e-ISSN 1734-9168
http://www.isez.pan.krakow.pl/en/folia-biologica.html

Folia Biologica (Kraków), vol. 70 (2022), No 4
https://doi.org/10.3409/fb_70-4.19

Sabahia polypodii gen. et sp. nov. (Hemiptera: Cicadellidae: Evacantihinae) and its Phylogenetic Position within the Nirvanini Tribe

Marcin WALCZAK, Cezary GĘBICKI, Marzena ZMARZŁY and Natalia SAWKA-GĄDEK

Accepted October 17, 2022 *Published online November 16, 2022* *Issue online December 06, 2022*

Original article

WALCZAK M., GĘBICKI C., ZMARZŁY M., SAWKA-GĄDEK N. 2022. *Sabahia polypodii* gen. et sp. nov. (Hemiptera: Cicadellidae: Evacantihinae) and its phylogenetic position within the Nirvanini tribe. Folia Biologica (Kraków) **70**: 151-162.

In this paper, a new genus *Sabahia* Walczak & Gębicki with a new species *Sabahia polypodii* Walczak & Gębicki within the tribe Nirvanini is described. It originates from Sabah Province on Borneo (Malaysia, Sabah) and is most closely related to *Decursusnirvana* Gao & Zhang and *Sinonirvana* Gao & Zhang. It differs from these genera primarily with regard to the morphology of the male genitalia. Although it shows some resemblance to representatives of the genus *Chudania* Distant in the structure of the aedeagus, it can be clearly separated from this genus by the absence of a median carina from the facial part of the head. Details of the external morphology, as well as those of the male and female genitalia are documented (including scanning microscopy images). In addition, the phylogenetic relationships of several species within the subfamily Evacanthinae and related groups are discussed, based on comparative analyses of the genetic sequences for histone (H3) and the mitochondrial gene of cytochrome oxidase c (COI).

Key words: Nirvanini, new taxon, taxonomy, morphology, ecology, Borneo, Malaysia, Sabah.

Marcin WALCZAK✉, Marzena ZMARZŁY, University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Biology, Biotechnology and Environmental Protection, Bankowa 9, 40-007 Katowice, Poland.
E-mail: marcin.walczak@us.edu.pl
Cezary GĘBICKI, Daszyńskiego 41, 42-400 Zawiercie, Poland.
Natalia SAWKA-GĄDEK, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland.

Nirvanini Baker, 1923 constitutes a relatively small tribe of a pan-tropical range, which is limited in its distribution to equatorial and subtropical humid forest zones (montane cloud forests) and other humid mountain habitats. It is associated with a variety of host plants belonging to the class Magnoliophyta. Its representatives feed on some trees (e.g. of the genus *Aesculus, Quercus, Acacia*), as well as shrubs (e.g. *Citrus, Camellia, Vitis*) and numerous perennials and grasses (SCHUMACHER 1915; AHMED & MAHMOOD 1970; MESHRAM & RAI 2017). Some species of the genus are regarded as pests among farmers growing sugarcane and horticultural crops (VIRAKTAMATH & WESLEY 1988), or even show features typical of an invasive species (WEBB & VIRAKTAMATH 2004; AGUIN-POMBO *et al.* 2007). The group was previously classified as the subfamily Nirvaninae Baker, 1923 (OMAN *et al.* 1990), which is now considered to be a junior synonym of Evacanthinae (DIETRICH 2004). In the past, numerous genera of the current Nirvanini were often placed in the subfamily Typhlocybinae (MATSUMURA 1931). However, five tribes have recently been assigned to the subfamily Evacanthinae Metcalf, 1939: Nirvanini Baker, 1923, Balbillini Baker, 1923, Evacanthini Metcalf, 1939, Pagaroniini Anufriev, 1978, and Pentoffiini Wang, Dietrich & Zhang, 2017 (WANG *et al.* 2017). The subfamily shows many similarities, and is most probably closely related, to the subfamily Cicadellinae (DIETRICH 2004). MESHRAM and RAI (2017) presented an updated review of the taxonomy of the Nirvanini tribe.

In spite of numerous morphological analyses and other comparative studies, no single and sufficiently

unambiguous features could be identified which would distinguish the Nirvanini tribe from the remaining ones (especially from Evacanthini) (DIETRICH 2004; WANG *et al.* 2017).

The Nirvanini tribe includes mostly medium-sized species with an elongated, slender body which is flattened dorsoventrally. Light colouration is dominant, generally with a species-specific colour pattern in the form of red, orange and black stripes, streaks and spots (on both the dorsum and the wings). The head is wide, equal to the pronotum or wider. The vertex is predominantly elongated (or strongly elongated) and flattened (but not concave), with a distinct sutura coronalis, rarely extending beyond the ocelli. Vertex margins are arcuate, converging at the apex, rounded or pointed. Typical of Evacanthini, the double lateral carinae are absent. In some species (e.g. of the genus *Chudania* Distant), the lateral parts of the vertex are covered with delicate sculpture. Ocelli are located near the vertex margins above compound eyes. In the lateral view, the frontoclypeus is usually flat, forming an acute angle with the vertex line (e.g. *Kana* Distant, *Nirvana* Kirkaldy, *Chudania* Distant and some species within the genus *Sophonia* Walker), more rarely broadening below the apex (e.g. in some species of *Sophonia* Walker), or sporadically forming an almost right angle (*Decursusnirvana* Gao & Zhang). Median carina of the frontoclypeus are short, and only sporadically longer (e.g. *Chudania delecta* Distant) or absent. Clypeus is wide, trapezoidal in shape and lacking median carinae. Lora are very fine. Lower edges of the gena (maxillary plates) are equal to the clypeus or extending beyond its apex. This is the only characteristic to unequivocally separate the Nirvanini species from those of Evacanthini and Pagaronini. Antennae are long, reaching at least the end of the pronotum or wing apices. Antennal carinae are distinct. Pronotum is with lateral carinae. There are long-winged forms. Forewings are with the transverse venation reduced, limited to the wing apex. The wing appendix is considerably reduced. Four external cells are subequal (e.g. *Kana* Distant), or the fourth (inner) is twice as long as the remaining ones, while being rectangular or irregular in shape (e.g. *Sophonia* Walker and *Nirvana* Kirkaldy). Hindwing is always developed, with three or four apical cells. In the latter case, a marginal vein runs close to the outer wing margin and joins its costal margin near the nodular area (e.g. *Kana* Distant, *Decursusnirvana* Gao & Zhang, *Sinonirvana* Gao & Zhang). Fore and middle tibiae are cylindrical. The ventral row of setae on the protibia are with a single seta distinctly longer than others. Metafemur is with a macrosetal formula 2+1+1, sometimes with supernumerary setae. Pygofer is cylindrical or flattened, with more or less clearly delineated lobes and ventral processes. Apices of the pygofer are with a numerous macrosetae. Anal tube is with processes or processes absent. Genital valve is relatively minute. Genital plates are usually elongated, almost equally narrow, and sometimes tapering (e.g. *Nirvana* Kirkaldy) or with a broadened and upwardly bent apex (e.g. *Decursusnirvana* Gao & Zhang). Style is differing in shape, hooked or awl-like elongate (e.g. *Nirvana* Kirkaldy). Connective is Y-shaped with sub-equal arms and T-shaped with an elongated basal arm. Aedeagus are with a single shaft and gonopore, often with long and numerous processes, rarely with processes absent. Some species characteristically have a strongly-reduced atrium at the shaft base (e.g. *Decursusnirvana* Gao & Zhang, *Sinonirvana* Gao & Zhang). Details of the ovipositors in Nirvanini have been described quite recently, while the sculpture, shape and distribution of teeth on the ovipositor valvules are of diagnostic value for some Nirvanini species (VIRAKTAMATH 1992; DIETRICH 2011a, 2011b; WANG *et al.* 2017). The assignment of *Sabachia polypodii* gen. et sp. nov. to the tribe Nirvanini, and the subfamily Evacanthinae, is confirmed by a set of characteristics including well-developed ocelli located near the anterior vertex margin, cylindrical fore tibia, macrosetal formula on the hind femur apex 2+1+1, medial carina on the frontoclypeus absent, basal seta in the fore femur ventral row that is distinctly longer than others, and a lower margin of the maxillary plate slightly extended beyond the lower margin of the anteclypeus.

Prior to now, the following 10 species representing 4 genera belonging to the Nirvanini tribe from Borneo have been described: *Kana illaborata* Distant, *Nirvana placida* (Stål), *N. sanguineolineata* (Baker), *Pythonirvana muiri* Baker, *Sophonia longitudinalis* (Distant), *S. malayana* (Baker), *S. ocellaris* (Baker), *S. picta* Viraktamath & Wilson, *S. sandakanensis* (Baker) and *S. similis* Viraktamath & Wilson (DISTANT 1908; STÅL 1859; BAKER 1923; METCALF 1963; NAST 1972; VIRAKTAMATH & WILSON 2018).

Materials and Methods

The research was carried out in 2011 on the research plots near D'Villa Rina Ria Lodge in Ranau District (Borneo, Sabah). The coordinates of the location are: 6°00′02″N, 116°32′45″E. The research was conducted in August at night (during a random night trip). The insects were found using a standard entomological sweep net (⌀35 cm), in accordance with the methodology commonly used for this type of research (GĘBICKI *et al.* 1977; KLIMASZEWSKI *et al.* 1980; STEWART 2002). The research with the use of an entomological sweeping net was supplemented by viewing the ferns (possibly the host plant of this species) with *Sabahia polypodii* gen. *et* sp. nov. specimens.

Dry-mounted specimens were studied under a Leica M205C microscope, Leica DM3000LED stereomicroscope and a Delta Optical IPOS-810 stereomicroscope. Measurements were made with an ocular micrometer. The SEM micrographs were obtained using a Phenom XL field emission scanning electron

microscope with a BackScatter Detector (BSD). The panoramic image stitcher Image Composite Editor 2.0.3.0 and the graphic editor Adobe Photoshop CS6 were used to prepare the figures. No procedures that could damage the specimens, e.g. washing, dehydration and sputter-coating with a film of electrically conducting material, were used. The specimens were only cleaned with a brush and were then mounted on aluminium stubs (by inserting an insect pin into a fragment of a sponge that was glued to the stub). Next, the specimens were covered with an anti-static spray. The specimens were measured using the Leica Application Suite 4.9.0 software. The genitalia of the insects were dissected after boiling the abdomen three times (about 10 minutes) in a 10% solution of potassium hydroxide (KOH). This preparation was performed according to the KNIGHT (1965) procedure. Then, the specific parts of the genital structures were separated from the abdomen using thin forceps and a needle blade. The whole was then placed in glycerine. The genitalia were subsequently dissected and examined using a Delta Optical IPOS-810 stereomicroscope and a Leica DM3000LED stereomicroscope. Photographs of the habitus were taken with a Canon EOS 50D digital camera equipped with a Canon 100 mm f/2.8 USM Macro and a Sigma 150 mm f/2.8 USM APO Macro DG HSM lens. Photographs of the genitalia were taken using a Nikon D7500 camera and the Nikon M Plan10 lens. The images were stacked, aligned and combined using the Helicon Focus 7 (the first author is the licence holder). The map was generated with the QGIS program (GNU General Public Licence) and using a vector map downloaded from the website: https://www.naturalearthdata.com/.

The holotype and nine paratypes are preserved in the entomological collection of the University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Biology, Biotechnology and Environmental Protection (Katowice, Poland), and one of the paratypes is in the collection of the author: Marcin Walczak.

Molecular data

Taxon sampling

The collected data on the specimens and their GenBank accession numbers are provided in Table 1.

Table 1

List of species and GenBank accession numbers used in the phylogenetic analysis

Species	H3	COI	Reference
Empoasca fabae	KY302505	KY264063	WANG *et al*. 2017
Narecho sp.	KY302559	KY264122	WANG *et al*. 2017
Onukia flavimaculata	KY302541	KY264102	WANG *et al*. 2017
Evacanthus stigmatus	KY302509	KY264070	WANG *et al*. 2017
Carinata ganga	KY302512	KY264073	WANG *et al*. 2017
Paraonukia ochra	KY302540	KY264101	WANG *et al*. 2017
Onukiades formosanus	KY302542	KY264103	WANG *et al*. 2017
Friscanus friscanus	KY302506	KY264067	WANG *et al*. 2017
Pagaronia confusa	KY302517	KY264079	WANG *et al*. 2017
Epiacanthus semifuscus	KY302546	KY264109	WANG *et al*. 2017
Decursusnirvana excelsa	KY302553	KY264117	WANG *et al*. 2017
Sabahia polypodii gen. *et* sp. nov. – isolate Ev1	OM992260	ON016095	Present study
Sabahia polypodii gen. *et* sp. nov. – isolate Ev2	OM992261	ON016096	Present study
Sabahia polypodii gen. *et* sp. nov. – isolate Ev3	OM992262	ON016097	Present study
Sabahia polypodii gen. *et* sp. nov. – isolate Ev4	OM992263	ON016098	Present study
Tortor sp.	KY302558	KY264121	WANG *et al*. 2017
Nirvana suturalis	KY302518	KY264081	WANG *et al*. 2017
Kasunga sp.	KY302557	KY264120	WANG *et al*. 2017
Sophonia orientalis	KY302554	KY264118	WANG *et al*. 2017
Ophiuchus sp.	KY302547	KY264110	WANG *et al*. 2017
Kosasia typica	KY302555	KY264119	WANG *et al*. 2017
Concaveplana sp.	KY302520	KY264083	WANG *et al*. 2017
Sophonia rosea	KY302549	KY264112	WANG *et al*. 2017
Sophonia sp.	KY302548	KY264111	WANG *et al*. 2017
Oniella honesta	KY302521	KY264084	WANG *et al*. 2017
Convexfronta guoi	KY302550	KY264113	WANG *et al*. 2017
Kana semela	KY302552	KY264116	WANG *et al*. 2017
Australnirvana adelaideae	KY302522	KY264085	WANG *et al*. 2017
Chudania emeiana	KY302519	KY264082	WANG *et al*. 2017

DNA extraction, amplification and sequencing

DNA was extracted from one leg of each specimen. The genomic DNA was isolated without modifying the protocol, using the Syngen DNA Mini kit (Syngen, Wrocław, Poland) under a laminar flow. To elute the purified DNA, we applied 50 µl of an Elution Buffer onto the silica membrane. Two of the genes were amplified: one mitochondrial COI and one nuclear H3. To amplify a fragment of the mitochondrial cytochrome c oxidase I (COI) gene, the primer pair LCO1490 and HCO2198 (FOLMER *et al.* 1994) was used. For the H3 amplification, the primers H3AF and H3AR (COLGAN *et al.* 1998) ware used. A polymerase chain reaction (PCR) amplification for all the DNA fragments that were analysed was carried out under a laminar flow in a final volume of 20 µl containing: 30 ng of DNA, 1.25 U Perpetual OptiTaq (EURx, Poland), 0.4 µl of 20 µM of each primer, 2 µl of 10x Pol Buffer B and 0.8 µl of 5 mM dNTPs in a Mastercycler ep system (Eppendorf, Hamburg, Germany). The cycling profile for the PCR was: 95°C for 2 min, 35 cycles of 95°C for 30 sec, Tm of oligos for 30 sec, 72°C for 1 min and a final extension period of 72°C for 7 min.

In order to assess the quality of the amplification, the PCR products were electrophoresed in 1% agarose gel, for 45 min at 85 V, with a DNA molecular weight marker (Mass Ruler Low Range DNA Ladder, Thermo-Scientific, Waltham, MA, USA). The PCR products were purified using the Syngen Gel/PCR Mini Kit (Syngen, Wrocław, Poland).

The samples were sequenced in both directions using the same primers as for the PCR reactions, combined with a BigDye Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems, (ABI) Foster City, CA, USA) using the chain termination reaction method (SANGER *et al.*1977). The sequencing reaction was carried out with the PCR product at a total volume of 20 µl containing: 2 µl of BigDye Terminator Reaction Ready Mix v. 3.1 (ABI), 2 µl 5× sequencing buffer (ABI), 3.2 mol/µl of the primer solution and 6 µl of the purified PCR product. The cycle-sequencing profile was 3 min at 94°C, followed by 30 cycles of 10 s at 96°C, 5 s at 50°C and 2 min at 60°C.

The sequencing products were precipitated using the ExTerminator (A&A Biotechnology, Gdynia, Poland), and were separated on an ABI PRISM 3130xl DNA Sequencer (Applied Biosystems, Foster City, CA, USA).

Sequence edition and alignment

The raw chromatograms were evaluated and corrected in Geneious v. R10.2.6 (https://www.geneious.com). In order to identify the NUMTs (BENSASSON *et al.* 2001; SONG *et al.* 2008), the mitochondrial COI sequences were translated into amino acid sequences with Geneious v. R10.2.6 using the standard invertebrate mitochondrial genetic code. All of the nucleotide sequences were verified using BLAST searches of the NCBI (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The alignment of the combined sequences that were studied was performed using the MAFFT (KATOH *et al.* 2002) plugin available within Geneious v. R10.2.6.

Molecular phylogenetic

Models for the Bayesian (BI) analyses were calculated in jModeltest (DARRIBA *et al.* 2012; GUINDON & GASCUEL 2003) using the Akaike information criterion (AIC). The BI analyses were performed in MrBayes v. 3.2.6 (RONQUIST *et al.* 2012) with four independent runs, each having three heated and one cold chain. Analyses were run for 2 million generations, with trees sampled every 1000 generations. The first 25% of each run was discarded as a burn-in. The convergence among the runs was assessed using Tracer (RAMBAUT *et al.* 2018). The ML analyses were performed using PhyML v. 3.0 (GUINDON *et al.* 2010). All the trees were visualised using FigTree (http://tree.bio.ed.ac.uk/software/figtree). The trees were edited and annotated in Corel Draw 17.1.0.572 (Corel Corporation, 2014).

Results

Phylogenetic inferences were obtained for the *H3* and COI genes using the Bayesian inference (BI) and Maximum likelihood (ML). The GTR+G+I model with a gamma correction of 1.389 and invariable sites of 0.548 was selected by the AIC in jModelTest for the matrix. Heuristic searches resulted in one ML tree (-ln= -9591.77984). The phylogenies were resolved and the main splits were supported by high bootstrap values and posterior probabilities. Only four nodes had bootstrap scores <80, and eight nodes had posterior probabilities <90 (Fig. 1).

Empoasca fabae (Harris) was used to root the topologies. Our phylogram shows two main clades. The first is formed by two subclades. Both of the subclades are composed of Nirvanini tribe species, with the first comprised of: *Concaveplana* sp., *Sophonia rosea* Li & Wang, *Sophonia* sp., *Oniella honesta* Melichar, *Kasunga* sp., *Kosasia typica* Distant, *Sophonia orientalis* (Matsumura), *Ophiuchus* sp., *Convexfronta guoi* Li, *Nirvana suturalis* Melichar and *Tortor* sp. The second subclade is formed by: *Decursusnirvana excelsa* (Melichar) and *Sabahia polypodii* gen. nov. and sp. nov. (Fig. 1).

The second clade is formed by two subclades. The first subclade is comprised of the following Nirvanini species: *Australnirvana adelaideae* (Evans), *Kana semela* (Linnavuori) and *Chudania emeiana* Zhang & Yang. The second is formed by two groups, with the

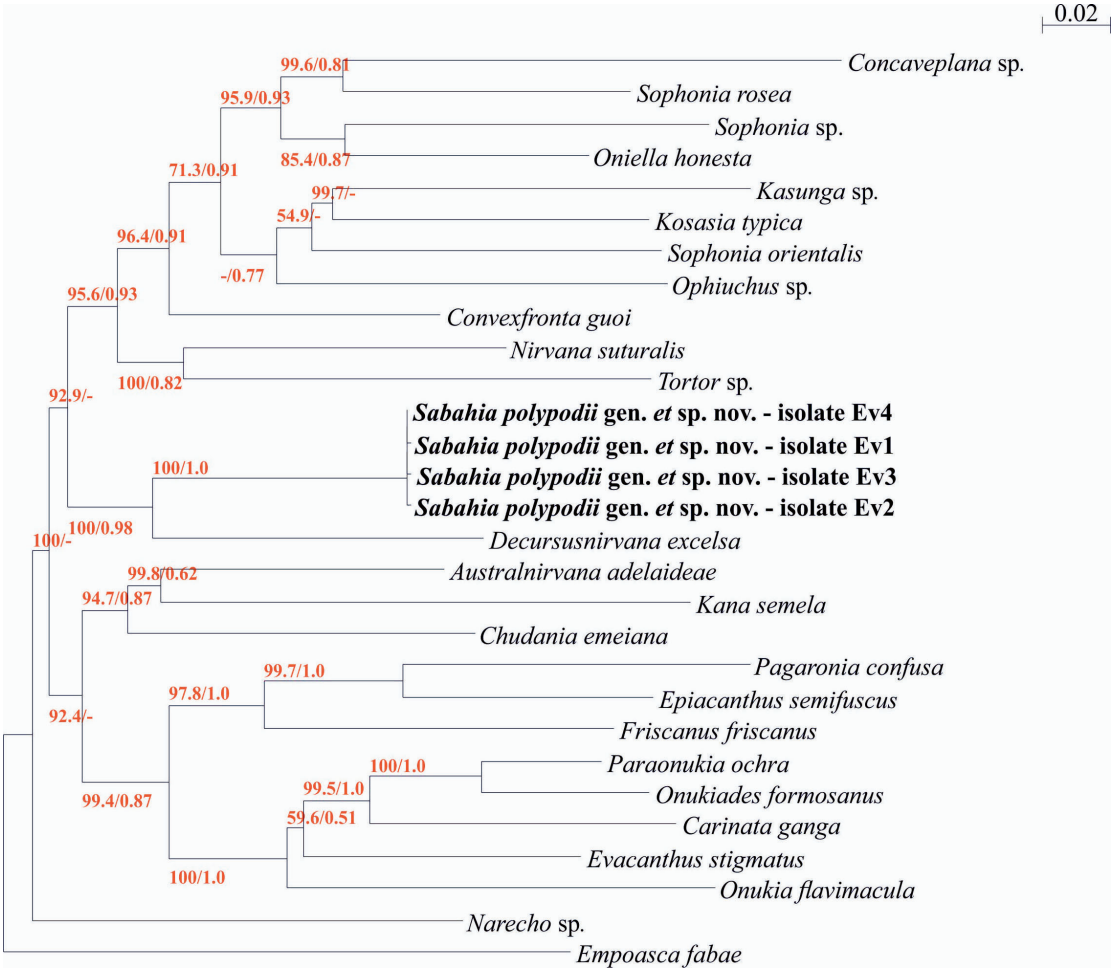

Fig. 1. Phylogenic tree showing the phylogenetic position of *Sabahia polypodii* gen. et sp. nov. among the Nirvanini and Evacanthini tribes, inferred from the maximum likelihood (ML) and Bayesian interference (BI) analyses of the histone H3 and cytochrome oxidase I (COI) gene sequences. The first number on the branch is the bootstrap support from PhyML and the second is the posterior probabilities from MrBayes. Scale bar unit: expected substitutions per site.

first consisting of representatives of the Paragonini tribe: *Pagaronia confusa* Oman, *Epiacanthus semifuscus* Motschulsky and *Friscanus friscanus* (Ball). The second group is formed by species belonging to the Evacanthini tribe: *Paraonukia ochra* Huang, *Onukiades formosanus* (Matsumura), *Carinata ganga* Li & Wang, *Evacanthus stigmatus* Kuoh and *Onukia flavimaculata* Li & Wang (Fig. 1).

Taxonomy

Family – Cicadellidae Latreille

Subfamily – Evacanthinae Metcalf

Tribe – Nirvanini Baker

Sabahia gen. nov.

(Figs 1-8)

Type species: *S. polypodii* sp. nov.

D i a g n o s i s. Medium-sized Nirvaninae. Vertex is slightly shorter than the pronotum, with the anterior margin arcuate. In the lateral view, the lines of the vertex and frontoclypeus form an almost right angle. Frontoclypeus is lacking median carina, with the lateral margins subparallel. Antennae are almost reaching the end of the body. Clypeus (anteclypeus) is elevated medially. Wings are considerably longer than the body. Apical cell 4 of the forewing is longest; marginal vein of the hindwing running close to the wing margin (especially in the apical part), with 4 apical cells present. Male pygofer is with a narrow rounded apex, divided into a dorsal and a ventral part by a horizontal groove, with a pair of hook-like ventral processes. Apical part of the style (with a ventral lobe) is distinctly shorter than the basal one, and is connective typical of the tribe. Aedeagus is lacking an atrium and is without spines or processes on the shaft, which is divided into two fused parts: the dorsal and the pointed, strongly sclerotised ventral one. Massive sternite VII plate in the female is slightly longer medially. Apex of the first pair of valvulae are elongate and pointed, while ventral margins of the second pair of valvules are arcuate.

D e s c r i p t i o n. A medium sized genus (females app. 4.9 mm, males app. 5.5-5.6 mm) (Tab. 2, Figs 2a-b, 3a-b).

H e a d. Vertex (crown) is relatively short, distinctly broader around than between the eyes (0.78 x) and between the antennae (0.66 x). Anterior margin of the vertex is gently arcuate, lateral margins undulated, edged by a weakly defined carina (more distinct in the apical part of the head). Vertex surface is almost flat, with small depressions on the sides apically, sutura coronalis is short, transforming into a low median carina extending somewhat above the line of the ocelli. Apical part of the vertex is slightly convex, covered with numerous cuticular wrinkles converging apically (Fig. 4a). Ocelli, relatively large, are located just above the upper margins of the compound eyes and are separated from the apical margin by a distance equal to 2x the ocellus width. The edge between the vertex and frons elevated, visible from above, is with numerous cuticular wrinkles (Fig. 4a). Lateral angle of the head formed between the line of the vertex and medial line of the frontoclypeus is almost a right angle (Fig. 2b). Facial part of the head with the labrum is evenly covered with cuticular nodules, and the surface of the gena is glabrous (Fig. 4b). Lateral margins of the upper part of the frontoclypeus are almost parallel in 2/3 of their course, and are distinctly narrowed along the basal 1/3 (Fig. 4c). Median carina are completely missing (Fig. 4b-c). Lateral surfaces of the frontoclypeus are with 7 indistinct pairs of cuticular carinae, which obliquely converge to a slightly elevated medial part of the face (where the mouthpart muscles are attached) (Fig. 4c). Clypeal groove is deep and gently arcuate. Clypeus is wide, app. 1.3 x shorter than the frontoclypeus. Median carinae are absent. A triangular protruding part of the clypeus is terminating on the sides with flatter fragments (Figs 4b-c). Lower margin of the clypeus are only 0.6 x shorter

Fig. 2. *Sabahia polypodii* gen. et sp. nov. habitus: a – male, dorsal view, holotype; b – female, lateral view, paratype (left view).

Fig. 3. *Sabahia polypodii* gen. et sp. nov. ventral view: a – male, paratype (legs and abdomen); b – female, paratype.

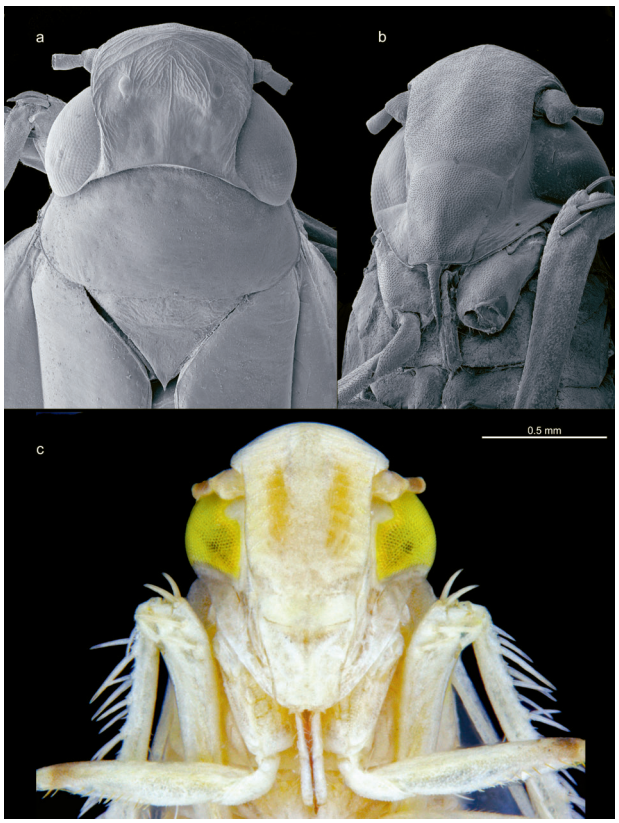

Fig. 4. Head and pronotum: a – male, paratype, dorsal view with details of the vertex, pronotum and scutellum (SEM); b – the same specimen, facial part of the head (SEM); c – female, paratype, facial part of the head.

than the upper one, straight and are slightly incised medially. Lora are very short and narrow, expanding from the vicinity of the clypeal groove to the subapical part of the clypeus. Lateral margins of the large maxillary plates are straight, reaching beyond the level of the clypeus. Rostrum is short, extending to the middle coxa (Figs 4b-c). Compound eyes are large, almost globular (in the lateral view), with a minute antennal incision on the inner margin (Fig. 2b). Antennal pit is broad, just anterad of the anterior eye margin (Figs 4b-c). Antennae are very long, reaching the end of the body, more than 8x longer than the head length (Figs 2a, 3a). Antennal scapus is slightly flattened, twice as wide as the cylindrical pedicellus (Fig. 4b).

T h o r a x. Pronotum is shield-shaped, smooth and somewhat longer than the head (app.1.3x), with the anterior margin arcuate and the posterior margin almost straight (slightly incised medially). Lateral margins (at the wing base) are deeply incised, lacking distinct carinae. Anterior part of the head capsule is basally distinctly swollen (Fig. 4a). Scutum (together with the scutellum) is shorter than the pronotum (0.8x), scutellar groove is deep and complete. Basal part of the scutum is furrowed and distinctly separated from a glabrous scutellum (Fig. 4a).

W i n g s. In both sexes, the wings reach far beyond the tip of the abdomen (Figs 3a-b). Forewings are elongate (especially in males) and relatively narrow, 3.4x as long as wide. Transverse venation is limited to r-m and m-cu in the apical part. Cells between the longitudinal veins and apical parts of three apical cells are covered with cuticular granulation and are opaque. Longitudinal veins are covered with macrosetae. There are four apical cells, including the fourth – the longest are regular in shape, resembling rectangles (especially cells 2 and 3). Appendix is strongly reduced, with veins PCu and A1 on the clavus distinct (Fig. 5a). Hindwing is elongate, 2.6x longer than wide. Four apical cells are present. Marginal vein runs close to the wing margin (especially in the apical part) joining vein R at the nodal part of the anterior margin, and vein m-cu is very short but distinct, located just below the M bifurcation (Fig. 5b).

L e g s. Fore femur basally with a 1 macroseta in the interior row (AV 1) and numerous microsetae; fore tibia is with a row of macrosetae gradually diminishing in length (Fig. 6a). Middle femur is slightly arcuate with 1 apical macroseta above the pit of the knee joint. Hind coxa is very wide, distinctly extending beyond the lateral margins of the abdomen, with a macrosetal formula on the femur apex 2+1+1 (Fig. 6a), and basitarsus almost 3x as long as the remaining tarsal segments (Figs 6b-d), with the apical margin straight, provided on the ventral side with two longer bristles (limiting the segment mobility) and a characteristic row of 6 short spines and 2 platellae. The margin of the shortest segment II is with 2 bristles, 4 spines and 2 platellae (Fig. 6b).

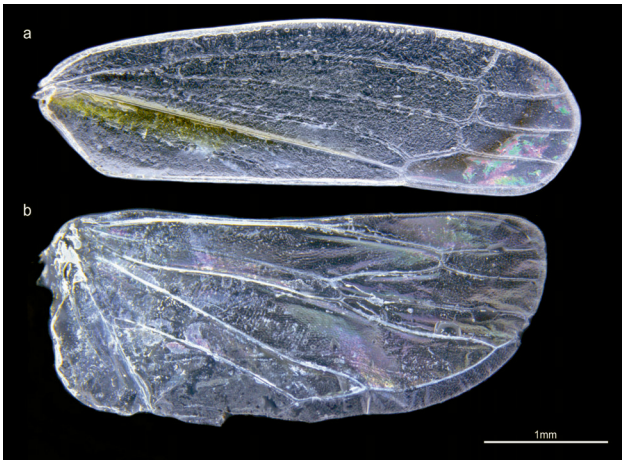

Fig. 5. Wings, male, paratype: a – forewing; b – hindwing.

Fig. 6. Legs: a – leg chaetotaxy in a female; b – hind tarsus (female); c – fore tarsus (male); d – middle tarsus (female).

A b d o m e n. Male pygofer are elongate and relatively narrow, divided by a longitudinal groove into a higher dorsal part and a broader ventral part with a pair of hooked processes. Apical and lateral surfaces are with long macrosetae (extending beyond the pygofer) with a characteristic longitudinal sculpture. Anal tube is short and strongly sclerotised (Fig. 7a). Broad genital plates are with apices tapering and strongly upward bent, basally distinctly broadened and equipped with a row of moveable margin macro-

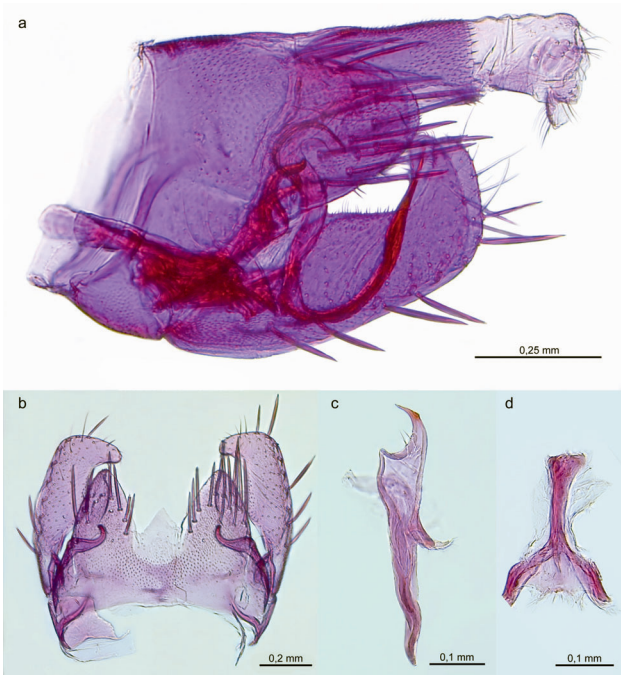

Fig. 7. Male genitalia: a – the whole male genital block with the anal tube (left view); b – pygofer and genital plates in a male, dorsal view (slide flattened); c – left style; d – connective.

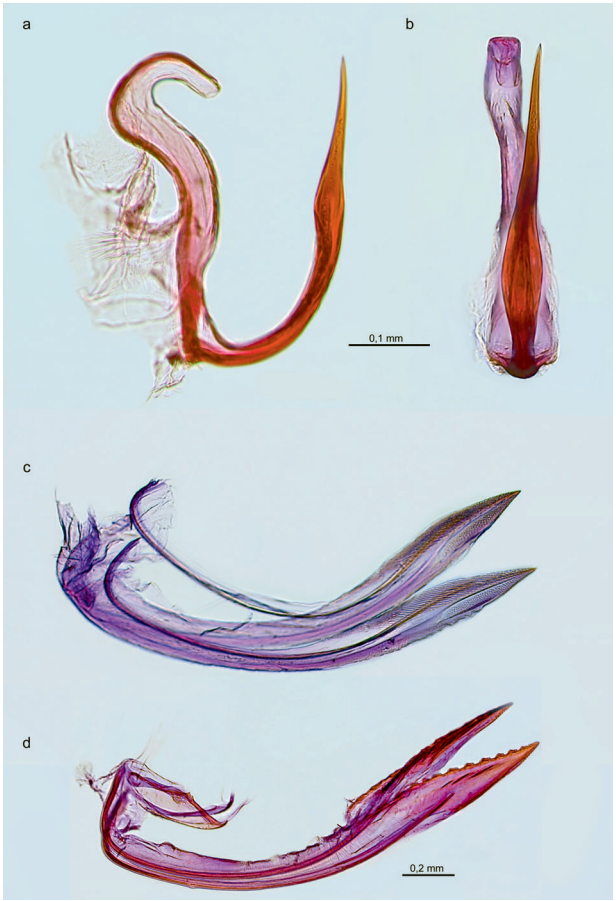

Fig. 8. Details of the genitalia: a – aedeagus, lateral view; b – aedeagus, ventral view; c-d – valvules (first and second pair), ovipositor (lateral view).

setae. Genital valve is triangular in the outline (Figs 7a-b). Style is hook-like, with the apical part (including an indistinct internal lobe) shorter than the narrower basal part (Fig. 7c). Connective is Y-shaped with short divergent arms (Fig. 7d). Aedeagus is lacking an atrium, differentiated into S-shaped curved dorsal part and a strongly sclerotised, pointed ventral part. Shaft processes are absent, with apical gonopore (Figs 8a-b). Female pygofer are uniform, with a long row of macrosetae and a very small anal tube. Sternite VII plate is slightly narrower than that of sternite VI, elongated medially (Fig. 3b). Valvula 1 is regularly arcuate (Fig. 8c). Valvula 2 is long and pointed at the apex, slightly folded to the ventral side and with sparse minute teeth on the ventral margin (Fig. 8d).

Sabahia polypodii, sp. nov.

(Figs 1-8, Tab. 2)

S p e c i e s d e s c r i p t i o n. Body is almost uniformly light in colouration, predominantly dark yellowish (Figs 2a-b). Ocelli are with a broad dark rim (Fig. 2a). Eyes are yellow, sometimes with a black, mottled, irregular colour pattern (Fig. 2b). Frontoclypeus is light with two longitudinal yellowish-brown streaks (Fig. 4c). Sides of the scutum are with blurry yellow patches and three characteristic longitudinal black stripes medially. Scutellum is yellow (Fig. 2a). Margins of the corium are yellowish. Along the forewing sutura coronalis (especially in 2/3 of its length) there is a dark yellow longitudinal stripe transforming into a dark, arcuate colour streak overlapping all anal cells (Figs 2b, 5a). Hindwing is colourless (Fig. 5b). Abdominal sternites are yellowish-brown with lighter posterior margins (Figs 3a-b). A relatively narrow pygofer with a rounded apex is endowed with 12 apicolateral macrosetae on each side. Macrosetae length and pygofer width are subequal – visible in the lateral view (Fig. 7a). Style apex is narrow and pointed, with a fine subapical tooth on the inner margin (Fig. 7c). S-bent shaft of the aedeagus is transforming into a strongly sclerotised and terminally pointed ventral part (Figs 8a-b). First valvula is with a pointed apex, second valvula is with the ventral margin regularly arcuate, marginal teeth are broad and equidistant (Figs 8c-d). Detailed dimensions of the species described here are presented in the table (Tab. 2).

T y p e m a t e r i a l. Holotype, male: MALAYSIA, BORNEO / SABAH D'Villa Village / near Ranau / 23 VIII 2011 rainforest / on ferns, at night / leg. Marcin Walczak // HOLOTYPE / *Sabahia polypodii* / gen. et sp. nov. / WALCZAK *et* GĘBICKI det. 2022 [red label]. Paratypes 3 males, 7 females (the same location); // PARATYPE / *Sabahia polypodii* / gen. et sp. nov. / WALCZAK *et* GĘBICKI det. 2022 [red labels].

E t y m o l o g y. The genus name is derived from the name of Sabah Province (Borneo: Malaysia) where the specimens were collected, while the species name *polypodii* draws attention to its trophic association with ferns.

Table 2

Sabahia polypodii gen. et sp. nov. – dimensions of typical specimens.

Mesurements (in mm)	Male (holotype)	Female (paratype)
Total body length (with forewings)	4.92	5.54
Head		
Face (length) – frons + clypeus (without labium)	1.19	1.34
Frons in the midline (length)	0.96	1.08
Clypeus (length)	0.27	0.30
Frons in the central part (width)	0.46	0.52
Vertex in the midline (dorsal side)	0.48	0.54
Vertex total length + eyes (dorsal side)	1.03	1.16
Vertex width between the eyes (dorsal side)	0.58	0.65
Eye width (najwieksza średnica z boku)	0.46	0.51
Antennae (total)	4.08	4.06
Scape	0.11	0.11
Pedicel length	0.13	0.13
Pedicel width	0.07	0.07
Flagellometres	3.84	3.82
Thorax		
Pronotum in the midline (dorsal side)	0.57	0.64
Pronotum total length (dorsal side)	0.67	0.75
Pronotum width (dorsal side)	1.04	1.17
Pronotum + scutellum in midline (dorsal side)	1.05	1.18
Legs		
Femur	1.35	1.55
Tibia	2.45	2.92
Tarsus	1.01	1.13
Tarsomere I	0.60	0.63
Tarsomere II	0.24	0.26
Tarsomere III	0.27	0.30
Wings		
Forewing length	3.83	4.40
Forewing width	1.10	1.26
Hindwing length	3.59	4.12
Hindwing width	1.39	1.60
Abdomen		
Abdomen (ventral side)	1.33	2.72

Discussion

Sabahia polypodii sp. nov. is most probably an endemic taxon limited in its distribution to north-eastern Borneo. It is trophically associated with ferns (Polypodiopsida Cronquist, Takht. & W. Zimm.). The representative specimens of the species were captured while sweeping ferns mostly by torchlight. The insects remained calm, sitting along the fern leaves. When touched, they moved away, jumped or even flew away for a longer distance. Some seemed to be feeding in spite of the late hour. All the specimens were collected from a small area at about 3 a.m. The temperature was relatively low (about 20°C), due to the influence of the Kinabalu Mts. Field studies have clearly indicated that the taxon is mono- or oligophagous and trophically associated with small ferns found on the cloud forest floor.

Sabahia polypodii gen. nov. and sp. nov. is most closely related to the species of the genus *Decursusnirvana* Gao & Zhang and to a monotypical genus *Sinonirvana hirsuta* Gao & Zhang, which come from central and southern China (GAO *et al.* 2014). This is reflected most clearly in the morphological characteristics of the head, wings and the structures of the male copulatory block, as well as by DNA sequences (the analyses did not include *Sinonirvana* Gao & Zhang).

Both of the previously described genera (GAO *et al*. 2014) are characteristically endowed with processes or spines on the shaft of the aedeagus, which is a feature that separates them from *Sabahia* sp. nov. In *Sinonirvana* Gao & Zhang, there is a pair of lateral processes at the base and a pair of apical lateral processes, whereas *Decursusnirvana* aedeagus possesses a triangular ventral process, as well as a pair of subapical and a pair of apical spines (GAO *et al.* 2014). The new taxon is also similar to some species of the genus *Chudania* Distant (especially to *Ch. guangxiana* Wu Dai & Yalin Zhang) in the general structure of the aedeagus, including the absence of an atrium and a division of the shaft into two angularly connected parts (DAI & ZHANG 2005). Other features of diagnostic value include the fact that the body is less dorsoventrally flattened and the median carina is completely missing on the frontoclypeus, which is more elevated than in most Nirvaninae (especially in the lateral view); also, lateral grooves on the frontoclypeus run parallelly. Within Nirvanini (particularly the Old World forms), two main groups of species are distinguished by their distinct morphological traits. This is at least partly confirmed by the analyses of DNA sequences from selected representatives of the tribe (Fig. 1). The first group comprises genera with four apical cells on the hindwing and a well-developed marginal vein, generally running close to the outer wing margin and merging with its nodal part. The forewing typically possesses an apical row of transverse veins forming four apical cells of an identical shape and size. Other less significant features include: short and apically hooked styles, small anal plates with rounded apices, relatively short Y-shaped connectives (only sporadically with a slightly elongate basal arm), and a pygofer usually with a distinct ventral lobe, often additionally provided with a process. It is noteworthy that the aedeagus has a reduced atrium, is often irregularly shaped and is species specific. The degree of body and head flattening,

as well as the length of the median carina on frontoclypeus are variable, even in the individual genera of these and other Nirvanini. The group comprises among others, species of the *Kana* Distant, *Chudania* Distant and *Australnirvana* Wang, Dietrich & Zhang genera, which on the diagram of genetic sequences form a separate subclade related to the species of the Pagaronini and Evacanthini tribes (Fig. 1).

The other morphologically distinct group of Nirvanini includes the genera with three apical cells on the hindwing and a marginal vein somewhat shifted from the outer margin and merged with the radial vein, which results in the formation of a large membranous lobe in the apical part. On the forewing, four apical cells are usually varied in shape and size, and the fourth cell (the inner one) is distinctly longer than the remaining ones. Other characteristics are more diverse: styles with a considerably elongate apex, longer and often tapering genital plates (e.g. *Nirvana* Kirkaldy), T-shaped connectives with an elongate basal arm, and a pygofer lacking clearly emarginated lobes but endowed with ventral processes. The aedeagus is typical of most Evacanthinae, with a fully developed atrium and often long processes. This group contains the species of the *Sophonia* Walker and *Nirvana* Kirkaldy genera. Genetic research has confirmed the uniformity of the group forming a single separate clade. Accordingly, it seems interesting to define the phylogenetic relationships between the genera *Sabahia* gen. nov., *Decursusnirvana* Gao & Zhang and probably *Sinonirvana* Gao & Zhang with those of other Nirvanini. They form a distinctive and separate group, which is morphologically similar to the genera *Kana* Distant, *Chudania* Distant and *Australnirvana* Wang, Dietrich & Zhang, but is genetically it is closer to the genera *Sophonia* Walker and *Nirvana* Kirkaldy.

The analysis of the genetic relationships of selected species within Nirvanini, Evacanthini and Pagaronini in the subfamily Evacanthinae confirmed most of the previous results (DIETRICH 2004; WANG *et al.* 2017). Close relationships between the Evacanthini, Nirvanini and Pagarononi tribes, and especially close genetic relations between Evacanthini and Pagaronini were indicated (Fig. 1). Also, the paraphyletic character of the genus *Sophonia* Walker (Dietrich 2004) was proven to be valid. Similarly to previous reports (WANG *et al.* 2017), a group of relationships was revealed which includes the genera *Kasunga* Linnavuori, *Kosasia* Distant, *Sophonia* Walker (some species) and *Ophiuchus* Distant, with *Sophonia* Walker (some species), *Oniella* Matsumura and *Convexfronta* Li being most closely related. On the other hand, a close relationship between the genera *Nirvana* Kirkaldy and *Tortor* Kirkaldy was not confirmed (Fig. 1). The results attest to the phyletic distinctiveness of the species within the *Narecho* Jacobi genus, which is closer to the Evacanthini tribe (WANG *et al.* 2017). Neither can we confirm a close relationship between *Decursusnirvana* Gao & Zhang and *Australnirvana* Wang, Dietrich & Zhang, which in our results belonged to separate phyletic lineages, where *Australnirvana* Wang, Dietrich & Zhang, *Chudania* Distant and *Kana* Distant formed a clade close to the Evacanthini and Pagaronini lineage (Fig.1).

However, the presented results must be further supplemented before a decision on the mono- or paraphyletic character of the subfamily Evacanthinae within the Nirvanini tribe is made (DIETRICH 2004; WANG *et al.* 2017).

Finally, we would like to add some comments regarding the biotope in which the insects were found. Figure 9 shows a photo of the biotope. The specimens were collected from ferns, which are also visible in the photo (Fig. 9). Professor Adam ROSTAŃSKI (Botany Team, Institute of Biology, Biotechnology and Environmental Protection, University of Silesia in Katowice) identified these ferns covering the bottom of the rainforest as belonging to the Nephrolepidaceae family, most likely *Nephrolepis brownii* (Desv.) Hovenkamp & Miyam or *Nephrolepis biserrata* (Sw.) Schott. based on the photos. The paper by JAMAN *et al.* (1999) was helpful in determining the fern species.

Fig. 9. The biotope of *Sabahia polypodii* gen. et sp. nov

Acknowledgements

First of all the authors would like to thank Prof. Adam ROSTAŃSKI (Botany Team, Institute of Biology, Biotechnology and Environmental Protection, University of Silesia in Katowice) for his efforts in determining the fern species. We would like to thank Dr Małgorzata KALANDYK-KOŁODZIEJCZYK (Zoology Team, Institute of Biology, Biotechnology and Environmental Protection, University of Silesia in Katowice) for her valuable comments and our colleague MSc Adam KOZIOŁ (from Poznań) for providing a photo of the biotope.

Author Contributions

Research concept and design: M.W., C.G.; Collection and/or assembly of data: M.W.; Data analysis and interpretation: M.W., C.G., M.Z., N.S.-G.; Writing the article: M.W., C.G., M.Z., N.S.-G.; Critical revision of the article: C.G.; Final approval of article: M.W., C.G.

Conflict of Interest

The authors declare no conflict of interest.

References

AGUIN-POMBO D., FRANQUINHO AGUIAR A.M., KUZNETSOVA V.G. 2007. Bionomics and taxonomy of leafhopper *Sophonia orientalis* (Homoptera: Cicadellidae), a Pacific pest species in the Macaronesian Archipelagos. Ann. Entomol. Soc. Am. **100**: 19-26. https://doi.org/10.1603/0013-8746(2007)100[19:BATOLS]2.0.CO;2

AHMED M., MAHMOOD S.H. 1970. A new genus and two new species of Nirvaninae (Cicadellidae: Homoptera) from Pakistan. Pak. J. Sci. Ind. Res. **12**: 260-263.

BAKER C.F. 1923. The Jassoidea related to the Stenocotidae with special reference to Malayan species. Philipp. J. Sci. **23**: 345-405.

BENSASSON D., ZHANG D.X., HARTL D.L., HEWITT G.M. 2001. Mitochondrial pseudogenes: Evolution's misplaced witnesses. Trends Ecol. Evol. **16**: 314-321. https://doi.org/10.1016/s0169-5347(01)02151-6

COLGAN J.D., MCLAUCHLAN A., WILSON G.D.F., LIVINGSTONE S.P., EDGECOMBE G.D., MACARANTAS J., CASSIS G., GRAY M.R. 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Aust. J. Zool. **46**: 419-437.

DAI W., ZHANG Y. 2005. A new species of *Chudania* Distant (Hemiptera: Cicadellidae: Nirvaninae) from China. Zootaxa **1057**: 61-64. https://doi.org/10.5281/zenodo.170118

DARRIBA D., TABOADA G.L., DOALLO R., POSADA D. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods **9**: 772. https://doi.org/10.1038/nmeth.2109

DIETRICH C.H. 2004. Phylogeny of the leafhopper subfamily Evacanthinae with a review of Neotropical species and notes on related groups (Hemiptera: Membracoidea: Cicadellidae). Syst. Entomol. **29**: 455-487. https://doi.org/10.1111/j.0307-6970.2004.00250.x

DIETRICH C.H. 2011a: Tungurahualini, a new tribe of Neotropical leafhoppers, with notes on the subfamily Mileewinae (Hemiptera, Cicadellidae). ZooKeys **124**: 19-39. https://doi.org/10.3897/zookeys.124.1561

DIETRICH C.H. 2011b: A remarkable new genus of Nirvanini (Hemiptera: Cicadellidae: Evacanthinae) from Southeast Asia. Zootaxa **2970**: 63-67. https://doi.org/10.11646/zootaxa.2970.1.5

DISTANT W.L. 1908. Rhynhota. IV. Homoptera and appendix (Pt.). The fauna of British India, including Ceylon and Burma. London, Taylor & Francis. XV+501 pp.

FOLMER O., BLACK W., HOEH W., LUTZ R., VRIJENHOEK R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Marine Biol. Biotechnol. **3**: 294-299.

GAO M., DAI W., ZHANG Y. 2014. Two new Nirvanini genera from China (Hemiptara: Cicadellidae). Zootaxa **3841**: 491-500. https://doi.org/10.11646/zootaxa.3841.4.2

GĘBICKI C., GŁOWACKA E., KARWAŃSKA J., KLIMASZEWSKI S.M., WOJCIECHOWSKI W. 1977. Zgrupowania piewików, mszyc i koliszków (Homoptera: Auchenorrhyncha, Aphidodea and Psyllodea) wybranych środowisk rejonu huty „Katowice". [The communities of Planthoppers and Leafhoppers, Aphids and Psylloidea (Homoptera: Auchenorrhyncha, Aphidodea and Psyllodea) from selected environments in the vicinity of Katowice steelworks]. Acta Biol., Prace Nauk. Uniw. lsk. **4**: 95-122. (In Polish with English abstract)

GUINDON S., DUFAYARD J.F., LEFORT V., ANISIMOVA M., HORDIJK W., GASCUEL O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst. Biol. **59**: 307-321. https://doi.org/10.1093/sysbio/syq010

GUINDON S., GASCUEL O. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood". Syst. Biol. **52**: 696-704. https://doi.org/10.1080/10635150390235520

JAMAN R., MAT-SALLEH K., LATIFF A. 1999. Provisional Account and Checklist of Ferns and Fern Allies in Bario, Kelabit Highlands, Sarawak. ASEAN Review of Biodiversity and Environmental Conservation (ARBEC). 1-12 pp.

KATOH K., MISAWA K., KUMA K.I., MIYATA T. 2002. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res. **30**: 3059-3066. https://doi.org/10.1093/nar/gkf436

KLIMASZEWSKI S.M., WOJCIECHOWSKI W., CZYLOK A., GĘBICKI C., HERCZEK A., JASIŃSKA J. 1980. Zgrupowania wybranych grup pluskwiaków równoskrzydłych (Homoptera) i różnoskrzydłych (Heteroptera) w lasach rejonu huty „Katowice". [The communities of Homoptera (Homoptera) and Heteroptera (Heteroptera) in the forests in the vicinity of Katowice steelworks]. Acta Biol., Prace Nauk. Uniw. lsk. **8**: 22-39. (In Polish with English abstract).

KNIGHT W.J. 1965. Techniques for use in the identification of leafhoppers (Homoptera, Cicadellidae). Entomol. Gaz. **16**: 129-136.

MATSUMURA S. 1931. A revision of the Palaearctic and Oriental Typhlocybid-genera, with description of new species and new genera. Insecta Matsumurana **6**: 55-91.

MESHRAM N.M., RAI S. 2017. A new species of genus *Nirvana* (Hemiptera: Cicadellidae: Evacanthinae) with note on female genitalia from India. Zootaxa **4303**: 264-272. https://doi.org/10.11646/zootaxa.4303.2.6

METCALF Z.P. 1963. General catalogue of the Homoptera (VI) Cicadelloidea, Part 7 Nirvanidae. Agricultural Research Service. United States Departament of Agriculture, Washington 35 pp.

NAST J. 1972. Palaearctic Auchenorrhyncha (Homoptera). An annotated check list. Warszawa: Polish Sci. Publ. 550 pp.

OMAN P.W., KNIGHT W.J., NIELSON M.W. 1990. Leafhoppers (Cicadellidae): a bibliography, generic chesk-list and index to the world literature 1956-1985. C.A.B. International Institute of Entomology Oxon, 368 pp.

RONQUIST F., TESLENKO M., VAN DER MARK P., AYRES D.L., DARLING A., HÖHNA S., LARGET B., LIU L., SUCHARD M.A., HUELSENBECK J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. **61**: 539-542. https://doi.org/10.1093/sysbio/sys029

RAMBAUT A., DRUMMOND A.J., XIE D., BAELE G., SUCHARD M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Syst. Biol. **67**: 901-904. https://doi.org/10.1093/sysbio/syy032

SCHUMACHER F. 1915. Der gegenwärtige Stand unserer Kenntnis von der Homopteren-Fauna der Insel Formosa unter besonderer Berücksichtigung von Sauter'schem Material. Mitt. Zool. Mus. Berl. **8**: 73-134.

SANGER F., NICKLEN S., COULSON A.R. 1977. "DNA sequencing with chain-terminating inhibitors". Proc. Natl Acad. Sci. USA **74**: 5463-5467.

STÅL C. 1859. Hemiptera. Species novas descripsit. [In:] Konglika Svenska Fregattens Eugenies resa omkring Jorden under befäl af C.A. Virgin åren 1851-1853 3. Zoologi, Insecter. Norstedt, Stockholm. 219-298.

STEWART A.J. 2002. Techniques for sampling Auchenorrhyncha in grasslands. Denisia **4** (N.F.): 491-512.

SONG H., BUHAY J.E., WHITING M.F., CRANDALL K.A. 2008. Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. Proc. Natl. Acad. Sci. USA **105**: 13486-13491. https://doi.org/10.1073/pnas.0803076105

VIRAKTAMATH C.A. 1992. Oriental nirvanine leafhoppers (Homoptera, Cicadellidae) – a review of Baker, C. F. species and keys to genera and species from Singapore, Borneo and the Philippines. Entomol. Scand. **23**: 249-273.

VIRAKTAMATH C.A., WESLEY C.S. 1988. Revision of the Nirvaninae (Homoptera: Cicadellidae) of the Indian subcontinent. Gt Basin Nat. Mem. **12**: 182-223.

VIRAKTAMATH C.A., WILSON M.R. 2018. New species of the leafhopper genera Sophonia and Stenotortor (Hemiptera: Cicadellidae: Evacanthinae) from the Oriental region. Zootaxa **4378**: 356-366. https://doi.org/10.11646/zootaxa.4378.3.4

WANG Y., DIETRICH C.H., ZHANG Y. 2017. Phylogeny and historical biogeography of leafhopper subfamily Evacanthinae (Hemiptera: Cicadellidae) based on morphological and molecular data. Sci. Rep. **7**: 45387. https://doi.org/10.1038/srep45387

WEBB M.D., VIRAKTAMATH C.A. 2004. On the identity of an invasive leafhopper on Hawaii (Hemiptera, Cicadellidae, Nirvaninae). Zootaxa **692**: 1-6. https://doi.org/10.5281/zenodo.158492