

Intergeneric Relationships in recent Nymphidae

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Abstract

Nymphidae, a family containing about 20 described species and mainly limited to the Australian region, is considered relatively primitive in the Myrmeleontoidea. It contains species more resembling Osmylidae and Psychopsidae in appearance and others more like Myrmeleontidae and, historically, has been treated as two families (Myiodactylidae and Nymphidae). Adult representatives of the seven described genera, including all generotypes, have been examined. Based on features, including genitalia, of most described species and a number of undescribed taxa, possible relationships between the genera are outlined and discussed.

Introduction

Nymphidae are a small family of distinctive Neuroptera and are almost entirely limited to the Australian region. They are of particular interest in being the most likely ancestral group of higher Myrmeleontoidea – including the antlions, ascalaphids and nemopterids. Most references to it are either descriptions of one or few species, or speculations on the family relationships. In general appearance, Nymphidae are diverse, and the supposedly more primitive members (*Myiodactylus*, *Osmylops*) have been placed by some early workers (HANDLIRSCH 1908, TILLYARD 1926, WITHYCOMBE 1925) in a separate family, Myiodactylidae, separated from other genera on the wing shape and absence of tibial spurs (Fig. 1). Occasionally, a more distant relationship of these taxa has been implied: WITHYCOMBE (1925) placed Myiodactylidae in the Superorder Osmyoidea and the Nymphidae in the Myrmeleontoidea. However, as ADAMS (1958) showed, the only character of the several adult features earlier used to separate the two “families” that appears valid is the wider forewing costal area of the “Myiodactylidae” and this may not be alone sufficient for separation at the family level. Tibial spurs, by analogy, are present or absent in clearly related genera of Myrmeleontidae. Adams thus followed ESBEN-PETERSEN (1917) and NAVÁS (1922) in discounting HANDLIRSCH's (1908) splitting of the Nymphidae, but MACLEOD (1970) tentatively suggested that further knowledge of larval features may lead to reappraisal of this idea. NAVÁS (1922) designated three “tribes” in the family Nymphini – not sensu BANKS 1913, Myiodactylini, Nymphyrini, but these have not been adopted by more recent authors.

In adult features, Nymphidae are in some ways transitional between Psychopsidae and Myrmeleontidae (RIEK 1970), but are clearly distinct from both. The following account includes considerations of genitalic data of all described genera, which data may lead to clarification of the family relationships when other Australian Neuroptera have been similarly appraised. Apparently the only previously published genitalic data on the family are those of TJEDER (1970), who figured the male terminalia of *Nymphes myrmeleonides* LEACH and “*Osmylops pallidus*” BANKS and of ACKER (1960). ESBEN-PETERSEN's (1917) drawings of *O. sejunctus* (WALKER) are sufficient to confirm his identification, but not for detailed morphological interpretation.

As considered here, Nymphidae are separable from all other Myrmeleontoidea by having at least some trichosors on the forewing margin, although these may be weakly defined. They are easily separable from Osmylidae by lacking ocelli, and further diagnostic features are given by RIEK (1970).

Genus	No. species known	Examined		
		♂	♀	Both
<i>Nymphes</i>	5	5	4	4
<i>Austronymphes</i>	1	1	1	1
<i>Nesydrion</i>	4	4	4	4
<i>Nymphydion</i>	1	—	1	—
<i>Norfolius</i>	1	1	1	1
<i>Myiodactylus</i>	5 (?+1)*	3	4	2
<i>Osmylops</i>	3	3	3	3

Tab. 1: Nymphidae: Recent Genera. **M. chrysopoides* NAVÁS has not been confirmed as belonging to this genus.

Types of many species, and all generotype species, have been examined, and a considerable amount of additional material also seen.

A revision of the family is to be completed shortly, and this paper is a preliminary assessment of generic relationships. Table 1 shows the numbers of species of the seven known genera that I have examined.

The major features used for specific and generic separation, and for suggesting relationships between them, are wing venation and genitalia.

Wing venation

With few exceptions, features of venation have been the primary characters used for generic separation by earlier authors and — although the extent of variation of some characters is greater than hitherto appreciated — such is clearly sound. The venation is complex, and in this account the interpretation of ADAMS (1958), as followed by MACLEOD (1979) is used.

Features referred to for taxonomic purposes are:

- a) The complexity of the costal field of the forewing. In *Nymphes*, *Austronymphes* and *Nesydrion* the costal crossveins are mainly simple. Other genera show some elaboration by forking, often only sporadically or near the wing margin and only *Norfolius* has crossveins linked to form more than one row of cells, for part of the costal length.
- b) Subcostal crossveins. Although the separation of genera with one basal crossvein from those having many crossveins is usually unambiguous, several species (or some individuals of species) of *Austronymphes*, *Osmylops* and *Myiodactylus* may have the crossveins incomplete posteriorly, and they may be represented only by small projections from the subcosta. A greater anomaly occurs in *Nymphes* in which both conditions of one and many crossveins are found in species which are clearly closely related. Although such variation has not been found in other genera, this plasticity may indicate the need for caution in interpreting this feature as of generic value in the family.
- c) Point of origin of Rs+MA. In most taxa this is near the wing base in both wings. In one species here referred to *Nymphes* its point of origin in the hindwing is at about one third of the wing length from the base, and in *Austronymphes* and in many individuals of *Nesydrion* it is also well removed from the wing base.
- d) Position of fork of MP, if present. Several positions of the forewing MP fork are found. In *Nymphes*, it is usually clearly beyond the separation of MA from Rs; in *Nesydrion* the position is more variable, and in *Austronymphes* the fork is absent. The latter feature is found also in some species of *Nymphes*, and in *N. modesta* the fork is usually present but is absent in a few otherwise similar individuals. The vein is usually simple in *Myiodactylus* and forked in *Osmylops*. Most taxa have MP forked near the wing base in the hind wing, and the position of the fork of MP₂ may be a specific character.

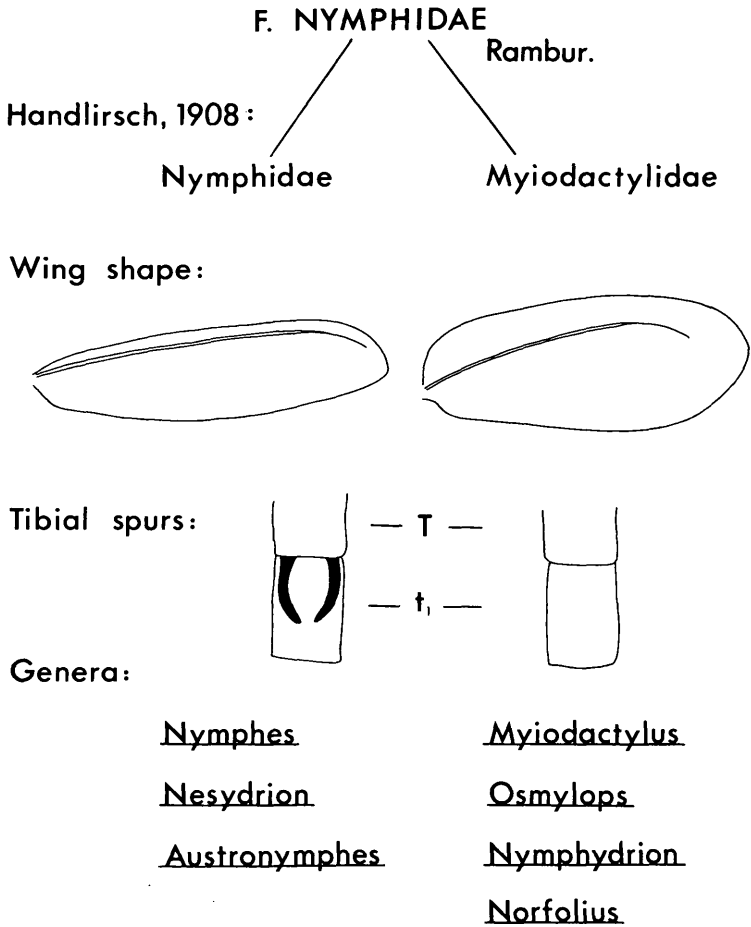


Fig. 1: Historical scheme of division of Nymphidae into two families: characters used and generic allocation.

- e) Cubital veins. The prominent CuA forewing fork of *Nymphes* and *Austronymphes* is generally somewhat less prominent in *Nesydrion*, and considerably less conspicuous in other genera, and may exemplify the greater superficial resemblance of *Nymphes* to many Myrmeleontidae in which the fork is very well developed. The presence of two rows of cells behind CuA in the hindwing is a useful generic character for *Nymphes* and the great length of the hindwing CuA in *Nymphydron* is currently the major basis for retaining the genus.
- f) Anal veins. In the forewing, all three anal veins are invariably distinct, but the extent of branching – particularly of 1A – varies somewhat, even in the same species of *Myiodactylus* and *Osmylops*. In the hindwing, 1A is often fused, even if for only a short distance, with CuP, and care is needed in interpretation of this region: 2A and 3A remain generally distinct.

Genitalic structures

Notwithstanding the pioneer work of TJEDER (1970) and ACKER (1960), genitalia of Nymphidae (especially homologisation and terminology of the male genitalia) remain diffi-

cult to interpret fully. Clearly, male genitalia are elaborate, and provide major suites of characters for species separation. Female structures are overall simpler, but they are still useful for distinguishing species. In both sexes of all species examined, a small median posterior cata-processus is present and the cercal callus is generally pale, although not well-differentiated from the surrounding area. It usually bears a large number of small trichobothria. In the male of *O. sejunctus*, however, the callus is expanded and bears digitate processes.

Female (Fig. 2)

In all genera the ectoproct and tergite IX are separated by a (sometimes indistinct) suture, and the ectoproct is usually distinctly dorsal and enclosed by the tergite along at least part of its ventral surface. Tergite VIII is expanded ventrally, and sternite VIII absent: a sub-genitale is invariably present and may represent this sternite. In a few species, however, the membrane ventral to tergite VIII contains a slightly sclerotised plate probably representing a postgenitale, which is not otherwise clearly evident. A pair of arcuate gonapophyses laterales are present and their shape is of some specific value. The spermatheca is usually a simple slender duct, often long and substantially coiled, but in *Austronymphes*, *Norfolius* and some species of *Nesydrion* and *Osmyllops* leads to an expanded and heavily sclerotised "sac" (?velva). The bursa is indistinct and membranous.

The tergite and sternite of segment VII are well-separated, and both are heavily sclerotised. The shape of sternite VII may be of specific value (*Nymphes*, for example) but may also vary slightly within a species.

Male (Fig. 3)

As in the female, the ectoproct is closely associated with, and sometimes partially enclosed by, tergite IX. I here follow TJEDER (1970) in referring the major posterior sternite to segment IX, although it often subtends tergite VIII and may prove to be sternite VIII or there represent a fusion of sternites of the two segments. In *Norfolius* and *Austronymphes*, however, its designation as IX is relatively unambiguous and, without investigation of muscle insertions of the other genera, it appears practical to consider the structure homologous between all genera of the family. Sternite VIII may, therefore, be distinct or not, and tergite VIII be correspondingly shallow or extended ventrally. A tignum is never present. A gonarcus is invariably present and is usually divided dorsally. It is usually fairly slender, although somewhat deepened in isolated species in several genera. Lateral entoprocessi from the gonarcus are sometimes well-developed but are more commonly small or absent. A median dorsal structure between the two parts of the gonarcus should perhaps be termed the arcessus: TJEDER (1970) refers to this in *Nymphes myrmeleonides* as the mediuncus — in this species, however, the structure is not as clearly separated from the gonarcus as in many others. As only one median dorsal structure is present in each species, and the extent of association with the gonarcus within a genus ranges from loosely attached to distinctly separate, it is likely that the same structure is represented in each. Whereas in some species of *Osmyllops* it has become slightly anterior to the gonarcus dorsal tips, in others it is produced posteriorly. The arcessus (mediuncus) is ornamented ventrally, usually towards its apex, with more or less elaborated, usually symmetrical spines — the hypocuspis of TJEDER.

The ventral tips of the gonarcus are usually widely separated, and each supports a movable and sometimes elaborate structure which I have here called the paramere*. Although TJEDER terms this the "hypostylus" in *Nymphes myrmeleonides*, the separate structure which he terms the paramere in this species is not present in others and the main structure is itself sometimes relatively simple. In *O. sejunctus*, the structure is more elaborated than in others of this genus but TJEDER's "adscensio" appears to be the major part of the paramere and TJEDER's "paramere", a membranous ventral lobe not prominent in any other species. The median bifurcate structure designated by TJEDER as the "paramere" (with superprocessus) in *N. myrmeleonides* is not always present: it is, for example, absent from other species

* During the Symposium, Dr. P. A. Adams suggested that this structure should properly be termed a gonocoxite.

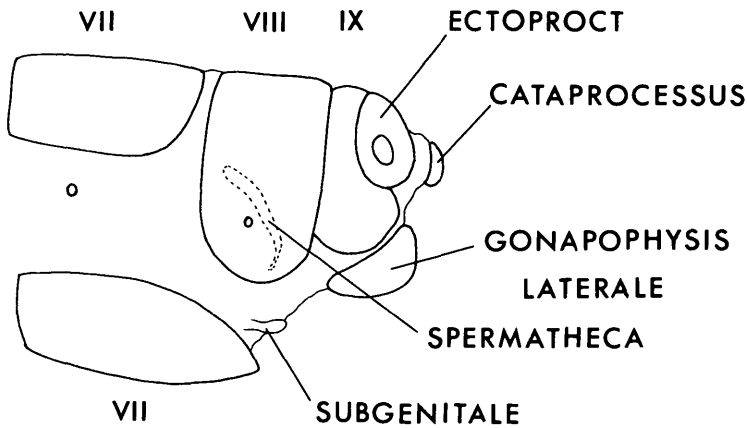


Fig. 2: Female terminalia of Nymphidae, generalised to indicate terminology.

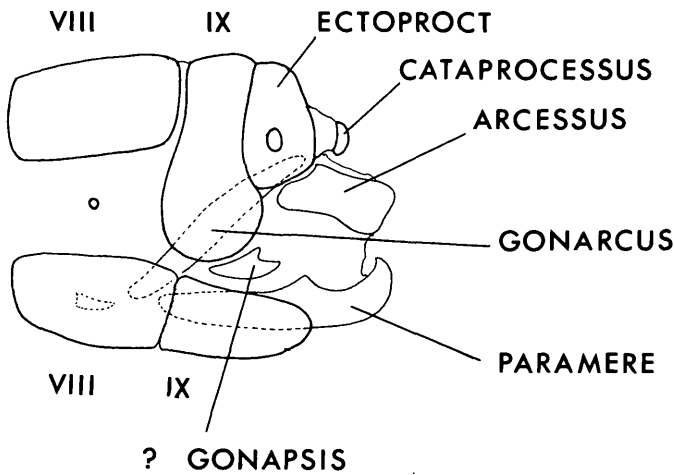


Fig. 3: Male terminalia of Nymphidae, generalised to indicate terminology.

of *Nymphes* and from *Austronymphes*. It is most elaborated in *Nesydrion* in which it is elongate and the apices variously spined. It is present in *Norfolius* and, whereas it is usually absent from *Myiodactylus* and *Osmyllops*, a small median structure associated ventrally with the arcessus in *O. placidus* appears to represent the same structure. In all, this structure is clearly separated from the gonarcus arch. It is tentatively termed the gonapsis, by analogy with the position of this structure in some Chrysopidae. A small hypandrium internum is present, although this is often greatly reduced, membranous, and difficult to detect.

The above interpretation of genitalic structures therefore differs in some details from that of TJEDER (1970), but terminology is based largely on his account. TJEDER's prime pur-

	Gonarcus	Arcessus	Parameres	'Gonapsis'
<i>Nymphes</i> LEACH	Separate	Large	Large/Small	+ ×
<i>Austronymphes</i> ESBEN-PETERSEN	Separate	Large	Large	×
<i>Nesydrion</i> GERSTAECKER	Separate	Large	Large	+ Large
<i>Norfolius</i> NAVÁS	Separate	Small	Large	+ Small
<i>Myiodactylus</i> BRAUER	Fused	Moderate	Large	×
<i>Osmylops</i> BANKS	Separate	Small	Large	(+) ×

Tab. 2: Nymphidae. Male Genitalic complements of each Genus (*Nymphydron* BANKS omitted);
× = absent, + = present.

pose was to provide a terminology “facilitating taxonomic descriptions“ rather than to clarify origins of structures. I agree with him in believing it currently impossible to morphologically define all structures of the male genitalia, which are extremely variable within the order. The presence or absence of the above structures in each genus is summarised in Table 2.

Discussion

- The family clearly contains two major elements, or groups of genera:
1. As shown by earlier authors, *Nymphes*, *Austronymphes* and *Nesydrion* form a closely – associated group of genera. One species here referred to *Nymphes* is in some respects annectant between *Nymphes* and *Austronymphes*. This group is united by their relatively elongate wings and by possession of tibial spurs, and comprises the former family Nymphidae in its restricted sense.
 2. The other genera, which lack tibial spurs and generally have more rounded wings, are more diverse and are those earlier referred to the separate family Myiodactylidae. *Myiodactylus*, with particularly broad fore wings is very different in general appearance from *Nymphes* but other genera have a wing shape more closely resembling the group 1 genera.
- As MACLEOD (1970) has reaffirmed, the family is of considerable antiquity, and a fossil species from the Jurassic period has been referred to it. The Baltic amber species, *Pronymphes mengeanus* KRUGER resembles the “group 1“ genera above in wing shape, and MACLEOD suggested the likelihood that this taxon may prove to be identical with *Nesydrion*.

The second of the above groups has been considered the more primitive (for example by ADAMS 1958), and the first group shares a number of structural features with many Myrmeleontidae. These include tibial spurs and the pronounced development of the fore wing CuA fork and hindwing MP₂ fork. Despite the wide range in general appearance of the Nymphidae, genitalia imply that they should be considered as a single, separate family; a division of Myiodactylidae from Nymphidae *sensu restricto* is not supported on the adult features. Females are remarkably similar in gross genitalic features, as in some other families of Neuroptera, and interspecific differences parallel intergeneric differences. Males differ more, but there is still considerable variation within a genus, and it may be difficult to assign males to a particular genus on genitalic features alone. In all, the structures here regarded as parameres are prominently developed and an arcessus (although sometimes small) is invariably present. Males of some *Myiodactylus* and *Osmylops* species have the gonarcus fused (or the arches closely associated) dorsally, and the separation of the arches in *Nymphes* and other genera may be an advanced trait. Likewise, the supposedly more primitive genera are less elaborate in usually lacking a “gonapsis“, and elaboration of this structure is a distinctive feature of *Nesydrion*. Within the first group of genera, *Nesydrion* appears relatively isolated.

Of the other genera, it is possible that reduction in width of the forewing costal field may be an advanced character. A wide field is found in both *Myiodactylus* and *Nymphydron* and the latter genus is maintained as distinct largely on hind wing venational features: discovery

of the male may necessitate some reappraisal of its status. *Norfolius* is distinct on venation features and in possessing a distinct "gonapsis".

Thus, the seven described genera of Nymphidae are considered to be distinct on venational features, and less so on genitalic structures. The "group 1" genera more closely resemble recent Myrmeleontidae in characters of wings and legs than do the "group 2" genera: this accords with earlier suggestions that they may be the "more advanced" genera. However, there is no evidence that the two "groups" form other than a single transition series from the more primitive *Myiodactylus* to the more advanced *Nymphes*.

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Since this paper was read, the following, containing figures of 20 species of Nymphidae has been published:
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