Debris-Carrying in Larval Chrysopidae: Unraveling Its Evolutionary History

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ABSTRACT   Larval debris-carrying, which occurs in many insect taxa, is a remarkable behavioral trait with substantial life history significance. For the Chrysopidae, information on the topic is scattered, and the habit's diversity and evolutionary history are unassessed. Here, we compile a comprehensive, annotated catalog on chrysopid debris-carrying and its associated larval morphology, and we identify emerging systematic patterns of variation, from larval nakedness to the construction of elaborate packets. Then, we examine these patterns in the context of available phylogenies with two objectives: 1) to begin unraveling the evolutionary history of chrysopid debris-carrying and 2) to evaluate the current and potential role of larval morphology (including debris-carrying modifications) in classification and phylogeny of this family. Debris-carrying: the literature revealed that debris-carrying occurs in the chrysopoid fossil record and in all three extant chrysopid subfamilies, including those proposed as basal (Nothochrysinae, Apochrysinae). Nevertheless, the family's ancestral state remains unresolved. The habit may have evolved at least once in Nothochrysinae or been lost several times. Larvae from only one genus of Apochrysinae are known, and they are debris-carriers. Each of the four tribes of the third subfamily, Chrysopinae, has distinctive debris-carrying characteristics. In ankylopterygine larvae, debris-carrying modifications seem relatively conserved. Among the ant-associated belonopterygine genera, debris-carrying is either highly evolved or, in one case, possibly absent. Within the large chrysopine tribe, nakedness and debris-carrying appear to have evolved independently numerous times; also, some reversals may have occurred. With one possible exception, leucochrysine genera have debris-carrying larvae. Larval morphology: scrutiny of the literature showed that all chrysopid genera whose larvae are known exhibit characteristic suites of anatomical structures related to carrying debris. Moreover, larval morphology provides strong (synapomorphic) evidence for the monophyly of four of the seven suprageneric chrysopid taxa: the subfamily Nothochrysinae and three of the four tribes of Chrysopinae (Ankylopterygini, Belonopterygini, and Leucochrysini). Larval morphological and debris-carrying characteristics appear to support some, but not all, previously proposed generic relationships within the tribe Chrysopini. Given the demonstrated potential advantages for including larval characters in chrysopid phylogenetic studies, it is essential to enhance the pool of available larval data. Therefore, we propose that citizen-scientists be involved in gathering verifiable data and that systematists develop comprehensive data matrices for comparative larval studies.

KEY WORDS   camouflage, phylogeny, larval morphology, trash-carrying, Neuroptera

Among insects, the larval habit of camouflaging or shielding the body with exogenous organic or inorganic material (= debris-carrying) is an elaborate behavioral attribute with far-reaching life history and evolutionary consequences (e.g., see Principi 1943, 1946; Eisner et al. 1978; Milbrath et al. 1993, 1994; Tauber et al. 1995b; Brandt and Mahsberg 2002; Bucheli et al. 2002). Examples exist in a wide range of insect orders,[4] including Hemiptera, Trichoptera, Lepidoptera, Coleoptera, and Neuroptera. Within the Chrysopidae, this behavior occurs in the majority (≈65%) of genera for which larvae are known (Appendix 1), and it appears closely associated with the

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[4] Hemiptera: Reduviidae (Butler 1923, Brandt and Mahsberg 2002); Trichoptera: most families (Wiggins 1977); Lepidoptera: Geometridae (Ferguson 1985), Coleophoridae (Bucheli et al. 2002, Falkovitsh 2003), Psychidae (Rhainds et al. 2009); Coleoptera: Derodontidae (Brown and Clark 1962), Curculionidae (Gressitt et al. 1968), Chrysomelidae (Chaboo et al. 2008, Chaboo 2011), Endomychidae (Leschen and Carlton 1993), Sphindidae (McHugh and Kiselyova 2003); Neuroptera: Ascalaphidae (Henry 1977); Myrmeleontidae (Robert Miller and Lionel Stange, personal communication), Sisyridae (Killington 1936, 1937), Chrysopidae (e.g., Smith 1926; Killington 1936, 1937; Catalog, Supp Table 1 [online only]).

evolutionary diversification of the family (Tauber and Tauber 1989, Tauber et al. 1993).

Much information on debris-carrying within the Chrysopidae has accumulated over the past ≈90 yr. During this period, systematic and natural history studies documented a wide range of variation in chrysopid debris-carrying and concomitant modifications in larval anatomy. However, the information has been neither compiled nor examined in detail, and the evolutionary history of debris-carrying has not been explored phylogenetically. To assess current knowledge and provide a foundation for future work, we: 1) assemble, in a systematically based catalog, the dispersed literature on the larval morphology and debris-carrying habits of chrysopids and their chrysopoid ancestors (Catalog, Supp Table 1 [online only]); 2) search for evolutionary patterns contained within the current literature; 3) highlight significant findings for specific taxa; and 4) identify taxa whose poorly known larvae might yield especially important comparative information.

Finally, despite the proven value of immatures in phylogenetic analysis in other insect groups (e.g., see Oberprieler et al. 2000, Meier and Lim 2009), we document their almost complete absence from chrysopid phylogenies. In doing so, we also provide a rationale for using larval characters, including those related to debris-carrying, in phylogenetic analyses of the Chrysopidae, and we offer recommendations whereby specialists and citizen-scientists can cooperate to accelerate the process.

Background

Debris-Carrying. Both the behavioral and morphological components of larval debris-carrying in chrysopids exhibit valuable taxon-specific variation. Although the behavior involved in constructing a dorsal cloak or packet (often referred to as "loading behavior"; see Fig. 2F) is described for only a very small number of species, many reports have focused on the packet as an indicator of the underlying behavior. For example, in nature, larvae of most species appear to be selective in the material they use for their coverings, and as a consequence, the composition of the packet can be taxonomically significant. Depending on the species, this material may include waxy flocculence from the sternorrhynchan prey; arthropod exoskeletons, exuviae, snail shells, or fragments thereof; small pieces of dried leaves or wood, trichomes, or lichens; silken threads from spiders or mites; and sand or soil (e.g., see Smith 1922, Eisner et al. 2002, Anderson et al. 2003).

Other aspects of the larval packet also vary among species, for example, the amount (weight) of the material carried, the size of the packet relative to the body, the mode of attachment, and the degree of the packet's cohesiveness. Any of these features could be taxonomically informative; regrettably, their value is unknown because reports in the literature are few and interspecific comparisons are meager. Typical coverings include a small number of scattered pieces of material loosely held by hooked setae on the dorsum, light layers of material intertwined with long setae,

loosely to tightly constructed cloaks that partially or completely cover the larval body, and very dense shields that are tightly attached and intertwined with silken strands and that extend well beyond the outline of the larval body.

Furthermore, larvae show interspecific variation in the frequency with which they carry debris: some species carry debris occasionally or during a specific instar, which is usually the first instar ("occasional debris-carriers"). Generally, the occasional debris-carriers carry scattered pieces of material. Ideally, if sufficient data were available, we could categorize each species (e.g., "debris-carrier" if all instars consistently have a distinct covering of material; "light debris-carrier" if all instars usually carry a few, scattered fragments of material; "occasional debris-carrier" if only some instars or some individuals carry material; or "naked" if all instars are usually without debris). In reality, for most species, data are only sufficient to differentiate "naked" (without debris) from "debris-carrying" in the broad sense of the term (see Figs. 1–3 for examples).

In contrast to the behavioral variation above, the numerous features of larval morphology implicated in debris-carrying are relatively well-documented, and a broader range of taxa is included. Table 1 describes the features that are typically associated with either naked larvae or with debris-carriers. What is especially striking is that larvae express great variation in these traits and yet no specific combination of features defines either of the two lifestyles.

Literature. Larval debris-carrying in Chrysopidae has been documented for >275 yr (since Réaumur's [1737] report). Many subsequent papers referred to the behavior, but often anecdotally and with varying amounts of detail. For some taxa, the information reflects numerous observations accumulated over many years; in others, only one observation may be available. Our catalog here (Catalog, Supp Table 1 [online only]) includes all the references to larval debris-carrying and larval morphology that we found for each chrysopid species.

Larval morphology has long been a key element in neuropteran systematics and phylogeny at the ordinal level (initiated by Withycombe [1922, 1924] and Tillyard [1926], advanced by Ellis MacLeod [1960, 1964], and continuing to the present by Aspöck and Aspöck [2007] and Monserrat [1996, 2008]). Moreover, at the family level, comparative larval morphology has constituted a substantial element in the classification of the two largest neuropteran families: Myrmeleontidae (e.g., Stange and Miller 1990, Stange 2004, Miller and Stange 2012) and Chrysopidae (see below).

For the family Chrysopidae, comparative descriptive studies that deal with larvae began mainly during the 1920s and 1930s, with studies by Smith, Lacroix, Withycombe, and Killington (Appendix 1; Catalog, Supp Table 1 [online only]). Later researchers, in the 1940s through the 1970s (Principi, Tjeder, Tauber, Monserrat, Tsukaguchi, and others), identified the value of larval morphology in deciphering the identity and relationships of chrysopid taxa especially at the
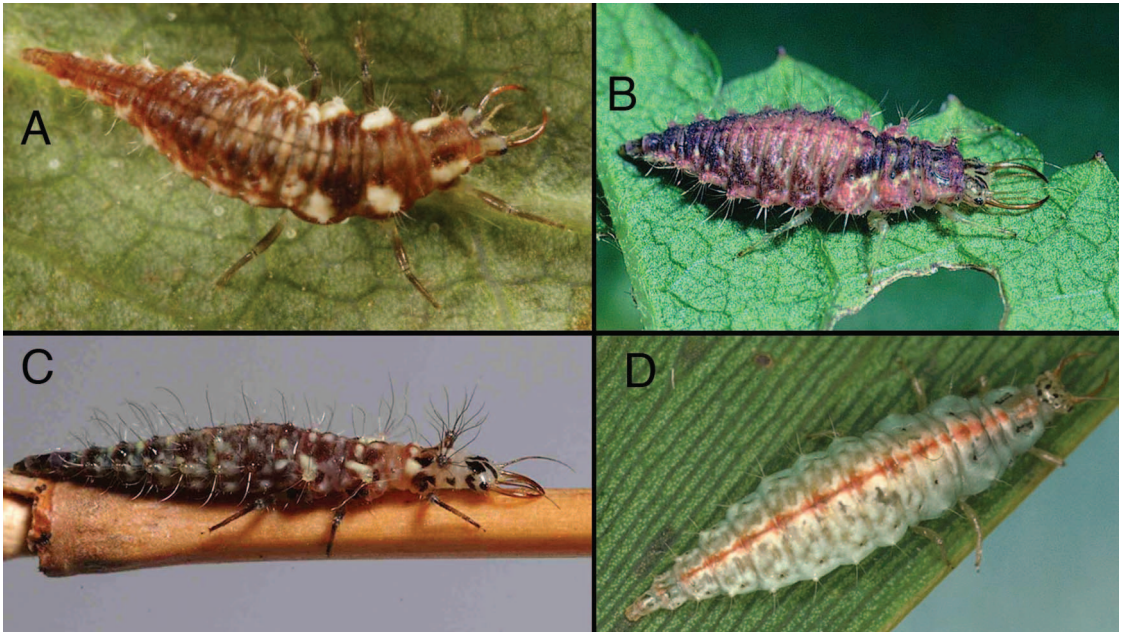
Fig. 1. Examples of naked chrysopid larvae: all Chrysopinae, Chrysopini. (A) *Chrysoperla rufilabris* (Burmeister), (B) *Meleoma signoretii* Fitch, (C) *Chrysopa oculata* Say, and (D) *Anomalochrysa hepatica* McLachlan. Photos by: Lyle Buss (A), Stephen A. Marshall (B and C), and M.J.T. (D). (Online figure in color.)

generic level; during the 1940s and 1950s, the work of Professor Maria Matilde Principi set the "gold standard" in morphological detail, clarity, and esthetics.

The last three decades saw a considerable increase in information on immature stages from various regions (Appendix 1; Catalog, Supp Table 1 [online only]): Africa (Hölzel and colleagues), Asia (Tsukaguchi), Australia and Micronesia (Adams; New; Boros), Hawaii (Tauber and Tauber), Europe (Gepp and colleagues; Monserrat and Díaz-Aranda), and the New World (Tauber, Tauber, Albuquerque, and colleagues; Freitas). Publications by these and other authors provide the basis for this review. The recent compilation of research on the Iberian fauna (Monserrat and Díaz-Aranda 2012) takes an in-depth view of the fauna, from subfamilies to species, and it emphasizes the great advantage of using immature stages (especially first instars) in chrysopid systematics at all hierarchical levels. It constituted a valuable resource for this work.

Our bibliographic record (Catalog, Supp Table 1 [online only]) is presented within a taxonomic framework. Each listing identifies the type of information that is contained in the reference cited: whether larvae are described and, if so, which instar(s); whether drawings or photos are provided and, if so, which instar(s); and, whether additional information is available (e.g., the type of material carried, the instar[s] carrying debris). We restricted our citations on the type of material used to those packets that larvae constructed in their natural habitat because in the laboratory, larvae often carry material not used in nature. Despite our efforts, we may have missed some publications.

Although the chrysopid larval stage includes three instars (L1, L2, and L3), most current information refers only to the first or third. The first instar (Semaphoront A) differs markedly in structure, setation, and often coloration from the other two instars (Semaphoront B), which differ from each other only in minor ways that are largely related to size and setal numbers. Thus, for systematic purposes, first and third instars constitute the most useful and phylogenetically informative larval stages for evaluation; they are the ones that we use here (see Wheeler 1990 for a discussion of phylogenetically relevant comparisons among instars).

Phylogenetic Framework. As a basis for our analysis, we used the three phylogenetic studies that are available for the Chrysopidae; all three offer provisional and restricted, but useful, results. One is based on morphological characters; it includes all genera in the family, but the phylogenetic comparisons are largely informative only at the subfamilial and tribal levels (Brooks and Barnard 1990, expanded by Brooks 1997). It is noteworthy that all but one of the morphological characters in this study stem from the adult stage. The other two phylogenetic studies (Winterton and Freitas 2006, Haruyama et al. 2008) are based on molecular data; their analyses extend to the generic level, but each included a very different range of taxa and each has significant limitations in the diversity and number of species it sampled.

Given the disparities among each of the above studies, it is not surprising that they differ in their support for the monophyly and relationships among the three chrysopid subfamilies (Apochrysinae, Chrysopinae, and Nothochrysinae). In the morphologically based
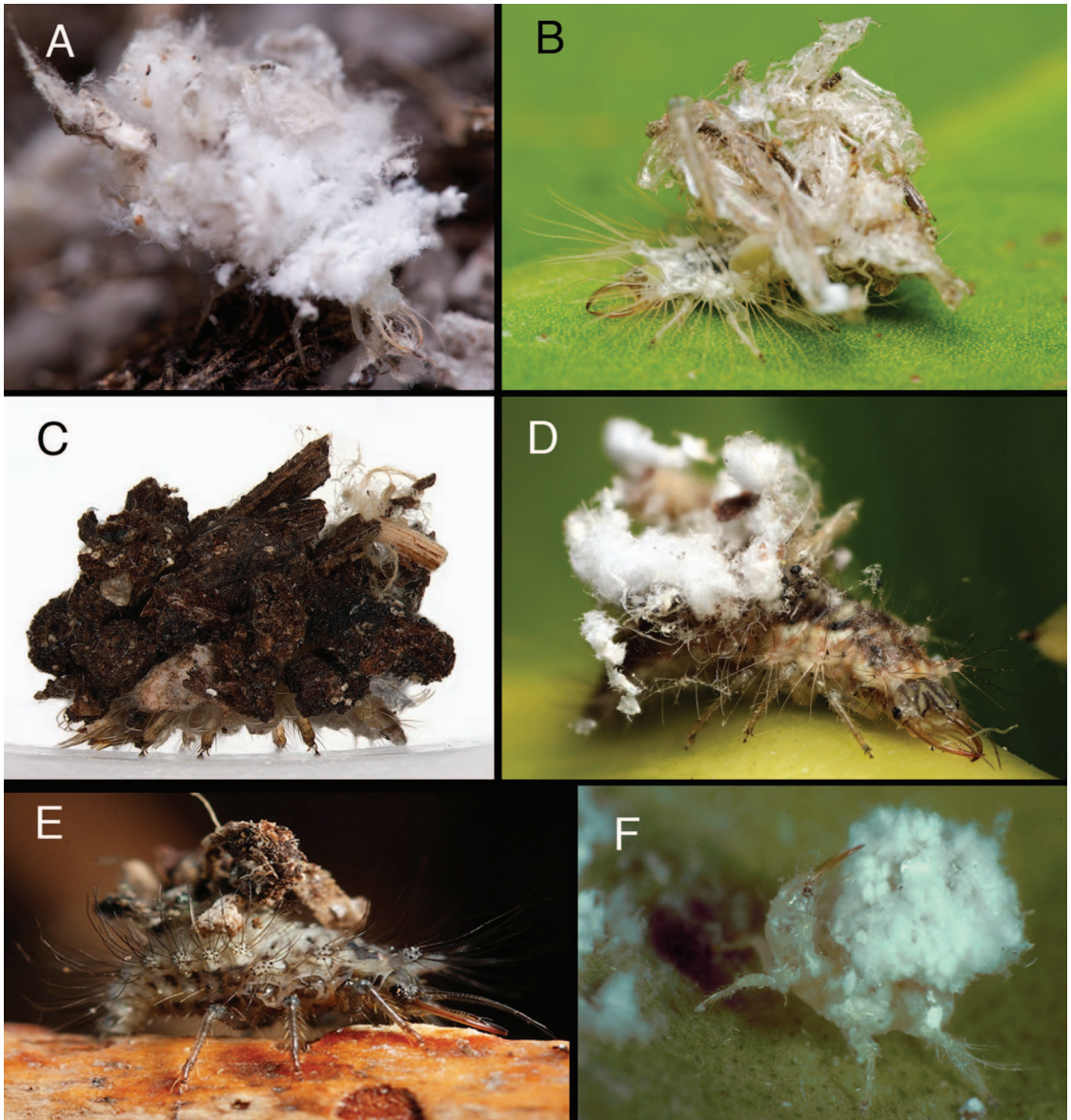
Fig. 2. Examples of debris-carrying chrysopid larvae. (A) Apochrysinae: *Apochrysa matsumurae* (Okamoto) (identification not confirmed), carrying flocculence and material from male "cocoons" of the coccoidean *Drosicha corpulenta* (Kuwana); (B) Chrysopinae, Ankylopterygini: *Semachrysa matsumurae* (Okamoto) (identification not confirmed), carrying exuviae and arthropod parts; (C) Chrysopinae, Belonopterygini: *Italochrysa italica* (Rossi) (identification by R. A. Pantaleoni), carrying pieces of woody material; (D) Chrysopinae, Chrysopini: *Cunctochrysa albolineata* (Killington) (identification by R. A. Pantaleoni), carrying flocculence, miscellaneous animal material; (E) Chrysopinae, Chrysopini: *Pseudomallada* sp. (identification not confirmed); (F) Chrysopinae, Chrysopini: *Chrysopa slossonae* Banks, first instar engaging in "loading behavior," with flocculence from wooly alder aphids (*Prociphilus tesselatus* [Fitch]). Photos by Yusei Hara (A and B), Roberto A. Pantaleoni and Carlo F. Cesaroni (C), Brian P. Valentine (D), Gilles San Martin (E), and Thomas and Maria Eisner (F). (Online figure in color.)

phylogeny (Brooks and Barnard 1990, Brooks 1997), all three subfamilies are considered monophyletic, and Nothochrysinae is sister and basal to the other two subfamilies.

In comparison, the first molecular study (Winterton and Freitas 2006) recovers only two of the subfamilies (Nothochrysinae and Chrysopinae) as monophyletic clades, and a weakly supported Apochrysinae (exclu-sive of one exceptional genus) is found to be sister to Nothochrysinae + Chrysopinae. This study involved 18 of the >80 known chrysopid genera; all suprage-neric taxa included at least one representative.

The second molecular study (Haruyama et al. 2008) included more genera ($n = 24$) than the first. Most were in Chrysopinae (tribe Chrysopini); tribe Leu-cochrysini was excluded. In this study, Chrysopinae is
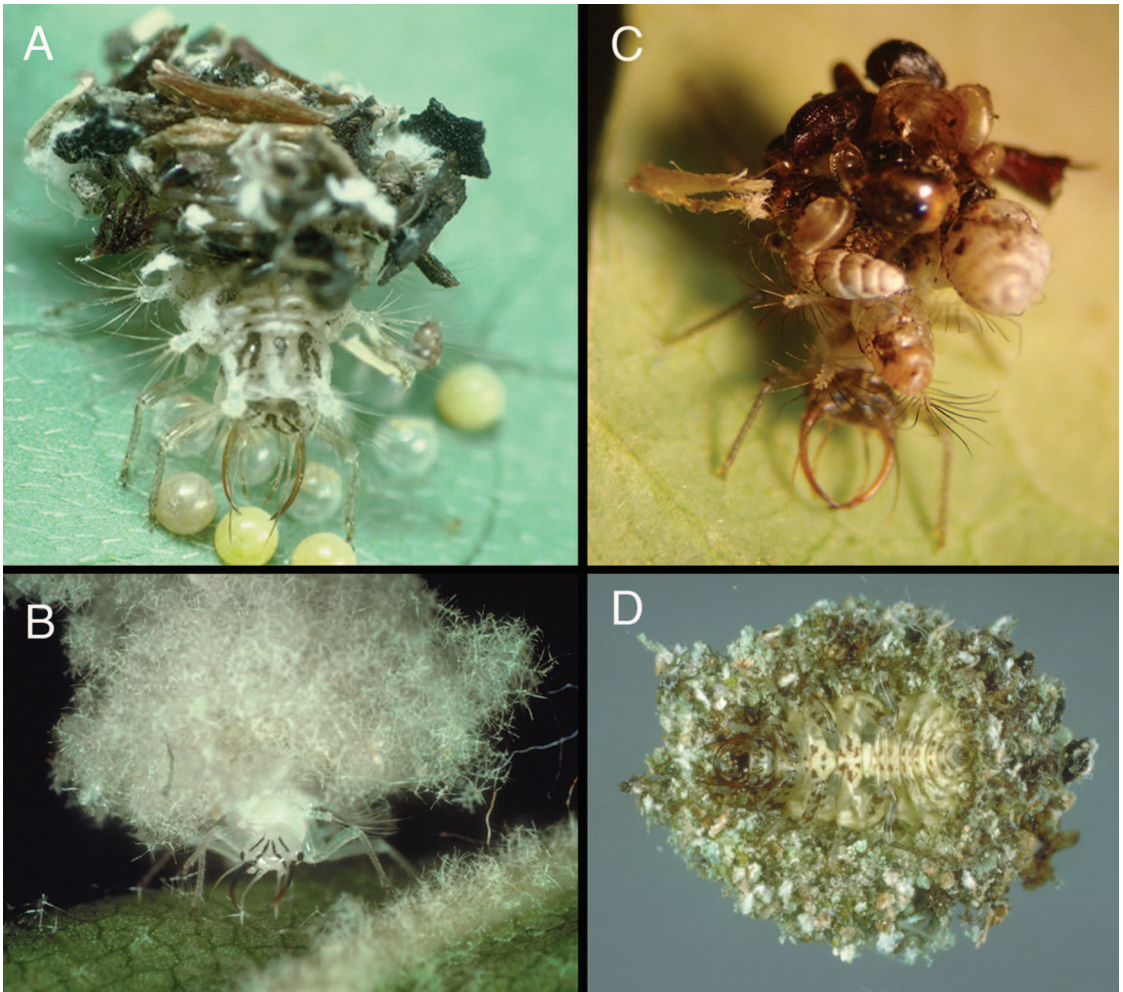
Fig. 3. Examples of debris-carrying chrysopid larvae. (A) Chrysopinae, Chrysopini: *Ceraeochrysa smithi* (Navás) carrying small fragments of dried plant material, (B) Chrysopinae, Chrysopini: *Ceraeochrysa lineaticornis* (Fitch) carrying trichomes from sycamore leaves, (C) Chrysopinae, Leucochrysini: *Leucochrysa (Leucochrysa) insularis* (Walker) carrying snail shells and living snails, and (D) Chrysopinae, Leucochrysini: *Leucochrysa (Nodita) pavida* (Hagen) carrying lichens (ventral view). Photos by Thomas and Maria Eisner (A, B, and D) and Daniel C. Dourson (C). (Online figure in color.)

the only subfamily with support for monophyly; it was recovered as sister to an unresolved Apochrysinae + Nothochrysinae. Thus, the early evolutionary history of the Chrysopidae remains largely enigmatic.

Despite the above limitations and differences, each of the three phylogenies presents some credible phylogenetic hypotheses for evaluating currently known patterns of chrysopid debris-carrying.

Evolutionary Patterns of Larval Debris-Carrying

Family Chrysopidae

At least some larvae are known from each of the chrysopid suprageneric taxa (Appendix 1; Catalog, Supp Table 1 [online only]). As a result, several general observations regarding debris-carrying in the Chrysopidae are apparent: 1) debris-carrying occurs within all the major lineages of Chrysopidae, including the three subfamilies and all four tribes of Chrysopinae. 2) The larvae of each chrysopid genus studied to date express a unique suite of anatomical features, most of which may be associated with the debris-carrying habit. 3) Because the available larval data and the phylogenetic trees lack sufficient sampling of basal taxa, it is not yet known whether debris-carrying or nakedness is the ancestral state for the family. 4) Larval synapomorphies support the monophyly of the subfamily Nothochrysinae and three of the four tribes in Chrysopinae (Ankylopterygini, Belonopterygini, and Leucochrysini). However, they have not yet been identified for subfamilies Apochrysinae and Chrysopinae or the tribe Chrysopini. 5) The larvae of each chrysopid genus express a unique suite of characteristics; in

Table 1. Major morphological features that are typically associated with debris-carrying and naked chrysopid larvae

Structure	Debris-carrier	Naked larva
Body		
Shape	Globose, humped	Fusiform, flat
Setae	Numerous, mid-length to long, hooked	Few to numerous, short, acute
Head		
Setae	Textured	Smooth
Thorax		
Lateral tubercles (LTs)	Cylindrical, digitiform	Absent, hemispherical
Setae on LTs	Elongate, textured, hooked, multipronged	Mid-length, smooth, acute
Setae on posterior T3	Numerous, robust, textured, hooked	Few, slender, smooth, acute (rarely modified)
Laterodorsal tubercles (LDTs)	Present	Absent
Dorsal setae	Sometimes numerous, often modified	Usually sparse, unmodified (acute, blunt)
Abdomen		
A1: LDTs	Present, sometimes large	Absent or very small
A1: setae on LDTs	Numerous, long, textured, hooked	Few, small, smooth, acute
A2–A5: LTs	Papilliform, digitiform	Absent, hemispherical, spherical
A2–A5: setae on LTs	Elongate, textured, hooked	Mid-length, smooth, acute
A2–A5: LDTs	Prominent	Absent or very small
A2–A5: setae on LDTs	Numerous, long, textured, hooked	Few, small, acute
Submedian setae (SMS)	Midlength to long (stout), often textured, hooked, or modified	Short to midlength (slender), smooth, acute or blunt, rarely modified

Larvae usually do not express all of the individual features associated with either of the life styles; in reality, there is a full range of variation between debris-carrying and nakedness.

some cases, individual character-states appear autapomorphic for the genus.

Our specific, taxon-based analysis begins below, with the two small, presumably basal, chrysopid subfamilies: Nothochrysinae and Apochrysinae. The larger subfamily Chrysopinae and its four tribes follow, and the analysis concludes with the chrysopoid fossil record and a brief summary of the resulting taxon-based patterns.

Subfamily Nothochrysinae

Despite its small size, the subfamily Nothochrysinae exhibits a broad range of variation in its debris-carrying habits. Larvae are known from four of its nine genera (Catalog, Supp Table 1 [online only]), of these, three are naked (*Hypochrysa*, *Dictyochrysa*, and *Kimochrysa*), and one is a debris-carrier (*Nothochrysa*).

None of the naked larvae in the subfamily are reported to have any of the usual morphological modifications for debris-carrying (New 1981; Monserrat and Díaz-Aranda 2012; C.A.T., unpublished data). The known larvae (L2 and L3) of *Hypochrysa* and *Kimochrysa* are green and very cryptic against a background of green foliage (Duelli et al. 2010), and they have very unusual "bacilliform" (= short, rodlike, blunt to slightly clavate) setae (Monserrat and Díaz-Aranda 2012, C.A.T., unpublished data). Those of *Dictyochrysa* (L1) are buff-colored with brown patches; they too have short, blunt dorsal setae (New 1981).

All of the known larvae of the fourth genus, *Nothochrysa* (*n* = 3 of 7 species), are debris-carriers (Catalog, Supp Table 1 [online only]). Typically, their packets are substantial to moderate in size, and they contain few, but relatively large, fragments of woody or leafy (dried) plant material, lichens, and frass. Their morphological modifications for debris-carrying are modest; for example, the bodies are only slightly thick-

ened, the lateral tubercles of the thorax and abdomen are small and carry few setae, and laterodorsal tubercles are absent from the abdomen (Toschi 1965, Monserrat and Díaz-Aranda 2012). Nevertheless, all instars have numerous hooked and filiform setae on the dorsum of the abdomen. The three described *Nothochrysa* species exhibit some variation in the morphological structures associated with carrying debris (e.g., in the degree of development of lateral tubercles and in the number of large setae associated with thoracic and abdominal tubercles).

Nothochrysinae is generally considered a relict group based on the retention of plesiomorphic conditions; as yet, adult morphology has provided no clear synapomorphies to unite the group (e.g., Adams 1967, Adams and Penny 1992, Brooks and Barnard 1990, Brooks 1997).[5] However, several larval synapomorphies (based on specimens from four genera) are now proposed (Appendix 1; also Monserrat and Díaz-Aranda 2012, C.A.T., unpublished data). All of them are on cranial appendages and are not associated in an obvious way with debris-carrying.

A cladogram for the nine genera of Nothochrysinae, based on adult (wing and genital) characters (Fig. 1 in Brooks 1997), depicts one well-supported clade con-

[5] As an aside, we propose that an overlooked possible source of informative characters (adult stage) is the unique form of reproductive behavior currently documented for two genera in Nothochrysinae (Principi 1956, Toschi 1965). After mating, *Hypochrysa* and *Nothochrysa* females retain the spermatophore externally, at the tip of the abdomen, for >1 hr; during this time the abdomen pulsates and the contents of the spermatophore appear to be drawn into the female abdomen; subsequently the female eats the shell of the spermatophore. In addition, during mating, a mass of frothy, granular material (distinct from the spermatophore) is transferred from the male to the female: onto the lateral surface of the female abdomen (*Nothochrysa*) or associated with the spermatophore (*Hypochrysa*). It would be of great interest to learn whether any of these reproductive features are shared by the other seven genera in the subfamily, and if they have associated anatomical modifications that would be pertinent to systematic study.

taining five of the genera; relationships among the remaining four genera (including *Kimochrysa*) are unsupported. Our recent studies of *Kimochrysa* larvae indicate that this genus is very closely related to *Hypochrysa*, which falls within the supported clade (C.A.T., unpublished data). Given that the ancestral larval condition of Nothochrysinae is unknown, this cladogram is consistent with two alternative hypotheses regarding the evolution of debris-carrying in the subfamily. The most parsimonious assumes nakedness as the basal state, in which case debris-carrying would have evolved at least once (*Nothochrysa*). However, if debris-carrying were ancestral, then nakedness would have evolved independently two times (*Dictyochrysa* and *Hypochrysa* + *Kimochrysa*).

Subfamily Apochrysinae

Although there are six valid genera in the Apochrysinae (Winterton and Brooks 2002), larvae are known from only one, *Apochrysa* (Appendix 1; Catalog, Supp Table 1 [online only]). The third instar of *Apochrysa matsumurae* (Okamoto) was described and reported to be a debris-carrier (Tsukaguchi 1995). Photos (one by P. Duelli in Aspöck and Aspöck [2007], and another, Fig. 2A here) show *Apochrysa* third instars carrying flocculence from sternorrhynchan prey.

The anatomy of the described *Apochrysa* larva is typical of debris-carriers or occasional debris-carriers. For example, the abdomen is moderately thickened, and it bears well-developed lateral tubercles and small laterodorsal tubercles (Tsukaguchi 1995). The setae are not especially modified for debris-carrying, but are numerous, with some weakly hooked and many relatively long.

The monophyly of Apochrysinae seems well-supported by the adult morphology (Brooks and Barnard 1990). However, the few known larvae of the group have not been shown to express features that distinguish them from debris-carrying larvae in the subfamily Chrysopinae. It is possible that larval support for Apochrysinae is absent because very few larval characters and very few taxa from Apochrysinae have been examined. Thus, additional studies are needed.

In this regard, we noted in Tsukaguchi's illustration of the *A. matsumurae* third instar a character that is worthy of exploration, that is, the mesothoracic and metathoracic lateral tubercles appear longer than those of the prothorax. This condition has not been reported for other chrysopid taxa.

Subfamily Chrysopinae

Currently, the large and diverse subfamily Chrysopinae is distinguished by two relatively strong apomorphies from adult morphology (antennal setae in four rings, alar tympanal organ enlarged; Brooks and Barnard 1990, Brooks 1997). Also, a unique suite of larval features distinguishes the subfamily; however, the individual features that comprise the suite are shared with either Apochrysinae or Nothochrysinae, and the

taxa comprising Chrysopinae, as yet, have no confirmed larval synapomorphies (Appendix 1).

The three phylogenies differ with regard to the monophyly and the relationships of the tribes included within Chrysopinae. First, with regard to monophyly, Brooks (1997) provides some morphological evidence for the monophyly of Belonopterygini, Leucochrysini, and Ankylopterygini, but the single apomorphy proposed for Chrysopini is inconsistent among the included taxa. The results of Winterton and Freitas (2006) provide evidence for the monophyly of each of the four tribes; those of Haruyama et al. (2008) support monophyly for Ankylopterygini and for Belonopterygini, but not for Chrysopini (Leucochrysini was not tested).

Second, with regard to the relationships among the four tribes, the morphological study places a monophyletic grouping of Belonopterygini + Leucochrysini in a sister relationship with a monophyletic grouping of Ankylopterygini + Chrysopini; however, the features proposed as apomorphies in support of these groupings are highly variable. One of the molecular studies (Winterton and Freitas 2006) places a monophyletic Chrysopini as sister to the monophyletic grouping of (Belonopterygini + [Leucochrysini + Ankylopterygini]). In the second molecular study (Haruyama et al. 2008), the Chrysopini is paraphyletic, and its relationship with the other tribes is unclear. The chrysopine genera that were examined fell into seven clades, all with various degrees of support.

Larval morphology provides support (synapomorphic character states) for the monophyly of two of the four tribes (Belonopterygini and Leucochrysini). Larvae in the other two tribes (Ankylopterygini and Chrysopini) are in need of further comparative study.

Tribe Ankylopterygini. Larvae from three of the five known ankylopterygine genera (*Ankylopteryx, Parankylopteryx, Semachrysa*) are classified as debris-carriers (Appendix 1; Catalog, Supp Table 1 [online only]). Detailed larval descriptions are available for two of the three genera (Hölzel et al. 1990, Tsukaguchi 1995). These larvae share a suite of anatomical features related to debris-carrying: their bodies are moderately humped; they have long, cylindrical lateral tubercles on the thorax and well-developed, hemispherical lateral tubercles on the abdomen; and the dorsal setae on abdominal segments A2 through A6 are hooked. In contrast, laterodorsal tubercles appear to be absent from abdominal segments A1 through A5, and setae on the lateral tubercles and thoracic nota are relatively sparse and unhooked. The two genera differ in the number of hooked setae, as well as their pattern of distribution.

Based on the small number of described larvae within the two genera, ankylopterygine larval debris-carrying modifications do not appear to be highly modified. At this time, one larval feature has been proposed tentatively as unique for Ankylopterygini (Tsukaguchi 1995; also see Appendix 1). More studies of the larvae are needed.

Tribe Belonopterygini. The ant-associated life history of one the belonopterygine species, *Italochrysa*
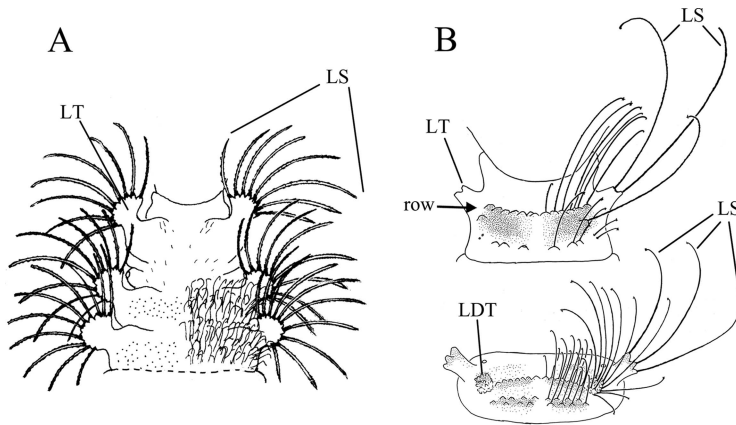
Fig. 4. Morphological variation in thoracic structure of belonopterygine first instars. (A) *Italochrysa stigmatica* (Rambur) (modified from Fig. 24 in Monserrat and Díaz-Aranda 2012); (B) *Vieira elegans* (Guérin-Méneville): upper, prothorax; lower, mesothorax (modified from Figs. 6 and 7 in Tauber et al. 2006). (Abbreviations: LDT, laterodorsal tubercle; LS, setae on lateral tubercles; LT, lateral tubercle; row, row of secondary prothoracic setae).

italica (Rossi), is well documented (Principi 1943, 1946). The few additional observations and unpublished notes that are available for larvae of this chrysopid tribe also mention an association with ant colonies (e.g., Weber 1942; E. G. MacLeod, personal communication; C.A.T. and S. L. Winterton, unpublished data).

The morphology and behavior of *I. italica* larvae indicate a high degree of modification for debris-carrying (Principi 1943, 1946). For example, the body of the third instar *I. italica* is extremely humped and compact, the thoracic and abdominal tubercles are stout and highly setose, and the dorsal surface of the larva, including the head, is covered with rough-surfaced setae and numerous small secondary setae. Moreover, the legs are short and the empodia and claws are relatively large; such features may enable larvae to retain purchase on the substrate and avoid attack directed at the ventral surface. Larvae also appear highly adept at maneuvering their bodies to take advantage of their dense protective covering. Also, the mode of moving debris along the surface of the body (through peristaltic contractions of the abdominal segments [as described by Principi], as opposed to lifting the head and abdomen and using the mandibles [as occurs in larvae of other Chrysopinae]) reduces exposure of the vulnerable ventral surface.

The first instars of two belonopterygine genera (*Italochrysa* and *Calochrysa*) are unique among chrysopids in that they express some traits that typify later-stage larvae, that is, second or third instars. For example, unlike the 2–3–3 pattern of setae (LS) on the pro-, meso-, and metathoracic lateral tubercles that is typical of first instars in all other chrysopid taxa, the first instars of these two genera have from six to nine LS on each of the thoracic tubercles (Fig. 4A; New 1983, 1986; Díaz-Aranda and Monserrat 1995; Monserrat and Díaz-Aranda 2012). The first instars of another belonopterygine genus (*Vieira*) retain the 2–3–3 LS pattern on the thoracic lateral tubercles, but the prothorax also has an anterior row of seven pairs of robust, hooked setae, and the mesonotum and metanotum each have a pair of laterodorsal tubercles bearing approximately nine robust, hooked setae (Fig. 4B; Tauber et al. 2006). This pattern of thoracic setation and notal tubercles is unique among chrysopid taxa, and its presence may indicate that the extraordinarily large number of setae on the thoracic lateral tubercles of *Italochrysa* and *Calochrysa* first instars are derived from secondary setae that became enlarged and were shifted from the notum to the tips of the lateral tubercles.

Italochrysa and *Calochrysa* first instars also have an exceptionally large number of dorsal abdominal setae, relative to first instars in other chrysopid taxa (New 1983, 1986; Díaz-Aranda and Monserrat 1995; Monserrat and Díaz-Aranda 2012). Again, the character state resembles that of second and third instars in other taxa. It appears that, in first instar *Italochrysa* and *Calochrysa*, natural selection for defensive modifications against ants may have resulted in the accelerated expression of features that typically occur in later instars. This pattern of accelerated development is in keeping with the relatively large eggs reported for *Italochrysa* and *Calochrysa* (Principi 1946; New 1983, 1986; Monserrat and Díaz-Aranda 2012; their eggs have volumes between 3 and 10 times greater than those of *Chrysopa* or *Chrysoperla* [see Tauber et al. 1991]).

The above shows that belonopterygine first instars express an extraordinary range of intergeneric variation in larval structures related to debris-carrying. Weber's (1942) intriguing note on the New World belonopterygine genus *Nacarina* indicates that the variation may be even broader. He reported finding a group of chrysopid larvae that resemble ant brood, in association with *Camponotus* ants. He reared one of the larvae to the adult stage and identified it as *Nadiva* (= *Nacarina*). Based on his findings, we suggest that naked *Nacarina* larvae, like the debris-carrying larvae

of other belonopterygines, may use ant brood as their prey. Perhaps they have a mechanism other than covering themselves with debris, e.g., defensive chemicals, for protection from brood-tending ants (see Dettner and Liepert 1994). Confirmation of Weber's 1942 report would be of great value to understanding the evolution of debris-carrying in Belonopterygini.

At this time, the monophyly of tribe Belonopterygini is well-supported by synapomorphies (adult: Brooks and Barnard 1990; larval: Appendix 1), but the taxonomic diversity of larvae that have been studied is relatively small.

Tribe Chrysopini. Not surprisingly, this tribe, the largest and most diverse within Chrysopinae, has a broad range of variation in larval debris-carrying habits and in associated morphological modifications. Of the 27 genera of Chrysopini whose debris-carrying status are known, 17 are classified as debris-carriers, whereas naked larvae or occasional debris-carriers are reported for 10 genera (Appendix 1; Catalog, Supp Table 1 [online only]); larvae are unknown from the other nine chrysopine genera.

Chrysopini With Naked Larvae. Larvae in the genera *Brinckochrysa*, *Chrysoperla*, *Peyerimhoffina*, *Atlantochrysa*, and *Nineta* are reported consistently as being naked or mostly naked; the rarely seen larvae of *Nipponochrysa*, have also been reported not to carry any debris (Catalog, Supp Table 1 [online only]). *Chrysoperla* species sometimes inhabit the flowers of composites (Asteraceae), where they become "liberally sprinkled with pollen" (Killington 1928). Species of *Chrysopa*, *Plesiochrysa*, *Anomalochrysa*, and *Meleoma* also are considered to have naked larvae, but within these genera the degree of nakedness varies among species and instars.

Naked larvae usually have bodies that are narrow and relatively flat, occasionally moderately thickened lateral tubercles are absent (*Brinckochrysa*), small (*Anomalochrysa*, *Chrysoperla*, *Peyerimhoffina*, and *Atlantochrysa*), hemispherical (*Chrysopa*, *Plesiochrysa*, and *Meleoma*), or well-developed and almost cylindrical (*Nipponochrysa*); see Figs. 1 and 5A. Abdominal laterodorsal tubercles may be present (*Chrysopa*, *Plesiochrysa*, *Meleoma*, and *Peyerimhoffina*), reduced (*Chrysoperla* and *Nineta*), or absent (*Brinckochrysa* and *Nipponochrysa*). Dorsal abdominal setae (submedian setae, SMS, of Tsukaguchi 1995) are smooth and usually relatively short, straight, and acutely tipped (sparse: *Chrysoperla*, *Nineta;* dense: *Nipponochrysa*). However, there are notable exceptions to the above: the dorsal abdominal setae on *Peyerimhoffina* are clavate; those on *Brinckochrysa* have star-shaped tips; in *Chrysopa* they are long and sometimes broadly curved and hooked; while those of *Meleoma* are straight and hooked.

Surprisingly, the third instar of one very unusual species of *Chrysoperla* has hooked dorsal SMS on abdominal segments A1 to A5 (Tsukaguchi 1995: *Chrysoperla furcifera* [Okamoto]). It is noteworthy that this species' unusual larval features are consistent with its exclusion from the *Chrysoperla* clade in one of the molecular phylogenies (Haruyama et al. 2008).

Also, unusual larval features may support that study's exclusion of *Chrysoperla suzukii* (Okamoto) from *Chrysoperla.* The larva in Tsukaguchi's (1995) drawings (see his Fig. 93i and j) appears more robust and setose than those of other *Chrysoperla* species.

Most species in the large genus *Chrysopa* are reported to have naked larvae or larvae (usually first instars) that occasionally carry scattered pieces of debris (e.g., Smith 1922, 1926; Killington 1936, 1937; Tsukaguchi 1978, 1995; Gepp 1983, 1988); however, there is considerable variation and one notable exception. The larvae of *Chrysopa slossonae* Banks are highly prey-specific; they feed on a single species of aphids and they have a conspicuous propensity to cover themselves with the wax that their prey secrete. In nature, this covering serves as a defense against several species of ants that tend the aphids (Eisner et al. 1978, Tauber and Tauber 1987).

In the laboratory, the debris-carrying *C. slossonae* was shown to be capable of interbreeding with its near relative, *Chrysopa quadripunctata* Burmeister, a species that has a wider prey range and larvae that are only occasional debris-carriers (Tauber and Tauber 1987). Comparative studies of the two species, their hybrids, as well as geographic populations of *C. quadripunctata*, revealed genetically based morphological and behavioral modifications for larval debris-carrying (Tauber et al. 1993, 1995a,b; Milbrath et al. 1994). They also showed that environmental factors can strongly influence the degree of debris-carrying behavior and that under some conditions larvae of the occasional debris-carrier express a strong tendency to apply debris on their dorsa.

We have collected larvae of four *Meleoma* species in the field: *Meleoma emuncta* (Fitch), *Meleoma dolicharthra* (Navás), *Meleoma signoretii* Fitch, and *Meleoma kennethi* Tauber, and all were either naked or carried only a few pieces of debris (Toschi 1965, M.J.T. and C.A.T., unpublished data). However, as in *Chrysopa*, *Meleoma* larvae have well-developed lateral tubercles on the thorax. Moreover, their dorsal abdominal setae are numerous, with small hooks or knobs at the tips, and apparently are held somewhat flat on the abdominal surface (Tauber 1969, C.A.T. and T. de León, unpublished data). We suggest that some *Meleoma* larvae may be debris-carriers or that the dorsal abdominal setae that usually subserve debris-carrying in other chrysopid larvae may have other, as yet unrecognized, functions in *Meleoma.*

Chrysopini With Debris-Carrying Larvae. Among the debris-carrying genera of Chrysopini, all larvae have thickened or globose bodies and well-developed, but not especially elongate, thoracic and abdominal lateral tubercles (Figs. 2D, 2E, 3A, 3B, 5B, and 5C). Typically, the metathorax has a row of four or more prominent, modified setae, and each of the anterior six to seven segments of the abdomen (A1 through A7) has two to three rows of dorsal setae that are hooked or otherwise modified for holding material.

Despite the above similarities among the debris-carrying genera of Chrysopini, striking differences exist. For example, the shape of the larval body (spe-
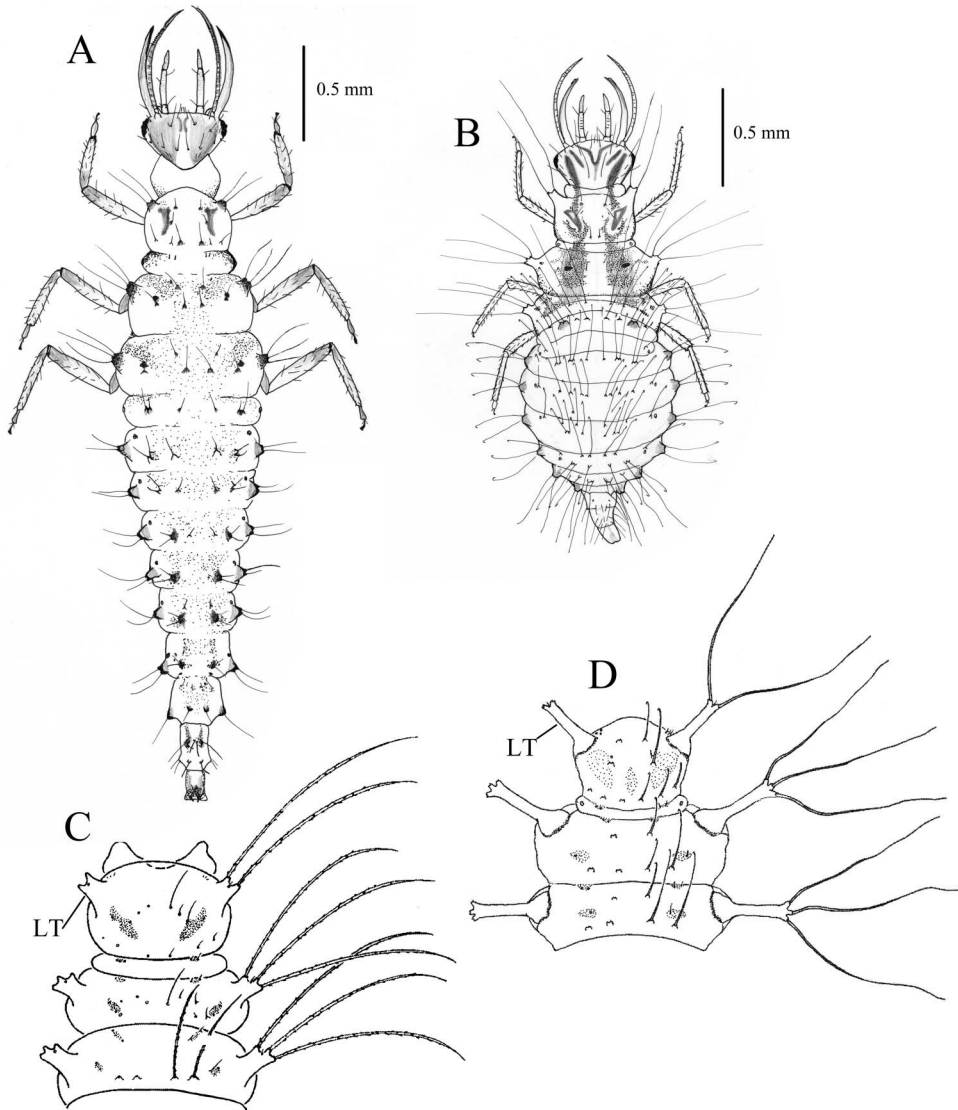
Fig. 5. Morphological variation among first instar Chrysopidae. (A) Typical naked larva: *Chrysoperla externa* (Hagen) (from Tauber 1974), (B) Typical debris-carrier: *Yumachrysa apache* (Banks) (from Tauber 1975), (C) Typical chrysopine prothorax: *Ceraeochrysa* (debris-carrier) (modified from Fig. 10 in Tauber et al. 2000), and (D) Typical leucochrysine prothorax: *Leucochrysa* (*Nodita*) (debris-carrier) (modified from Fig. 22 in Mantoanelli et al. 2011). (Abbreviation: LT, lateral tubercle).

cifically the degree of thickening and the height of the mesothorax and metathorax, as well as the size of the first abdominal segment) varies notably among debris-carrying genera; *Chrysopodes*, *Yumachrysa*, and *Ceraeochrysa* illustrate the variation well. For example, the posterior section of the *Chrysopodes* metanotum rises steeply above the anterior section, and the row of robust metanotal setae extend from large chalazae along the top of the raised posterior section (Tauber 2003, Silva et al. 2013). Each of these large chalazae has an oval marking that extends onto the integument in front of the seta. In *Ceraeochrysa*, the metathorax rises gradually above the mesothorax, but the first abdominal segment is constricted and the

second segment is wide, a situation that gives the body somewhat of an hourglass appearance (Tauber et al. 2000, Tauber and de León 2001). In *Yumachrysa*, the first abdominal segment is enlarged and bears substantial setose laterodorsal tubercles (Tauber 1975).

The broad range of variation in larval chaetotaxy among the debris-carrying genera of Chrysopini is exemplified by the following: 1) Setae on the lateral or laterodorsal tubercles often are smooth or slightly granular (*Cunctochrysa*, *Pseudomallada*, *Rexa*, and *Titanochrysa*), but they may be thorny in *Chrysopodes*, *Ceraeochrysa*, and *Yumachrysa*. 2) The posterior region of the metanotum usually has a transverse row of long setae, but the mesonotum varies in having

such a row (present: *Cunctochrysa*, *Chrysopidia*, and *Ceraeochrysa*; absent: *Chrysopodes*, *Mallada*, *Apertochrysa*, *Pseudomallada*, *Rexa*, *Yumachrysa*, and *Suarius*; Fig. 5B and C). 3) Dorsal setae on the abdomen may be long (*Yumachrysa* and *Suarius*), intermediate length (*Ceraeochrysa*, *Chrysopodes*, *Pseudomallada*, and *Cunctochrysa*), or short (*Titanochrysa*). Also, they may range from smooth, hooked, and without a flattened tip (*Ceraeochrysa* and *Chrysopidia*), to smooth, with a long, laterally flattened terminal hook (*Chrysopodes*), or broadly hooked with a spatulate or slightly spatulate tip (*Cunctochrysa* and *Pseudomallada*). In *Titanochrysa*, the posterior setae on the dorsum of each segment, i.e., A2 through A4, are short, stout, and hooked. 4) Finally, the presence or absence of small dorsal tubercles on various abdominal segments and the number and characteristics of the setae they bear varies considerably among genera. The larvae of most debris-carrying genera have the tubercles only on segments A6 and A7. Indeed, among the debris-carrying genera, *Pseudomallada* and *Yumachrysa* are exceptional in having the tubercles on each of abdominal segments A5 through A7; *Yumachrysa* also has an exceptional, large dorsal tubercle on the first abdominal segment.

Phylogeny of Debris-Carrying in the Chrysopini. Below, we discuss the diversification of larval features among the chrysopine genera in relation to the two molecular-based chrysopid phylogenies.

The first study (Winterton and Freitas 2006) included only 9 of the 36 genera in Chrysopini; all 9, except 1 (*Mallada*), were found to be monophyletic. Moreover, relationships among some of the genera seemed reasonably well-resolved. *Chrysopodes* (a debris-carrier) was recovered as the sister genus to the other eight genera, of which *Ceraeochrysa* (a debris-carrier) is sister to *Chrysoperla* (naked) and the *Plesiochrysa–Chrysopa* clade (naked) is sister to the *Apertochrysa–Mallada–Glenochrysa–Pseudomallada* clade (all debris-carriers: Catalog, Supp Table 1 [online only]).

When larval morphology is viewed within the context of the above phylogeny, we find agreement with some of the proposed relationships. First, the sister relationship between *Chrysopodes* and the eight other genera is in concordance with larval morphology; indeed, *Chrysopodes* larvae express several larval features that are not reported for any other chrysopid genus whose larvae are known. These distinctive features include the structure of the metathorax and the robust metathoracic setae arising from modified chalazae (Tauber 2003, Silva et al. 2013, Catalog, Supp Table 1 [online only]). It is noteworthy that the phylogeny based on adult morphology (Brooks 1997) identified *Chrysopodes* as having "unknown affinities," a status that also may attest to a distant relationship with other chrysopine genera.

Second, larval characters strongly support the distinction and the close relationship between *Chrysopa* and *Plesiochrysa* (shown by the two molecular studies and the adult morphological data). Larvae of the two genera share many morphological features (see Tsu-

kaguchi 1978, 1995; Tauber et al. 2001). (Note: The relationship between *Chrysopa* and *Plesiochrysa* has been fraught with misinterpretation. 1) Winterton and Freitas [2006] apparently misread the findings of Tauber et al. [2001], instead of differences existing between the molecular and larval-based studies, both sets of data concur that the two genera are distinct, but closely related. 2) Also, Monserrat and Díaz-Aranda (2012) erroneously dismissed the relationship between *Chrysopa* and *Plesiochrysa.* Their conclusion was based on a larva that Adams [1959] described and whose identity as *Plesiochrysa* had been shown to be in error [Tauber et al. 2001]).

Third, the *Apertochrysa–Mallada–Glenochrysa–Pseudomallada* clade in the phylogeny of Winterton and Freitas (2006) is not contradicted and is tentatively supported by shared larval features, many of them associated with debris-carrying. The larvae of all four genera are debris-carriers, and the described larvae of three of these genera (Tsukaguchi 1995, Monserrat and Díaz 2012, Catalog, Supp Table 1 [online only]) express a relatively broad range of overlapping features (*Apertochrysa*, *Mallada*, and *Pseudomallada*, especially the latter two). Larvae of *Glenochrysa* are undescribed.

Fourth, the proposed sister relationship between *Chrysoperla* and *Ceraeochrysa* finds little or no support in current larval data. Similarly, larval support for Brooks' grouping of *Chrysopa* + *Plesiochrysa* with *Ceraeochrysa* is not forthcoming. These hypothesized relationships warrant further examination, including detailed comparisons of the larval anatomy.

To summarize our thoughts on the evolution of debris-carrying in Chrysopini in relation to the Winterton and Freitas (2006) phylogeny: 1) The most parsimonious interpretation is that debris-carrying represents the basal state for the tribe. 2) Nakedness apparently evolved independently at least twice among the taxa tested: once in *Chrysoperla* and once in the *Chrysopa–Plesiochrysa* clade. In evaluating these conclusions, it should be remembered that only one-fourth of the chrysopine genera are included in the phylogeny.

In comparison, the second molecular study (Haruyama et al. 2008) examined a slightly broader range of taxa in the tribe Chrysopini (approximately one-third of the genera), and it recovered seven reasonably well-supported clades. Relationships among the clades are not well-resolved, but some hypothesized generic groupings are noteworthy. First, the close relationship between *Chrysopa* and *Plesiochrysa* is corroborated, and as shown above, this relationship is strongly supported by morphological (larval and adult) data. Second, the study provides additional evidence for a close association between the debris-carrying genera *Pseudomallada* and *Apertochrysa*, as do both the earlier molecular study and larval morphological data (see above). Third, a relationship between *Chrysoperla* and *Peyerimhoffina* was recovered; it, too, is supported with larval data (Monserrat and Díaz-Aranda 2012) and by adult morphology (Brooks 1997). Finally, although adult morphological data sup-

port a close relationship between the above two genera (*Chrysoperla* and *Peyerimhoffina*) and *Mallada* (Brooks 1997), supporting larval data are not obvious at this time; this proposed relationship deserves further study.

To summarize the evolution of debris-carrying in Chrysopini in relation to the phylogeny of Haruyama et al. (2008), two alternate patterns are apparent: 1) in the most parsimonious interpretation (i.e., when debris-carrying is the presumed basal state of the tribe) nakedness evolved independently within the tested chrysopine genera approximately six times, with one reversal (Clades 1, 3, 4 [and one reversal], 5 [two events], and 6). 2) In contrast, if nakedness were the basal state, then debris-carrying would have evolved independently approximately eight times (Clades 2, 3, 4 [two events], 5 [two events], 7, and *Borniochrysa*).

Tribe Leucochrysini. The debris-carrying habits (in nature) of only a few species in one leucochrysine genus have been reported, but those that are known exhibit a diverse and thought-provoking range of debris selectivity (Fig. 3C and D). One species, *Leucochrsya* (*Nodita*) *pavida* (Hagen), largely carries lichens (Skorepa and Sharp 1971), and careful analysis of the dorsal packets shows that the larvae are highly discriminating in the lichen species and the specific parts of the lichens they use for covering themselves (Wilson and Methven 1997). The larvae may serve as important dispersal agents for the lichens, and as a result the disparate organisms may have a mutualistic relationship (Slokum and Lawrey 1976).

Another species, *Leucochrysa* (*Leucochrysa*) *insularis* (Walker), carries very small terrestrial snail shells (sometimes living snails!) in its packet (Jones 1929, 1941). Here again, the larvae appear to be narrowly selective as to the types and sizes of snails they choose. Other *Leucochrysa* species are reported to carry sternorrhynchan flocculence, but these reports are unconfirmed.

Larvae have been described from most leucochrysine genera (*Leucochrysa*, *Gonzaga*, *Santocellus*, and *Berchmansus;* Appendix 1; Catalog, Supp Table 1 [online only]), and they all express strikingly elongate, digitiform lateral tubercles on the thoracic segments (Figs. 3D and 5D; Appendix 1). Because of these elongate tubercles and other features (e.g., humped body shape, papilliform abdominal lateral tubercles, and hooked abdominal SMS) leucochrysines generally are assumed to be debris-carriers (Mantoanelli et al. 2011).

However, recently *Berchmansus* larvae were shown to have a fusiform and somewhat flat body, elongate lateral tubercles on the abdominal and thoracic segments, and spatulate (not hooked) thoracic and abdominal setae (Tauber and Tauber 2013). Given these attributes, it is now apparent that leucochrysine larval anatomy has a much larger range of intergeneric variation than previously assumed. Moreover, the *Berchmansus* larval features lead us to question whether they carry debris. It is likely that in nature the somewhat flat but setose larvae of *Berchmansus*

either are naked or carry only a sparse packet of material.

Regrettably, the phylogenetic relationships among leucochrysine genera have not been examined with either morphological or molecular approaches. Nevertheless, based on larval characters included in current descriptions, it appears that *Santocellus* and *Berchmansus* are characterized by strong larval apomorphies (*Santocellus:* relatively short mandibles and uniquely shaped labial palpomeres; *Berchmansus:* elongate abdominal lateral tubercles and knobbed dorsal abdominal setae; Tauber et al. 2008b, Tauber and Tauber 2013). In addition, *Leucochrysa* (both subgenera) and *Gonzaga* appear to be more closely related to one another than to either of the two above genera (Tauber et al. 2008a,b); indeed, consistent features differentiating the two genera have not been identified.

Ancient Chrysopid Relatives (Superfamily: Chrysopoidea)

Recently, a very large, debris-carrying chrysopoid larva, *Hallucinochrysa,* was discovered in early Cretaceous amber from Spain; the presence of fossilized "debris" (fern trichomes) entwined in its elongate lateral setae offers evidence that the larva was a debris-carrier (Pérez-de la Fuente et al. 2012). This fossil demonstrates that debris-carrying behavior, with its associated morphological modifications, has deep roots in the chrysopoid lineage. Furthermore, the larva has a remarkable set of structures that are unlike any known among the extant chrysopids. These include extremely long, slender lateral and sublateral tubercles on each thoracic segment, equally long and slender lateral tubercles on the abdomen, and uniquely shaped setae (LS) extending from the lateral tubercles. The unusual anatomy of the *Hallucinochrysa* larva underscores that the ancient trait of chrysopid debris-carrying has evolved through multiple pathways.

A more modern fossilized chrysopid larva (Miocene amber, second or third instar, Dominican Republic) also presents features that the discoverers attributed to debris-carrying (Engel and Grimaldi 2007). These include well-developed lateral tubercles with elongate setae and a relatively flat body with a laterally upturned dorsal surface. Together, these structures were described as comprising a "corbicula," or basket, for carrying debris. However, we, and others (see Pérez-de la Fuente et al. 2012), propose that this specimen could have been either naked or a debris-carrier. First, unlike the *Hallucinochrysa* fossil above (which was embedded in amber with debris entwined in its setae), this larva was not reported to be associated with debris. Second, the anatomical characteristics of the larva also occur in naked larvae, especially those of *Chrysopa;* they share similarly well-developed lateral tubercles, relatively long lateral setae, and flattened bodies. Also, it is noteworthy that the Miocene larva has well-developed lateral tubercles on abdominal segment A1; among extant species, only the larvae

of a few *Chrysopa* species are known to have lateral tubercles on this segment (Principi 1940, Tsukaguchi 1978).

Apart from the question of the Miocene larva's debris-carrying status, we noted that the description and illustration of the larva (Engel and Grimaldi 2007) include two unusual traits: a pair of small setose tubercles on the sides of the prothorax behind or below the large lateral tubercles and the absence of dorsal setae on the prothorax, mesothorax, and abdominal segments posterior to A4. These features attracted our attention because they are not known to occur in any currently described extant chrysopids.

General Taxon-Based Patterns in Chrysopid Debris-Carrying

Because of sparse information on the larval behavior and morphology of many chrysopid taxa, we emphasize that most statements (including our own below) regarding the origin and evolutionary patterns in chrysopid debris-carrying are, at best, subject to confirmation. Given that caveat, we summarize our thoughts on the topic below with the goal of stimulating discussion and additional research.

Based on existing data from extant and fossil chrysopoids, it is now known that debris-carrying and its associated larval morphology express a relatively high degree of evolutionary plasticity. The data also indicate that this plasticity may be subject to significant constraints. Specifically, we conclude that:

1. Debris-carrying is an ancient characteristic that has arisen or been lost repeatedly during the evolution of the Chrysopoidea.
2. The morphological modifications that underlie the diverse forms of chrysopoid (and chrysopid) debris-carrying are numerous and diverse.
3. Among the extant chrysopids, the morphological adaptations that support debris-carrying involve a relatively large, well-defined group of anatomical structures, each of which apparently can be enhanced, reduced, or modified independently over evolutionary time (Table 1). Prominent among these structures are the shape of the body; the thoracic and abdominal lateral tubercles and laterodorsal tubercles, as well as the setae they bear; the dorsal setae of the thorax; and the transverse rows of submedian abdominal setae. The legs, cephalic appendages, and cephalic setae may also be involved. Debris-carrying larvae often show extensive modification of some but not all of these structures; moreover, the alteration of one structure does not always appear to be dependent on the alteration of others.
4. Given the evolutionary flexibility implied in the statements above, it also appears that the morphological modifications for chrysopid debris-carrying evolve within a defined and constrained framework. Evidence for this restriction stems from the consistent pattern in which basic larval structures are retained in all genera but are modified to sub-

serve debris-carrying. For example, chrysopid larvae have one pair of relatively large lateral tubercles on each thoracic segment and on each abdominal segment A2 through A7. The size, shape, orientation, and setation of these tubercles vary among genera. Indeed, in a few cases the basic structures (e.g., the lateral tubercles themselves) appear to have been lost, but in no case have additional ones been added. Similar statements could be made for many other larval features involved in debris-carrying (e.g., thoracic and abdominal laterodorsal tubercles, thoracic and abdominal setae, and thoracic folding). Thus, it seems that each genus evolved a unique set of modifications to a fundamental, shared, ground plan of anatomical structures, and in each genus these modifications support a specific habit of debris-carrying, occasional debris-carrying, or nakedness.

We have found only one exception to the fourth point above, and that is the case of two belonopterygine genera *Italochrysa* and *Calochrysa* in which the typical chrysopid pattern of first-instar setation is altered (discussed above). However, this deviation could be explained by the accelerated development and displacement of secondary thoracic setae, and not the de novo evolution of LS (Tauber et al. 2006).

Integration of Debris-Carrying, Larval Morphology, and Chrysopid Systematics

Several authors have expressed some misgivings about using larval characters related to debris-carrying in phylogenetic studies of Chrysopidae, because they suspected that the repeated evolution of larval debris-carrying may result in excessive homoplasy (Tauber 1975, Monserrat and Díaz-Aranda 2012, Pérez-de la Fuente et al. 2012). However, in view of the comparative morphological studies of chrysopid larvae during the last two decades, we believe that these reservations now need reevaluation.

The following recent quote from Pérez-de la Fuente et al. (2012): pg. 2, Supporting Information) provides a useful focus for our discussion of the issue:

"It is interesting to note that the current high-level classification within Chrysopidae is almost solely based on adult characters (12) [Brooks and Barnard 1990], because parallelisms and convergence in larval traits are rampant across the family (28) [Tauber 1975]. However, larval anatomy and morphology have proven to be of great importance for recovering lower-level relationships within the family (29, 30) [Tauber et al. 2008a,b]." (References in square brackets are those that the authors cited by number).

Below, we review whether this type of well-intentioned cautionary statement could be misinterpreted and lead to the unfortunate marginalization of larval morphology as a source of characters for phylogenetic studies. We evaluate three assertions in the quotation:

1. Indeed, the current higher-level classification of Chrysopidae is based almost solely on adult char-

acters (Brooks and Barnard 1990, Brooks 1997). However, it is now known that larval characters also are systematically very informative at supragneric levels (see Appendix 1). Nothochrysinae, Belonopterygini, Leucochrysini, and Ankylopterygini provide significant examples (Díaz-Aranda and Monserrat 1995, Tsukaguchi 1995, Monserrat and Díaz-Aranda 2012, Tauber and Tauber 2013). Thus, the informative value of larval characters should also be emphasized in statements that evaluate the sources of characters for phylogenetic study.

2. As with any other characters, larval traits can be subject to parallelism and convergence, especially if they are not chosen and defined carefully. For example, if larvae were scored on the basis of "debris-carrying present or absent," "humped abdomen present or absent," "well-developed thoracic tubercles present or absent," "dense, long, setae present or absent," the characters undoubtedly would introduce homoplasy into the data set (Tauber 1975). However, specific larval morphological features that support debris-carrying (if precisely defined and presented with alternative character states) would be no more subject to parallelism or convergence than any other type of well-delineated feature. Examples include "posterior section of metathorax raised above anterior section abruptly or gradually," "laterodorsal tubercles on abdominal segment A1 (or A5) present or absent," "clavate SMS present or absent." Thus, the careful choice and definition of characters is crucial, but this note of caution applies equally to both adult and larval characters (e.g., see Miller and Wenzel 1995).

3. Larval morphology has proven to be highly significant for recovering lower-level (i.e., generic) relationships within the family; in fact, all currently recognized chrysopid genera (whose larvae are known) are distinguished by a unique set of larval features. We suggest that the acquisition, modification, and loss of debris-carrying may have left visible and useful markers along a retrievable course of evolutionary change. Because of their diversity and generic-level consistency, these larval morphological features may play a major role in unraveling the tangled branches that currently comprise the chrysopid phylogenetic tree.

Recommendations

While preparing this article, we noted opportunities where modest but focused efforts could accelerate investigations of chrysopid debris-carrying. One involves increasing the larval database. The other focuses on developing comprehensive larval data matrices.

Gathering Larval Data: Citizen-scientists and Professionals

The lack of specimens with useful data is one of the most significant reasons why immature insects are generally not included in phylogenetic studies (Meier and Lim 2009). This problem reflects the situation with chrysopid larvae. However, given popular Web sites, including social media, it is now possible for amateur scientists, photographers, and hobbyists to share images and information with specialists in a quick and efficient manner (see Figs. 1–3). Such images, if associated with the preserved specimens, could provide valuable information for systematic and other studies. Thus, we recommend that professionals encourage and work with citizen-scientists to retain voucher specimens for their photographs.[6] For example, such interactions, initiated through social media and followed up with exchange of voucher specimens, led to the description of a new chrysopid species from Thailand (Winterton et al. 2012), and the discovery of a unique pattern of oviposition in a North American chrysopid species (Tauber et al. 2013).

Developing Larval Data Matrices: Chrysopid Systematists

Chrysopid systematists have made considerable progress in promoting uniformity and clarity in the terminology for larval characters. A similar but more focused communal effort would help develop an extensive analysis of chrysopid larvae and their inclusion within a comprehensive phylogenetic study of the family. Using immature stages in phylogenetic studies requires that comparisons be made across homologous larval characters on equivalent semaphoronts (equivalent developmental stages) of all included taxa (see Wheeler 1990, Meier and Lim 2009). Thus, we suggest two areas in need of discussion and cooperation among chrysopid systematists: 1) identification of morphological and behavioral homologies among larvae across the full range of chrysopid taxa and 2) development of an extensive taxon–character data matrix (with precise, well-described, and well-illustrated character states) for systematists worldwide to use in evaluating chrysopid larvae in any taxon. We propose that the recent compendium on the chrysopid larvae of the Iberian Peninsula (Monserrat and Díaz-Aranda 2012) offers a valuable prototype upon which to build an extensive taxon–character data matrix.

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[6] For voucher specimens of chrysopid larvae, we recommend preservation in 95% ethyl alcohol (larvae and packet), unless the packet includes waxy material. In that case, the packet should be dry-mounted on a point or stored in a gelatin capsule. All images and specimens should carry specific locality and collection data. Preservation of larval specimens in alcohol and prompt mailing to a specialist will facilitate identification via DNA procedures.

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Appendix 1. Chrysopid larval habits and larval descriptions: summary of current information

I. Subfamily Nothochrysinae (2% of chrysopid species)
Nine genera, larvae from four known

Genera with detailed larval descriptions (no. = 3)
    Dictyochrysa (1 species, L1) naked
    Hypochrysa (1 species, L1, L3) naked
    Nothochrysa (3 species, L1, L3) debris-carrier, occasional debris-carrier

Larval synapomorphies
    Several shared, unique larval features (enumerated by Díaz-Aranda and Monserrat 1995, Monserrat and Díaz-Aranda 2012)
    Antenna: terminal segment short (approximately 10 times shorter than remainder of antenna); terminus with group of small apical setae, not an elongate seta (L3)
    Labial palpus: terminal segment with more than three lateral sensilla[a]

Larval features with intergeneric variation
    Habit: naked to debris-carrier
    Body: fusiform, elongate, flattened dorsoventrally to slightly thickened
    Head: setae (L1) clavate or filiform, (L3) blunt or filiform
    Thorax: lateral tubercles (LTs) absent to very small with a few (2–3) setae (LS), or fairly well developed with numerous straight or hooked LS, and if present, not more developed than abdominal LTs
    Abdomen: LTs absent to small; laterodorsal tubercles (LDTs) absent or very small, with only one seta (LDS)
    Types of setae: thoracic notal setae–short, bacilliform or filiform; abdominal submedian setae (SMS) (A1–A6)–short, bacilliform or elongate, hooked or elongate, blunt without hook

II. Subfamily Apochrysinae (1% of chrysopid species)
Six genera, larvae known from one

Genera with detailed larval descriptions (no. = 1)
    Apochrysa (1 species, L3 only) debris-carrier or occasional debris-carrier

Larval synapomorphies
    None currently identified (Tsukaguchi 1995; possible apomorphy: mesothoracic and metathoracic LTs longer than those on prothorax)
    Larvae of subfamily currently distinguished by set of features shared with Chrysopinae or Nothochrysinae

Distinguishing larval characteristics: based solely on *Apochrysa*
    Body: elongate, weakly humped
    Head: jaws longer than head capsule, antenna with terminal segment long (only approximately three times shorter than remainder of antenna), antennal terminus with elongate apical seta
    Thorax: LTs larger than those on abdomen; LTs considerably longer than broad (especially on T2 and T3); dorsum without tubercles
    Abdomen: dorsum of A1–A7 with small LDTs, each with more than one seta
    Types of setae: thoracic notal setae filiform, abdominal SMS of A1–A6 moderately hooked

III. Subfamily Chrysopinae (97% of chrysopid species)
Larvae known from all four tribes

Larval synapomorphies
    None confirmed

Distinguishing larval characteristics
    Antenna[b]: terminal segment long (only three to four times shorter than remainder of antenna), terminus with relatively long apical seta
    Labial palpus: terminal segment with three or fewer lateral sensilla[a]
    Thorax: prothoracic LTs equal to or longer than mesothoracic or metathoracic LTs[c]

Larval structures with intertribal variation
    Head: jaw length and breadth, labial palpus (second segment) size, flagellar spur presence or absence, location of cephalic setae on cranium
    Thorax: presence or apparent absence of thoracic dorsal sclerites; no. of setae in metathoracic posterior row, presence or absence of secondary setae on thoracic nota

IIIA. Tribe Ankylopterygini (five genera, larvae known from three)

Genera with detailed larval descriptions (no. = 2)
    Ankylopteryx (4 species, L3; 1 species, L1) debris-carrier
    Semachrysa (1 species, L3) debris-carrier

Larval synapomorphies
    One possibly unique feature proposed by Tsukaguchi (1995): metathorax with posterior row behind suture between laterodorsal sclerites bearing only four setae (however, see *Peyerimhoffina*)

Distinguishing larval characteristics (L3)
    Absence of secondary setae on dorsum of thorax

Larval structures with intergeneric variation
    Abdomen: A1 with one or two setae on laterodorsal tubercle

Appendix 1. Continued

IIIB. Tribe Belonopterygini (15 genera, larvae known from five)

Genera with detailed larval descriptions (no. = 3)
   Calochrysa (1 species, L1) debris-carrier
   Italochrysa (2 species, L1; 1 species, L3) debris-carrier
   Vieira (1 species, L1) debris-carrier

Larval synapomorphies (all instars unless noted otherwise)
   Many unique, shared features (for the first instar, see Tauber et al. 2006, modified below, also Monserrat and Díaz-Aranda 2012; for third instar, see Principi 1946)
   Head: jaws short (shorter than three-fourths the length of the head capsule); mandible stout (basal width approximately one-third the length); flagellum with robust, spur-like subapical seta (L1); labial palpus with second segment short, stout, much broader than apical segment; terminal segment of labial palpus with two lateral sensilla (L3)[a]; cephalic setae blunt, ornamented (rough), located anteriorly on the head capsule
   Thorax: dorsal sclerites apparently absent or very small (L1)

Larval (L1) features with intergeneric variation
   Habit: debris-carriers or naked
   Body: thickened, hunched, head partially withdrawn into prothorax
   Head: flagellar spur small to large
   Thorax: prothorax either with LTs bearing six to nine LS and without enlarged dorsal setae, or with LTs bearing two LS and pronotum with anterior row of long, hooked setae; mesothorax, metathorax either with LTs bearing eight to nine LS and without setose LDTs, OR with LTs bearing three LS and with LDTs bearing approximately nine long setae.
   Types of setae: elongate setae on LTs hooked or blunt, with single or multi-pronged tips; abdominal SMS smooth or rough

IIIC. Tribe Chrysopini (36 genera, larvae known from 27)

Genera with detailed larval descriptions (no. = 22)
   Anomalochrysa (1 species, L1, L3) occasional debris-carrier, naked
   Apertochrysa (1 species, L3) debris-carrier
   Atlantochrysa (1 species, L1, L3) naked
   Brinckochrysa (1 species, L1, L3; 1 species, L3) naked
   Ceraeochrysa (10 species, L1, L3; 1 species, L3) debris-carrier
   Ceratochrysa (1 species, L3) debris-carrier
   Chrysopa (10 species, L1, L3; 2 species, L3) naked to debris-carrier
   Chrysoperla (9 species, L1, L3; 2 species, L3) naked
   Chrysopidia (1 species, L1, L3) debris-carrier
   Chrysopodes (*Chrysopodes*) (5 species, L1, L3) debris-carrier
   Chrysopodes (*Neosuarius*) (2 species, L1, L3) debris-carrier
   Cunctochrysa (2 species, L1, L3) debris-carrier
   Mallada (5 species, L1, L3) debris carrier
   Meleoma (7 species, L1, L3; 2 species, L3) naked to light debris-carrier
   Nineta (3 species, L1, L3; 2 species, L3) naked
   Nipponochrysa (1 species, L3) naked
   Peyerimhoffina (1 species, L1, L3) naked
   Plesiochrysa (2 species, L1, L3) naked
   Pseudomallada (11 species, L1, L3; 5 species, L3) debris-carrier
   Rexa (1 species, L1, L3) debris-carrier
   Suarius (3 species, L1, L3) debris-carrier
   Titanochrysa (1 species, L1, L3) debris-carrier
   Yumachrysa (2 species, L1, L3) debris-carrier

Larval synapomorphies
   None confirmed

Distinguishing larval characteristics
   Head: jaws about same length as head capsule; terminal segment of labial palpus with three lateral sensilla[a]; cranial setae located mesally on cranium
   Thorax: differentiated from Apochrysinae and Ankylopterygini by presence of small secondary setae on nota; metanotum with posterior row of eight or more setae behind suture between dorsolateral sclerites (Sc2)

Larval features with intergeneric variation
   Habit: naked to debris-carriers
   Body: fusiform, elongate, flattened dorsoventrally to thickened or globose
   Head: cranial seta S12 present or absent; setal surface smooth or rough
   Thorax: LTs spherical or hemispherical, rarely absent or cylindrical; LDTs present or absent, with one or more setae
   Abdomen: LTs spherical or hemispherical, rarely absent or cylindrical; LDTs present or absent, with one or more setae
   Types of setae: LS elongate to short, with stalk straight or curved, smooth, thorny, or denticulate, with tip acute, hooked, or clavate/knobbed; SMS long, short, or bacilliform, with stalk straight to mildly or deeply curved, narrow, tapered, or robust, with tip acute, hooked (sometimes flattened), knobbed (spatulate), or multipronged

Appendix 1. Continued

IIID. Tribe Leucochrysini (seven genera, larvae known from four)

Genera with detailed larval descriptions (no. = 4)
     Berchmansus (1 species, L2, L3) unknown, naked or specialized debris-carrier
     Gonzaga (1 species, L1, L3) debris-carrier
     Leucochrysa (*Leucochrysa*) (3 species, L1, L3) debris-carrier
     Leucochrysa (*Nodita*) (8 species, L1, L3) debris-carrier
     Santocellus (1 species, L1; 1 species, L3) debris-carrier

Larval synapomorphies
     Several shared, unique larval features (see Mantoanelli et al. 2011, Tauber and Tauber 2013)
     Head: jaws about same length as cranium to ≈1.7 times longer; antenna with pedicel more than three times length of flagellum,
        terminal seta approximately one-half the length of flagellum (L1, L3)
     Thorax: LTs elongate (prothoracic LTs extending at least to middle of cranium; meso- and metathoracic LTs longer than half the width
        of the corresponding segment) (L3); LTs digitiform, not clavate; pronotum with primary setae S1, S3, S4, and S5 present, S2 absent
        or indistinguishable from secondary setae (L1, L3)

Distinguishing larval characteristics
     Thorax: metathorax with posterior row of four setae behind suture between dorsolateral sclerites (Sc2)
     Types of setae: all setae smooth

Larval features with intergeneric variation
     Body: variable, from globose with terminal segments withdrawn to fusiform, flattened dorsoventrally, elongate
     Head: terminal segment of labial palpus with two to three small lateral sensilla or depressions; secondary setae present or absent
     Abdomen: LT shape ranging from papilliform to elongate digitiform
     Types of setae: elongate setae on thoracic and abdominal tubercles (LS) with tips acute, hooked or knobbed (spatulate); thoracic notal
        setae hooked, knobbed or filiform; abdominal (A1–A6) SMS hooked or knobbed

Only larval descriptions with sufficient data for informative comparisons are included in the counts. For references and a full compilation
of larval descriptions, notes, published photos and illustrations, see Catalog, Supp Table 1 [online only].
    [a] Character state unknown for Apochrysinae and Ankylopterygini (Chrysopinae).
    [b] Both character states shared with Apochrysinae.
    [c] Shared with Nothochrysinae.