

FOUR JUMPING SPIDER GENERA OF THE *COCALODES*-GROUP ARE MONOPHYLETIC WITH GENERA OF THE SPARTAEINAE (ARANEAE: SALTICIDAE)

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ABSTRACT

Rodrigo, A.G. & Jackson, R.R. (1992). Four jumping spider genera of the *Cocalodes*-group are monophyletic with genera of the Spartaeinae (Araneae: Salticidae). *New Zealand Natural Sciences* 19: 61-67.

Wanless (1984a) erected a new sub-family, the Spartaeinae, to contain all members of the incorrectly named Boethinae except the genera *Allococalodes*, *Cocalodes*, *Holcolaetis*, and *Sonoita*. These were excluded from the sub-family because they possessed a median tegular apophysis on the male palp, a feature which Wanless believed to be synapomorphy of the group, and one which separated the group from members of the Spartaeinae. Our phylogenetic analysis of the extant members of the Spartaeinae, and the "*Cocalodes*-group" indicate that the latter are monophyletic with other genera of the sub-family. An amended definition of the sub-family is provided.

KEYWORDS: Spartaeinae - "*Cocalodes*-group" - phylogeny - monophyly - quasi-polymorphic coding.

INTRODUCTION

Wanless (1984a) erected the jumping spider sub-family Spartaeinae to accommodate members of the incorrectly named Boethinae. He also removed the genera *Cocalodes* Pocock, *Sonoita* Peckham & Peckham, and *Holcolaetis* Simon from the sub-family on the grounds that males of these genera possess a median apophysis on the palpal tegulum, a feature not possessed by other genera of the Spartaeinae. Wanless (1984a) suggested that another sub-family should be erected to contain these aberrant genera and a closely related genus, *Allococalodes* Wanless, and he informally referred to them collectively as the "*Cocalodes*-group". He was later to reassess this claim on the grounds that *Holcolaetis* and *Sonoita* share little in common with *Cocalodes* and *Allococalodes*, apart from the presence of a tegular median apophysis, the homology of which he doubted (Wanless 1985). There is little doubt,

however, that these genera are closely affiliated with members of the Spartaeinae and another allied sub-family, the Lyssomaninae (Wanless 1984a).

These three groups are considered to be primitive salticids (Blest & Carter 1987), and our interest in them stems from a desire to test the hypothesis first proposed by Jackson & Blest (1982) that jumping spiders evolved from web-building ancestors. As a consequence, we reconstructed the phylogeny of the Spartaeinae using morphological characters, and we included the genera *Cocalodes*, *Allococalodes*, *Holcolaetis*, and *Sonoita* in the analysis. Our results indicate that the "*Cocalodes*-group" forms a monophyletic clade within the Spartaeinae and, in accordance with current phylogenetic systematic practice, should be included as members of the sub-family. Here, we describe the phylogenetic analysis, as well as the implications of its results.

METHODS AND MATERIALS

TAXA STUDIED

Descriptions of the taxa listed in Table 1 were obtained from published literature (cited in Table 1). A list of characters were obtained from these descriptions and these are described below.

MORPHOLOGICAL CHARACTERS

The following morphological characters were used to construct a taxon-character dataset. The reader is directed to the excellent papers by Wanless (1984a, 1984b) for more complete descriptions of the characters. The method of maximum parsimony (Kluge & Farris 1969, Wiley 1981) was used to reconstruct the phylogeny of the group. As is appropriate for this method, only characters whose states partition the taxa into two

or more groups, with at least two groups having more than one taxon as a member, were used. Characters which satisfy this criterion are phylogenetically informative (*sensu* Hennig 1965). Characters which are monomorphic for all taxa offer no information on within-group relationships. Characters for which there is only one partition with more than one taxon are similarly uninformative, for it implies that all other taxa possess unique character states (*ie.* autapomorphies).

Table 1. List of genera studied. *Asemonea* is a member of the Lyssomaninae, and was included as an outgroup. *Allococalodes*, *Cocalodes*, *Holcolaetis*, and *Sonoita* have been informally referred to by Wanless as the "Cocalodes-group".

| GENUS | REFERENCE |
|----------------------------------|-------------------|
| <i>ALLOCOCALODES</i> Wanless | Wanless 1982 |
| <i>ASEMONEA</i> | Wanless 1980 |
| <i>BRETTUS</i> Thorell | Wanless 1979 |
| <i>COCALODES</i> Pocock | Wanless 1982 |
| <i>COCALUS</i> Koch | Wanless 1981a |
| <i>CYRBA</i> Simon | Wanless 1984b |
| <i>GELOTIA</i> Thorell | Wanless 1984a |
| | Wijesinghe, 1991b |
| <i>HOLCOLAETIS</i> Simon | Wanless 1985 |
| <i>MELEON</i> Wanless | Wanless 1984a |
| <i>MINTONIA</i> Wanless | Wanless 1984a |
| <i>NEOBRETTUS</i> Wanless | Wanless 1984a |
| <i>PHAECIUS</i> Simon | Wanless 1981b |
| | Wijesinghe 1991a |
| <i>PORTIA</i> Karsch | Wanless 1978 |
| | Wanless 1984a |
| <i>SONOITA</i> Peckham & Peckham | Wanless 1985 |
| <i>SPARTAEUS</i> Thorell | Wanless 1984a |
| | Wanless 1987 |
| <i>TARAXELLA</i> Wanless | Wanless 1984a |
| | Wanless, 1987 |
| <i>VEISSELLA</i> Wanless | Wanless 1984a |
| <i>YAGINUMANIS</i> Wanless | Wanless 1984a |

1. Posterior median eyes (PMEs): 1-small and vestigial; 0-large (Wanless 1984a, p. 137). Only some extant and extinct (*ie.* amber fossil) members of the Spartaeinae, Lyssomaninae and *Cocalodes*-group possess large and functional PMEs. These are vestigial in other advanced salticids. Wanless (1984a) notes that with the exception of *Taraxella*, all salticids can be placed easily into one or the other category.
2. PME in relation to anterior median/anterior lateral eyes (AMEs/ALEs) and posterior lateral eyes (PLEs): 1-closer to AME/ALEs than to PLEs; 0-closer to PLE (Wanless 1980, p. 217). The closeness of the PMEs to the anterior eyes is most marked in the lyssomanine genera *Asemonea* O.P.-Cambridge, *Goleba* Wanless, *Macopaeus* Simon, and *Pandisus* Simon, where the tubercles on which the PMEs are situated abut those which hold the ALEs. The PMEs of some spartaeine genera are also found close to the ALEs, although not to the extent found in the lyssomanine genera.
3. Femoral organ: 1-present; 0-absent (Wanless 1984a p. 139). This structure takes the form of a perforated region situated either on a tubercle or in a gully on the underside of the femora of Legs I in the males of some genera. An amorphous exudate is often associated with the organ, and it may have a pheromone secreting function.
4. Minute tarsal and metatarsal setae: 1-present; 0-absent (Wanless 1984a, p. 169; 1984b, p. 450). Numerous minute setae may be found on the underside of tarsi and metatarsi of some genera.
5. Retrolateral tibial apophysis (RTA): 1-membraneous base present; 0-membraneous base

- absent (Wanless 1984a, p. 139). The RTA is found on the male palpal tibia. The presence of a membraneous base to the RTA allows it to have some mobility. This feature is only present in some genera.
6. M1 apophysis of the distal haematodocha: 0-absent, 1-minute lobe, 2-large and petal-like, 3-long and filamentous, 4-membraneous patch (Wanless 1984a, p. 140). The distal haematodocha of the male palps of some genera are made up of two apophyses which are labelled by Wanless (1984a) as M1 and M2. The reader is referred to Wanless (1984a) for more complete descriptions of these structures, but it is noteworthy that these apophyses are absent from the *Cocalodes*-group. Wanless (1984a) therefore suggested that the presence of M1 and M2 may be a synapomorphy (*ie.* a shared-derived character) of the Spartaeinae.
 7. Median tegular apophysis: 1-present; 0-absent (Wanless 1982, p. 264; Wanless 1984a, p. 141). This apophysis takes the form of a bifid prong arising from the palpal tegulum, and is only found in members of the "*Cocalodes*-group", as well as some lyssomanine genera.
 8. Tegular furrow: 0-lacking; 1-short and shallow; 2-deep (Wanless 1984a, p. 140). Part of the tegulum, usually found on its dorsal side. It is often obscured by other structures of the palp, and information on this feature is not always available. Wanless (1984a) makes the point that the furrow is found on the palps of all male spartaeines, and considers it to be a synapomorphy of the sub-family.
 9. Palpal patellar protuberance: 0-lacking; 1-membraneous; 2-rigid; ?-variable (Wanless 1984a, p. 141). The patellar protuberances, together with tibial protuberances, are part of the architecture of the male palps and define their potential for articulation.
 10. Eyes on well-developed tubercles: 0-yes; 1-no. Many spartaeine and lyssomanine genera have their ALEs, PME's, and PLE's set on well developed tubercles. In others, however, these tubercles are poorly developed or lacking.
 11. Mytiliform fields: 0-absent; 1-present (Wanless 1984b, p. 446). These "mytiliform" fields are so-called by Wanless because of the presence of structures (30-40 μm in length) which resemble mussel shell valves. These fields are situated on the dorsal surface of the abdomen, and are associated with pores of some form or other, suggesting a secretory function. They are difficult to find in all but fresh specimens, and have only been found in some species. We have been conservative in our estimation of their presence, and have only recorded them as present in those genera with species which are known to possess these fields. All other genera have been treated as not possessing these fields.
 12. Cymbial flange: 0-absent; 1-present (Wanless 1978, p. 84). A flange-like protuberance is found on the pro- or retrolateral dorsal surface at the base of the cymbium of some genera.
 - 13-16. Number of pro-marginal teeth on chelicerae (Wanless 1984a, p. 138). Salticids, like many other spiders, possess dentate armature on their chelicerae. The numbers of these cheliceral teeth have often been used as diagnostic characters. However, because of the variability in numbers of these teeth between species within genera, such characters have recently been rejected as having systematic value. Nonetheless, while the numbers of cheliceral teeth may be variable, this variability, as measured by its range, may itself be phylogenetically informative.

We have coded these continuous characters using Quasi-Polymorphic Coding (QPC; Rodrigo & Ritchie in prep.), a coding method which takes account of the range of a character and its overlap amongst taxa. Briefly, for any continuous character, QPC treats the regions of overlap between two or more taxa, and the regions unique to each taxon as separate quasi-alleles. For any given area of overlap, all taxa which share that region are coded as having the same quasi-allele whereas at the unique areas only one taxon possesses the quasi-allele and this is taken to be uninformative. Quasi-alleles are coded as being absent from a taxon (character state 0) or present in the taxon (character state 1). Fig. 1a illustrates how the method is used to code the numbers of pro-marginal teeth.

17-23. Number of retromarginal teeth on chelicerae (Wanless 1984a, p. 138). Again, this character has been coded using QPC (Fig. 1b).

PHYLOGENETIC ANALYSIS

A taxon-character dataset was constructed by assigning to each taxon, a character state for every character (Table 2). Where information was unavailable on any particular character for a given taxon, that character was coded as "unknown" or "missing" (this is indicated by a "?" in Table 2).

The computer program PAUP 3.0L (Phylogenetic Analysis Using Parsimony: Swofford 1990) was used to reconstruct the phylogeny of the group under the principle of maximum-parsimony. According to the parsimony criterion, a tree is selected as a plausible phylogenetic hypothesis if it requires the fewest number of character state changes (Kluge & Farris 1969, Farris 1983). All characters were treated as unordered, *ie.* no prior assumption was made about the evolutionary sequence of transformations of each char-

acter. In order to obtain a directed evolutionary hypothesis, the trees were rooted using the outgroup method (Watrous & Wheeler 1981). According to this method, a closely related sister taxon (= the outgroup) of the group under study (= the ingroup) is selected. For each character, if a state is found in both the ingroup and the outgroup then that state is treated as ancestral (= plesiomorphy). Other states of the character are taken to be derived (= apomorphies). If two taxa share derived states, it is an indication of phylogenetic relationship. Outgroup analysis is implemented automatically in PAUP 3.0L. We chose the genus *Asemonea*, a member of the *Lyssomaninae*, as an outgroup.

Eleven most parsimonious trees were found using the tree-bisection reconnection (TBR) option in PAUP 3.0L (Swofford 1990). All trees had a length (*ie.* number of character changes) of 64 and a consistency index of 0.422. The consistency index lies in the range (0,1) and can be taken as a measure of how well the characters are indicators

Table 2. Morphological character-taxon dataset. See text for details of the characters and their codes. Missing or variable information is indicated by "?".

| Taxon | Characters | | | | | | | | | | | | | | | | | | | | | | |
|----------------------|------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 |
| <i>Brettus</i> | 0 | 1 | 1 | 1 | 0 | 2 | 0 | ? | 2 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Cocalus</i> | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Cyrba</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | ? | ? | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Gelotia</i> | 1 | 0 | 1 | 1 | 0 | 0 | 0 | ? | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Meleon</i> | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 2 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Mintonia</i> | 0 | 1 | 1 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| <i>Neobrettus</i> | 0 | 1 | 0 | 0 | 0 | 3 | 0 | ? | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Phaecius</i> | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Portia</i> | 0 | 0 | 0 | 1 | ? | 3 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Spartaeus</i> | 0 | 1 | 1 | 1 | 0 | 3 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Taraxella</i> | ? | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Veisella</i> | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Yaginumanis</i> | 0 | 1 | 0 | 0 | 0 | 3 | 0 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| <i>Cocalodes</i> | 0 | 1 | 0 | 0 | 0 | 4 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Allococalodes</i> | 0 | 1 | 0 | 0 | 0 | 4 | 1 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Holcolaetis</i> | 1 | 1 | 0 | 0 | 0 | 4 | 1 | ? | ? | 1 | 1 | ? | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| <i>Sonoita</i> | 0 | 1 | 0 | 0 | 0 | 4 | 1 | ? | ? | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| <i>Asemonea</i> | 0 | 1 | 0 | 0 | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |

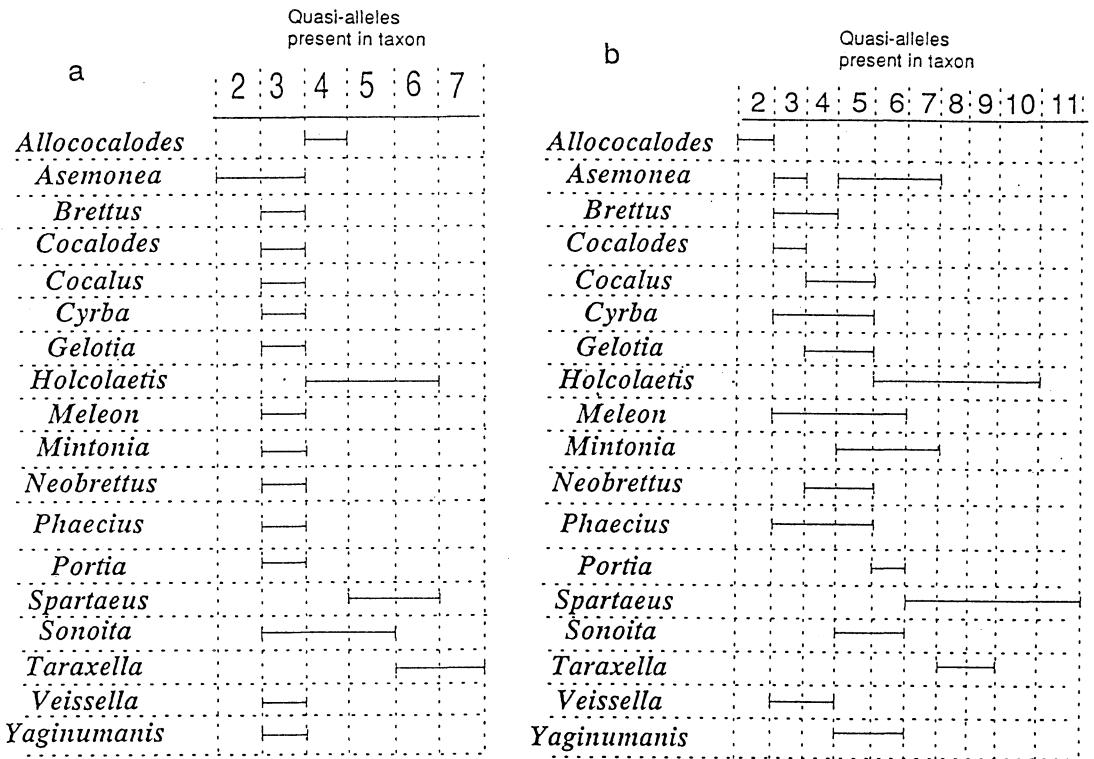


Figure 1. Quasi-polymorphic coding: a) numbers of pro-marginal cheliceral teeth; b) numbers of retro-marginal cheliceral teeth. Horizontal bars represent quasi-alleles present in each taxon. Quasi-alleles are not necessarily related in a one-to-one manner with the character states. For instance, in (b), some taxa have members with both 8 or 9 cheliceral teeth. However, there are no taxa in which members have 8 teeth without other members having 9, or vice versa. Therefore, "8 or 9 cheliceral teeth" is represented by one quasi-allele.

of phylogenetic relationship. A consistency index of 1 indicates that every character is a perfect indicator of phylogenetic affiliation. A strict consensus of the 11 trees, showing only those clades supported by all most parsimonious trees, indicate that *Cocalodes*, *Allococalodes*, *Holcolaetis*, and *Sonoita* are part of the Spartaeineae and form a monophyletic group with two spartaeine genera, *Spartaeus* and *Taraxella* (Fig. 2).

DISCUSSION

The monophyly of the "*Cocalodes*-group" and the Spartaeineae is supported not only by our phylogenetic results, but also by studies on eye ultrastructure (Blest & Carter 1987, Blest *et al.* 1990, A. D. Blest pers. comm.). David Blest and co-

workers at the Australian National University, Canberra, have studied the retinal organisation of the principal eyes of a number of jumping spiders, including spartaeineae and members of the genus *Allococalodes*. Their studies indicate that the retinal organisation found in *Allococalodes* is very similar to that of other spartaeineae.

Given the support that a phylogenetic analysis and ultrastructural information offer for the monophyly of the spartaeineae and the "*Cocalodes*-group", there is no compelling reason not to include the latter as members of the Spartaeineae. Diagnostically, as well, the two groups are very similar: for instance, Wanless (1984a), in his diagnosis of the Spartaeineae, noted that to separate the females *Cocalodes*-group from those of the Spartaeineae, literature descriptions, particularly of the

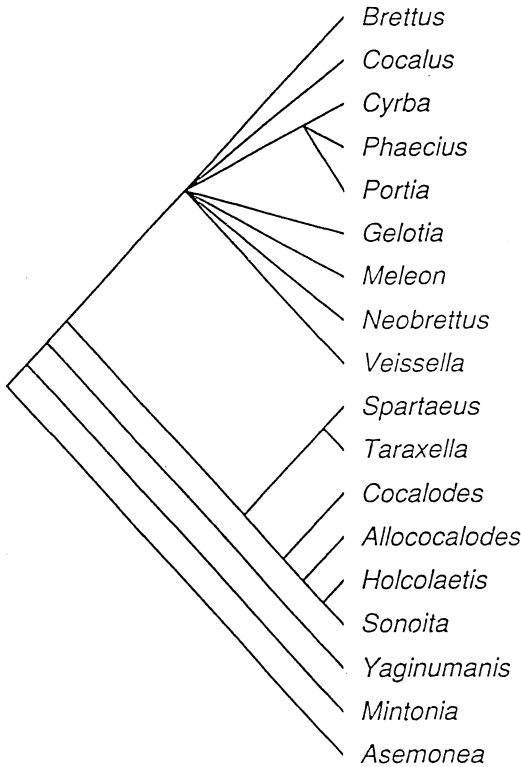


Figure 2. A strict consensus of the 11 most-parsimonious phylogenetic trees of the Spartaeinae and "Cocalodes-group".

epigynes, need to be consulted. Furthermore, separating the Spartaeinae and "Cocalodes-group" from the Lyssomaninae is not difficult: members of the latter sub-family have their eyes arranged in four rows, and have a typically lyssomaniform carapace (see Wanless 1980 for details). The following, then, is an amended classification of the sub-family Spartaeinae.

Sub-family **SPARTAEINAE** Wanless, 1984
Amended definition. As defined by Wanless (1984) but with the following amendments:
Body length, 3.0 mm to 16.0 mm;
Chelicerae, retromargin with two to ten teeth;
Type genus, *Spartaeus* Thorell;
Other genera,

Extant: *Allococalodes* Wanless, *Brettus* Thorell, *Cocalodes* Pocock, *Cocalus* Koch, *Cyrba* Simon, *Gelotia* Thorell, *Holcolaetis* Simon, *Meleon* Wanless, *Mintonia* Wanless, *Neobrettus* Wanless, *Phaenius* Simon, *Portia* Karsch, *Sonoita* Peckham & Peckham, *Taraxella*

Wanless, *Veissella* Wanless, *Yaginumanis* Wanless.

Extinct: *Almolinus* Petrunkevitch, *Cenattus* Petrunkevitch, *Eolinus* Petrunkevitch, *Paralinius* Petrunkevitch, *Prolinus* Petrunkevitch.

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