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An Overview of the Current Status of Chrysopidae (Neuroptera) Systematics

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Abstract

There has been significant progress over the last ten years in resolving some of the major taxonomic problems afflicting chrysopid systematics. Genera are now well-defined, ensuring the possibility of accurate generic assignation of most specimens; the number of monotypic genera have been reduced; and the use of new, non-morphological characters has clarified the relationships of certain species-complexes. However, several problems still remain and these are discussed in this paper. The relationships between the subfamilies and tribes of the Chrysopini are reassessed. A new generic phylogeny is proposed for the Nothochrysinae. Genus-groups are proposed for the Chrysopini in an attempt to clarify generic relationships within the tribe. Three new generic synonyms are proposed. Finally, a series of revisionary priorities is proposed for the Chrysopini.

Key words: Phylogeny, green lacewings, cladistics

Introduction

Over ten years ago New (1984) wrote that Chrysopidae provided numerous problems for systematists and echoed Killington's (1937) plea for a world revision of the family. Peter Barnard and I rose to this challenge and later published the first revision of the world genera of Chrysopidae (Brooks & Barnard, 1990). The intention of our work was to provide a taxonomic framework for the family within which systematists could tackle particular taxa. Since 1990 other workers have revised certain genera, supra-generic groupings or regional chrysopid faunas and further developed the systematics of the family (e.g. Yang & Yang, 1991; Hölzel & Monserrat, 1992; Adams & Penny, 1992; Brooks, 1994; Hölzel, Ohm & Stelzl, 1994; Yang, 1995; Tsukaguchi, 1995; Winterton & Brancatini, 1996). Table 1 provides a list of the new genera and subgenera described since 1990. So, progress has been made to address New's (1984) rather gloomy prognosis that "elucidation of the status and integrity of all taxa in the Chrysopidae remains unlikely in the foreseeable future".

Nevertheless, despite these developments, there still remain many aspects of chrysopid systematics that are inadequately resolved. The purpose of this paper is to examine which of the issues raised by New (1984) have been dealt with, what questions remain to be answered and to discuss any new problems that have arisen. Chrysopidae is a large family

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Table 1
New genera and subgenera described since 1990 and therefore not appearing in the checklist in Brooks & Barnard (1990).

Crassochrysa Hölzel, 1990 [Chrysopini, Afrotropics]
Odontochrysa Yang & Yang, 1991 [= *Plesiochrysa* Adams, 1982] **syn. n.**
Xanthochrysa Yang & Yang, 1991 [= *Chrysacanthia* Lacroix, 1923] **syn. n.**
Chrysopa (Euryloba) Yang, 1991 [Chrysopini, China]
Dichochrysa Yang 1991 n.n. for *Navasius* Yang & Yang, 1990 [Chrysopini, Worldwide]
Asthenochrysa Adams & Penny, 1992 [Nothochrysinae, Neotropics]
Leptochrysa Adams & Penny, 1992 [Nothochrysinae, Neotropics]
Lauraya Winterton, 1995 [Apochrysinae, Australia]
Nipponochrysa Tsuikaguchi, 1995 [Chrysopini, Japan]
Pseudomallada Tsukaguchi, 1995 [= *Dichochrysa* Yang, 1991] **syn. n.**

that includes over 1200 species, some of which are of considerable importance as biocontrol agents. Resolution of the systematics of the family and provision of a stable nomenclature is, therefore, of importance to field biologists and agro-entomologists as well as a priority for taxonomists.

Past problems in chrysopid systematics

New (1984) highlighted several problems that were hindering progress in resolving the taxonomic difficulties in Chrysopidae. These were:

1. The difficulty of generic allocation of species;
2. Inadequately resolved subfamily and tribal classification;
3. Large proportion of monotypic genera;
4. Generic and suprageneric classification based on a limited range of adult characters;
5. Little known about specific variability.

These problems have been aggravated by authors publishing taxonomic papers based on insufficient data or incomplete research. Typical examples include:

1. Inadequate appraisal of intraspecific variation, especially of widespread species, which may lead to species being unnecessarily split and the introduction of synonymy.

2. Parochial outlook. Sometimes authors of regional revisions have failed to consider taxa occurring outside the area under consideration and have erroneously re-described taxa as new.

3. *Chrysopa incertae sedis*. Another recurrent problem is that there are over 150 described chrysopine species for which generic affinities are still unknown (Brooks & Barnard, 1990). These taxa are known only from the rather inadequate original descriptions and it is a priority to locate and redescribe the types of these species. It is also, of course, essential that future authors do not add to the confusion by poor descriptions of new species. Some taxonomists have taken a pragmatic approach. They have described a taxon as new, and at least have provided a detailed description with fully illustrated genitalia, leaving it to later revisers to establish whether any synonymy exists. The chrysopid faunas of South America, India and southeast Asia remain inadequately studied. There is a priority for basic descriptive work and reappraisal of type specimens from these regions.

4. Single female descriptions. A further remaining problem has been the description of many species based on single female specimens. This fault is often compounded by inad-

equate comparisons with previously described, closely-related taxa. Such practices take no account of variability and may confound the correct identification of specimens of the opposite sex. Moreover, in most cases, male genitalic characters have proven to be the most consistent in distinguishing species. Species based on single female specimens may thus be defined on unreliable, variable characters that have not been adequately evaluated in the family and that have little phylogenetic significance.

Towards a resolution

Some of the problems discussed above were addressed by Brooks and Barnard (1990) in their generic revision of the Chrysopidae.

1. Difficulty of generic allocation.

A large number of morphological characters, many of which had not been considered by previous authors, were surveyed throughout the family for their reliability in defining taxa. To assist with phylogenetic analysis the character states of each character in every genus was assessed. These included external characters as well as those of the male and female genitalia. This resulted in most genera being defined by robust apomorphic characters and has provided a framework into which new genera can be easily slotted. Correct generic assignment of species of either sex is now relatively straight-forward for most taxa, as is the recognition of new genera.

2. Inadequate tribal and subfamily classification.

Using a similar approach Brooks and Barnard (1990) also defined the supra-generic chrysopid taxa. However, some problems still remain. Initial cladistic analysis demonstrated that the tribes and subfamilies were monophyletic but failed to resolve adequately the relationships, leaving a trichotomy between the Leucochrysini, Ankylopterygini and Chrysopini. In addition, no apomorphic character could be found to define the Nothochrysinae.

3. Large proportion of monotypic genera

Following Brooks & Barnard (1990), the number of monotypic genera in the Chrysopinae has been reduced by synonymy from thirty to ten. Four of the remaining monotypic genera are still inadequately known (i.e. *Neula* (Neotropical leucochrysine): no specimens extant in collections; *Nuvol* (Neotropical leucochrysine): only one specimen known, but lacks abdomen; *Chrysaloysia* (Afrotropical belonopterygine): one male specimen known; *Turnerochrysa* (Afrotropical belonopterygine): female unknown. It is a priority to obtain more specimens of these genera, to provide detailed descriptions of both sexes and fully assess the status of these taxa.

4. Limited range of adult characters.

Many new adult characters have now been established to be of value in chrysopid systematics. Other characters, particularly certain features of the wing venation or the colour and position of markings, upon which much reliance had been placed by authors in the past, have been shown to be variable and, therefore, unreliable. Less progress has been made in the assessment of the value of egg or larval characters in phylogenetic analysis, although the work of Gepp (1983) and Diaz-Aranda & Monserrat (1995) is a useful starting point.

The recent description of the eggs and larvae of *Ankylopteryx collarti* Navás (Hölzel, Stelzl & Ohm, 1990) was the first for any ankylopterygine taxon and has the potential for shedding more light on the relationships of this tribe.

Traditional morphological taxonomic studies have recently been supplemented by new techniques, such as multivariate analysis (Thierry *et al.*, 1992), electrophoresis (Cianchi & Bullini, 1992), DNA analysis (Wells, 1991) and courtship song analysis (summarised in Henry, 1992), and have begun to show promise in resolving taxonomic problems.

5. Specific variability.

This still remains inadequately studied within the Chrysopidae. Genitalic variability can be a particular problem and may lead to the incorrect generic allocation of species.

Summary of progress since 1984

1. Genera are now based on apomorphic characters, so more robust.
2. Genera defined on a wide range of characters, many not used before; the same characters analysed in each genus and surveyed throughout family.
3. Male and female characters used in generic definitions so females can be allocated to genus.
4. Tribes and subfamilies defined and phylogenetic analysis attempted.
5. Monotypic genera in Chrysopinae reduced to 10; but still 5 out of 12 Apochrysinae genera monotypic.

Problems still remaining

Nothochrysinae

No defining apomorphic character has been established for the subfamily, although Adams & Penny (1992) suggested that the possession of 6 rings of flagellar setae could be apomorphic for the subfamily. Nevertheless, retention of many archaic features suggests that it is the least derived subfamily (Brooks & Barnard, 1990). A generic phylogeny for the extant genera is proposed in Fig. 1. This indicates that five of the genera fall into one monophyletic group, the *Nothochrysa*-group. The remaining four genera are more problematic and no convincing autapomorph has been found to link them. The presence of microtholi appears as a stem character defining the *Nothochrysa*-group although this character has apparently been secondarily lost in *Asthenochrysa*. The placement of *Kimochrysa* outside the *Nothochrysa*-group is also open to debate. The genus lacks microtholi, and tergite 9 is not fused with the ectoproct suggesting it should be placed among the primitive nothochrysines. This is further supported by the unique apomorphy it shares with *Pamochrysa* in that veins Sc and R are fused based of the pterostigma in the hind wing. However, in females of *Kimochrysa* the spiracle of the 8th abdominal segment opens onto the membrane rather than into the tergite and this is regarded as a stem apomorphic character for the advanced Nothochrysinae-group.

Most Nothochrysinae genera include few species, and three out of the nine genera are monotypic. This, together with the disjunct world distribution, probably reflects the long evolutionary history of the subfamily, and the extant taxa may be relicts of a more speciose group.

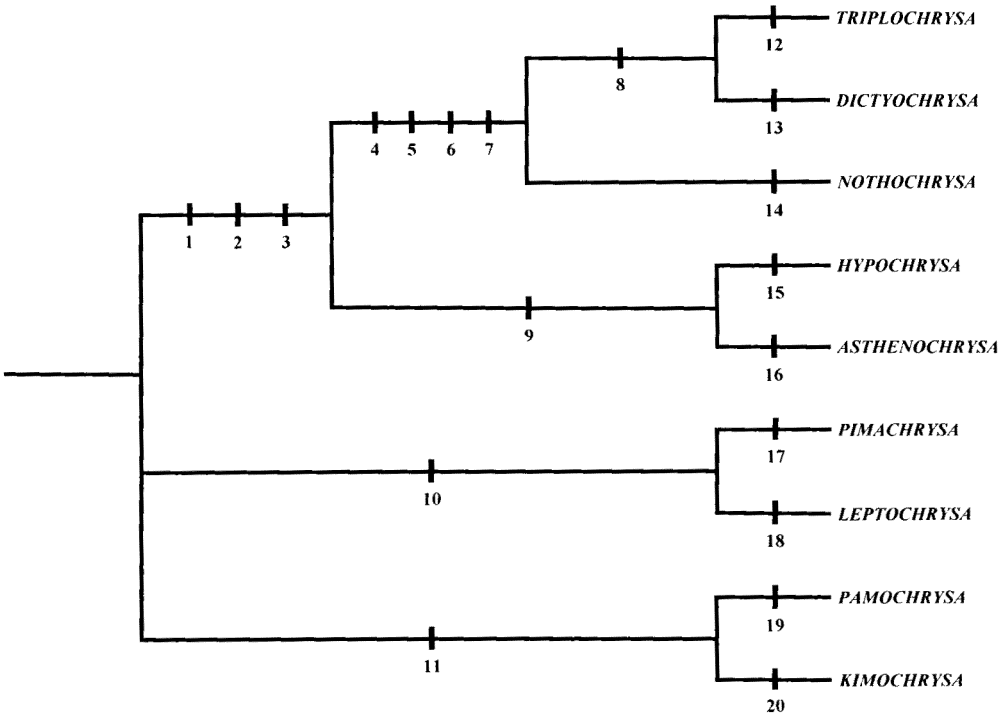

Fig. 1
Cladogram showing the relationships of the Nothochrysinae genera. Apomorphies are numbered as follows: 1. Tergite 9 and ectoproct fused in male; 2. Microtholi present in male; 3. Spiracle on segment 8 of female opens onto membrane not tergite; 4. Cell c1 > c2; 5. Tarsal claws basally dilated; 6. Vein 1A forked; 7. Psm distinct; 8. Multiple gradate series; 9. Apodeme in male tergite 9 elongate and extending beyond apex of abdomen; 10. Fore wing narrow; 11. Sc and C fused in hind wing based of pterostigma; 12. Gradates arranged in three series; 13. Wing veins with dense reticulation; 14. Entoprocessus reduced; 15. Veins 2A and 3A fused apically; 16. Spinose plate present in male genitalia; 17. Eyes very small; 18. Gradate cells rectangular; 19. Intramedian cell rhomboidal; 20. Sc fuses with C proximad of pterostigma.

Apochrysinae

The genitalia of most apochrysine genera are rather conservative, only in *Apochrysa* are they distinctive. This has led to most of the genera being defined by wing venational characters and, due to the great variability in wing venation, many are monotypic. Winterton (1995) recently described a new Australian genus based on venational characters. In addition, the wing venation of specimens of an undescribed Indian species in the collections of the Natural History Museum, London are not assignable to any of the currently described genera. Despite these venational differences, the genitalia of these two new species closely resemble other apochrysine genera. It seems that almost every newly discovered species may be allocated to a new genus because of the extreme plasticity of venational characters in this subfamily. This is clearly unsatisfactory since the plethora of monotypic genera tells us little about the phylogenetic relationships within the subfamily.

Another problem is the tentative inclusion of *Nothancyla* within the Apochrysinae. Some apochrysine synapomorphies are absent from the genus and the male genitalia more closely resemble Chrysopinae. However, absence of chrysopine synapomorphies (5 rows of antennal setae) preclude the assignment of the genus to the subfamily. One solution would be to erect a new subfamily for the genus, leaving it a monotypic subfamily.

Chrysopinae

Brooks and Barnard (1990) established the monophyly of the subfamily. However, the status of the tribes remains problematic since the proposed phylogeny failed to resolve the relationships between tribes. An alternative phylogeny is shown in Fig. 2. Synapomorphic genitalic characters suggest that Leucochrysini and Belonopterygini are sister groups.

Five of the 14 Belonopterygini genera are monotypic but they all appear to be well-defined and may represent a relict fauna. The larvae of only three genera are known, but all are ant-associated. It would be of considerable phylogenetic significance to establish whether the other genera have similar life histories. The phylogenetic relationships between genera remain unclear.

Ankylopterygini is defined on the basis of the synapomorphic morphology of the scythe-like, untoothed mandibles and elongate palps. However, a species-group within the genus

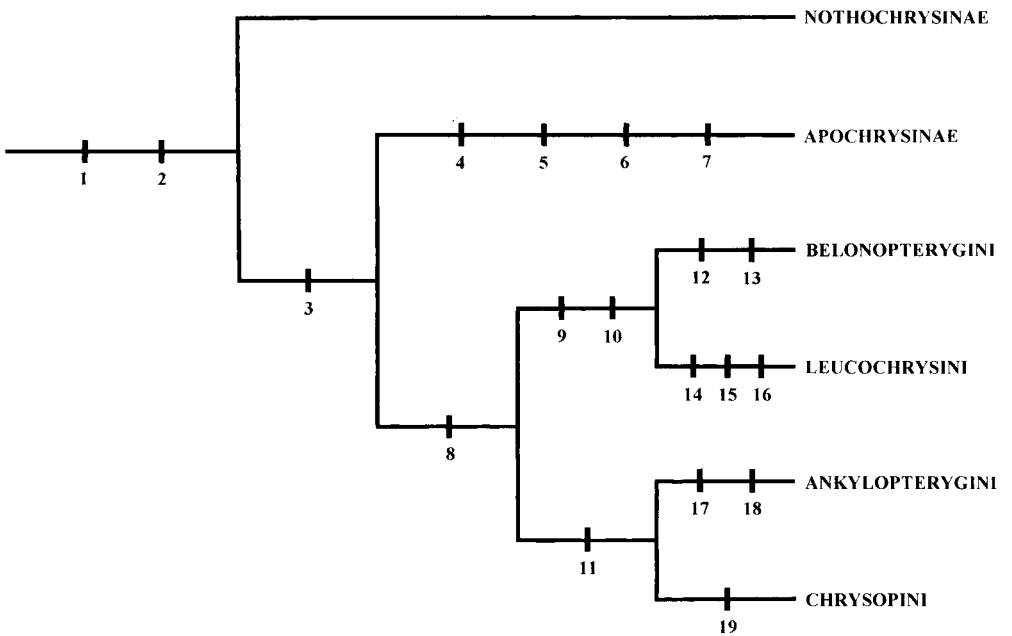

Fig. 2
Cladogram showing relationships of the subfamilies and tribes of Chrysopidae. Apomorphies are numbered as follows: 1. Larvae with empodia; 2. Larvae carry debris; 3. Psm meets outer gradate series; 4. Psm and Psc close together; 5. Basal Sc crossvein absent; 6. Pedicel constricted; 7. Antennal setae in 5 rings; 8. Antennal setae in 4 rings; 9. Gonocornua present; 10. Gonarcus transverse; 11. Arcessus narrow; 12. Cell c1 > c2; 13. Flagellar segments broad; 14. Pterostigma marked black; 15. Antennae >1.5 length of fore wing; 16. Psm curved upwards apically; 17. Palps constricted apically; 18. Mandibles scythe-like; 19. Tignum and gonapsis present.

Chrysopodes, which is unambiguously placed within the Chrysopini, shares these characters with Ankylopterygini. Such mandibular characters are suggestive of prey specialisation (perhaps a carnivorous diet, although no insect remains were found in the gut) and so could be convergent. Two genera currently included in Ankylopterygini, *Signochrysa* and *Retipenna*, although sharing the mandibular synapomorphies, otherwise differ markedly from the *Ankylopteryx*-group, especially in the morphology of the genitalia. This further suggests that the Ankylopterygini may be based on unreliable convergent characters. Hölzel (1992) provides a useful review of the systematics of the tribe.

A major challenge is the resolution of the generic affinities and relationships of the Chrysopini and to establish whether it is even monophyletic. The genitalic compliment (e.g. presence or absence of the tignum or gonapsis) may not be a reliable guide since the presence of these structures appears to be plesiomorphic for Chrysopini and the loss of these structures appears to have occurred on more than one occasion. Some chrysopine genera can be grouped on the basis of synapomorphies but many remain enigmatic. However, tentative groupings are suggested below.

Mallada group: (tignum and/or gonapsis present)
Anomalochrysa, Mallada – ectoprocts narrow; lobe on sternite 8 + 9;
Brinckochrysa, Chrysoperla, Eremochrysa, Peyerimhoffina – narrow wings, short intramedian cell, courtship songs;
Atlantochrysa, Cunctochrysa – ventral hook in male genitalia;
Apertochrysa – finger-shaped projection on entoprocessus;
Dichochrysa – plesiomorphic retention of full genitalic components;
Himalochrysa, Rexa – dorsal horns on arcessus;
Borniochrysa, Parachrysopiella – extended ectoprocts in male.

Chrysopa group: (gonocornua and/or pseudopenis present)
Ceratochrysa – gonocornua, gonocristae present;
Chrysopa, Ceraeochrysa, Plesiochrysa – pseudopenis, gonocornua, gonocristae present;
Nineta, Tumeochrysa – gonocornua present;
Yumachrysa, Meleoma – pseudopenis present.

Ungla group: (tergite 9 rounded, sternite 8 + 9 elongate)
Ungla, Kostka, Chrysopidia.

Unknown affinities:
Austrochrysa, Chrysemosa, Chrysopodes, Glenochrysa, Suarius.

Revisionary priorities

Within the Chrysopidae there are several large genera for which generic revision is a priority. These include *Dichochrysa, Mallada, Leucochrysa, Ankylopteryx* and *Italochrysa*. Brooks and Barnard (1990) listed 122 described species assignable to *Dichochrysa* which included eight species from the eastern Palaearctic. Subsequently, Yang (1995) listed 44 species from China alone, including many new species. An assessment of the Chinese fauna within the context of the *Dichochrysa* fauna in the region as a whole would be of great value. The division of the genus into discrete species-groups should also be a target in

order to establish the phylogeny and biogeography of the genus, and its relationships within the Chrysopini.

Mallada includes several very common widespread species that exhibit considerable variation throughout the range. A revisionary study would help to determine whether these species were monophyletic, and also establish the validity of many other morphologically similar taxa in the genus. In addition, the status of the *M. krakatauensis*-group (Brooks, 1994) and its relationship with *Chrysoperla* needs to be resolved.

Italochrysa currently includes a bewildering number of species, many described from female specimens and often distinguished by wing markings alone. A thorough revision of the genus based on male genitalia would help to clarify the status of these species and establish their relationships within the genus and with other closely related genera.

A revision of *Brinckochrysa* would be of value, especially if a thorough survey of the morphology of the stridulatory apparatus (Brooks, 1987) was included in the character analysis. Differences in the fine structure of the stridulatory organs are likely to reflect subtle differences in songs. If songs are an important part of courtship in the genus then it is possible that taxa with rather similar male genitalia are separable by morphological differences in the stridulatory organs.

Conclusions

There is still much basic taxonomic work to be done on the Chrysopidae. Some of the priorities include the need to:

1. Further resolve the higher classification of the family;
2. Revise certain large genera;
3. Intensify alpha taxonomic work on the faunas of South America, India and south-east Asia which are currently badly neglected;
4. Further explore non-morphological taxonomic methods;
5. Expand life-history investigations and morphological analysis of larval stages.

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