

SYNONYMY OF THE GENERA
PROTOPOLYBIA AND *PSEUDOCHARTERGUS*
(HYMENOPTERA: VESPIDAE; POLISTINAE)*

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INTRODUCTION

Protopolybia and *Pseudochartergus* are two genera of small paper wasps, both described by Ducke (1905a). They are clearly closely related, having the synapomorphy of a medial posterior process on the metanotum (Carpenter, 1990). Bequaert (1938) questioned the validity of these taxa, but later (1944a) accepted Weyrauch's view that there are "fundamental differences" in nest architecture. The recognition of these genera as distinct has prevailed since, and published keys appear to allow their separation with ease (Bequaert, 1944b and slightly modified in Snelling, 1981; Richards, 1978). This appearance is an illusion; the characters purported to distinguish the taxa simply do not. While engaged in phylogenetic studies on Polistinae (see Carpenter, 1990; Wenzel, 1990), we have independently come to the conclusion that neither morphology nor nest architecture support the recognition of two genera. It is our aim in this paper to establish the synonymy of these genera.

TAXONOMIC HISTORY

Ducke (1905a) established *Protopolybia* for five species: *Chartergus nitida* Ducke, *Polybia bella* Ihering, *Chartergus rufiventris* Ducke (= *emortualis* (Saussure) *fide* Ducke, 1907), *Polistes minutissima* Spinola and *Polybia holoxantha* Ducke. He stated that *Polybia pumila* Saussure (= *sedula* (Saussure) *fide* Richards, 1978), *picteti* Saussure, *nana* Saussure (a *Leipomeles*; Ducke, 1907, and Richards, 1978) and *laboriosa* Saussure (unidentified; Richards,

*Manuscript received by the editor October 11, 1989.

1978) also probably belonged in this genus, although he had not seen specimens. Bequaert (1944a) selected *bella* as the type species, and Bequaert (1944a) and Richards (1978) revised the genus. Richards (1978) recognized 23 species and two additional subspecies in *Protopolybia*.

Pseudochartergus was described for *Charterginus cinctellus* Fox (= *chartergoides* (Gribodo) *fide* Ducke, 1905b, 1907) and *C. fuscatus* Fox. Bequaert (1938) selected *cinctellus* as the type species. Bequaert (1938) and Richards (1978) subsequently revised *Pseudochartergus*. In Richards' monograph five species and two additional subspecies are recognized.

These genera have been shown as closely related in the phylogenetic diagrams of Ducke (1910, 1914), Richards (1978) and Carpenter (1990), and in the latter two they are each other's closest relatives. The strongest evidence for this is the medial posterior process on the metanotum, a feature unique within Polistinae (Carpenter, 1990).

MORPHOLOGICAL CHARACTERS

These genera were separated in Ducke's (1905a) morphological key by a couplet giving as alternatives: the clypeus much longer than wide and apically truncate, and the tempora extremely narrow (leading to *Pseudochartergus*) versus the clypeus not longer than wide and apically pointed, and the tempora variable but not extremely narrow (leading to *Protopolybia*). Ducke's later key (1910) separated these genera at the same couplet, adding the characters of the metanotum with a narrow dorsal surface and then vertically abrupt, and the metasoma always sessile (*Pseudochartergus*) versus metanotum uniformly oblique (*Protopolybia*). This constituted the first recognition that the two genera were closely related. Richards' (1978) key added the distinguishing features of the scrobal sulcus very weak (*Pseudochartergus*) versus distinct (*Protopolybia*), but otherwise the published keys have used Ducke's characters. Richards' discussion of *Pseudochartergus* (1978: 154) also mentioned a "short, stout body" and short wide metanotal process as characteristic of the genus. In what follows each of these characters is discussed in turn. Specimens of all species except *Protopolybia alvarengai*, *cameranii*, *iheringi*, *nitida*, *rotundata* and *rugulosa* have

been examined by JMC; they are deposited primarily in the collection of the Museum of Comparative Zoology, and the U.S. National Museum of Natural History.

Clypeal apex

The clypeal apex is truncate in *Pseudochartergus*, with the truncation being wider than an ocellar diameter. This a derived state from the primitive one of a bluntly pointed apex, found in most *Protopolybia* and other related genera (Carpenter, 1990). This indicates monophyly of *Pseudochartergus*, but its strength as a distinguishing feature is vitiated by the fact that it is approached in species of *Protopolybia*, including *minutissima* and *scutellaris*. The truncation is somewhat narrower in these species than in *Pseudochartergus*, being approximately an ocellar diameter. Furthermore, the clypeal apex is quite broadly rounded, almost truncate, in other species of *Protopolybia*, including *chanchamayensis*, *exigua*, *holoxantha* and *rubrithorax*. This indicates the continuous nature of the variation in this trait. Those *Protopolybia* with intermediate conditions may be more closely related to *Pseudochartergus*, but cladistic inferences based on continuously varying traits are often problematic (see Pimentel and Riggins, 1987). Whatever the case, this character is a poor diagnostic feature.

Clypeal proportions

The female clypeus longer than wide is supposed to characterize *Pseudochartergus*, but in *duckeianus* it is wider than long, and its length is really barely greater than its maximum width in the other species. Some of the species of *Protopolybia* have the clypeus much wider than long (*emortalis*, the *picteti* group), but most have it almost as long as wide, and in *scutellaris* it is actually longer than wide. The variation in the relative width of the clypeus played an important role in Bequaert's (1944a) key to species of *Protopolybia*, maintained to some extent in Richards' (1978) key, so not only is this character not diagnostic for either genus, it also varies continuously.

Tempora

The upper part of the female gena (tempora) "very narrow" is supposed to distinguish *Pseudochartergus* from *Protopolybia*, which has it "very broad" (Richards, 1978). This character has never been precisely described, but in *Pseudochartergus* the tempora is

narrower than the eye in lateral view. Richards (1978: 154), while characterizing his new species *duckeianus* as "rather intermediate", stated that "but the gena is narrower than in *Protopolybia*". However, while the gena is wider than the eye in lateral view in *Protopolybia emortualis* and the *picteti* group, other species have it narrower than the eye, and in *scutellaris*, *sedula* and *weyrauchi* it is no wider than in *duckeianus*. Not only is this feature variable within *Protopolybia*, it varies within *Pseudochartergus*: *fuscatus* and *pallidibalteatus* have it clearly narrower than the other three species. As with the clypeal proportions, not only is this character not really diagnostic for either genus, it also varies continuously.

Metanotal process

Richards' (1978) key characterized the metanotal process as short and broad in *Pseudochartergus*, versus long and tongue-like in *Protopolybia*. However, on p. 154, he stated that *emortualis* has the same condition. This is not actually correct; *emortualis* has it more rounded apically than any *Pseudochartergus*. On the other hand, in *Pseudochartergus fuscatus* the process is longer and narrower than in the other species, and in *pallidibalteatus* it is also quite narrow, although shorter. In *Protopolybia holoxantha* and *minutissima* the process is no longer or narrower than these two species of *Pseudochartergus*, and in *scutellaris* it is shorter and broader. The shape of the process varies considerably among the other species of *Protopolybia*, and thus this character too is not diagnostic for either genus.

Metanotal dorsum

The metanotum is compressed in most of the species of *Pseudochartergus*, so that it slopes almost vertically into the propodeal concavity, and has a very short horizontal surface. This is derived in comparison to the state of a single oblique surface, as in most *Protopolybia* and other related genera (see Carpenter, 1990). However, *Pseudochartergus dückeianus* has the plesiomorphic condition, while *Protopolybia emortualis* has the derived state. This character thus diagnoses neither genus.

Scrobal sulcus

As mentioned in Richards' (1978) key, the scrobal furrow is very weak in *Pseudochartergus*. But it is not distinct in all *Protopolybia*: *emortualis* has it no stronger than *Pseudochartergus*. An evanescent

scrobal furrow is a derived condition within Polistinae (Carpenter, 1990), and so this feature supports the monophyly of *Pseudochartergus*, but then also indicates paraphyly of *Protopolybia*, with *emortualis* evidently more closely related to *Pseudochartergus*.

Mesosomal proportions

Most species of *Pseudochartergus* have a relatively robust mesosoma in comparison to *Protopolybia*, which may well be derived, but as noted by Richards (1978: 154) *Protopolybia emortualis* has the same condition. Furthermore, the mesosomal proportions in *Pseudochartergus duckeianus* are similar to the other species of *Protopolybia*. Again, this character diagnoses neither genus.

Mesosomal segment I

In *Pseudochartergus* the first metasomal segment is said to be sessile, since it is broader than long and not petiolate. The polarity of this character at this level is unclear, since the sister-group of these genera is as yet unresolved, and the shape varies in the likely candidate genera (see Carpenter, 1990). In any event, the shape varies within *Protopolybia*, with *exigua* showing the same condition as *Pseudochartergus*. Most other species have the segment sessile, but narrower than in *Pseudochartergus*. As before, this character diagnoses neither genus.

NEST CHARACTERS

As with most taxa, the nests are less well known than the animals. Reports in the literature are often too brief to be of value and critical elements are left undescribed. Reliably determined nests of the following species have been examined by JWW (the collections containing critical specimens are identified below): *Pseudochartergus chartergoides*, *fuscatus*, *pallidibalteatus*, *panamensis*, *Protopolybia acutiscutis*, *chanchamayensis*, *exigua*, *holoxantha*, *minutissima*, *picteti*, *sedula*, *scutellaris* and *weyrauchi*. Considering that nests of only about half the species have been studied carefully by the same observer, we will no doubt need to revise our impressions of the distribution of given characters or the direction of character transformations when our knowledge is more complete.

To date, *Pseudochartergus* has been characterized as building naked combs sheltered by curled or adjacent leaves, the natural cavity being closed by a clear, hard sheet of salivary secretion with-

out vegetable fiber (Jeanne, 1970). Unlike most other neotropical genera, no paper envelope conceals the combs. In contrast, *Protopolybia* bears a simple, domed, paper envelope from the margin of the comb, some species later expanding the nest by building new cells upon this envelope and covering them with another. In his discussion of the distinction between *Pseudochartergus* and *Protopolybia*, Bequaert (1944) wrote, quoting a letter from Weyrauch:

“There is, however, one fundamental difference between the two genera. *Pseudochartergus* builds no envelope whatsoever of plant fibers around the comb. *Protopolybia* on the other hand covers with a fibrous envelope all parts of the combs not otherwise protected. The ability to build a paper envelope or its lack mark among all social wasps such a fundamental biological departure that in my opinion *Protopolybia* could not be regarded as a subgenus of *Pseudochartergus*.”

Thus, as has been traditional in polistine taxonomy, Bequaert relied in large part on architectural differences for generic separation. Unfortunately, each of Weyrauch's declarations about the state of the envelope in these genera and about the importance of envelopes in social wasps is now known to be compromised. Firstly, Richards (1978) reports that *Pseudochartergus pallidibalteatus* builds a paper envelope quite like that of *Protopolybia*, and JWW has confirmed the observation for nests of this species (Rijksmuseum, Leiden) as well as for another, unidentified one (Muséum National, Paris). In addition to the sheet of clear secretion between leaves, Schremmer's (1984) photographs of two *Pseudochartergus chartergoides* nests show several important features. This species will build a paper envelope from the comb margin and cells upon it, both traits considered typical of *Protopolybia* (see Ducke's 1905a key). Also evident are the multiple entrance holes corresponding to successively built sections, a trait long believed unique to *Protopolybia* (Ducke, 1910; Richards, 1978). Consequently, at least two of the five currently recognized species of *Pseudochartergus* violate the architectural boundaries other authors believed to be valid.

Secondly, *Protopolybia scutellaris*, in Colombia (Richards 1978) and Panama (Snow Entomological Museum, Lawrence, Kansas) do not build envelopes at all, but rather have a comb completely exposed beneath the broad leaves of *Heliconia*. Further contradicting the stereotype of a fibrous envelope in *Protopolybia*, *acutiscutis*,

sedula, *weyrauchi*, and likely others, often fix leaves together with clear salivary secretion, or use copious amounts of it in regions where the fibrous envelope is fastened to leaves.

Thirdly, recent studies have shown that an envelope or protective sheet has arisen or been lost independently in many lineages (Wenzel, 1990). For the genera in question we can infer that presence of the envelope is the primitive state: only one of 23 swarm-founding, neotropical genera contains no species known to produce envelopes (Apoica). From this perspective, then, the fiber-free veil of *Pseudochartergus* can be interpreted as a loss or reduction of the more ordinary, fibrous, ancestral envelope. Such reduction is known to have occurred in other taxa that nest in cavities, including species in the widely separated genera *Agelaia*, *Metapolybia*, *Polybioides*, *Vespa*, and *Vespula* (Wenzel, 1990, and unpublished data). More strikingly, the Indomalayan *Ropalidia opifex* builds nests in natural cavities between leaves, just as the neotropical *Pseudochartergus* does, and joins leaves together with a transparent sheet of oral secretion devoid of vegetable fiber, just like *Pseudochartergus* (van der Vecht, 1962). Thus, it now appears that the traits in which Weyrauch had so much faith are neither as clearly segregated as he thought nor as deeply significant as indicators of phylogeny.

The nests of *Protopolybia* and *Pseudochartergus* display a mosaic of ancestral and derived traits. Various presumably plesiomorphic characters appear in some *Pseudochartergus* and no *Protopolybia*. At least some nests of *Pseudochartergus chartergoides* (those without comb-borne envelopes), *panamensis* and *fuscatus* expand by gradually adding cells to the margin and elongating the cell walls as the larvae within grow larger, while *Pseudochartergus* nests bearing envelopes from the combs and nests of *Protopolybia* are expanded suddenly in large blocks of cells which are built to full height, the outermost wall becoming the envelope. Clearly, the first scheme is the primitive one displayed by most social wasps while the latter is derived.

Furthermore, *Pseudochartergus* appears to have no architectural autapomorphy since each trait is shared with at least some *Protopolybia*. For example, using pure secretion to close gaps between leaves is derived within the clade of South American swarming wasps and conspicuous in *Pseudochartergus* (Jeanne, 1970). Yet, this trait is also seen in what seems to be a highly derived design in

Protopolybia, such as that of *acutiscutis* (above), comprised of tens of thousands of cells, often with separate envelopes dissociated from the actual comb walls and expanding helically downward (Wenzel, 1990).

SYNONYMY

As shown by the foregoing, the recognition of two genera in this clade is untenable. *Pseudochartergus sensu* Richards may be a monophyletic group, as shown by the diagnostic apomorphy of an apically truncate clypeus, and supported by the non-unique evanescent scrobal sulcus. If these characters are accepted as synapomorphies, *Protopolybia* is apparently paraphyletic; there are no apomorphies defining the genus, the truncate clypeus is approached in several species, and the evanescent scrobal sulcus found in another species (*emortualis*) which shares other derived features with some species of *Pseudochartergus*. The classification must then be adjusted to remove the paraphyletic taxon (Hennig, 1966). Yet some of the apomorphies shared by *Protopolybia emortualis* with species of *Pseudochartergus* conflict with the clypeal apex apomorphy; *Pseudochartergus duckeianus* does not have the compressed metanotum or robust mesosoma. Thus, it may be that *Pseudochartergus* as presently constituted is not monophyletic, with *duckeianus* possibly misplaced (*cf.* Richards, 1978: 155). And if our inferences about nest architecture polarity are correct, this suggests *Pseudochartergus* may be paraphyletic but *Protopolybia* is monophyletic—the reverse of the morphological characters. In any event, most of the morphological characters show essentially continuous variation or are not diagnostic, while within a species of either of these groups, nests generally show far more variability than that found within species of virtually all the other neotropical swarming genera. Hence the diagnosis of two genera is dubious solely for these reasons. We are therefore synonymizing them.

Protopolybia and *Pseudochartergus* were described in the same paper. The Principle of the First Reviser (Article 24 of the International Code of Zoological Nomenclature) therefore applies in determining the relative precedence of these names. Bequaert (1938: 104) stated that he was “inclined to regard it [*Protopolybia*] as a subgenus only” of *Pseudochartergus*, but he did not take any explicit action. Accordingly, we are acting as first reviser, and select

Protopolybia as the name of this genus. The name appeared first in Ducke (1905a), on p. 7, with *Pseudochartergus* first mentioned on p. 8.

It should be noted that, as pointed out by Bequaert (1938), *Polistella* Ashmead (1904: 133), monotypic for *Polistes manillensis* Saussure, was based on misidentified specimens of *Protopolybia exigua* (see Richards, 1978, for species synonymy). *Polistella* is now treated as a subgenus of *Polistes* (e.g. van der Vecht, 1971; Richards, 1973). Under Article 70b of the Code it is to be referred to the Commission to designate as type species of *Polistella* whichever nominal species will in its judgement best serve stability of nomenclature. That clearly would be *Polistes manillensis*, despite the misidentification in the original designation. We will continue the established usage, rejecting *Polistella* as an available name for *Protopolybia*. The synonymy of this genus follows.

Protopolybia Ducke (1905a: 7, 9, 17)

Type species *Polybia bella* von Ihering, 1904, by subsequent designation of Bequaert (1944a: 97).

Pseudochartergus Ducke (1905a: 8, 9, 15). Type species *Charterginus cinctellus* Fox, 1898 (= *Nectarina chartergoides* Gribodo, 1891), by subsequent designation of Bequaert (1938: 103). NEW SYNONYMY.

ACKNOWLEDGMENTS

We thank Arnold Menke for commenting on the manuscript. This research was supported by NSF grant BSR-8817608.

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