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Biogeography and Phylogeny of the Crocinae (Neuroptera: Nemopteridae)

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ABSTRACT

The biogeography of the world fauna of Crocinae (Neuroptera: Nemopteridae) is outlined. 47 species in 17 genera are known, and larvae of 21 species have been described. A theory is proposed to explain the present-day distribution of the subfamily. The relationships between the various crocine genera, and their evolutionary progress, are discussed on the basis of a set of characters which have emerged from this study, and from the work of HöLZEL (1975b).

INTRODUCTION

The Crocinae, a subfamily of Nemopteridae, is a group of highly specialized lacewings with a wide distribution. The adults are delicate insects with long filamentous hind wings, and the larvae of some species have remarkably elongated prothoraxes. Both adults and larvae are cavernicolous, inhabiting small caves, crevices, rock overhangs and even buildings which provide dry equable microclimates.

The question of how Crocinae became distributed in the south Palaearctic and on the southern continents is intriguing, and a theory is proposed to explain these phenomena.

The phylogeny of the Crocinae was discussed by HöLZEL (1975b), and this is reviewed and elaborated in the light of additional characters and new taxa which have been discovered since then. An attempt is made to arrange the genera into groups reflecting an evolutionary hierarchy or progression.

1.1 PRESENT DISTRIBUTION AND CENSUS. Fig. 1.

Crocinae are distributed in five main areas in arid and semi-arid regions of the world. Forty-seven species in 17 genera are currently recognised, and of these, 21 species occur in the southern Palaearctic, ranging from Spain and Algeria in the west to Pakistan in the east. Four of these species also extend their ranges into the northern Afrotropical Region as far south as Kenya. Ten species are recorded from southern Africa, with two of these also known from Angola and Malawi. Six species are known from Australia and five from South America, whilst of the remaining five, two are known from each of Socotra Island and Chad, and one from India.

The following table provides a list of crocine genera, the number of species in each and an indication of their distribution. Information on the Palaearctic and northern Afrotropical genera is largely derived from HÖLZEL (1975b) and MEINANDER (1980), whilst that for the southern Afrotropical, Australasian and Neotropical taxa is from MANSELL (1980, 1981a, 1981b, 1983a, 1983b).

Afghanocroce Hölzel, 1968	(1)	Palaearctic
Amerocroce Mansell, 1983b	(1)	South America
Anacroce Hölzel, 1975a	(1)	Palaearctic
Apocroce Tjeder, 1974a	(1)	Socotra Island
Austrocroce Tjeder, 1974b	(4)	Australia
Carnarviana Mansell, 1983a	(2)	Australia
Concroce Tjeder, 1967	(3)	Southern Africa
Croce MacLachlan, 1885	(3)	Palaearctic/India/Afrotropical
Dielocroce Cowley, 1941	(16)	Palaearctic/Afrotropical/Chad
Josandreva Navás, 1906	(3)	Spain/Chad/Socotra Island
Laurhervasia Navás, 1914	(4)	Southern Africa
Moranida Mansell, 1983b	(1)	South America
Pastranaia Orfila, 1955	(1)	South America
Pterocroce Withycombe, 1923a	(1)	Palaearctic
Thysanocroce With., 1923b	(1)	Southern Africa
Tjederia Mansell, 1977	(2)	Southern Africa
Veurise Navás, 1927	(2)	South America

Table 1. Genera of Crocinae, indicating number of species and distribution.

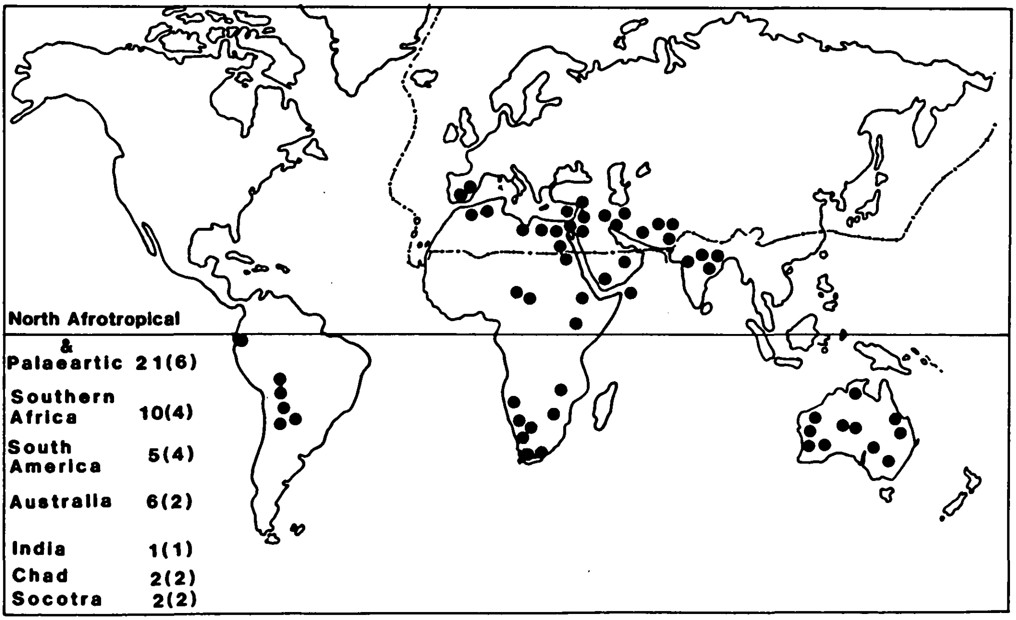

Fig. 1. Recorded distribution of the subfamily Crocinae. The dotted line indicates the southern limits of the Palaearctic Region.

1.2 HISTORICAL BIOGEOGRAPHY

Although it is convenient to evoke plate tectonics in explaining distributions of closely related organisms occurring on different continents, it is certainly justifiable in the case of the Crocinae. They do not lend themselves to other means of dispersal for several reasons: firstly, specialized habitats of larvae restrict them to particular areas; secondly, adults have weak powers of flight, and they, too, are associated with cave habitats, which render them poor candidates for long-range flight dispersal; thirdly, as the adults are short-lived they could probably not survive the time-span required for an intercontinental crossing by flight of wind; fourthly, local distribution patterns reveal that most species are localized, and apparently have low powers of vagility; finally, as they are not associated with man, crops or animals, they are unlikely to be accidentally dispersed.

The present distribution of Crocinae on the southern continents suggests a Gondwanian origin. This is supported by the fact that, despite ideal conditions, Crocinae are absent from North America which did not constitute part of Gondwanaland. The first group to be isolated would have been the Australian crocines, when Australia separated from Africa and South America during the early Jurassic (about 180 million years ago). These species have retained very generalized features and appear to be most closely related to the southern African **Concroce**. The remaining southern African genera form a fairly homogeneous group, with their closest relatives among the more advanced Palaearctic genera. There are major differences, however, between those two groups, indicating that they were isolated early, possibly by a barrier across equatorial Africa in the form of tropical forests. A great radiation of Crocinae took place along the southern Palaearctic and northern Afrotropical Region and across as far as India in the Oriental Region. As will be suggested below, some of the most advanced taxa are to be found in this area. The South American genera appear to be most closely related to the Palaearctic fauna, and were probably derived from this source before the final separation of north Africa and South America towards the end of the Cretaceous, about 65 million years ago (DIETZ & HOLDEN, 1970).

2.1 PHYLOGENY

Crocinae are most closely related to the Nemopterinae and share a sister group relationship with them (HöLZEL, 1975b). The Crocinae show several apomorphies not shared by the Nemopterinae (HöLZEL, 1975b), for example, filamentous hind wings in the adults and elongated prothoraxes in some larvae, which indicate that they are the more advanced subfamily, and are probably descended from the Nemopterinae. TJEDER (1967) suggested that the Crocinae are less advanced, but this view is not shared by HöLZEL (1975b) or myself.

In this study, numerous characters were assessed, including those mentioned by HöLZEL (1975b), and about 21 emerged as potentially significant in arranging the subfamily to genus level. In turn, only a few of these, listed below, can be utilized in placing the genera into groups, which may eventually lead to a tribal arrangement when more data are available.

Although information on Crocinae is fairly comprehensive, with larvae and biology of 21 species in 13 genera now known, there are still major lacunae in our knowledge. These include deficient information on the Neotropical taxa, especially **Pastranaia**; some **Austrocroce** larvae are still unknown and the larvae and biology of the largest genus, **Dielocroce**, and its close relatives, remain virtually unstudied. However, we are in a better position to consider the evolution of Crocinae, where 45% of larvae are known, than is the case in any other group of Neuroptera. It is premature to start constructing cladograms, but we can attempt to evaluate characters and use them to determine the relationships between genera, and to tentatively arrange these in an evolutionary sequence.

The only attempt at an interpretation of crocine phylogeny was that of HöLZEL (1975b), and the purpose of the present study is to review and expand upon his ideas in the light of new information. As more data become available, a better insight into crocine phylogeny will emerge, and it is hoped that this account will stimulate discussion and further research to this end.

2.2 CHARACTER STATES

After considering about 50 characters, the following emerged as potentially significant in arranging the Crocinae from family to genus-group level. They include most of the features used by HöLZEL (1975b). The character state on the left hand side is considered to be the apomorph or derived condition, whilst the alternative on the right is the plesiomorph or generalized state.

1	Hind wings modified	Hind wings normal
2	Mouthparts elongated	Mouthparts short
3	Hind wings threadlike	Ribbon- or spoon-shaped
4	Maxillae tubular	Maxillae normal
5	Larval prothorax sclerotized	Unsclerotized
6	Antennae shortened	Antennae long
7	Reduction in size of insect	Insects larger
8	Posterior cubitus and first anal vein in forewing fused	CuP and 1A separate
9	Male parameres not fused	Parameres fused apically
10	Male without pleuritocavae	Male with pleuritocavae
11	Larva with long prothorax	Larva with short prothorax
12	Males with bullae on wings	Bullae absent
13	Female with sternite 8 absent or fused	Female with S8 distinct
14	Radial sector thickened, with many radial crossveins in proximal radial field	Rs unmodified
15	First branch of Radial sector branched	Rs1 unbranched
16	Rs originates close to wing base	Rs originates distal of wing base
17	Adults tiny	Adults normal
18	Male with complete tergite 9	Tergite 9 divided dorsally
19	Sternite 8 in female fused with lateral gonopophyses	S8 not fused with gonopophyses
20	Male with long ectoprocts	Male with short ectoprocts
21	Rostrum long	Rostrum (mouthparts) short

2.3 DISCUSSION OF CHARACTERS

1 and 2. These derived characters define the Nemopteridae, which is the only family in the Neuroptera which has developed long ribbon- or thread-like hind wings, and has the mouthparts elongated into a rostrum.

3 to 7; are unique to the Crocinae and delimit the subfamily. HöLZEL (1975b) has discussed 3 to 5. Numbers 6 and 7, the shortening of antennae and a reduction in size of the insect, are apomorphic relative to the Nemopterinae and have contributed to the cavernicolous habit of Crocinae, which is also an advancement over the sister group.

8. The separation of Cup and 1A in the forewing is plesiomorph (HöLZEL, 1975b) and is the prevailing condition in Nemopterinae. The fusion of these two veins in most crocine genera must be seen as an advance. Only **Pastranaia** and **Josandreva** retain the plesiomorphic state.

9. HöLZEL (1975b) maintains that 'fused parameres' is apomorphic. However, on outgroup comparison it must be considered plesiomorphic as it is the condition manifest in the Nemopterinae. Genera retaining fused paramere lobes are **Josandreva, Croce, Amerocroce** and **Veurise** (?).

10. The presence of pleuritocavae is considered plesiomorphic by HöLZEL (1975b) and their loss is the derived condition. None of the genera which have pleuritocavae also possess bullae, and it seems as though bullae may have arisen subsequent to the loss of the intersegmental invagination. Pleuritocavae are present in **Josandreva, Croce, Veurise** and **Moranida.**

11. The elongation of the larval prothorax is certainly derived as Crocinae are unique among the insects in this respect. Genera whose larvae have developed long prothoraxes are **Laurhervasia, Tjederia, Amerocroce, Moranida, Pterocroce,** and **Dielocroce** (only one species known).

12. The development of bullae is also unique to Crocinae, and the occurrence of bullae in both fore- and hind wings must be considered the most advanced condition. Bullae are present in the wings of **Laurhervasia, Thysanocroce, Anacroce, Afghanocroce** (hind wings only), **Pterocroce** (forewings only) and **Dielocroce** (both fore- and hind wings).

13. HöLZEL (1975b) maintains that a sclerotized or partly sclerotized sternite 8 in the female has arisen independently several times. However, the view held here is that it is the plesiomorphic condition, as in the Nemopterinae, and that its gradual disappearance or fusion with other sternites is derived. Only **Moranida, Apocroce, Afghanocroce, Veurise** and **Dielocroce** show no signs of an eighth sternite, although in some of these it may be fused with sternite 7 (e.g. **Veurise, Moranida**).

14. In which the Rs has become thickened and runs closely parallel to the radius, with many crossveins in the proximal part of the radial field, but absent from the distal part. It is a development of the radial field not found in other Neuroptera, and is a derived character manifest in **Moranida, Anacroce, Apocroce, Pterocroce, Afghanocroce** and **Dielocroce.**

15, is another derived character mentioned by HöLZEL (1975b), and is found in **Moranida, Amerocroce, Apocroce, Pterocroce, Afghanocroce** and **Dielocroce.**

16. The position close to the wing base and the angle of origin of Rs is unique to only two genera, **Josandreva** and **Croce.**

17. **Josandreva** and **Croce** are remarkably small relative to other Crocinae, and following on from character 7 this is a derived condition relating to a cavernicolous habit.

18 and 19. These two characters are peculiar to **Thysanocroce**, **Tjederia** and **Laurhervasia**. TJEDER (1967) maintains that an undivided tergite 9 in the male is a primitive condition, but it is considered to be apomorphic here, as it is found nowhere else in the Crocinae or Nemopterinae. The same applies to the fusion of sternite 8 with the lateral gonopophyses in the female.

20. Ectoprocts are well developed in **Moranida**, **Amerocroce** and, to a lesser extent, **Afghanocroce**. Relative to other crocines and nemopterines it must be considered a specialized character.

21. The development of a long rostrum seems to correlate with a high degree of advancement in the Crocinae, but it may also be an adaptation to the environment (type of flower available) of particular species. Caution should be exercised when assessing its value as an evolutionary character.

2.4 ARRANGEMENT OF GENERA IN EVOLUTIONARY SEQUENCE

Based on the above-mentioned characters and their interpretation, the genera and groups of genera could be arranged in the following evolutionary progression, starting from the most generalized.

Pastranaia: Lack of information on the female and larva of this genus precludes an accurate assessment of its position. It could be an isolated primitive group (see character 8) as suggested by HöLZEL (1975b). His criticism of its association with **Josandreva** in the tribe Pastranaiini ORFILA (1955) on the basis of a single plesiomorphic character is well founded, and the tribe is unsubstantiated.

Josandreva/Croce: Form a homogeneous group as suggested by HöLZEL (1975b). They share the characters 9 to 13 in the plesiomorphic state and **Josandreva** also has CuP and 1A separate, but this character is apomorphic in **Croce**. Characters 16 and 17 are synapomorphies which unite the two genera into a distinct group.

Austrocroce/Carnarviana/Concroce: Show an advance over the **Josandreva/Croce** group in that all three have characters 8, 9 and 10 in the apomorphic condition. However, they still retain the remaining characters, 11 to 21 in the plesiomorphic state. They are placed together on the basis of their overall similarity and the three synapomorphies, which they also share with some of the higher taxa. As yet, no unique synapomorphy has been found that could prove that they are a monophyletic group. The larvae of three species of **Austrocroce** are still unknown.

Veurise: Uncertainty also surrounds this South American genus and more information is required. It shows an advance over the previous group in that S 8 in the female is not a distinct sclerite, but apparently fused with S 7 (STANGE & WILLINER, 1981). It also has 8 and 9 as apomorphies, whilst 10 to 21 (excluding 13) are plesiomorphic.

Thysanocroce/Tjederia/Laurhervasia: In this group of genera, two additional apomorphies, bullae in the hind wings of the males (except **Tjederia**) and larvae with long prothoraxes (except **Thysanocroce**), appear for the first time (11 and 12). In addition, characters 8, 9 and 10 are in the derived state. Two synapomorphies, 18 and 19, are unique to these three genera and apparently unite them into a monophyletic group.

Amerocroce: Is enigmatic in that it shows several apomorphies, namely 8, 10, 11, 15 and is one of only two genera in which the male ectoprocts are very long (20), and the rostrum is also remarkably long (21). Conversely, the plesiomorphic state is retained in characters 9, 12, 13 and 16 to 19. The radial field (14) is starting to become modified, but has not reached the condition manifest in the next group.

Moranida/Apocroce/Pterocroce/Anacroce/Afghanocroce/Dielocroce: This is the most advanced group of genera, sharing the most synapomorphies, namely 8, 9 and 10 (except **Moranida**), 11 and 12 (except **Moranida, Apocroce**), 13 (except **Pterocroce**), 14 and 15 (except **Anacroce**). The development of the radial field is characteristic for this group, as is the development of bullae, especially in the most advanced genus, **Dielocroce.**

(a) **Moranida** shows affinities with the previous genus, **Amerocroce,** especially in the development of the ectoprocts. However, whilst retaining two plesiomorphies, 10 and 12, it shares more synapomorphies with this group than it does with **Amerocroce.**

(b) **Apocroce** retains 12 in the plesiomorphic state, otherwise it fits well into the group. The larva is unknown.

(c) **Pterocroce** still has character 13 in the generalized state, but also shows an advance in having the unique feature of bullae in the forewings only.

(d) **Anacroce** has an unbranched Rsl, which is plesiomorphic for this group (character 15), but only the holotype is known, otherwise it seems closely related to the next genus. The larva has yet to be discovered.

(e) **Afghanocroce** is closely related to the next genus, but has bullae only in the hindwings. The larva is also still unknown.

(f) **Dielocroce** is probably the most highly evolved crocine genus, and also the most successful. Its unique apomorphy is the presence of bullae in both pairs of wings. In addition, the males have dorsal projections on the extremities of the parameres (see HöLZEL, 1975b: eg. fig. 77), a character shared with **Pterocroce, Afghanocroce** and **Anacroce.** The only known larva, **D. baudii** (Griffini), has a long prothorax, the rostrums tend to be long, and of all genera, it shows the least number of plesiomorphies, based on the above table.

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