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Notes on the nest of the social wasp *Pseudopolybia langi*  
(Hym., Vespidae, Polistinae)

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ABSTRACT

Detailed descriptions of the architecture of *Pseudopolybia langi* nests are presented for the first time. Structural variations in the arrangements of nest parts are described and compared with features observed in other species of *Pseudopolybia* and other epiponine genera.

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Introduction

The subfamily Polistinae is known for the great diversity and beauty of its nest architecture (Richards, 1971; Wenzel, 1991, 1993, 1998). Some genera, such as *Polistes* and *Mischocyttarus*, usually have small nests with simple structures and unenveloped single combs, often with less than a hundred cells. The nests of several species of epiponine genera, however, may be quite large, with hundreds to thousands of cells in several combs, and are usually covered by an envelope (Carpenter, 1991; Jeanne, 1975, 1991; Richards, 1978).

*Pseudopolybia* von Dalla Torre 1894 is a wasp genus of the tribe Epiponini that is normally found in forested areas, with four species distributed from Nicaragua to southern Brazil (Richards and Richards, 1951; Richards, 1978). It is distinguished by the third segment of the labial palpi bearing a short, stout, curved bristle near its apex, and the number of palpal segments being six maxillary and four labial (Richards, 1978; Andena et al., 2007). The nests of most species in the genus are oval to spherical arboreal objects, presenting a pale yellow to brown envelope composed of laminate or imbricate sheets (much like those of vespine species), with a simple entry; each comb is attached to the comb above by vertically positioned pedicels. Comb diameters gradually decrease from the

first comb to the last (Jeanne, 1975; Andena et al., 2007). Details of such distinctive architectures can be observed in the Fig. 4E in this paper showing a nest of *P. difficilis* (Ducke 1905), which is also representative of the internal structure of the nests of *P. vespiceps* (Saussure 1864) and *P. compressa* (Saussure 1854). Other images of nests of these species may be found in Ducke (1914, p. 318), and Richards (1978, p. 4). In the papers by Wenzel (1993, 1998) about vespine nest architecture, information on the genus *Pseudopolybia* was only based on features observed in the above three species (i.e. envelope laminate; combs round or oval, secondary combs suspended from those above by central pedicel; cocoon caps simple; entrance simple at lowest point).

*Pseudopolybia langi* Bequaert, 1944 differs from its congeners in several aspects, being a much smaller wasp (6–8 mm long versus 13–15 mm in other species), and with a more elongated body. It has been recorded for the Guyanas, Ecuador, and Brazil. In the latter country, it is known from the states of Amapá and Amazonas in areas covered by relatively undisturbed “terra-firme” rainforest. Due to the relative rarity of *P. langi*, its nests were unknown to Bequaert (1944) and even to Richards (1978), only being mentioned (but not described) in a paper by Dejean et al. (1998) in association with palm trees of the genus *Astrocaryum*. Later, one of us (OTS) encountered a fully developed (although damaged) nest in Amapá State (IEPA collection; not found in recent visits by the authors). A photograph of this specimen was used by Andena (2007; thesis) to prepare a brief description that was used in a phylogenetic analysis published by Andena et al. (2007). We recently collected a new well-preserved nest specimen in Amapá State (MPEG collection)

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which better demonstrates both external and internal aspects of the architecture of the species – making it relevant to present a full description of the nest architecture of *P. langi* and analyze some observed variations in terms of *Pseudopolybia* nest architecture as well as some other epiponine genera.

## Methods

### Specimens examined

The nests used here as references for the description of nest architecture of *P. langi* were both encountered in areas covered by ombrophilous “terra-firme” rain forest in the following localities in Brazil:

Specimen #1: Amapá. Laranjal do Jari, RESEX Cajari, comunidade Marinho (00°34'44"S/52°13'16"W), 01/ix/2001, O.T. Silveira (IEPA collection; not found in recent visits by the authors). The nest was brought to OTS by a boy who found it in an orchard tree (probably Annonaceae). It had been transported in a plastic bag and showed some damage caused by crushing. Photographs were taken just a few hours after receiving the specimen. The nest was removed from the plastic bag, the envelope carefully detached, and the broken and loose combs were set apart from the remaining nest elements still

affixed to the substrate leaf (see Fig. 1). This nest was not reexamined recently, and our present comments are based on OTS's knowledge and memory of the specimen in 2001, as well as available photographs.

Specimen #2: Amapá. Ferreira Gomes, Floresta Nacional do Amapá (FLONA Amapá; 0°58'03.36"N/51°38'19.09"W), 08/iii/2016, Felizardo S.P.S. & Santos I.P. (MPEG). The nest was located along a trail in the Amapá plot of the PPBio biodiversity research program. It was found in a relatively dry area, approximately 2 km from the Araguari River, and at least 500 meters distant from any other smaller water course. The nest was in a young tree of the family Annonaceae (2.5 m tall) with small leaves, and was attached to two of the leaves, approximately 2 m above the ground. The entire nest was collected in a plastic bag (together with wasps present at the moment, numbering about 40 individuals). The brood in the nest cells consisted only of eggs and small to medium-sized larvae. Due to the fragility of the envelope, some deformation occurred around the entrance, but this did not prejudice the observation of its original form.

Information concerning a third nest specimen was also used for comparative purposes. It consists of a fragmented nest in the collection of the American Museum of Natural History (AMNH; Amazonas, 03/x/1991; catalog 910310-1). A photograph is available on the internet at <http://research.amnh.org/iz/hymenoptera/collection/display.php?sid=401491>.

### Measurements

Measurements of the FLONA-Amapá specimen were made using a pachymeter. Nests available only from photographs were measured indirectly using ImageJ software (<https://imagej.nih.gov/ij/>), based on scale information available in the photographs (a ruler in the case of the IEPA – Cajari nest; cell size in the case of the AMNH specimen). Measurements were obtained (when possible) of: combs (major and minor diameters and height), cell dimensions, pedicel lengths, the envelopes, and associated substrate leaves.

### Comparative analysis of the evolution of *P. langi* nest features

To compare some of the architectural features of *P. langi* with those of other epiponine taxa within a phylogenetic framework, we performed the parsimonious optimization of these nest characters with the program Winclada (Nixon, 2002) on a phylogenetic tree for the Polistinae adapted from a tree published by Wenzel and Carpenter (1994) based on morphological adult and larval characters, as well as on nest characteristics. Character states were generally coded according to the phylogenetic study by Wenzel (1993). In the adapted tree showed in Fig. 5 (for Epiponini only), *Occipitalia* and *Synoecoides* are omitted, since they have been synonymized to *Clypearia* and *Polybia*, respectively (see Carpenter et al., 1996, 2000). For its distinctive nest architecture, *Marimbonda* is maintained and represented in the tree as sister-group of *Leipomeles* (see Carpenter, 2004); *P. langi* is added to the tree as sister-group of other *Pseudopolybia* species, according to Andena et al. (2007).

## Results

The FLONA-Amapá nest was used as a primary reference, as it was collected undamaged and its original shape was well-preserved. The envelope is a small inverted flask-shaped structure, fixed laterally to two small leaves (1.7 cm wide, 6.5 cm long) (Fig. 2A, B); the combs are in a vertical series, connected to each other by short vertical pedicels, and connected laterally to the substrate leaves by equally short lateral pedicels, except for the downmost smaller developing comb (Fig. 3A).



Fig. 1. Nest of *P. langi* from RESEX Cajari; scale: 2 cm.

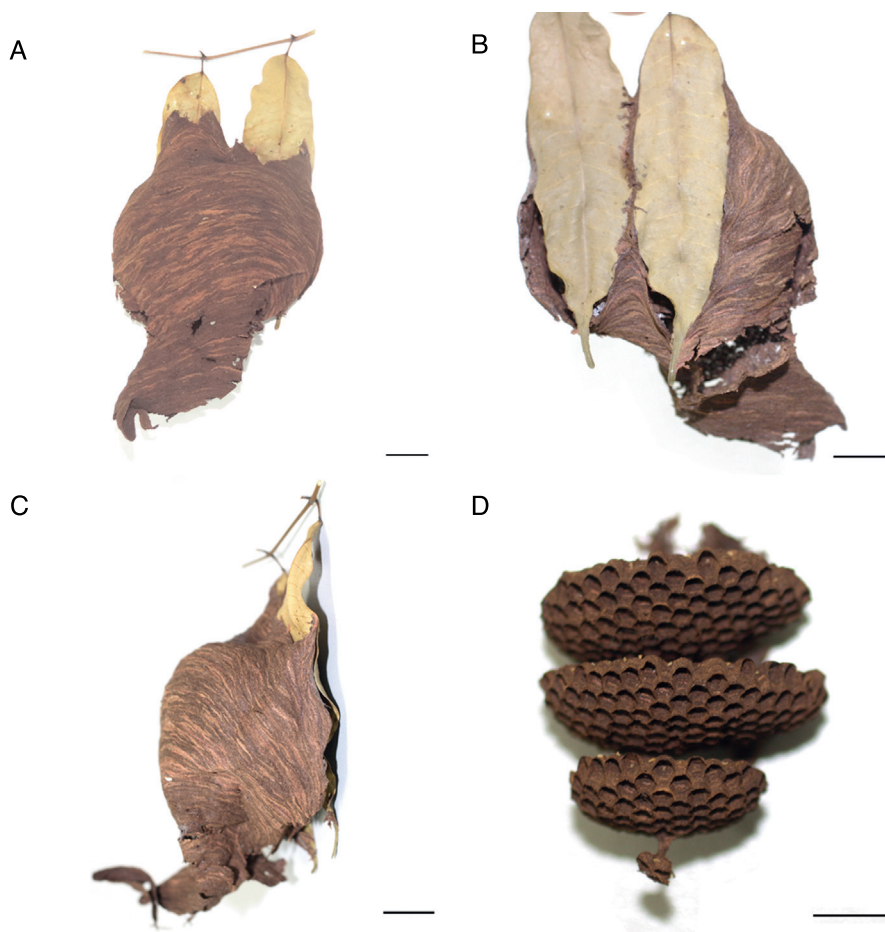


Fig. 2. Nest of *P. langi* from FLONA-Amapá, showing the envelope A and C; substrate B; and combs D; scales = 1 cm.

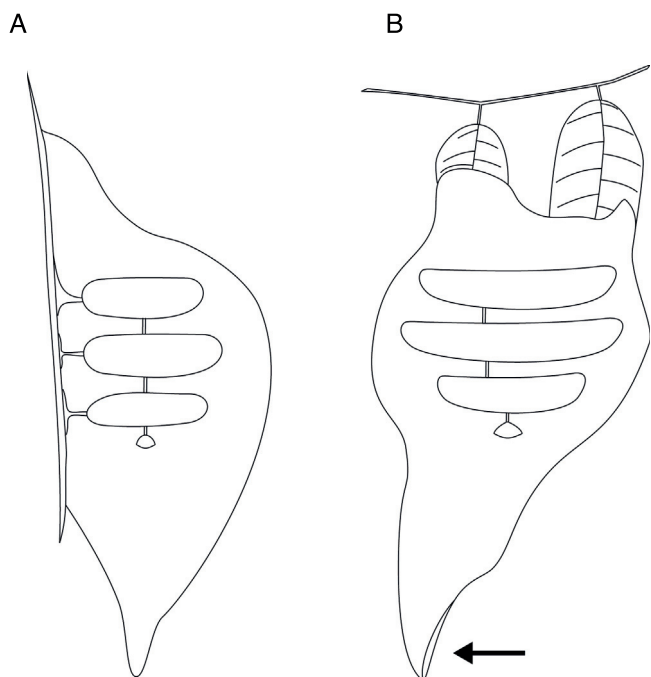


Fig. 3. Nest scheme of *P. langi* from FLONA-Amapá. A – lateral view; B – frontal view; arrow: nest entrance.

**Combs:** The nest has four combs (the last one very small, apparently having just been initiated) of the same color as the envelope, mostly dark-brown with some small, light-brown spots (Fig. 2D). The combs are semicircular to oval in shape, with the border facing the substrate being roughly straight; the dorsal surfaces of the combs are slightly concave (Fig. 3A, B). The larger two upper combs both have approximately 150 cells; the third comb has approximately 70 cells; the fourth comb has only three incomplete cells. The first comb has a major diameter of 3.1 cm and a minor diameter of 2 cm; the second comb is 3.3 × 2.1 cm; the third comb is 2.2 × 1.8 cm; the fourth comb is only approximately 5 × 4 mm (Fig. 2D).

**Pedicels:** The pedicels are rather flat in cross-section, with the lower section tending to be wider; the first pedicel (connected to the substrate) is distinctly oblique, and very wide and buttress-like. Vertical pedicels 2–3 are laterally and backwardly displaced, being closer to the substrate side of the comb (Fig. 3A, B). The larger, more fully developed combs were connected to the substrate leaves by short lateral pedicels; the first comb was connected by two such lateral pedicels; the second by three pedicels; and the third comb by only one; the recently initiated downmost comb hangs from the upper one without connections to the substrate (Fig. 3A).

**Cell size:** The comb cells are 2 mm wide and about 5 mm deep. The total number of cells was estimated to be about 370.

**Envelope:** The envelope consists of a single sheet, apparently made of long fibers, predominantly dark-brown, with light-brown narrow bands along the construction lines, giving it a streaked appearance; without ridges or corrugations (Fig. 2A–C). The nest was lighter brown in color at the time of collection, with

yellowish stripes. A few hours after collecting it, however, the envelope became darker, eventually reaching the tone shown in the photograph. The envelope resembles an inverted flask, wider at the top, and gradually decreasing to the base, where it takes on a rather short bottleneck shape (Figs. 2A, 3A). The entrance is a relatively short tube, with an aperture diameter of 1.5 cm (Fig. 3A). The envelope is fragile and brittle, different from other *Pseudopolybia* which have it with more supple consistency (*P. difficilis*, *P. compressa*; see Wenzel, 1998). It has a total length of about 9 cm, and its largest width is 5 cm.

**Variations:** We were not able to confirm the original shapes of the envelopes of the other two nests of *P. langi* (evaluated as photographs) as they had become broken or deformed, although other aspects of the architecture of the RESEX Cajari specimen, such as the type of nesting substrate, comb arrangement, and envelope color can be discussed.

**Position relative to substrate:** The nest collected in the RESEX Cajari was constructed under (i.e., on the abaxial surface) a single relatively large leaf (approximately 11 cm long and 5 cm wide) whose position was inferred to be roughly horizontal (based on the relative orientation of nest cells), with the nest being attached to the substrate dorsally. This indicates that the position of the comb series relative to the substrate can vary in this species, or that it can use (or adjust to) substrates with different or varying spatial orientations (like species in *Angiopolybia*, *Leipomeles*, and *Parachartergus*; see Wenzel, 1991, 1998).

**Combs:** The nest combs appear to be arranged in two adjacent vertical columns. Five combs are clearly visible in the photograph of Fig. 1; the somewhat hidden border of a sixth subjacent comb can be seen under the most distally placed stack of combs (at the bottom of the photograph). Remains of the envelope can be seen around the combs, near the margin of the substrate leaf.

It was not possible to identify elements of the main vertical comb-to-comb pedicels in this photograph of the fragmented nest, so that the positions of those connections are uncertain. An aspect of interest in Fig. 1 is that the two detached combs (both measuring ca. 3.7 cm in major diameter) in the photograph seem to be larger than those still in their original positions (2.6 and 3.2 cm in major diameter) – the attached combs necessarily being older than the detached combs. The combs in this nest specimen are a slightly larger than those of the FLONA-Amapá nest, the total number of cells being estimated as ca. 700 (about twice as many as in the first specimen described here, based on comb number and area), but the oval or roughly semicircular combs of both are similar. The widths of the cells of the Cajari specimen are also estimated to be similar (ca. 2 mm; based on combs that appear according to a plane nearly horizontal with respect to the photograph) to those of the FLONA-Amapá nest, although several of the cells of the former are capped.

**Envelope:** The envelopes of the studied nests are quite similar, with construction lines delimiting differentially colored bands. The proportions of yellow and brown colors may vary from nest to nest. Unfortunately, essentially nothing can be said about the shapes of the envelopes of the broken/damaged specimens.

## Discussion

The FLONA-Amapá specimen appears to be the first fully-developed undamaged nest of *P. langi* available for detailed architectural study. In some respects, it very much resembles the nests of some basal epiponine genera rather than other *Pseudopolybia* species, especially with regards to the retention of the plesiomorphic character of a “single sheet” envelope (Andena et al., 2007). The shape of the envelope was highly convex (character 17 of Wenzel, 1993), as in other *Pseudopolybia*, but was shortly prolonged

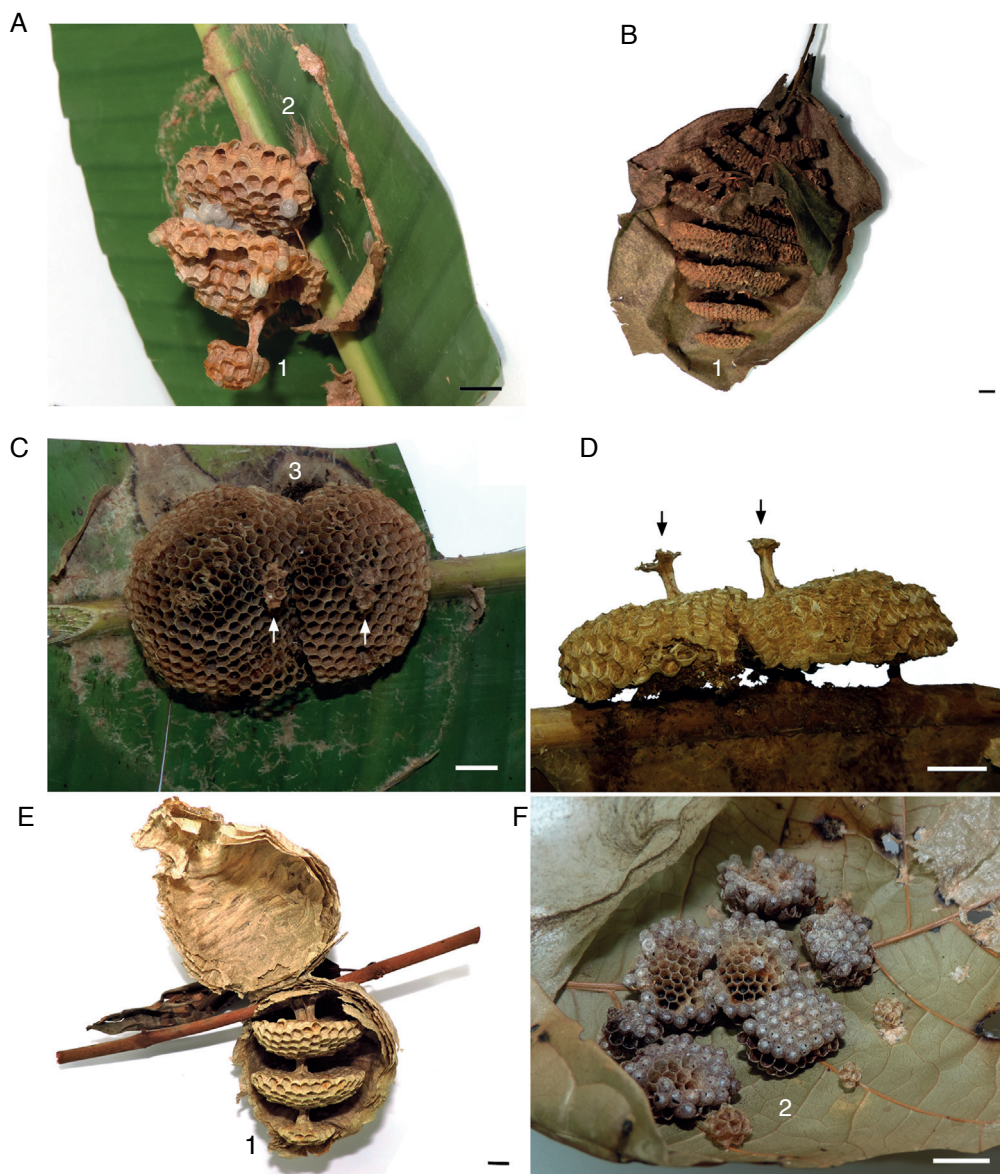
downwards to form a small “spout” (character 10 of Wenzel, 1993), very similar to those observed in some species of the related genera *Parachartergus* and *Chartergellus* (see our Fig. 5; and Richards, 1978: Pl. 3, Fig. 23; Wenzel, 1998: Fig. 18A and B), and the epiponine genus *Angiopolybia* (Fig. 5; and Jeanne, 1975; Wenzel, 1998: Fig. 23F).

Parsimonious optimization of the above mentioned character “shape of nest entrance” (corresponding to Wenzel’s 1993 character 10) in a genus level phylogenetic tree with topology like that of Wenzel and Carpenter (1994) and with *P. langi* added as sister-group to other *Pseudopolybia* (Fig. 5, terminal *Pseudopolybia*\*), resulted ambiguous with respect to the plesiomorphic state in *Pseudopolybia* (Fig. 5, tree node 3), as well as to the ancestor of the clade *Pseudopolybia*–*Nectarinella* (Fig. 5, tree node 2); i.e., under fast optimization, the state observed for *Pseudopolybia langi* resulted “primitive” in that genus (and in the whole component *Pseudopolybia*–*Nectarinella*), with the alternative state in the other three species (“entrance simple at lowest point”; see Wenzel, 1998) being inferred to be a synapomorphy of that species group (Fig. 5, terminal *Pseudopolybia*\*). Conversely, under the slow optimization mode, the elongated nest entrance of *P. langi* is treated as an independent development with respect to similar shapes in related genera like *Parachartergus* and *Chartergellus*. Whatever the optimization method used, the very typical elongated nest entrance of *Angiopolybia pallens* appeared as independently derived relative to similar features in taxa of the *Pseudopolybia*–*Nectarinella* component (actually, at least for one of the two large-sized species of *Angiopolybia*, i.e. *A. paraensis*, the nest has been described as lacking such elongated entrance; see Richards, 1978).

The lateral attachment of combs by pedicels to a vertical substrate in the FLONA Amapá nest appears to be similar to species of other related genera, such as *Parachartergus* and *Chartergellus* (see Fig. 5). However, this feature concerns only to the appearance of secondary combs in an already “finished” condition, which actually hides the fact that they are initiated through a pedicel hanging from the comb just above, only being connected to the substrate when the comb margin comes close to the latter (see the downmost comb in Fig. 2D). This is the same condition observed in other *Pseudopolybia* (Fig. 4E), and *Angiopolybia* (Fig. 4A, B), and similar to some *Agelaia* (Fig. 5), and is distinct from most *Parachartergus*, *Chartergellus* (Fig. 5), and part of *Leipomeles* (actually, part of this genus corresponding to former genus *Marimbonda*, and the species of *Nectarinella* construct sessile combs; Fig. 5) (see Jeanne, 1975; Richards, 1978; Wenzel, 1998).

Parsimonious optimization of such a character (with three states: 0 – single pedicellate comb; 1 – multiple independent pedicellate combs; 2 – multiple pedicellate stacked combs; other conditions as non-applicable, and setting *Polistes*, *Ropalidia*, *Agelaia*, and *Parachartergus* as polymorphic; see Jeanne, 1975) on the phylogenetic tree mentioned above yields results ambiguous (as before) as to the ancestral condition in the *Pseudopolybia*–*Nectarinella* clade (Fig. 5, tree node 2). Fast optimization makes “multiple stacked combs” ancestral to the whole epiponine clade *Agelaia*–*Clypearia* (Fig. 5, tree node 1), while slow optimization assigns to this same ancestral the condition “multiple independent pedicellate combs”, thus implying that the similar states observed in *Angiopolybia* and *Pseudopolybia* should be considered independently derived. Evidently, these analyses are preliminary, and may be reconsidered in future broad-spectrum studies of nest architecture in the Polistinae.

The presence of two comb stacks, as observed in the Cajari specimen of *P. langi* is apparently very unusual among Neotropical polistines, and additional specimens will be needed to determine the frequency of that type of comb arrangement. That condition has been observed, however, in at least one other species that makes pedicellate multiple-stacked combs (see the abandoned nest remains of *Angiopolybia pallens* in Fig. 4C, D), and it is indeed



**Fig. 4.** Images of nests or their remains: (A) *Angiopolybia pallens* (envelope removed) 1 – downmost secondary comb hanging by a pedicel from the one just above, 2 – adjustment to vertical orientation of comb series from an oblique pedicel (and substrate); (B) *A. pallens* nest (envelope partially removed) adapted to a vertical substrate consisting of twigs and leaves, 1 – same as A-1; (C) remains of *A. pallens* nest showing two stacks of combs (arrows indicating secondary pedicels), showing lateral fusion (on upper side of the photograph; 3); (D) same as (C), lateral view; (E) *Pseudopolybia difficilis*, envelope structure and comb arrangement; (F) *Leipomeles dorsata*, 2 – combs at marginal oblique sector of the substrate–leaf adjusting to a vertical orientation. All nest specimens in MPEG collection.

possible that the rarity of that situation may be a consequence of comb fusion, something that can be observed in Fig. 4C. A relationship between this organizational structure and the construction of larger nests seems plausible, as double comb stacks would allow larger numbers of combs without creating a longer single vertical series (which would presumably be more unstable when attached dorsally to the substrate). Jeanne (1975) discusses in detail the occurrence of, and different implications of, those two comb arrangement modes, i.e., multiple independent combs versus multiple stacked combs.

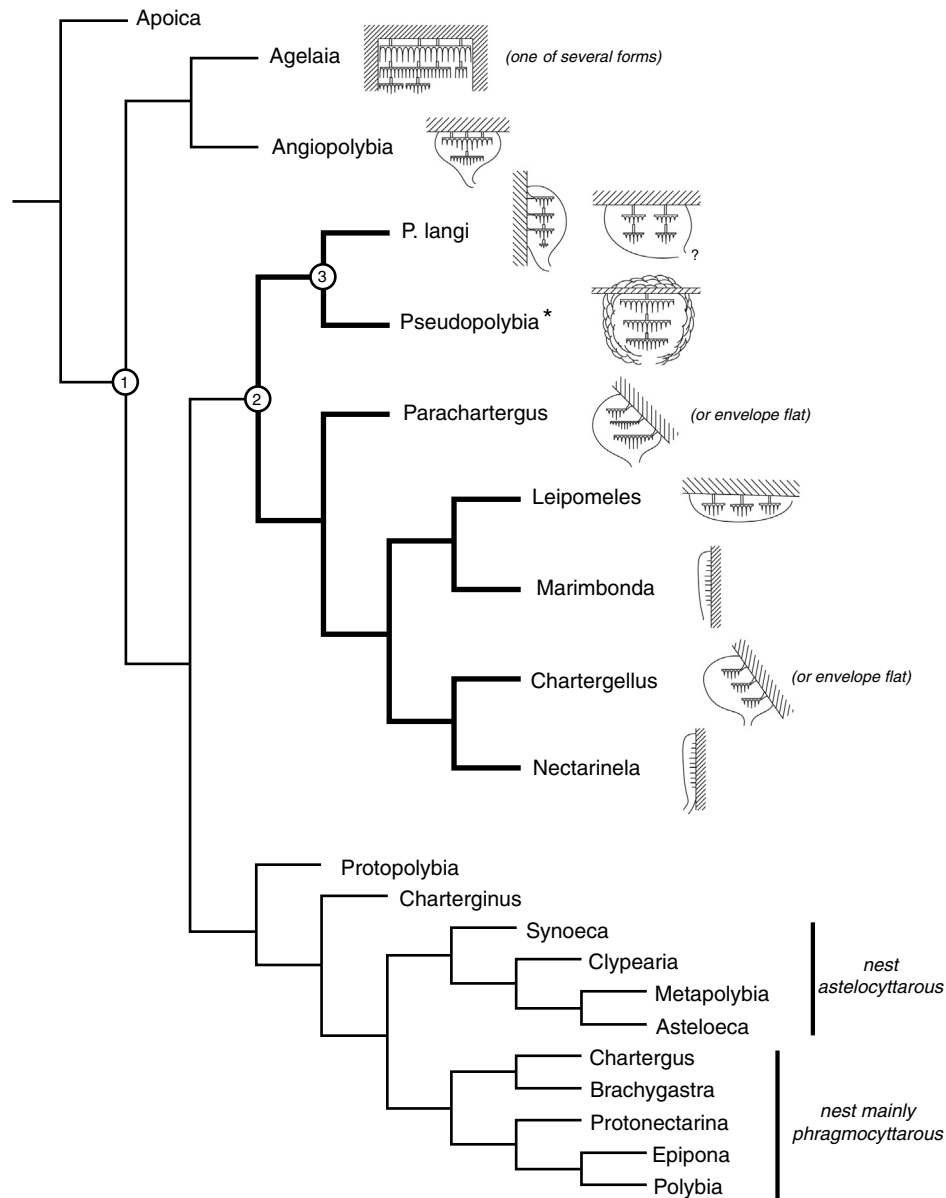
Based on available specimens, the nests of *P. langi* appear to have the capacity to adapt to substrates with differing spatial orientations (i.e., the nests can be attached to either laterally or dorsally positioned substrates), while the comb series still maintains a vertical orientation. Adjustments to such different kinds of substrates can be observed in the nests of a single species (e.g. *Angiopolybia pallens*, Fig. 4A, B), or even in a single nest, in cases

of curved surfaces or surfaces that may change spatial orientation with time (i.e., on leaves; see nest of *Leipomeles dorsata* in Fig. 4F).

The nests of *P. langi* described in this paper show that the simple monolayer envelope and a spout-shaped nest entrance are the main differences in respect to other *Pseudopolybia* species. However, the manner of adding secondary combs is the same in all of those species, with each new secondary comb being initiated from a pedicel hanging from the comb just above it. In *P. langi*, lateral comb–substrate pedicels are added in cases of vertical substrates.

#### Conflicts of interest

The authors declare no conflicts of interest.



**Fig. 5.** Phylogenetic relationships for the genera of Epiponini, adapted from [Wenzel and Carpenter \(1994\)](#); omitting *Occipitalia* and *Synoecoides*; *Marimbonda* is maintained and represented as sister-group of *Leipomeles*; *P. langi* added as sister-group of other *Pseudopolybia* species (terminal marked with an \*). Schematic representations of architectural types adapted from [Wenzel \(1991\)](#). “astelocytтарous”: sessile comb with cells constructed directly on substrate, covered by an envelope; and “phragmocyttarous”: multiple stacked combs with cells of secondary combs constructed on the envelope of preceding comb (see [Richards, 1978](#); [Wenzel, 1998](#)); a question mark (?) indicates uncertainty on the shape and position of nest entrance of the “Cajari nest specimen” of *P. langi*.

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