, dorsal. (b) Body, lateral. (c) Body, ventral. (d) Head, dorsal. (e) Head, ventral. (f) Head, lateral. (g) Thorax, dorsal. (h) Hind leg, anterior. (i) Tarsus, dorsal.

with three small setae (as drawn on Figure 4(a)) or two setae and pore; labrum with three pairs of setae (one mesally, two laterally); dorsum without secondary setae.

Cervix full laterally, ventrally, slightly withdrawn from cranium dorsally; with row of 6–8 pairs of setae along anterior margin, dorsum to venter.

4.1.3. Cephalic Appendages (Figures 2(d)–2(f), 4(a), and 4(b)). Mandible long, thin, length ~ 0.88 – 0.90 mm (along curved exterior margin), length 0.74 – 0.78 mm (straight line), width

(at base) 0.10 – 0.13 mm; ratio mandible length (curved margin) to head width = 1.11 – 1.13 ; ratio mandible length (curved margin) to head length (dorsal) = 1.37 – 1.40 . Mandible very slightly upturned distally, with single acute basolateral seta; terminus sharp, with four very small teeth. Antennal length 0.94 mm, $\sim 1.5\times$ length of cranium; width ~ 0.04 mm (at widest part of pedicel); scape with relatively straight sides, two pairs of distal setae (one lateral, other dorsal); pedicel annulate, with ~ 18 – 22 medium-length annulations mesally, one elongate annulation basally, one distally, distal annulations with two small setae, one lateral, one mesal, distomesal margin

FIGURE 3: *Pimachrysa fusca* Adams (Joshua Tree National Park, Riverside Co., CA), thoracic (a, b) and abdominal (c, d) integument and setae, dorsal. Note slight differences in size of setae and chalazae between second (a, c) and third (b, d) instars. All images are the same magnification ($\times 100$).

FIGURE 4: Head of *Pimachrysa fusca* Adams, second instar. (a) Dorsal. (b) Ventral. co: cardo; c.m.: cranial margin; fl: flagellum; l.p.x: labial palps, number of segment; md: mandible; mx: maxilla; ped: pedicel; pg: palpiger; sc: scape; stp: stipes; Sx: primary seta number; Vx: Vx setae.

FIGURE 5: Thorax (dorsal) of *Pimachrysa fusca* Adams, second instar. dep: smooth-surfaced, intrasegmental depression between subsegments; Sc1, Sc2, and Sc3: first, second, and third primary sclerites of each segment; sp: spiracle; Tx: number of thoracic segment.

concave, bearing small claw; flagellum short, stubby, ~0.08 times length of pedicel, terminus with one short apical seta, surrounded by three or four microsetae. Labial palp long, slender, ~0.85 times length of mandible (straight line); basal segment with four distal setae, two dorsally, two ventrally; middle segment long, with long, undivided basal subsegment bearing ~three setae mesally, with ~six mesal subsegments, one mesal seta; terminal subsegment elongate, with two long setae distally, one basally; terminal labial segment ~one-third length of middle segment, slightly tapered distally, heavily sclerotized, no setae observed, ventrolateral margin with five closely spaced, elongate sensilla. Palpiger erect, with relatively straight sides, one mesal seta, one lateral seta; prementum broad, with three pairs of setae; cardo, stipes elongate, narrow, longitudinally arranged, cardo behind stipes, stipes with long seta.

4.1.4. Thorax (Figures 2(g) and 5). Lateral tubercles absent; dorsum with scattered, short, acute setae; pleurum with longitudinal, dorsal band of short bristles, spines; primary setae unidentified (except as noted below and in Figure 5). Legs (Figures 2(h) and 2(i)) white, with white-to-cream-colored setae; coxa dark brown; distal one-third of femur, basal one-fifth of tibia dark brown, with margins of all adjoining segments black distally; tarsus, claw, empodium dark brown.

Prothorax (T1) with two well-delineated subsegments separated by transverse depression. Paired Sc1 dark brown, elongate, extending full length of anterior subsegment, slightly narrow anteriorly, broader mesally, posteriorly, underlaid by dark brown, pigmented lateral stripe. Sc2 broadly ovate, extending from middle to posterior margin of anterior subsegment, with longitudinally elongate, brown marking posteromesally.

Mesothorax (T2) consisting of three well-delineated subsegments separated by distinct depressions. Anterior subsegment with pair of ovate sclerites (Sc1) on anterior margin, with single lateral seta (probably S1Sc1); spiracles simple, sessile, circular, brown, with cylindrical atrium. Second subsegment with pair of small sclerites (Sc2) on anterior margin, each with single seta (S1Sc2), juxtaposed much smaller seta (S2Sc2); subsegment separated mesally from posterior subsegment by transverse depression with pair of large, brown, circular sclerites (Sc3) laterally, each with small mesal seta (S1Sc3).

Metathorax (T3) consisting of three well-delineated subsegments separated by transverse depressions, each with pair of small setae laterally (probably S1Sc1, S1Sc2), but sclerites Sc1, Sc2 not identified. Sc3 medium-sized, brown, circular, with small mesal seta (S1Sc3).

4.1.5. Abdomen (Figures 2(a), 2(b), 2(c), and 6). Lateral tubercles (LTs), laterodorsal tubercles (LDTs) absent; spiracles (A1–A8) circular, sessile, with simple atrium. Each segment (A1–A7) roughly quadrangular, divided into three subsegments (or raised folds) separated by transverse depressions, anterior one extending to margin of segment; spiracle located laterally on dorsum of second subsegment; dorsum of all subsegments with acute submedian setae (SMS) on chalazae of small to medium sizes, arranged in transverse rows on each subsegment; pleura with patches of small, mostly acute, sometimes blunt setae, spines. A1: anterior subsegment short, dorsum with four pairs of SMS; second, third subsegments longer, similar in size to each other, each with row of ~ten to twelve pairs of SMS, most stemming from relatively small chalazae. A2–A7: dorsum of each subsegment with ~nine to twelve pairs of SMS; number and length of SMS, size (plumpness) of chalazae becoming progressively larger posteriorly. A7: first subsegment with four pairs of short SMS stemming from relatively large, plump chalazae; second and third subsegments each with five to seven pairs of SMS, most with plump chalazae. A8: segment divided into three subsegments; anterior subsegment narrow, well-delineated from subsequent subsegment; second, third subsegments not well-delineated from each other; dorsum of anterior subsegment with one pair of SMS, middle subsegment with two pairs of SMS; posterior subsegment with ~seven pairs of SMS; pleural region of segment with two, unsclerotized, lateral swellings, each bearing ~five medium length setae. A9: cylindrical, with two visible subsegments; anterior subsegment without setae anteriorly, with ~three pairs of robust dorsal setae posteriorly, lateral-most pair on swelling; posterior subsegment with row of ~seven pairs of medium length setae on robust chalazae posteriorly. A10: dorsum with ~six pairs of setae laterally, ~eight pairs of setae extending from posterior membrane on terminus. Venter with subsegmentation poorly demarcated; each segment (A1–A8) with two transverse bands of acute setae and spines (microsetae), pair of large, sublateral patches of relatively robust setae and spines (microsetae); setae often longer than those on dorsum, but without enlarged chalazae.

4.2. Third Instar. Similar to second instar except for measurements and noteworthy features, as follows.

FIGURE 6: Abdomen (dorsal) of *Pimachrysa fusca* Adams, second instar. (a) First and second segments. (b) Fifth and sixth segments. (c) Seventh and eighth segments. (d) Ninth and tenth segments. Ax: number of abdominal segment; dep: smooth-surfaced, intrasegmental depression between subsegments; Sc1, Sc2, and Sc3: first, second, and third primary sclerites of each segment; sp: spiracle.

4.2.1. Body (Figures 1(a)–1(c), 7, 8(a), and 8(b))

Body length (measured in lateral view through spiracles) 8.5–9.0 mm (L2: 5.5 mm).

Body depth (thickest) 1.5–1.6 mm (L2: ~0.94 mm).

Subsegmentation, setation, coloration as in L2.

Setal size approximately same as L2. Thoracic, abdominal setal bases sometimes slightly swollen, sclerotized (Figures 3(b) and 3(d)).

4.2.2. Head (Figures 7(a) and 8(c))

Head width (across eyes) 0.77–0.78 mm (L2: 0.79 mm).

Head length (dorsum) 0.63–0.64 mm (L2: ~0.64 mm).

Head depth (midregion to top of eye) 0.18–0.19 mm (L2: ~0.20 mm).

4.2.3. Cephalic Appendages (Figures 7(a) and 8(c))

Mandible length (along curved exterior margin) 0.93–0.97 mm (L2: ~0.88–0.90 mm).

Ratio, mandible length to head width = 1.19–1.29 : 1 (L2: 1.11–1.13 : 1).

Ratio mandible length to head length (dorsal) = 1.46–1.57 : 1 (L2: 1.37–1.40).

Antennal length ~0.96 mm, ~1.5x length of cranium (L2: ~0.94 mm, ~1.5x length of cranium).

FIGURE 7: *Pimachrysa fusca* Adams, third instar (Joshua Tree National Park, Riverside Co., CA). (a) Head, dorsal. (b) Thorax, dorsal. (c) Abdominal segments 1 through 3, dorsal. (d) Abdominal segments 4 and 5, dorsal. (e) Abdominal segments 6 through 10, dorsal.

Flagellar length 0.06–0.07 mm (L2: 0.06 mm); terminus with single very short apical seta, few, if any, surrounding microsetae.

Ratio, length of flagellum : length of pedicel 0.08 : 1 (L2: 0.07 : 1).

Ratio, length of labial palp : length of mandible (straight line) $\sim 0.78 : 1$ (L2: $\sim 0.85 : 1$).

Labial palp: middle segment with $\sim$ seven subsegments; ventrolateral margin of terminal segment with four to five closely spaced, elongate sensilla.

4.2.4. Thorax (Figures 7(b) and 8)

Legs as in L2, except coxa white distally; basal one-third of tibia dark brown.

4.2.5. Abdomen (Figures 7(c)–7(e), 8(a), and 8(b)). As in L2, with following exceptions:

A1: anterior subsegment dorsally with eight pairs of SMS; second, third subsegments each with row of $\sim$ twelve to fifteen pairs of SMS, most stemming from relatively small chalazae.

A2–A7: dorsum of each subsegment with $\sim$ nine to fifteen pairs of SMS—one to three more than L2.

A8: dorsum of anterior subsegment with two pairs of SMS; pleural region with single pair of broad, unsclerotized, lateral swellings, each bearing $\sim$ ten setae.

A10: basal portion of segment withdrawn and shorter than on L2.

Venter similar to L2.

FIGURE 8: *Pimachrysa fusca* Adams, third instar (Joshua Tree National Park, Riverside Co., CA). (a) Body, lateral. (b) Body, ventral. (c) Head, prothorax, ventral. (d) Hind leg, anterior.

4.3. Size Differences between Second and Third Instars. Among our specimens, the L2 ($n = 1$) and L3 ($n = 2$) express some unusual variation in the relative sizes of body parts. The L3s, as expected, have much larger bodies than the L2, and yet the head size is almost identical among our specimens of the two instars. Also, while the L3 mandibles appear somewhat larger than those of the L2, the antennae and labial palps do not. In addition, the L3 setal size is approximately the same as in the L2, but the degree of enlargement and sclerotization of the abdominal setal bases is less than on L2 (Figures 3(a) and 3(c) versus 3(b) and 3(d)). Thus, the L3 setae seem less prominent than those of the L2 (Figure 3).

Given the small number of specimens, we are puzzled by the above variation in the relative sizes of larval body parts. First, we do not know whether our observations represent the normal situation for this species. Second, if it does, we suggest that the variation could be related to some unusual pattern of annual or seasonal variation in the availability of food or perhaps seasonal or generational differences in physical factors.

4.4. Cocoon (Figures 16(a) and 16(b)). White, oblong longitudinally, round transversely, with basal side spun directly against substrate; attached base with single layer of thin, transparent silk; upper surface with two layers of silk: inner layer: dense, relatively smooth and outer layer: sparse, mixed with debris.

5. Comparative Information on *Nothochrysa californica* Banks

Previously, the three instars and cocoon of *N. californica* were described in detail [16]. However, full comparisons with other described nothochrysin immatures are hampered because the descriptions lack adequate illustrations and several larval characters were not included. Here, we provide images and drawings of the *N. californica* second instar (Figures 9–13) and the following notes on all instars for use in comparisons. All observations and measurements below are based on one to two specimens per instar:

Mandible length (along curved exterior margin) = L3: 1.63–1.66 mm; L2: 1.15 mm; L1: 0.80 mm.

FIGURE 9: *Nothochrysa californica* Banks, second instar (Strawberry Canyon, University of California Campus, Alameda Co., CA). (a) Head, dorsal. (b) Head, ventral. (c) Thorax, dorsal. (d) Abdominal segments 1 through 4, dorsal. (e) Abdominal segments 5 through 7, dorsal. (f) Abdominal segments 8 through 10, dorsal.

Antennal length = L3: ~1.65 mm, 1.5x length of cranium; L2: 1.24 mm, 1.8x length of cranium; L1: 0.84 mm, 1.6x length of cranium.

Pedicle with claw at tip = L3: yes; L2: yes; L1: yes.

Pedicle length = L3: 2.16 mm; L2: 0.97 mm; L1: 0.58 mm.

Flagellar length = L3: 0.18 mm; L2: 0.17 mm; L1: 0.17 mm.

Length of flagellar seta = L3: 0.03 mm; L2: 0.03 mm; L1: 0.04 mm.

Labial palp, number of lateral sensilla on terminal segment = L3: 4; L2: 4-5; L1: 0.

6. Unique Larval Characters for Nothochrysinæ

Three larval features have been proposed as unique, and perhaps apomorphic, for the subfamily Nothochrysinæ [5, 13, 18]. Given the recent data from *Hypochrysa* and now *Pimachrysa*, as well as our reexamination of the *N. californica* larvae, we were led to reevaluate the diagnostic and phylogenetic value of these characters. In addition, we propose an addition larval character that may be unique to the Nothochrysinæ. For our larval comparisons, we used our own measured values and estimated others from published drawings (*Dictyochrysa*: Figure 3 by New [14]; *N. capitata*, *N. fulviceps*: Figures 46 and 47 by Monserrat and Díaz-Aranda [13]).

FIGURE 10: *Nothochrysa californica* Banks, second instar (Strawberry Canyon, University of California Campus, Alameda Co., CA). (a) Body, dorsal. (b) Body, lateral. (c) Body, ventral.

FIGURE 11: Head of *Nothochrysa californica* Banks, second instar. (a) Dorsal. (b) Ventral. co: cardo; c.m.: cranial margin; fl: flagellum; l.p.1–3: labial palps, number of segment; md: mandible; mx: maxilla; ped: pedicel; pg: palpiger; sc: scape; sen: sensilla; stp: stipes; Sx: primary seta number; Vx: Vx setae.

FIGURE 12: Thorax (dorsal) of *Nothochrysa californica* Banks, second instar. dep: smooth-surfaced, intrasegmental depression between subsegments; Sc1, Sc2, and Sc3: first, second, and third primary sclerites of each segment; sp: spiracle; Tx: number of thoracic segment.

6.1. Length of Flagellum. The nothochrysinine antenna is characterized as having a terminal segment (flagellum) that typically is short and stubby, that is, approximately 10 or more times shorter than the pedicel; in larvae of Apochrysinæ and Chrysopinæ, the flagellum is considerably longer—only about 3–6 times shorter than the pedicel. For *Hypochrysa* and *Pimachrysa* second and third instars, as well as *N. fulviceps* and *N. californica* third instars, this character is consistent (their flagella are ~12–20 times shorter than the pedicel). Also, for the *Dictyochrysa* first instar, it is close at ~9 times shorter than the pedicel. However, there are interesting examples of interspecific and developmental variation in *Nothochrysa*. For example, the third instar of *N. fulviceps*, with a flagellum that is 12.5 times shorter than the pedicel, is consistent with the character, and the third instars of both *N. capitata* and *N. californica* (with flagella 8.3–9.1 times shorter than the pedicel) are near the 10x designation (Box 2). However, the flagella of the first and second instars of *N. californica* are noticeably longer, with the first instar being the most deviant (L3: flagellum 9.4–9.5 times shorter, L2: 5–7 times shorter, L1: only 4 times shorter than the pedicel; see Figure 14). Whether this pattern of developmental variation applies to the first instars of the European *Nothochrysa* species is unknown. However, if the old maxim “ontogeny recapitulates phylogeny” holds for this genus, the pattern could have phylogenetic importance.

6.2. Terminal Flagellar Setae. The nothochrysinine flagellum is typified as bearing several, very small terminal setae; in contrast, the tip of the flagellum in Chrysopinæ and Apochrysinæ bears a single long seta with a robust base. Upon reevaluation, this trait holds for most of the known nothochrysinine larvae—*Dictyochrysa* (L1, one species), *Hypochrysa* (L1, L2, and L3, one species each), *Pimachrysa* (L2, L3, one species,

Figure 14(a)), and *Nothochrysa* (L3, two European species). However, the structure differs in *N. californica*; in this species the flagellum terminates with a single elongate seta having a broad base (Figure 14(b)). The length of the terminal seta varies from 0.18 to 0.25 times the length of the flagellum. Again, the deviation from the typical nothochrysinine pattern is most pronounced in the *N. californica* first instar. Unfortunately, the situation with the first and second instars of the European species is unknown.

6.3. Number of Sensilla on Terminal Segment of Labial Palp. Thus far, this character appears to be a consistent means of distinguishing nothochrysinine larvae (second and third instars, Semaphoront B; there are no sensilla on the palps of the first instar). A number of four or more sensilla is typical of nothochrysinine larvae. Three or fewer sensilla are present on larvae of Apochrysinæ and Chrysopinæ (note: this character is difficult to examine; it requires careful placement and often manipulation of a cleared specimen with labial palps in ventrolateral position and under sufficient lighting.)

6.4. Cocoon Structure. As described here, the *Pimachrysa* cocoon is sessile and strongly oblong; the basal membrane of the cocoon is single, thin, and highly transparent, whereas the upper layer is double, thick, and opaque. Among the Nothochrysinæ, this cocoon structure is shared with *Nothochrysa* (Toschi 1965: *N. californica*); however, the situation is not clear for *Hypochrysa*. *Hypochrysa africana* shares the oblong (“barrel”) shape of *Pimachrysa* and *Nothochrysa* (Duelli et al. 2010, as *Kimochrysa*), but it is unknown if its cocoon is sessile or entire. In any case, the *Pimachrysa* and *Nothochrysa* cocoons appear unlike the entire, more spherical cocoons spun by larvae of many Chrysopinæ (Chrysopini, Leucochrysinini) that we have observed.

6.5. Synapomorphies? Whether the above characters constitute apomorphies or symplesiomorphies is unconfirmed, and available evidence from the hemerobiids (the presumed sister group of Chrysopidae) is inconclusive. For example, among the hemerobiids, (1) the length of the flagellum exhibits intergeneric variability: in *Boriomyia fidelis* (Banks), the flagellum is short relative to the pedicel [19]; in *Hemerobius* species, it is elongate [20]; in *Micromus* species, it is indistinguishable from the pedicel [20]. (2) The length of the terminal flagellar seta also shows variability among hemerobiid genera: in *B. fidelis* and *Drepanacra binocula* (Newman) the flagellum is elongate [19, 21]; in *Micromus* it is short and accompanied by a very small seta [20]; in *Hemerobius* it is also short, but without a small seta [20]. To our knowledge, no hemerobiids have been shown to have a cluster of very short setae on the terminal antennal segment as found in *Hypochrysa*, *Pimachrysa*, and *Dictyochrysa*. (3) To our knowledge, lateral sensilla have not been reported from the terminal segment of hemerobiid labial palpi. They appear to be unique to Chrysopidae; however, the plesiomorphic number is unknown. (4) At this point, reports on the structural features of Neuropteran cocoons are not sufficient for meaningful phylogenetic comparisons.

FIGURE 13: Abdomen (dorsal) of *Nothochrysa californica* Banks, second instar. (a) First and second segments. (b) Fifth and sixth segments. (c) Seventh and eighth segments. (d) Ninth and tenth segments. Ax: number of abdominal segment; dep: smooth-surfaced, intrasegmental depression between subsegments; Sc1, Sc2, and Sc3: first, second, and third primary sclerites of each segment; sp: spiracle.

From the above, it is obvious that the choice of an out-group is of crucial importance for the interpretation of an apomorphic versus plesiomorphic state for the various larval characters. Unfortunately, there has been relatively little comparative systematic work that compares hemerobiid and chrysopid larvae (see [22]).

7. Nothochrysine Phylogeny

When Adams [1] revised the subfamily Nothochrysinæ, it comprised seven extant genera and four fossil genera attributed to the Miocene. Later, two extant and eight fossil genera were added, and one extant genus was synonymized [3, 6, 23]. So, now the subfamily includes eight extant genera

and twelve extinct fossil genera from the early Eocene (Ypresian) to the Miocene (Aquitainian, Burdigalian?).

Although Adams [1] included *Nothochrysa* within the subfamily because it retained many archaic and/or unusual features that are not expressed in the Chrysopinæ, he pointed out that it has other advanced features that are more typical of Chrysopinæ and Apochrysinæ than Nothochrysinæ (e.g., in its development of the pseudomedia and pseudocubitus, its wing folds). And recently, an extensive study of all known fossil chrysopids identified patterns of evolutionary progression in certain venational features among the nothochrysine fossils that support a distinct position for *Nothochrysa* [3]. But, the relationships among the extant genera remain unresolved.

Based on his morphological studies, Brooks [2] proposed that the extant genera of the subfamily fall into two groups.

Nothochrysinæ*Dictyochrysa* – **Naked***fulva* Esben-Petersen

New 1981 [14] [Desc-L1; Draw-L1; Note]

Hypochrysa – **Naked***elegans* (Burmeister)Brauer 1867 [15], as *Hypochrysa nobilis* Heyd. [Desc-L3; Draw-L3; Note]Lacroix 1925, as *Hypochrysa nobilis* Schneider [Note]Principi 1956b, as *H. nobilis* Schneider [Note: svelt, agile, green larva, no mention of debris]

Gepp 1983 [Photo-L3; Note]

Gepp 1988 [Photo-L3; Note]

Díaz-Aranda and Monserrat 1995 [18] [Draw-L1, L3; Note]

Gepp 1999 [Photo-L3]

Díaz-Aranda et al. 2001 [Draw-L1, L3; Note]

Monserrat and Díaz-Aranda 2012 [13] [Desc-L1, L3; Draw-L1, L3; Note]

africana (Kimmins)

Duelli et al. 2010 [4] [Photo-L3]

Tauber 2014 [6] [Desc-L2; Draw-L2; Photo-L2; Note: Synonymy of *Kimochrysa* with *Hypochrysa*, largely based on larval characters]

Tauber and Faulkner, this paper [Draw-L2; Note]

Nothochrysa – **Varied, with both Debris-carrier & Occasional Debris-carrier***californica* Banks

Toschi 1965 [16] [Desc-L1–L3; Draw-L1–L3; Note; Mat: not specified; Beh]

Tauber and Tauber, unpublished data [Mat: bracts from *Quercus* catkins, frass, plant fragments]

Tauber and Faulkner, this paper [Redesc-L2; Draw-L2; Photo-L2]

capitata (Fabricius)*

Withycombe 1922 [Desc-L1–L3; Draw-L3; Note: a few large pieces; Mat: not specified]

Lacroix 1925 [Note: packet loosely attached, not elaborate; Mat: not specified]

Killington 1931 [Note: a few large pieces; Mat: not specified]

Killington 1937 [17], as *Nathanica* [Desc-L1–L3; Draw-L3; Note: information from Withycombe 1922]Kimmins 1939, as *Nathanica* [Desc-L1; Draw-L1]Fraser 1959, as *Nathanica* [Draw-L2 or L3; Note; Mat: not specified]New 1969, as *Nathanica* [Note: L2, L3 – most carried some to much debris; Mat: mainly animal remains; Beh]

Gepp 1983 [Photo-L3; Note; Mat: frass, twisted plant material, lichens]

Barnard et al. 1986 [Desc: dorsal coloration]

Gepp 1988 [Note: packet loose, on central part of abdomen; Mat: bud scales, frass]

Monserrat and Díaz-Aranda 2012 [13] [Desc-L3; Draw-L3; Note; Mat: few large, diverse fragments]

fulviceps (Stephens)

Lacroix 1925 [Note: packet loosely attached, not elaborate; Mat: not specified]

Killington 1935, as *Nathanica* [Desc-L1; Draw-L1; Note; Mat: not specified]Killington 1937 [17], as *Nathanica* [Desc-L1; Draw-L1; Note; Mat: not specified]

Gepp 1983 [Photos-L3, with and without debris; Note; Mat: large pieces of plant material, shed bark etc.]

Gepp 1984a [Photo-L3; Note; Mat: not specified]

Gepp 1988 [Draw-L3, Photo-L3; Note: packet on abdomen; Mat: bud scales, frass, coleophorid cases]

Díaz-Aranda & Monserrat 1995 [18] [Draw-L3; Note; Mat: not specified]

Díaz-Aranda et al. 2001 [Draw-L3; Note; Mat: not specified]

Monserrat & Díaz-Aranda 2012 [13] [Desc-L3; Draw-L3; Note; Mat: few large pieces of different nature]

Pimachrysa – **Naked***fusca* Adams

Tauber & Faulkner, this paper [Desc-L2, L3; Draw-L2; Photo-L2, L3; Note]

Asthenochrysa – **Larvae Unknown***Leptochrysa* – **Larvae Unknown***Pamochrysa* – **Larvae Unknown***Triplochrysa* – **Larvae Unknown**

Box 1: Catalog of larval descriptions for Nothochrysinæ (updated from Tauber et al. [5], where the citations not listed in the references here can be found). * See Monserrat and Díaz-Aranda 2012 [13] regarding problems in distinguishing *N. capitata* and *N. fulviceps*.

FIGURE 14: Flagellum and distal annulations of pedicel on (a) *Pimachrysa fusca* Adams and (b) *Nothochrysa californica* Banks, second instar antenna. Note: stubby flagellum and short terminal setae on *P. fusca* and elongate flagellum and single, more robust terminal seta on *N. californica*.

FIGURE 15: Head of *Hypochrysa africana* Kimmins, second instar. (a) Dorsal. (b) co: cardo; c.m.: cranial margin; fl: flagellum; l.p.x: labial palps, number of segment; md: mandible; mx: maxilla; ped: pedicel; pg: palpiger; sc: scape; sen: sensilla; stp: stipes; Sx: primary seta number; Vx: Vx setae.

In his scheme *Nothochrysa* was included with *Dictochrysa* and *Hypochrysa*, separate from *Pimachrysa* and *Kimochrysa*. These groupings subsequently were found to be weak; indeed *Kimochrysa* was synonymized with *Hypochrysa* [6]. Finally, in another study that used molecular and other data, Duelli et al. [4] proposed that the small bodied, pollen-feeding nothochrysine genera (e.g., *Hypochrysa* sen. lat. (including *Kimochrysa*), *Pamochrysa*, *Pimachrysa*, and *Asthenochrysa*) are very similar to each other. These authors concurred with the opinion that although *Nothochrysa* shows some

affinities with these nothochrysine genera, they also resemble Apochrysinæ and Chrysopinæ in other respects. Given their findings, they conjectured that the small bodied, pollen-feeding nothochrysines represent the most ancient group of extant chrysopids. Moreover, they concluded that pollen-feeding is the likely ancestral condition for chrysopid adults.

It appears from the descriptions of now four of the eight nothochrysine genera (Box 1) that larval characters support the conclusions of Adams, Archibald and Makarkin, and Duelli et al. [1, 3, 4]. The pattern of larval differences between

Pimachrysa (L2, L3)

Larvae naked, without a layer of camouflaging material.

Small to medium sized larvae (L2: ~5.5 mm; L3: 8.5–9.0 mm); shape fusiform, narrow, abdomen rounded, slender.

Cephalic markings obvious, lateral epicranial markings elongate; mesal epicranial and/or postfrontal markings reduced; with a conspicuous median stripe.

Cephalic setae: all primary setae except S10 and S12 present; Vx obscure, probably two setae and a pore.

Antennae with terminal segment (flagellum) stubby, short (0.07–0.08x length of pedicel).

Mouthparts elongate (mandible ~1.4–1.6x longer than head capsule).

Mandible with single seta on basolateral margin.

Thorax without lateral tubercles.

Paired prothoracic sclerites (Sc1) elongate.

Metanotum with three distinct folds, each bearing a transverse band of unhooked setae with acute tips.

Legs fairly long in relation to body; tarsi dark brown throughout.

Abdominal segments II–VII without lateral tubercles, with some lateral setae slightly elongated, but without distinct lateral setae (LS).

Abdominal segments I–VII dorsally with transverse bands of numerous short, acute setae (SMS).

Abdominal segments V–VII without laterodorsal tubercles, without LDS (but with some laterodorsal setae slightly elongated).

Nothochrysa (all instars, unless noted otherwise)

Larvae usually bearing a camouflaging layer of debris.

Large larvae (L3: 9–12 mm; L2: 6–7 mm; L1: 4–5 mm); shape very slightly fusiform, abdomen convex, almost flattened to globular.

Cephalic markings obvious, epicranial markings large, fused with postfrontal markings, occupying almost the entire cephalic dorsal surface.

Cephalic setae: all primary setae including S12 present; Vx = two short anterior setae, pore, single posterior seta, in longitudinally elongate row.

Antennae with terminal segment (flagellum) of variable length.

Pedicel length/flagellar length (= number of times flagellum shorter than pedicel):

N. capitata L3 = ~8.8 (from Figures 47-6 [13])

N. fulviceps L3 = ~13.0 (from Figures 47-12 [13])

N. californica L1 = ~3.6, L2 = 5.1–6.2, L3 = 9.4–9.5

Flagellar terminus and terminal bristle variable.

N. capitata, *N. fulviceps* L3 with rounded flagellar terminus, very short terminal bristle (from Figure 1b [18], Figures 47-6, 47-12 [13])

N. californica L3–L1 with flagellum tapered, slightly elongate seta (setal length/flagellar length: L3 = 0.18, L2 = 0.18, L1 = 0.25)

Mouthparts noticeably longer than the head capsule.

N. capitata, *N. fulviceps* L3 (from Figures 46-1, 46-5 [13])

N. californica L1–L3 (mandible length/head length: L1 = 1.36, L2 = ~1.60–1.65, L3 = 1.30–1.48)

Mandible with two setae on basolateral margin.

Thorax with lateral tubercles present, carrying 1-2 or few elongate lateral setae (LS).

Paired prothoracic sclerites (Sc1) triangular.

Metanotum with transverse row of filiform (hooked or straight) setae posteriorly.

Legs very long in relation to body size; tarsi pale to dark brown.

Abdominal segments II–VII with lateral tubercles well developed, hemispherical, bearing filiform or hooked (“uncinate”) setae (LS).

Abdominal segments VI–VII (sometimes also V, VIII) with laterodorsal tubercles present, bearing single long seta (LDS?) (sometimes also a shorter seta).

Dorsum of abdominal segments I–VI with transverse rows or bands of hooked submedian setae (SMS).

Hypochrysa (L1, L3)

Larvae naked, without a layer of camouflaging material.

Small to medium sized larvae (L2: 6–7 mm); shape fusiform, narrow, abdomen rounded, slender.

Cephalic markings light or dark; lateral epicranial markings narrow, elongate; mesal epicranial and/or postfrontal markings faint, either with a conspicuous median stripe or with pair of small frontal markings.

Cephalic setae: all primary setae including S12 present; Vx obscure, probably two setae and a pore or three setae.

Antennae with terminal segment (flagellum) stubby, short (~0.05–0.06x length of pedicel).

Mouthparts elongate (mandible ~ 1.7 – $1.8\times$ longer than head capsule).
 Mandible with single seta on basolateral margin.
 Labial palp with terminal segment bearing 4 lateral sensilla.
 Thorax without lateral tubercles.
 Paired prothoracic sclerites (Sc1) elongate.
 Metanotum with three distinct folds, each bearing a transverse band or row of unhooked, blunt to clavate (bacilliform) setae.
 Legs of normal size in relation to body; tarsi dark brown throughout.
 Abdominal segments II–VII without lateral tubercles, without distinct lateral setae (LS).
 Abdominal segments I–VII dorsally with transverse rows or bands of numerous short, blunt to clavate (bacilliform) setae (SMS).
 Abdominal segments V–VII without laterodorsal tubercles, without LDS.

Dictyochrysa (L1)

Larvae naked, without a layer of camouflaging material.
 Small to medium sized larvae (L1: ~ 2 mm); shape fusiform, narrow, abdomen rounded, slender.
 Cephalic markings unknown.
 Cephalic setae: S12 absent; S8–10 unknown; Vx short.
 Antennae with terminal segment (flagellum) rounded apically, pedicel length/flagellar length = 9 (number of times flagellum shorter than pedicel) (from Figure 3 [14])
 Mouthparts nearly twice as long as head capsule.
 Number of setae on mandible unknown.
 Thorax without lateral tubercles.
 Paired prothoracic sclerites (Sc1) triangular.
 Metanotum with three distinct folds, each bearing a transverse band of unhooked setae with acute tips.
 Legs fairly long in relation to body; tarsi dark brown throughout.
 Abdominal segments II–VII without lateral tubercles.
 Abdominal segments I–VII dorsally with transverse bands of blunt setae (SMS).
 Abdominal segments V–VII without laterodorsal tubercles, without LDS.

Box 2: Summary of larval features of nothochrysine genera with described larvae. In addition to information in this paper; see [6, 13–18].

FIGURE 16: *Pimachrysa fusca* Adams, cocoon (Joshua Tree National Park, Riverside Co., CA). (a) Basal surface attached to glass vial. (b) Round exit hole on upper surface (head end) of cocoon. b.s.: basal surface; e.h.: exit hole.

Nothochrysa and the other known nothochrysine genera is consistent with the pattern of variation expressed in adult morphology. Most notable among the larval traits is the difference in larval life style between the small-bodied genera and *Nothochrysa*. Three of the small-bodied genera—*Hypochrysa*, *Pimachrysa*, and *Dictyochrysa*—are now known

to have naked larvae; they have narrow, fusiform bodies that lack lateral tubercles on the thorax and abdomen and are without laterodorsal tubercles on all abdominal segments. In marked contrast, the larvae of the European *Nothochrysa* species and the North American *N. californica* are debris-carriers; they have broad, somewhat flattened bodies, small

but distinct, sclerotized, lateral tubercles on the thorax and abdominal segments A2 through A7, as well as other morphological adaptations for holding debris (Box 1).

It is noteworthy that within the family Chrysopidae, life style (larval nakedness versus debris-carrying) is associated with numerous morphological and behavioral adaptations, and yet it is an evolutionarily very labile trait. Debris carrying occurred very early in chrysopid evolutionary history [24], and both naked and debris-carrying forms have evolved numerous times within the family [5, 24]. Thus, it could be argued that the characters above are redundant—all an expression of the naked versus debris-carrying life styles. However, it is important that, in addition to features associated with life style, the larvae of *Nothochrysa* species also differ from other nothochrysinines in features that appear unrelated to their debris-carrying habit (Box 2). For example, as discussed above, larvae of *Nothochrysa* species show a broad range of interspecific and developmental variation in flagellar length and in the length and structure of the terminal seta(e) on the flagellum. They also differ in their head markings and in the shape and size of the pronotal sclerites. Each of these characters provides independent support that *Nothochrysa* is distinct from the smaller-bodied nothochrysinine genera and that species within *Nothochrysa* present a series of intermediate conditions between the more archaic extant nothochrysinines (e.g., *Dictyochrysa*, *Hypochrysa*, and *Pimachrysa*) and the Apochrysininae-Chrysopinae lineage(s). If this hypothesis proves true, not only would pollen-feeding likely be an ancestral adult feature of the extant Chrysopidae (as proposed by Duelli et al. [4]), but also nakedness would likely be their ancestral larval life style.

(Note: a previous description [6] of the *H. africana* second instar had some errors in the designation of setal numbers on the dorsum of the head. For accuracy in comparisons with *Pimachrysa* and other nothochrysinine larvae, Figure 15 here corrects those errors.)

Disclosure

This study is part of Regional Project W-3185.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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References

- [1] P. A. Adams, “A review of the mesochrysininae and nothochrysininae (Neuroptera: Chrysopidae),” *Bulletin of the Museum of Comparative Zoology*, vol. 135, no. 4, pp. 215–238, 1967.
- [2] S. J. Brooks, “An overview of the current status of Chrysopidae (Neuroptera) systematics,” *Deutsche Entomologische Zeitschrift*, vol. 44, no. 2, pp. 267–275, 1997.
- [3] S. B. Archibald and V. N. Makarkin, “A new species of *Archaeochrysa* Adams (Neuroptera: Chrysopidae) from the early Eocene of Driftwood Canyon, British Columbia, Canada,” *Canadian Entomologist*, vol. 147, no. 4, pp. 359–369, 2015.
- [4] P. Duelli, H. Hölzel, and M. W. Mansell, “Habitat and larvae of the enigmatic genus *Kimochrysa* Tjeder (Neuroptera: Chrysopidae) in South Africa,” in *Proceedings of the Tenth International Symposium on Neuropterology (22–25 June 2008, Piran, Slovenia)*, D. Devetak, S. Lipovsek, and A. E. Arnett, Eds., pp. 153–158, University of Maribor, Maribor, Slovenia, 2010.
- [5] C. A. Tauber, M. J. Tauber, and G. S. Albuquerque, “Debris-carrying in larval Chrysopidae: unraveling its evolutionary history,” *Annals of the Entomological Society of America*, vol. 107, no. 2, pp. 295–314, 2014.
- [6] C. A. Tauber, “Nothochrysininae (Neuroptera: Chrysopidae): new larval description and generic synonymy, with a consideration of generic relationships,” *Psyche*, vol. 2014, Article ID 839261, 10 pages, 2014.
- [7] S. Winterton and S. de Freitas, “Molecular phylogeny of the green lacewings (Neuroptera: Chrysopidae),” *Australian Journal of Entomology*, vol. 45, no. 3, pp. 235–243, 2006.
- [8] N. Haruyama, A. Mochizuki, P. Duelli, H. Naka, and M. Nomura, “Green lacewing phylogeny, based on three nuclear genes (Chrysopidae, Neuroptera),” *Systematic Entomology*, vol. 33, no. 2, pp. 275–288, 2008.
- [9] F. W. Stehr, “Techniques for collecting, rearing, preserving, and studying immature insects,” in *Immature Insects*, F. W. Stehr, Ed., pp. 7–18, Kendall/Hunt Publishing Company, Dubuque, Iowa, USA, 1987.
- [10] A. Rousset, *Morphologie Céphalique des Larves de Planipennes (Insectes Névroptéroïdes)*, vol. 42 of *Memoires du Museum National d'Histoire Naturelle Series A: Zoology*, Éditions du Muséum, Paris, France, 1966.
- [11] S. Tsukaguchi, *Chrysopidae of Japan (Insecta, Neuroptera)*, S. Tsukaguchi, Nishinomiya-shi, Japan, 1995.
- [12] C. A. Tauber, M. J. Tauber, and G. S. Albuquerque, “*Berchmansus elegans* (Neuroptera: Chrysopidae): larval and adult characteristics and new tribal affiliation,” *European Journal of Entomology*, vol. 103, no. 1, pp. 221–231, 2006.
- [13] V. J. Monserrat and L. M. Díaz-Aranda, “Los estadios larvarios de los Crisópidos ibéricos (Insecta, Neuroptera, Chrysopidae), nuevos elementos sobre la morfología larvaria aplicables a la sistemática de la familia,” *Graellsia*, vol. 68, no. 1, pp. 31–158, 2012.
- [14] T. R. New, “Some early stages of *Dictyochrysa* Esben-Petersen (Neuroptera, Chrysopidae),” *Neuroptera International*, vol. 1, no. 3, pp. 136–140, 1981.
- [15] F. Brauer, “Larve von *Hypochrysa nobilis* Heyd,” in *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, vol. 17, pp. 27–30, Zoologisch-Botanische Gesellschaft in Wien, 1867.
- [16] C. A. Toschi, “The taxonomy, life histories, and mating behavior of the green lacewings of Strawberry Canyon (Neuroptera: Chrysopidae),” *Hilgardia*, vol. 36, no. 11, pp. 391–433, 1965.

- [17] F. J. Killington, *A Monograph of the British Neuroptera*, vol. 2, Ray Society, London, UK, 1937.
- [18] L. M. Díaz-Aranda and V. J. Monserrat, "Aphidophagous predator diagnosis: key to genera of European chrysopid larvae (Neur.: Chrysopidae)," *Entomophaga*, vol. 40, no. 2, pp. 169–181, 1995.
- [19] E. G. MacLeod, "The immature stages of *Boriomyia fidelis* (Banks) with taxonomic notes on the affinities of the genus *Boriomyia* (Neuroptera: Hemerobiidae)," *Psyche*, vol. 67, no. 1-2, pp. 26–40, 1960.
- [20] A. H. Krakauer and C. A. Tauber, "Larvae of *Micromus*: generic characteristics and a description of *Micromus subanticus* (Neuroptera: Hemerobiidae)," *Annals of the Entomological Society of America*, vol. 89, no. 2, pp. 203–211, 1996.
- [21] T. R. New, "The immature stages of *Drepanacra binocula* (Neuroptera: Hemerobiidae), with notes on the relationships of the genus," *Australian Journal of Entomology*, vol. 14, no. 3, pp. 247–250, 1975.
- [22] J. D. Oswald and C. A. Tauber, "Recognition of larval Neuroptera. Preimaginal stages of the family Hemerobiidae," in *Lacewings in the Crop Environment*, P. K. McEwen, T. R. New, and A. E. Whittington, Eds., pp. 50–60, Cambridge University Press, Cambridge, UK, 2001.
- [23] P. A. Adams and N. D. Penny, "Review of the South American genera of Nothochrysinæ (Insecta: Neuroptera: Chrysopidae)," in *Current Research in Neuropterology, Proceedings of the Fourth International Symposium on Neuropterology (24–27 June 1991, Bagnères-de-Luchon, Haute-Garonne, France)*, M. Canard, H. Aspöck, and M. W. Mansell, Eds., pp. 35–41, M. Canard, Toulouse, France, 1992.
- [24] R. Pérez-de la Fuente, X. Delclòs, E. Peñalver et al., "Early evolution and ecology of camouflage in insects," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 109, no. 52, pp. 21414–21419, 2012.