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SHORT COMMUNICATION

Tip of the clade on the top of the World—the first fossil Lophopidae (Hemiptera: Fulgoromorpha) from the Palaeocene of Tibet

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Abstract Lophopidae is a family of planthoppers (Hemiptera: Fulgoromorpha) present today in tropical and subtropical zones of the Old World. The most recent taxonomic studies and phylogeny of these insects do not include the extinct representatives. Therefore, each new discovery of a fossil lophopid is of high interest, giving new insights to their evolutionary history and enabling to test the proposed relationships. The recent findings of extinct Lophopidae in Europe, in various Palaeogene deposits, put in doubts their proposed evolutionary and biogeographic scenario. The new fossil from the Palaeocene of Northern Tibet is related to one of the Lophopidae clades, Apia$^+$ group, believed to be the most advanced one, and recently distributed in the recent Sundaland-New Guinea-Queensland area. A new genus and species *Gesaris gnapo* gen. et sp. n. provide information on early lophopids diversity and relationships and demonstrates the necessity for a revision of the existing hypotheses for the initial diversification and distributional pattern of the Lophopidae.

Keywords Insecta · Lophopidae · Palaeocene · Tibet · Phylogeny · Biogeography · Taxonomy

Introduction

The planthopper family Lophopidae Stål, 1866 is one of the smallest within Fulgoroidea, with 43 genera and over 140 species recognized, both recent and extinct (Bourgoin 2015; Szwedo 2011; Stroiński and Szwedo 2012). This tropical Old World family (except *Carriona* Muir, 1931 from Peru, Ecuador and Panama) is the first to have a modern generic level phylogenetic analysis, biogeographic scenarios proposed and host plants relationships discussed (Soulier-Perkins 1998, 2000, 2001; Soulier-Perkins et al. 2007, 2013; Szwedo and Soulier-Perkins 2010). The members of the family could be identified by unique combination of characters of head, legs, and tegmina (Soulier-Perkins 1998; Soulier-Perkins et al. 2013). There are a few known fossils ascribed to Lophopidae (see Supplementary Material for a full list and Fig. 2) known since Palaeocene to late Eocene.

Material and methods

The specimen was examined using dissecting stereoscopic microscope Nikon 1500 and illustrated with the aid of the drawing tube. Photographs were taken using Nikon Digital camera DXM and Zeiss SteREO Discovery.V20 system. The venation nomenclature follows Bourgoin et al. (2015). The generic groups are marked according to the convention proposed by Amorim (1982), i.e., the name given to a

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monophyletic group is the name of the more basal taxon in this, followed by the sign $^{+}$

Systematic paleontology

Family Lophopidae Stål, 1866

Gesaris gen. n.

Type species *Gesaris gnapo* sp. n. by monotypy and present designation.

Diagnosis Pattern of venation close to the recent genus *Maana* Soulier-Perkins 1998. Costal area narrow at base without transverse veinlets, apical portion distinctly widened with a few veinlets (similar pattern in *Maana*); three rows of veinlets—nodal, subapical, and apical one present (as in *Maana* and other genera of the Apia^{+} group); it differs from *Maana* and other genera of Apia^{+} group by the sequence of forking of main stems—M→ScP+R=CuA (model ScP+R→M→CuA in the other genera of the Apia^{+} group); branches M_{3+4} and CuA_1 without common portion (branches M_{3+4} and CuA_1 with a short common portion in *Maana* and other members of the Apia^{+} group present).

Etymology Gesaris—name of the warrior king from the Tibetan, Chinese, and Mongolian mythology. Gender: masculine, third declension.

Composition Only type species *Gesaris gnapo* sp. n.

Description Tegmen narrow, about 3.5 times as long as wide, veins on membrane strongly elevated, carinate, with three rows of veinlets: nodal, subapical, and apical ones. Costal margin almost straight, costal area very narrow, parallel to costal margin, distinctly widened in the apical portion, forming 'stigmal area' (near nodal line); basal portion of costal area without veinlets, apical, widened portion ('stigmal area') with five oblique veinlets. Stems ScP+R, M, and CuA leaving basal cell separately. Stem ScP+R forked apicad of stem M forking, at same level as stem CuA forking. Branch ScP+RA forked slightly apicad of nodal line, with three terminals reaching margin. Branch RP forked apicad of nodal line, then forked subsequently at level of subapical and apical lines, reaching margin with four terminals. Stem M forked at basal $\frac{1}{3}$ of tegmen length, distinctly basad of stems ScP+R and CuA forkings. Stem M forked basad of stems ScP+R and CuA forkings. Branch M_{1+2} forked at level of nodal line, branch M_{3+4} forked distinctly basad of nodal line, branch M_4 forked at nodal line. Stem CuA forked at same level as stem ScP+R forking. Nodal line composed of veinlets: *pccp-scpra* (between Pc+CP and ScP+R), *1ir*, *1r-m*, and two veinlets *1im*. Subapical line present was composed of veinlets *2ir*, *2r-m*, and *2im*. Apical line present was composed of veinlets *3ir*, *3r-m*, and *3im*.

Cell C1 narrower than postcostal cell, closed apically with nodal line veinlet *1ir*. Cell C3 longer and wider than cell C1, closed with nodal veinlet *1im*. Cell C3a present basad of nodal line. Cell C5 narrower than cells C1 and C5, elongate, lancet-shaped.

Postnodal cells about as long as apical cells, subapical cells shorter than apical cells.

Remarks Based on the venational patterns, *Gesaris* gen. n. belongs to the Apia^{+} clade as delimited by Soulier-Perkins (2000, 2001). This generic group comprises nine extant genera: *Acarna* Stål, 1863; *Apia* Distant, 1909; *Jugoda* Melichar, 1915; *Kasserota* Distant, 1906; *Maana* Soulier-Perkins 1998; *Magia* Distant, 1907; *Megacarna* Baker, 1925; *Onycta* Fennah, 1955; and *Zophiuma* Fennah, 1955. Within this group, the subunit encircling *Maana*, *Kasserota*, *Acarna*, *Magia*, and *Onycta* form a separate subclade. This subclade could be delimited by the elongate tegmina with sparse but regular lines of veinlets on membrane: nodal, subapical, and apical ones; very narrow costal area, with veins CA and Pc+CP very close each other in basal portion, always without veinlets in between and widened in apical part, with veinlets in 'stigmal area'.

Gesaris gnapo sp. n.
(Fig. 1a–d)

Diagnosis Tegmen hyperpterous in RP and M (sensu Bourgoin et al. 2015). Stem ScP+RA reaching margin with three terminals: $ScPRA_1$, RA_2, and RA_3; stem RP forking pectinate, reaching margin with four terminals. Stem M reaching margin with eight terminals. Cell C3a 0.35×as long as cell C3.

Etymology Specific epithet is derived from the Tibetan word 'gna' po' meaning primeval, ancient.

Holotype Specimen No. NIGP 135805. Imprint of tegmen with clavus missing and postclaval margin partly destroyed. Deposited in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Type locality, horizon, and age Gangni Village, Anduo County, Dazhuoma area of the Qiangtang Basin in northern Tibet; Niubao Formation; Palaeocene.

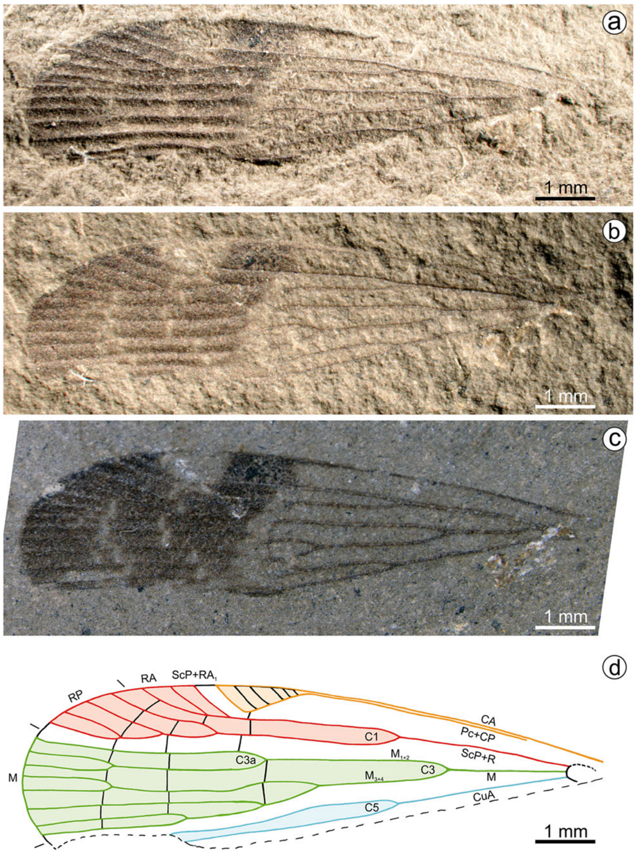

Fig. 1 *Gesaris gnapo* gen. et sp. n. **a**–**c** Photographs of the specimen under different light conditions. **a**, **b** Dry specimen under light from sides, **c** specimen under alcohol. **d** Reconstruction of tegmen venation

Description As for the genus. Length of tegmen 9.6 mm, width 2.72 mm. Cell C1 2.48 mm long, cell C3 3.32 mm long, cell C3a 1.16 mm long.

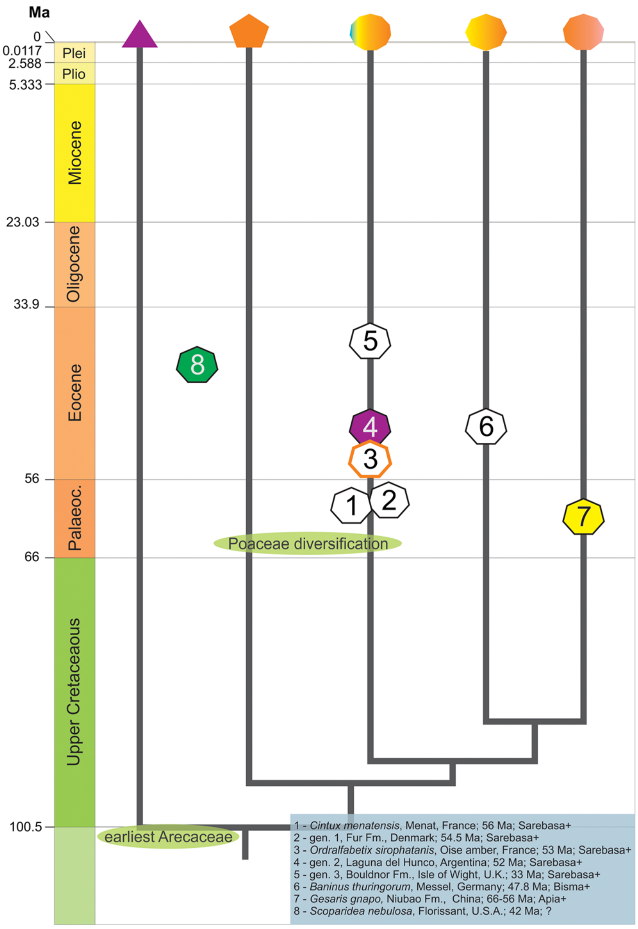

Fig. 2 Time and space distribution of fossil Lophopidae on the phylogenetic tree of lineages (generic groups) as proposed by Soulier-Perkins (2000, 2001)

Discussion

The ancestor of the family Lophopidae was postulated as feeding on Arecaceae (Fig. 2), with two later changes to Poaceae and Musaceae (Soulier-Perkins et al. 2007). Three scenarios were made to explain the paradoxical biogeographic distribution of the Lophopidae based on different geological events and times (Soulier-Perkins 2000). After a new assessment of the existing data on fossil and recent Lophopidae and their postulated host plants, any of them match to the observed facts. The oldest fossil species of Lophopidae are now from Tibet (*Gesaris gnapo* gen. sp. n.—Apia$^+$ group) and Europe (*Cintux menatensis* Stroiński et Szwedo, 2012—Sarebasa$^+$ group). Then, it could be assumed that Lophopidae has separated in Late Cretaceous, benefited from exploitation of the new habitats and host plants expansion due to Mid-Cretaceous re-organisation of biosphere (Szwedo and Soulier-Perkins 2010; Stroiński and Szwedo 2012). It seems probable that this separation took place somewhere in the ancestral area of Arecaceae and that Lophopidae committed a rather rapid diversification and spreading coincident with them. The ecological shift of Sarebasa$^+$ clade to Poaceae was postulated to take place in South-East Asia (Soulier-Perkins et al. 2007). This shift could be related to Poaceae massive diversification end expansion in the Palaeogene (Jones et al. 2014; Magallón et al. 2015). Only a sole species of monotypic genus—*Megacarna albosparsa* (Melichar, 1913) shifted to Musaceae. Soulier-Perkins (2000) postulated that ancestors of the Bisma$^+$ group (to which the Apia$^+$ clade comprises) originated in the West Pacific islands arc. Eleven of the concerned genera are found in terranes originating from this arc. However, the oldest fossil ascribed to the Bisma$^+$ group—*Baninus thuringiorum* Szwedo et Wappler, 2006—comes from the Middle Eocene Messel Maar (Szwedo and Wappler 2006). Finding of the representative of the Apia$^+$ group, the group believed to be the most advanced among the Lophopidae in the Palaeocene of Qiangtang Basin pushes back the time of separation of at least of this group of genera, but also questions the postulated area of origination. Ancestors of the modern Apia$^+$ group could originate earlier than formerly supposed (Soulier-Perkins 2000). The presence of extinct members of the Bisma$^+$ group in Europe (Szwedo and Wappler 2006) could support this statement. The early diversification and westward migrations of ancient Lophopidae probably took place in the early Palaeocene, due to suitable palaeogeographic and climatic conditions (Martin et al. 2013). It could be assumed that the 'invasion' of lophopids to the Indian subcontinent resulted from docking of it to mainland Asia. The palaeogeographic situation of the area is very complicated, a number of competing models for the Cretaceous evolution of the Tethys ocean between India and Eurasia were proposed, and these need to be understood both in the context of deformation in SE Asia, as well as in the Himalayas (Hall 2012). Also climatic changes—the Eocene Thermal Maximum (ETM2) and the subsequent Early Eocene Climatic Optimum (Zachos et al. 2008) influenced this expansion. Following climatic and biotic events of late Palaeogene and Neogene (Shukla et al. 2013) left the isolated genus *Bisma* Distant, 1907 in Ceylon as a relic of wider distribution in the past. Ancestors of the recent genera of the Apia$^+$ group could reach New Guinea at about 25–20 Mya, when the East Philippines−Jalmaher−South Caroline Arc collided with the Australian Plate at the north New Guinea margin (Hall et al. 2011). Ancestors of recent *Magia* species probably 'invaded' Australia later, during Pliocene-Pleistocene (Soulier-Perkins 2000). The recent genera placed in the Apia$^+$ group seem to be relatively young descendants of the much older ancestral forms, present in the Palaeocene. Such evolutionary history of the Apia$^+$ group seems to be reflected in its recent distribution (Soulier-Perkins 2000) and trophic relationships of the recent taxa (Soulier-Perkins 2007).

Conclusion

It could be concluded that discovery of fossil Lophopidae in Palaeocene deposits of Tibet gives a new clue to evolutionary and distributional patterns of the Lophopidae. The recent distribution of this group and its subunits seems to be result of millions of years of dispersal and extinction events, as well as vicariance events in some areas, influenced by changes of the availability of host plants, host-plants shifting and biotic and climatic changes at global and local scale. Scarce data on fossil insects from the most crucial period of Palaeogene faunistic turnover in Asia after the collision with Indian plate are available (Lin et al. 2010; Szwedo et al. 2013). Fossils from Tibet can bring new insights not only to evolution of groups, but also into paleoevents of biotic reorganization and formation of modern fauna of Asia.

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Supplementary material

Fossil site

A geological team from the Jianghan Institution of Petroleum and Gas collected a large number of fossils in the Qiangtang Basin of the Northern Tibet, China; insects collected near Gagni village were sent to one of us (QBL) for identification. Preliminary, 19 insect morphospecies attributed to 17 genera and 11 families are recorded from the Dazhuoma Entomofauna (near Gangni village), indicating a rather distinct diversity (Lin and Huang 2006). Only a single species of Prophalangopsidae (Orthoptera) and single species of Flatidae (Hemiptera) were described so far (Lin and Huang 2006; Szwedo et al. 2013). The fossil insects occur mainly in the lower part of the second member of the Niubao Formation (beds 179–249). The assemblage is diversified and quite abundant in individuals. The age of Dazhuoma Entomofauna was estimated as Palaeocene to Early Eocene in age (Cai and Fu 2003) and more recently aged Palaeocene (Lin and Huang 2006). Lithology of the fossil site was not reported and no more precise data are available (Zhang S 2009).

Fossil Lophopidae

Fossil Lophopidae are not very common and fossil record of the family comprises: *Cintux menatensis* Stroiński et Szwedo, 2012 from the Palaeocene of Menat in France, *Ordralfabetix sirophantes* Szwedo, 2011 from Lowermost Eocene Oise amber of France and *Baninus thuringiorum* Szwedo and Wappler, 2006 from the middle Eocene of Messel in Germany (Stroiński and Szwedo 2012; Szwedo 2011; Szwedo and Wappler 2006). Two more fossils of Lophopidae were reported by Petrulevičius et al. (2010a, b): one coming from the Upper Palaeocene Fur and Ølst Formations in Denmark, and the second from the Lower Eocene Laguna del Hunco, Argentina. The last European record of Lophopidae comes from the late Eocene deposits of Isle of Wight, U.K. (Szwedo, unpubl. data). The taxonomic placement of the only fossil lophopid from North America, i.e. *Scoparidea nebulosa* Cockerell, 1920 from the Eocene Green River Formation, Roan Mountain, Colorado, U.S.A. (Cockerell 1920) remains uncertain (Szwedo 2011), though it presents some salient features of the family.

Arecaceae as ancestral host plants of Lophopidae

The ancestor of the family Lophopidae was postulated as feeding on Arecaceae, with two later changes to Poaceae and Musaceae (Soulier-Perkins et al. 2007). According to Stevens (2015) and Magallón et al. (2015) all these families are placed in well supported monophyletic clade of monocotyledons (monocots) plants – commelinids. Arecaceae is a monophyletic group recently including 188 genera and approximately 2585 species (Govaerts and Dransfield 2005; Dransfield et al. 2008; Baker and Couvreur 2012, 2013a, b; PALMweb 2015). They are recently distributed in the tropics, with a few species reaching subtropical areas (Henderson et al. 1997, Eisenhardt et al. 2011). Their fossil records from the tropics are less common, however, than those from middle and high latitudes (Harley and Morley 1995; Harley and Baker 2001; Harley 2006; Palazessi and Barreda 2007; Dransfield et al. 2008; Gomez-Navarro et al. 2009; Futey et al. 2012). Fossil record of Arecaceae reflects their broader latitudinal distribution in the late Mesozoic and early Cenozoic because of warmer global climate (Zachos et al. 2008, Friedrich et al. 2012), but also lack of study in the early Cenozoic deposits in the tropics (Pan et al. 2006). The earliest unequivocal Arecaceae fossils are from the late Mid-Cretaceous to early Upper Cretaceous (Harley 2006; Dransfield et al. 2008; Couvreur et al. 2011, Futey et al. 2012). Australasia (including New Guinea, New Caledonia, and New Zealand) was hypothesized as ancestral area of Arecaceae and their crown node is estimated to be ca. 110 Myr old (Janssen and Bremer 2004; Bremer and Janssen 2006; Harley 2006; Taylor et al. 2009; Couvreur et al. 2011; Stevens 2015).

The oldest known Lophopidae represent Sarebasa$^+$ group, Bisma$^+$ group and Apia$^+$ group. This situation match well to the most parsimonious model proposed by Soulier-Perkins et al. (2007) and to statement about 'taxonomic conservatism' of Lophopidae in selection of the host plants as documented in Carriona$^+$, Macota$^+$, Bisma$^+$ and Apia$^+$ groups. The Sarebasa$^+$ group ancestor switched to another monocot family, the Poaceae (commelinid clade; Stevens 2015, Magallón et al. 2015). Rich and widespread fossil record of fossil representatives of Sarebasa$^+$ group could result from Poaceae massive diversification end expansion in the Palaeogene (Jones et al. 2014, Magallón et al. 2015). This switch appears to have been profitable, permitting an important radiation resulting in eleven recent genera and a total of fifty-six described species. Within Sarebasa$^+$ group ancestors of genera *Elasmoscelis* Spinola, 1839 (21 species) and *Lophops* Spinola, 1839 (13 species) apparently extended their distributions into Africa, and may have followed the expansion of the savannah on this continent during the Miocene (around 23 Ma). The genus *Elasmoscelis* being related to Poaceae, is more oligophagous, including a few records on core eudicots (Soulier-Perkins

2007, Stevens 2015) and their diversity benefit from the ‘diet relaxation’ (Attié et al. 2008, Wang et al. 2014).

The ancestors of Arecaceae seem to spread rapidly as in late Cretaceous times they were dispersed from their area of origin to Europe, North Africa, India, North and South America (Harley 2006, Manchester et al. 2010, Futey et al. 2012, Srivastava and Srivastava 2014). Taking into consideration the known fossil record of Lophopidae, they had been dispersing coincidently with early Arecaceae.

The distribution of Apia$^+$ group

Ancestors of Bisma$^+$ group (comprising Apia$^+$ clade to which newly described genus belongs) were postulated originating in the West Pacific islands arc (Soulier-Perkins 2000). Eleven of the concerned genera are found in the terranes originating from this arc. The fossils questions the postulated area of origination of Bisma+ group and its subclade, Apia+ group and the times of their origination. *Baninus thuringiorum* Szwedo et Wappler, 2006 representing Bisma+ group, was reported from the Middle Eocene Messel Maar (Szwedo and Wappler 2006); present finding in the Palaeocene of Qiangtang Basin implies earlier than formerly supposed (Soulier-Perkins 2000) time of separation of Apia+ group. These findings support the opinion on early diversification in continental part of Asia rather, and westward migrations of ancient Lophopidae in the early Palaeocene, as suggested by Szwedo and Soulier-Perkins (2010). This migration could be related to possibility of rapid dispersal due to suitable palaeogeographic and climatic conditions (DeCelles et al. 2007; Zachos et al. 2008; Zhang et al. 2008, 2011; Polissar et al. 2009; Hetzel et al. 2011; Wang et al. 2011; Dai et al. 2012). The knowledge of the dispersal events on the northern continents has greatly improved since it has been correlated with a negative Carbon Isotope ($\delta^{13}C$) Excursion – CIE linked to a short greenhouse effect called the Paleocene-Eocene Thermal Maximum – PETM (Röhl et al. 2000, Magioncalda et al. 2004, McInerney and Wing 2011). This PETM is a 150,000 years lasting abrupt global warming event that represents the warmest period of the last 65 million years, followed by the second major hyperthermal, Eocene Thermal Maximum 2 (ETM-2), that occurred approximately 53.7 million years ago (Zachos et al. 2008). Warm and uniform climatic and biotic conditions resulted in extension of geographic ranges and rapid migration of plants and animals (Smith et al. 2006, Wedmann and Makarkin 2007, Akhmetiev 2010, Lin et al. 2010, Rust et al. 2010, Grimaldi and Singh 2012), and Palaeogene Lophopidae were subject of these events as well as their Arecaceae host plants. The earliest Eocene, since the

Eocene Thermal Maximum (ETM2) and the subsequent Early Eocene Climatic Optimum (Zachos et al. 2008), could be a good estimation for migration of ancient Bisma+ group lophopids to the Indian subcontinent. Such statement is supported also by analysis of Cercopoidea and Fulgoroidea biogeography presented by Liang (1998). As the Earth's climatic belts changed dramatically during the Cenozoic, the isolated genus *Bisma* Distant, 1907 in the Ceylon appears as the relic of wider distribution in the past, according to the 'ousted relicts' concept (Eskov and Golovatch 1986, Eskov 1987).

Soulier-Perkins (2000) discussed the possible routes of Apia+ taxa migration. Collision of the East Philippines−Jalmaher−South Caroline Arc with the Australian Plate at the north New Guinea margin at about 25–20 Mya (Hall 2002, 2009; Hill and Hall 2002; Hall et al. 2011) enabled the first appearance of the Apia^{+} group in the New Guinea. Later, during the Pliocene-Pleistocene, the ancestors of modern *Magia* species possibly migrated to the Australia. From the middle Miocene until the Pliocene (15–5 Ma) increasing levels of aridity were influencing the habitats and vegetation in Australia (Martin 2006). However, at the beginning of the Pliocene, a brief period of warm and moist conditions occurred, which was followed by strong periods of aridity. Period that fluctuated between increasing aridity and a brief return of mesic conditions, may support dispersal and may have fractured populations among multiple, localized refugia, which resulted in increased diversification of taxa (Maekawa et al. 2003; Rowe et al. 2008; Fujita et al. 2010). Notwithstanding of these dispersal, extinction and diversification events the Bisma+ (including the Apia+ group) Lophopidae present 'taxonomic conservatism' in respect to their host plants selection (Soulier-Perkins et al. 2007). The modern taxa of the Apia^{+} group appears as relatively young descendants of the Palaeocene ancestors, with evolutionary history reaching mid-Cretaceous and reflected in fossil record (Szwedo and Wappler 2006, Szwedo and Soulier-Perkins 2010), distribution (Soulier-Perkins 2000) and trophic relationships (Soulier-Perkins et al. 2007).

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