

## Afrocranus gen. nov. (Hemiptera: Fulgoromorpha) from the Afrotropical region and its phylogenetic affinities within Delphacidae planthoppers

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Accepted May 13, 2025

Published online June 30, 2025

Issue online July 23, 2025

Original article

WALCZAK M., GĘBICKI C., ROMANIAK A., SAWKA-GĄDEK N., ŚWIERCZEWSKI D. 2025. *Afrocranus* gen. nov. (Hemiptera: Fulgoromorpha) from the Afrotropical region and its phylogenetic affinities within Delphacidae planthoppers. *Folia Biologica (Kraków)* 73: 36-54.

A new genus *Afrocranus* (Delphacidae Leach, 1815, Stenocraninae Wagner, 1963) has been established for two species: *Afrocranus ujodensis* Gębicki, Walczak & Świerniewski from continental Africa (Namibia); and *Afrocranus mixtus* Walczak, Gębicki & Świerniewski from Madagascar. A set of distinguishing characteristics is provided to differentiate this new taxon from the closely related Afrotropical genus *Embolophora* Stål, 1853, as well as the Neotropical species *Tanycranus elongatus* Bartlett, 2010 and other representatives of the subfamily Stenocraninae. Additionally, a DNA analysis was performed, and a phylogram illustrating the relationships among selected Stenocraninae planthopper species is presented.

Key words: Auchenorrhyncha, Stenocraninae, morphology, biodiversity, Namibia, Madagascar.

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Stenocraninae Wagner, 1963 is a small subfamily of Delphacidae Leach, 1815 planthoppers represented by 94 species belonging to ten genera, which is distributed mainly in the Holarctic (temperate regions of the Northern Hemisphere). A few species belonging to four genera have also been reported from other zoogeographical regions (Bourgoin 2025).

For Stenocraninae, the genus *Stenocranus* Fieber, 1866 (type genus for the family) is the most numerous (74 known species) and widespread, while being comprised of two subgenera: *Stenocranus* (type species *Fulgora minuta* Fabricius, 1787) and *Codex*

Hamilton, 2006 (type species *Delphax vittata* Stål, 1862) (Fabricius 1787; Stål 1862; Fieber 1866; Hamilton 2006; Bourgoin 2025). Most representatives of the genus have a similar distribution as the subfamily and are found in the Holoarctic, ranging from Alaska, the western provinces of Canada (British Columbia), western states of USA and Northern Mexico, across the whole of Europe, to Middle Siberia, Maritime Territory, Kurile Islands, Korea, Japan, China (Schanxi, Sichuan) and Taiwan (Nast 1972, 1987; Anufriev & Emeljanov 1988; Bartlett 2010). Some species are also known from the Oriental and



Neotropical regions (Berg 1879; Bartlett 2014), Australia (Fennah 1956) and there are even records from the Indo-Pacific Archipelago (Kirkaldy 1906; 1907). The biogeographic pattern resulting from this large distribution area points out a possible polyphyly of the taxon.

The remaining genera are represented by several species: *Stenokelia* Ribaut, 1934 known exclusively from France; *Terauchiana* Matsumura, 1915 from the Eastern Palaearctic (Matsumura 1915; Emeljanov 1982); *Preterkelisia* Yang, 1989 from China and Taiwan (Esaki & Ishihara 1950; Ding & Kuoh 1981; Yang 1989); and *Embolophora* Stål, 1853 (Stål 1853; Wagner 1963) from Africa. The American fauna is represented by the Nearctic *Kelisicranus arundiniphagus* Bartlett, 2006 (central USA) and two species of *Obtusicranus* Bartlett, 2006 (Western USA, Northern Mexico), together with five species of Neotropical *Frameus* Bartlett, 2010 and *Tanycranus elongatus* Bartlett 2010, as well as the Australian *Protersydne arborea* Kirkaldy, 1907 (Bartlett 2006, 2010).

Stenocraninae planthoppers can be characterised by the following combination of characteristics (Bartlett 2006): spur wide, flattened, rectangular in cross section, with numerous minute teeth on the inner margin; second abdominal sternite with small apodemes directed caudad; second abdominal tergite with a distinct central plate; male terminalia characteristics: central sperm-conducting shaft of the aedeagus strongly sclerotised, flagellum completely reduced, apical phallotreme smooth, phallotheca with curved processes in the apical or subapical part, its distal part membranous, aedeagus connected with phallotheca in a movable way, giving it the possibility of a far extension from the phallotheca, anal segment (10th) without a subanal process (with the exception of *Kelisicranus arundiniphagus*; phallotheca connected with an anal tube by a short suspensorium, formed partly by phallotheca and partly by the anal tube; anal tube with one pair (rarely two pairs) of ventral appendages; female terminalia characteristics: strongly widened ovipositor in many species, two separate genital pores – the first for eggs ovipositing and the second for copulation (Bartlett 2006).

Interestingly, the tendency of protruding in the preocular part of head can be observed in different stenocranines and the phenomenon of head hypertrophy is clearly visible in the species belonging to the genera *Frameus*, *Tanycranus* Bartlett 2010 (both Neotropical), *Terauchiana* (Palaearctic) and *Embolophora* (Afrotropical), with the latter being the most similar to the newly described genus (Matsumura 1915; Bartlett 2010).

The genus *Embolophora* is comprised of three species: *Embolophora monoceros* Stål, 1853 recorded from KwaZulu – Natal (Stål 1853, 1855), Democratic Republic of Congo (Fennah 1958) and Sudan (Fennah 1969); as well as *Embolophora britmusei* Asche, 1983 and *Embolophora theroni* Asche, 1983, which are known exclusively from Zululand, Natal (South Africa) (Asche 1983).

Hypertrophy of the preocular part of head, visible on the vertex above the upper margin of the eyes, is a feature rarely known from representatives of the Delphacidae family. Apart from Stenocraninae (especially in *Embolophora*, *Terauchiana*, *Tanycranus* and *Frameus*), we observe such a head shape in Asiracinae Motschulsky, 1863; e.g. *Idiosemus xiphias* (Berg, 1879) and Delphacinae Leach, 1815, mostly of the tribe Delphacini Leach, 1815 (*Ambarvalia pyrops* Distant, 1917, *Dictyophorodelphax mirabilis* Swezey, 1907, *Rhinodelphax hargreavesi* Muir, 1934, *Rhinotettix fuscipennis* Stål, 1855, *Sardia rostrata* Melichar, 1903, *Sardia campbelli* Muir, 1921), Tropidocephalini Muir, 1915 (*Pseudembolophora macleayi* Muir, 1920, *Tropidocephala butleri* Muir, 1921) and Saccharosydnnini Vilbaste, 1968 (especially *Saccharosydne rostrifrons* Crawford, 1914) (Leach 1815; Stål 1853, 1855; Motschulsky 1863; Berg 1879; Melichar 1903; Swezey 1907; Crawford 1914; Matsumura 1915; Muir 1915, 1920, 1921, 1934; Distant 1917; Vilbaste 1968; Asche 1985a; Bartlett 2010). The species belonging to the abovementioned Delphacini are characterised by a different degree of the head prolongation, ranging from 1.5 of the compound eye length (females of *Rhinotettix fuscipennis*) or even less (females of *Ambarvalia pyrops*), to the length of the vertex exceeding five times the preocular part of head (*Dictyophorodelphax mirabilis*). However, this characteristic weakly reflects sexual dimorphism.

Afrotropical Stenocraninae have been represented only by the genus *Embolophora* so far, but in this paper we describe another genus *Afrocranus* gen. nov. with two species: *Afrocranus ujotensis* sp. nov. from continental Africa (Namibia) and *Afrocranus mixtus* sp. nov. from Madagascar.

## Materials and Methods

### Material

The specimen depositories are as follows:

Upper Silesian Museum, Department of Natural History, Bytom, Poland – (USM)

Muséum national d'histoire naturelle, Paris, France – (MNHN)

The specimens from the USM were collected by Dr Roland Dobosz during the research expedition organised by the institution to Namibia in 2012. The specimens from the MNHN were collected during the expeditions organised by the institution to Madagascar in 2011 and 2016. For the holotype the labels are numbered, while for the paratypes the content of particular labels is separated with (//). The individual lines of data in the label are separated by a slash (/). The labels are written verbatim.

## Methods

### Morphology

The morphological features of the specimen were imaged using a Leica M205C stereo microscope with a Leica DFC495 digital camera and the Leica application suite ver. 4.9.0 software. All measurements are given in millimetres.

SEM pictures were obtained using a Phenom XL field emission scanning electron microscope with a Back-Scatter Detector (BSD). The panoramic image stitcher Image Composite Editor ver. 3.0 and the graphic editor Adobe® Photoshop CS6 were used to prepare the figures. The specimen was only cleaned with a brush because other methods, e.g. washing or dehydration, may have damaged the individual. Next, the specimen was mounted on aluminium stubs (an insect pin was inserted into a piece of the sponge glued to the stub). In the next stage, the specimen was covered with an anti-static spray.

**Genitalia preparation.** The abdomen was boiled three times (about ten minutes in total) in a 10% solution of potassium hydroxide (KOH), according to Knight's method (Knight 1965). The genitalia were detached from the abdomen after the boiling and washed in distilled water for cleaning. The specific parts of the genital structures were separated from the abdomen using thin forceps and a needle blade. Next, these structures were placed in glycerine. The genitalia were studied and the photographs were taken with a Leica M205C (high diffuse dome illuminator) light microscope with the digital camera Leica DFC495. The drawings were made in Firealpaca program using a Wacom Intuos pen tablet.

**Terminology.** The morphological terminology of the head, thorax and legs follows Holzinger *et al.* (2003), Bartlett (2006) and Ceotto & Bourgoin (2008); for the male genitalia it follows Bourgoin (1987) and Bartlett (2006), and for the female geni-

alia it follows Bourgoin (1993). The terminology of the venation of the fore- and hindwings is after Anufriev & Emeljanov (1988) and Bourgoin *et al.* (2015). The terminology and classification of the sensilla is according to Bourgoin & Deiss (1994), Holzinger *et al.* (2002), Romani *et al.* (2009) and Wang *et al.* (2018).

### DNA isolation, amplification and sequencing

Four specimens representing *Embolophora monoceros* (F18), *E. britmusei* (F19), *Afrocranus mixtus* (F20) and *Kelia praecox* Haupt, 1935 (F21) were used for the DNA isolation. The Syngen DNA Mini kit (Syngen, Wrocław, Poland) was used without a protocol modification to isolate the genomic DNA. To elute the purified DNA, we applied 50 µl of an Elution Buffer onto the silica membrane. The COI fragment was amplified using C1J2183 (Simon *et al.* 1994) and UEA8 (Lunt *et al.* 1996) oligonucleotides. A polymerase chain reaction (PCR) was carried out 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 the oligos for 30 sec, 72°C for 1 min and a final extension period of 72°C for 7 min.

The PCR results were electrophoresed in 1% agarose gel for 45 minutes at 85 V using a DNA molecular weight marker (Mass Ruler Low Range DNA Ladder, Thermo-Scientific, Waltham, MA, USA). The amplified 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 10 µl containing 1 µl of BigDye Terminator Reaction Ready Mix v. 3. 1 (ABI), 1 µl 5×sequencing buffer (ABI), 3.2 mol/µl of the primer solution and 3 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. Ex-Terminator (A&A Biotechnology, Gdynia, Poland) was used to precipitate the sequencing products, which were then separated on an ABI PRISM 3130xl DNA sequencer (Applied Biosystems, Foster City, CA, USA). The sequences were placed with the fol-

lowing accession numbers in GenBank: PQ150066-PQ150069.

**Sequence edition and alignment.** The raw chromatograms were analysed and corrected using Geneious vR10.2.6 (<https://www.geneious.com>). All nucleotide sequences (563bp) were validated using NCBI BLAST searches (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). The Clustal Omega (Sievers *et al.* 2011) plugin in Geneious R10.2.6 was used to align the concatenated sequences under study. The study sequences were aligned with other Delphacidae sequences obtained from GenBank (Table 1).

**Molecular phylogenetic.** Models for the Bayesian (BI) analyses were calculated in jModelTest (Darriba *et al.* 2012) using the Bayesian information criterion (BIC). The BI analyses were performed in MrBayes v3.2.6 (Ronquist *et al.* 2012) with four independent runs, each having three heated and one cold chain. The analyses were run for 1.2 million

generations with trees sampled every 1000 generations. The first 25% of each run was discarded as the burn-in. Convergence among the runs was assessed using Tracer (Rambaut *et al.* 2018). The ML analyses were performed using the IQTree web server (Trifinopoulos *et al.* 2016) with an ultrafast bootstrap analysis and aLRT SH-like test. All trees were visualised using FigTree v.1.3.1 (Rambaut 2010). The trees were edited and annotated in Corel Draw 17.1.0.572, 2014 Corel Corporation.

Phylogenetic inferences were made for the COI region using the Bayesian inference (BI) and Maximum likelihood (ML). For the BI analysis, the TVM+I+G model was selected by the AIC in jModelTest for the matrix. Heuristic searches resulted in one tree (-ln=4908.1524). For the ML analysis, the TIM2+F+I+G4 model was selected under BIC in jModelTest for the matrix. The phylogenies were resolved and the main splits were supported by high bootstrap values and

Table 1  
Sequences used in the phylogenetic analysis

Species name	GenBank accession number	Reference
<i>Embolophora monoceros</i>	PQ150066	Present study
<i>Embolophora britmusei</i>	PQ150067	Present study
<i>Afrocranus mixtus</i>	PQ150068	Present study
<i>Kelisia praecox</i>	PQ150069	Present study
<i>Stenocranus agamopsyche</i>	HM233920	GenBank database
<i>Anakelia fasciata</i>	AF304411	Dijkstra <i>et al.</i> 2003
<i>Stenocranus sp.</i>	HM017481	Urban <i>et al.</i> 2010
<i>Stenocranus sp.</i>	HM017476	Urban <i>et al.</i> 2010
<i>Stenocranus major</i>	AF304412	Dijkstra <i>et al.</i> 2003
<i>Laodelphax striatellus</i>	JN391182	Shi <i>et al.</i> 2011
<i>Dicranotropis hamata</i>	HM017498	Urban <i>et al.</i> 2010
<i>Megamelus notula</i>	EU183622	Ceotto <i>et al.</i> 2008
<i>Megamelus notula</i>	AF304414	Dijkstra <i>et al.</i> 2003
<i>Chloriona vasconica</i>	AF304419	Dijkstra <i>et al.</i> 2003
<i>Chloriona smaragdula</i>	AF304418	Dijkstra <i>et al.</i> 2003
<i>Chloriona unicolor</i>	AF304417	Dijkstra <i>et al.</i> 2003
<i>Javesella pellucida</i>	HM017472	Urban <i>et al.</i> 2010
<i>Saccharosydne procerus</i>	HM233884	GenBank database
<i>Burnilla sp.</i>	HM017502	Urban <i>et al.</i> 2010
<i>Ugyops stigmata</i>	HM017501	Urban <i>et al.</i> 2010
<i>Prolivatis hainanensis</i>	HM233904	Genbank database
<i>Ugyops sp.</i>	HM017503	Urban <i>et al.</i> 2010
<i>Asiraca clavicornis</i>	AF304409	Dijkstra <i>et al.</i> 2003
<i>Ugyops sp.</i>	AF304408	Dijkstra <i>et al.</i> 2003
<i>Cixius similis</i>	EU183620	Ceotto <i>et al.</i> 2008
<i>Cixius nervosus</i>	EU183619	Ceotto <i>et al.</i> 2008

posterior probabilities. The sequences of *Cixius nervosus* (Linnaeus, 1758) and *Cixius similis* Kirschbaum, 1868 were used to root the topologies.

A matrix of pairwise differences was used to es-

timate evolutionary divergence between the species using MEGA X (Kumar *et al.* 2018). Variance was estimated using the p-distance model and the bootstrap method at 1000 repetitions (Table 2).

Table 2

Estimates of evolutionary divergence between partial COI gene sequences to demonstrate the intra and inter generic variability by the percentage nucleotide difference (bottom left) and standard error (top right)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 <i>Afrocratus mixtus</i> sp.nov.	<b>0.016</b>	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.015</b>	<b>0.015</b>	<b>0.016</b>	<b>0.016</b>	<b>0.014</b>	<b>0.015</b>	<b>0.018</b>	<b>0.018</b>	<b>0.016</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.016</b>	<b>0.016</b>	<b>0.016</b>							
2 AF304417 <i>Chlorionta unicolor</i>	0.169	<b>0.012</b>	<b>0.012</b>	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.018</b>	<b>0.016</b>	<b>0.016</b>	<b>0.016</b>	<b>0.016</b>	<b>0.018</b>	<b>0.018</b>	<b>0.017</b>							
3 AF304418 <i>Chlorionta smaragdula</i>	0.192	0.081	<b>0.010</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.019</b>	<b>0.017</b>	<b>0.017</b>	<b>0.019</b>	<b>0.018</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.018</b>	
4 AF304419 <i>Chlorionta vasconica</i>	0.192	0.091	0.056	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.018</b>	<b>0.017</b>	<b>0.016</b>	<b>0.019</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>							
5 HM017502 <i>Burnilia</i> sp.	0.167	0.171	0.183	0.179	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.018</b>	<b>0.016</b>	<b>0.017</b>	<b>0.018</b>	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>							
6 HM017472 <i>Janevella pellucida</i>	0.181	0.165	0.179	0.190	0.165	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.018</b>	<b>0.018</b>	<b>0.018</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.019</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>
7 AF304414 <i>Megamelus notula</i>	0.198	0.196	0.192	0.187	0.204	0.196	<b>0.004</b>	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>	<b>0.016</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>	<b>0.018</b>	<b>0.017</b>	<b>0.016</b>	<b>0.020</b>	<b>0.019</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>	<b>0.018</b>
8 EU183622 <i>Megamelus notula</i>	0.196	0.192	0.192	0.185	0.198	0.194	0.10	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>	<b>0.015</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.016</b>	<b>0.019</b>	<b>0.019</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	
9 HM017498 <i>Dicranotropis hamata</i>	0.175	0.181	0.188	0.181	0.183	0.165	<b>0.014</b>	<b>0.017</b>	<b>0.015</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.019</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.019</b>	<b>0.017</b>	<b>0.017</b>	
10 JN391182 <i>Laelodiphas striatellus</i>	0.187	0.177	0.190	0.190	0.188	0.159	0.153	0.145	0.125	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.015</b>	<b>0.016</b>	<b>0.019</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.019</b>	<b>0.017</b>	
11 <i>Kelisia praecox</i>	0.149	0.167	0.185	0.190	0.187	0.203	0.202	0.198	0.192	0.185	<b>0.016</b>	<b>0.017</b>	<b>0.015</b>	<b>0.015</b>	<b>0.017</b>	<b>0.015</b>	<b>0.015</b>	<b>0.015</b>	<b>0.019</b>	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	
12 AF304411 <i>Anakelisia fasciata</i>	0.141	0.167	0.183	0.171	0.157	0.181	0.163	0.153	0.151	0.147	0.141	<b>0.017</b>	<b>0.015</b>	<b>0.015</b>	<b>0.017</b>	<b>0.015</b>	<b>0.015</b>	<b>0.019</b>	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	
13 AF304412 <i>Stenocranus major</i>	0.167	0.212	0.208	0.214	0.192	0.192	0.190	0.187	0.190	0.185	0.202	0.177	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.019</b>	<b>0.019</b>	<b>0.018</b>	<b>0.019</b>	<b>0.018</b>	<b>0.018</b>	<b>0.018</b>	
14 HM017476 <i>Stenocranus</i> sp.	0.139	0.167	0.190	0.190	0.181	0.194	0.190	0.188	0.169	0.187	0.147	0.137	0.155	<b>0.010</b>	<b>0.016</b>	<b>0.014</b>	<b>0.015</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	
15 HM017481 <i>Stenocranus</i> sp.	0.135	0.161	0.185	0.185	0.187	0.204	0.198	0.192	0.177	0.190	0.143	0.131	0.163	<b>0.015</b>	<b>0.015</b>	<b>0.016</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>	<b>0.018</b>	<b>0.018</b>	
16 HM233920 <i>Stenocranus agamopsycle</i>	0.146	0.167	0.192	0.183	0.169	0.183	0.171	0.164	0.157	0.148	0.141	0.130	0.162	0.116	0.118	<b>0.015</b>	<b>0.016</b>	<b>0.018</b>	<b>0.017</b>	<b>0.017</b>	<b>0.018</b>	<b>0.016</b>	<b>0.018</b>	<b>0.019</b>		
17 <i>Embolophora monoceros</i>	0.127	0.153	0.173	0.177	0.181	0.161	0.155	0.173	0.139	0.141	0.123	0.159	0.115	0.125	0.104	<b>0.013</b>	<b>0.018</b>	<b>0.017</b>	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>		
18 <i>Embolophora britomisei</i>	0.137	0.159	0.173	0.169	0.167	0.173	0.167	0.163	0.185	0.157	0.143	0.127	0.161	0.127	0.147	0.123	0.097	<b>0.018</b>	<b>0.018</b>	<b>0.016</b>	<b>0.017</b>	<b>0.018</b>	<b>0.018</b>	<b>0.018</b>	<b>0.016</b>	
19 HM233904 <i>Prolifatis hainanensis</i>	0.196	0.191	0.224	0.210	0.161	0.203	0.233	0.224	0.205	0.194	0.224	0.194	0.210	0.198	0.207	0.157	0.184	0.177	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.019</b>	<b>0.020</b>	<b>0.019</b>
20 HM017503 <i>Ugropis</i> sp.	0.218	0.202	0.220	0.216	0.212	0.232	0.224	0.216	0.185	0.210	0.188	0.214	0.181	0.183	0.178	0.175	0.188	0.168	<b>0.016</b>	<b>0.016</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>	<b>0.017</b>	<b>0.018</b>
21 HM017501 <i>Ugropis stigmata</i>	0.181	0.194	0.214	0.210	0.173	0.208	0.198	0.194	0.194	0.175	0.177	0.177	0.198	0.190	0.204	0.169	0.163	0.163	0.161	0.173	<b>0.016</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	<b>0.017</b>	
22 AF304408 <i>Ugropis</i> sp.	0.171	0.183	0.204	0.210	0.190	0.198	0.196	0.192	0.204	0.196	0.179	0.188	0.194	0.177	0.179	0.164	0.155	0.167	0.157	0.165	0.143	<b>0.015</b>	<b>0.017</b>	<b>0.017</b>	<b>0.016</b>	
23 AF304409 <i>Asiraca clavicornis</i>	0.181	0.190	0.204	0.204	0.187	0.190	0.214	0.204	0.202	0.179	0.194	0.181	0.218	0.200	0.196	0.174	0.169	0.190	0.196	0.183	0.181	0.133	<b>0.018</b>	<b>0.017</b>	<b>0.016</b>	
24 HM233984 <i>Saccharosydne procerus</i>	0.145	0.191	0.203	0.198	0.168	0.194	0.187	0.184	0.189	0.198	0.187	0.152	0.189	0.164	0.168	0.147	0.168	0.177	0.200	0.147	0.152	0.173	<b>0.018</b>	<b>0.019</b>	<b>0.019</b>	
25 EU183619 <i>Cixius nervosus</i>	0.185	0.173	0.206	0.210	0.194	0.202	0.194	0.190	0.204	0.194	0.188	0.187	0.198	0.190	0.202	0.185	0.171	0.188	0.214	0.200	0.177	0.159	0.173	0.196	<b>0.016</b>	
26 EU183620 <i>Cixius similis</i>	0.173	0.173	0.206	0.192	0.173	0.188	0.198	0.192	0.179	0.190	0.175	0.165	0.204	0.192	0.214	0.181	0.171	0.153	0.187	0.194	0.159	0.149	0.165	0.187	0.129	

## Results

### Taxonomy

Class: Insecta Linnaeus, 1758  
 Order: Hemiptera Linnaeus, 1758  
 Suborder: Fulgoromorpha Evans, 1946  
 Superfamily: Delphacoidea Leach, 1815  
 Family: Delphacidae Leach, 1815  
 Subfamily: Stenocraninae Wagner, 1963

**Afrocranus** gen. nov.  
 Gębicki, Walczak & Świerczewski

(Figs 1-11)

urn:lsid:zoobank.org:act:A90FBBF4-2E9E-4BB1-9E15-E116E058DBF7

Type species. *Afrocranus ujotensis* sp. nov.

**Diagnosis.** The genus *Afrocranus* belongs to the subfamily Stenocraninae taking into account morphological characteristics such as: head hypertrophy, structure of the phallotheca, shape of the parameres (similar to those in species of the genus *Embolophora*), anal tube, movable connection of the aedeagus with the phallotheca, and the morphology of the hind leg spur. This conclusion is further supported by the presence of a strongly developed, single subanal process and a wide suspensorium that connects the basal part of the anal tube to the dorsal part of the phallotheca.

The genus *Afrocranus* can be distinguished from other representatives of Stenocraninae by its single, long, wide subanal process, which bears apical spines. Superficially, it resembles the genus *Embolophora*, particularly due to the hypertrophy of the preocular part of the vertex, fore- and hindwing venation and the arrangement of the frontal carinae. The unique presence of the subanal process can be also observed in the North American genus *Kelisicranus* Bartlett, 2006, but here it forms a narrow, falciform projection. The presence of subanal processes is a feature typically associated with the Kelisiinae Wagner, 1963, in which they are strongly elongated and smooth, located on the anal tube suspensorium.

**Description.** Head. Preocular part of head strongly prolonged, vertex medially three times longer than the compound eye (Figs 1a-c, 4a-c, 6a, 7a); carinae well visible, area between the carinae slightly depressed; posterior margin of the vertex almost equals the length of the compound eye, sinuate, slightly incised medially and laterally. Median carina

strongly prolonged, reaching almost 3/4 of the vertex length, well visible in the basal part, arms of the median carina reduced. Apical compartment fused with the basal compartments, their surface covered with transverse, cuticular grooves, with numerous, minute tubercles and scattered trichoidal sensilla. Submedian carinae strongly prolonged, straight, in some parts slightly ridged, clearly thickened near the compound eyes, connected in the form of an arch at the top of the head. Longitudinal lateral carinae clearly diverged externally of the head. Lateral compartments, reaching the top of the head, narrower than the median part of the vertex, with microsculpture and sensilla as in the median part. Lateral part of the vertex between submedian and lateral carinae clearly narrower than the part between the lateral carinae of the vertex and frons, almost two times near the compound eye.

Dorsal margin of the fastigium arcuate, lateral margins forming an acute angle of about 45° (Figs 1a-c, 4a-c, 6a, 7a).

Frons narrow, strongly prolonged above the upper margin of the eyes. Median carina single in the basal part, diverged above the upper margin of the eyes; sutura epistomalis arcuate. Lateral carinae of the frons refracted at an angle at the top of the head, meeting with the vertex below the top of the fastigium (Figs 6b-c).

Postclypeus triangular, approximately twice as long as it is wide at the apical part, with both median and lateral carinae. Anteclypeus long and narrow, without carinae, almost two times shorter than the postclypeus; sutura clypealis weakly visible. Genal carina almost straight, extending from the compound eye to the sutura epistomalis.

Compound eye, in the lateral view, slightly longer than wide, anterior margin arcuate, posterior margin almost straight (Figs 1b, 6a, 7a).

Antennae reaching the posterior margin of the mesonotum; scapus about three times shorter than the pedicel, a bit widened at the apex, with the surface delicately wrinkled, covered with scattered, long trichoidal sensilla. Pedicel cylindrical; basal part (1/6 of its length) without sensory structures, dorsal surface with about ten plaque organs, in pairs. Third segment of the antenna spherical, petioles very short, atrium narrow, atrial wall low. Basal part of the arista flattened dorsally, with Bourgoin's organ and special organ with one internal appendage (Figs 1b, 6a, 7a).

**Thorax.** Pronotum medially shorter than the compound eye length. Disc of the pronotum flat and narrow, inserted between the eyes, with three carinae, posterior margin sinuate. Mesonotum medially

two times longer than the pronotum, lateral margins sinuate, with three carinae: median carina reaching the scutellum, lateral carinae shorter than the median, almost reaching the posterior margin (Figs 1c, 5a-b).

**Wing s.** Fore wings (tegmina) with apex rounded. Sc vein diverging from R near *ir* (longest of all the transverse veinlets). Common stem of CuA<sub>1</sub> and CuA<sub>2</sub> very short, *icua* veinlet absent (Figs 8a-b). Hind wings a bit shorter than the tegmina. The length of the M vein measured from the *r-m* transverse veinlet to the point of M<sub>1</sub> and M<sub>2</sub> fork the same as the M<sub>2</sub> vein; *r-m* transverse veinlet clearly placed before the *m-cu* veinlet (Fig. 8c-d).

**Legs.** Metatibia with two lateral spines (basal and subapical) and a row of six apical teeth (3+3) (Fig. 7b-f). Spur narrow, with a basal width almost the same as the tarsus; internal side concave, external side convex and densely covered with minute cuticular hairs up to mid-length; ventral margin with 19 small teeth and one apical, curved spine (Figs 7c, e). Metabasitarsus two times longer than the cumulative length of the second and third tarsomeres, apex with a row of seven teeth (2+5) and a characteristic groove on the dorsal side; apex of the second tarsomere of the metatarsus with five teeth of different sizes, third tarsomere with claws and arolium (Figs 7c, e).

**Male terminalia.** Pygopher triangular, in the lateral view; ventral margin slightly convex, dorsal margin more than two times shorter than the ventral margin (Figs 2a, 3a, 9b, 11a). Parameres directed dorso-caudad, apical part strongly constricted and curved (Figs 2a, 3a, 9c, 10c). Aedeagus elongated, tubular, widened in the proximal part, S-shaped, well sclerotised, closed in membranous phallotheca, protruding beyond the anal tube base. Flagellum absent (Figs 2a, 2d, 3a, 3d, 9b, 10c, 11a). Phallothrema apically, smooth, without appendages. Phallotheca rectangular weakly sclerotised, slightly narrowed proximally, with three strongly sclerotised appendages of different lengths and shapes, located in the upper-distal part. Phallobase narrow, suspensorium (anal tube connective) wide, with a long and massive subanal appendage. Subanal appendage longer than the phallotheca, flattened (in the lateral view) and sinuate, apex with three short and wide, well sclerotised teeth. Anal tube trapezoid, two times shorter than the pygopher, with two long and strong, symmetrical, acute pointed dorso-lateral appendages (Figs 2b-c, 3b-c, 10a-b, 11b-c). Anal style long and narrow (Figs 2a, 3a, 9b-c, 11a).

**Distribution.** Sub-Saharan Africa (Namibia) and Madagascar.

**Etymology.** The generic name is the result of the amalgamation of two words: Africa – *terra typica* of the new genus with the terminus of *Stenocranus*. Gender – masculine.

***Afrocranus ujotdensis* sp. nov.**  
Gębicki, Walczak & Świerczewski

(Figs 1-3)

urn:lsid:zoobank.org:act:91F0353F-E4BD-47B8-B407-AC1331ADB554

**Diagnosis.** The species differs from *Afrocranus mixtus* sp. nov. according to the following characteristics: vertex medially about three times longer than the compound eye width, in the dorsal view; wings – M vein length from the *r-m* veinlet to the M<sub>1</sub> and M<sub>2</sub> fork equals the M<sub>2</sub> vein length; transverse veinlet *r-m* placed clearly before the *m-cu* veinlet; male terminalia – pygofer posterior margin almost straight, first appendage of the phallotheca longest, strongly curved in the ventral view; subanal process with three distinct apical teeth.

**Measurements.** Total length (with tegmina): male (holotype) – 6.27 mm, females (paratypes) – 7.44-7.88 mm (n = 3). Additional measurements are indicated in Table 3.

**Description.** Vertex medially about 3 times longer than the compound eye width (in the dorsal view) (Fig. 1). Frontal lateral carinae broken at the

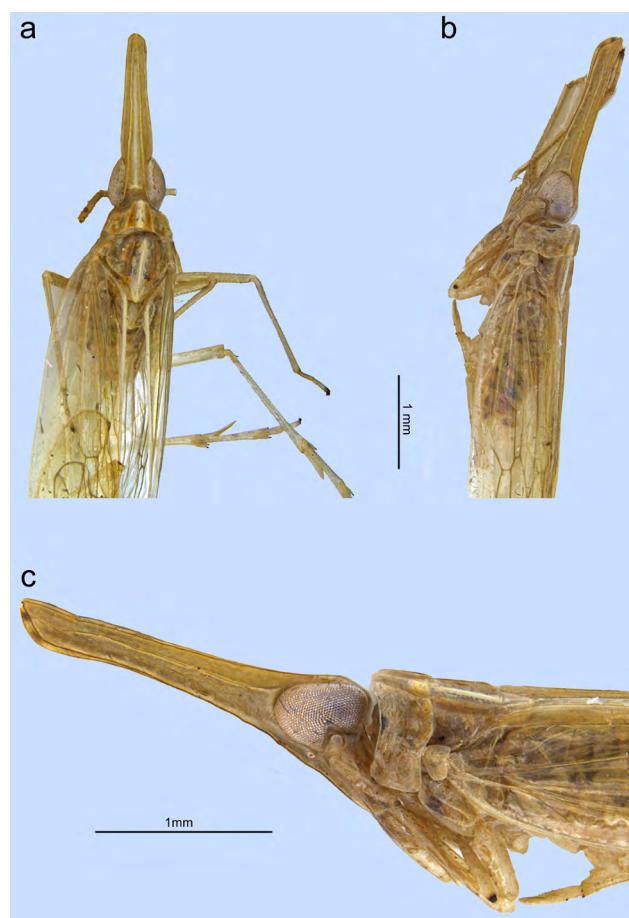


Fig. 1. *Afrocranus ujotdensis* gen. et sp. nov., habitus, male; a – dorsal view, paratype; b – left lateral view, holotype; c – left lateral view, head and thorax details in the larger scale, holotype.

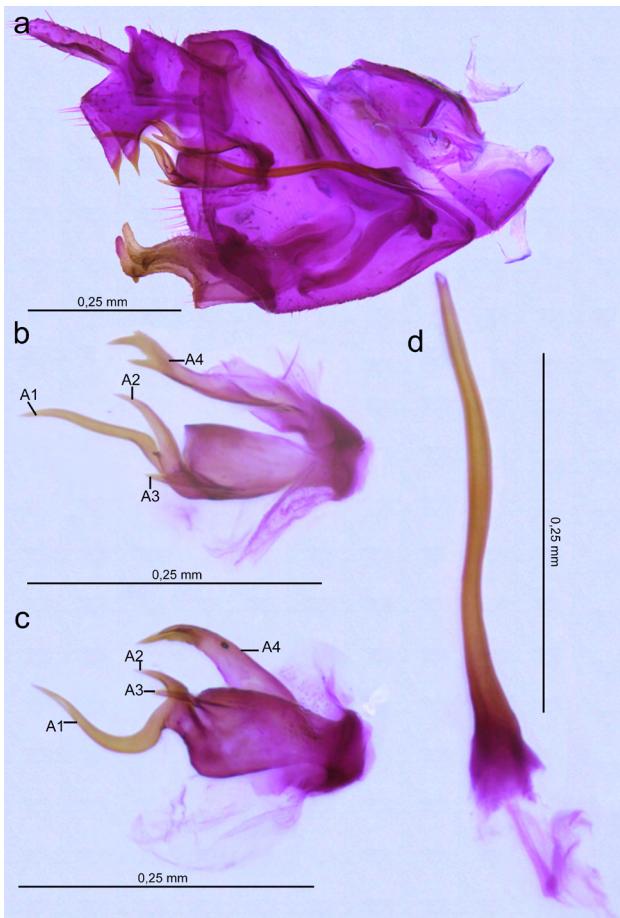


Fig. 2. *Afrocranus ujotdensis* gen. et sp. nov., male, holotype: a – terminalia, lateral view; b – phalloteca with subanal appendages, lateral view; c – same, ventral view; d – aedeagus.

apex of the head, connected with the lateral carinae of the vertex clearly below the apex of the fastigium (Figs 1b-c). In wing, the M vein length from the  $r-m$  veinlet to the  $M_1$  and  $M_2$  fork equals the  $M_2$  vein length (Figs 1a-b). Transverse veinlet  $r-m$  placed clearly before the  $m-cu$  veinlet.

Male terminalia – pygofer posterior margin almost straight (Figs 2a, 3a). Apical ventral side of the phallotheca with three, strongly sclerotised appendages: first and second long, connected at the base and directed backwards, and the third very short and wide, directed aside (Figs 2b-c, 3b-c). First appendage is the longest, reaching almost 1/2 the aedeagus length, strongly curved, in the ventral view (Figs 2d, 3d). Second appendage a bit shorter than the first, with a small spine at the base.

**Colouration.** Specimens examined (dried) were uniformly brightly coloured, with a weakly visible colour pattern. Vertex with a wide and white stripe alongside 4/5 of the median carina. Frons with a median carina yellowish-white with brown margins, top of the fastigium with two pairs of bright brown spots (the third pair weakly visible), located

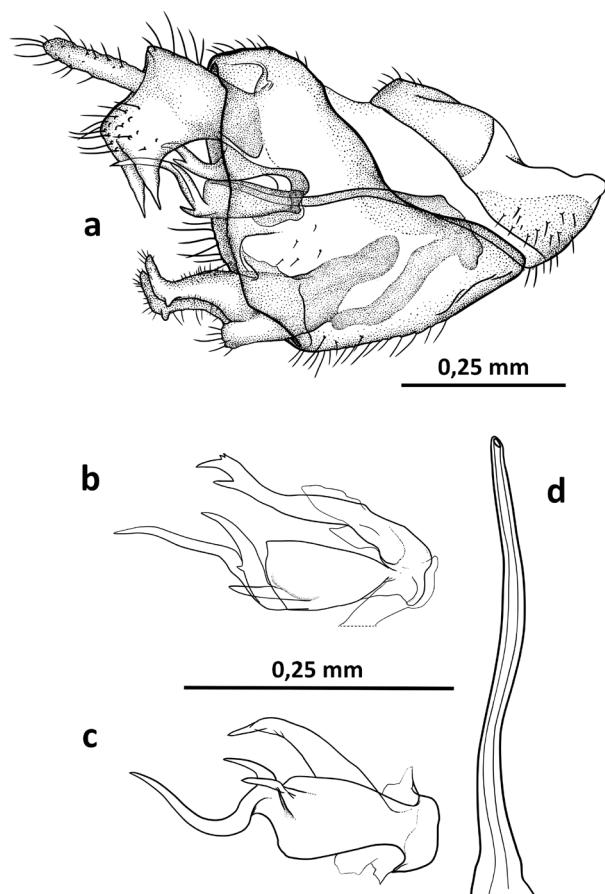


Fig. 3. *Afrocranus ujotdensis* gen. et sp. nov., male, hand drawing: a – terminalia, lateral view; b – phalloteca with subanal appendages, lateral view; c – same, ventral view; d – aedeagus.

alongside the frontal lateral carinae. Anteclypeus bright yellow; postclypeus with the carinae bright yellow with brown margins. Pedicellus uniformly brightly coloured. Pronotum and mesonotum with a white stripe alongside the median carina; lateral carinae marginated with bright brown stripes. Apical part of the rostrum black. Tegmina uniformly bright, with the claval margin white; hind wings with dark venation. Legs uniformly bright; apical parts of the metatibia spines, spur margin, metatarsus and claws of the third tarsus black (Figs 1a-c).

**Habitat.** Gallery forest/savanna, upland area (780 m a.s.l.).

**Distribution.** Southwest Africa, Namibia; species known from one locality in Kaokoland.

**Material (USM).** Holotype, ♂: 1st label (white) – NAMIBIA, Kaokoland / 17°24'23,8"S 14°13'02,6"E / Ruacana Waterfall (camp) / 11.02.2012 780 m, at light / gallery forests, savanna / leg. R. Dobosz & G. Kopij, 2nd label (red) – HOLOTYPE ♂ / *Afrocranus ujotdensis* / gen. & sp. nov. / Gębicki, Walczak & Świerczewski 2025.

Paratypes, 1♂, 3♀: 2♀ – NAMIBIA, Kaokoland / 17°24'23,8"S 14°13'02,6"E / Ruacana

Table 3

Measurements for *Afrocranus ujotdensis* and *Afrocranus mixtus* (in mm)

Measurements	<i>Afrocranus ujotdensis</i> sp. nov.		<i>Afrocranus mixtus</i> sp. nov.	
	♂ (H)	♀♀ (Pt)	♂ (H)	♀♀ (Pt)
Head				
length in lateral view (from top of rostrum to posterior edge of eye)	1.73	2.15-2.50	2.35	2.47-2.81
total length of frons	2.02	2.46-2.74	2.56	2.79-3.13
length of frons in midline	2.00	2.48-2.75	2.54	2.77-3.11
width of frons	0.24	0.24-0.25	0.23	0.23-0.24
length of visible part of rostrum	0.46	0.52-0.58	0.60	0.66-0.71
interocular distance	0.18	0.21-0.22	0.21	0.22-0.23
head, maximum width in top view (with eyes)	0.65	0.67-0.70	0.65	0.67-0.69
length of vertex in midline	1.58	2.03-2.25	2.03	2.28-2.56
total length of vertex	1.59	2.04-2.27	2.04	2.29-2.58
maximum width of eye	0.53	0.54-0.56	0.50	0.52-0.53
length of clypeus in midline	0.58	0.58-0.60	0.54	0.65-0.67
length of pedicel	0.46	0.42-0.44	0.42	0.40-0.42
Pronotum				
length in midline	0.32	0.33-0.34	0.34	0.36-0.40
total length	0.36	0.39-0.42	0.38	0.41-0.44
width	0.70	0.82-0.85	0.84	0.88-0.90
Mesonotum				
length in midline	0.58	0.66-0.71	0.60	0.68-0.83
width (with tegulae)	0.88	0.96-0.98	0.87	0.96-1.06
Leg I				
profemur	0.88	0.96-1.02	1.01	1.08-1.10
protibia	1.02	1.16-1.22	1.10	1.13-1.20
protarsus	0.35	0.46-0.48	0.39	0.41-0.43
Leg II				
mesofemur	0.91	1.10-1.20	1.03	1.10-1.14
mesotibia	1.20	1.36-1.44	1.28	1.35-1.40
mesotarsus	0.45	0.56-0.60	0.41	0.46-0.51
Leg III				
metafemur	0.96	1.16-1.21	1.08	1.09-1.20
metatibia	1.28	1.54-1.66	1.48	1.60-1.65
spur	0.37	0.40-0.44	0.44	0.52-0.54
metatarsus	0.85	0.99-1.06	1.06	1.10-1.20
metabasitarsus	0.45	0.65-0.70	0.79	0.81-0.85
metatarsomere II	0.23	0.32-0.35	0.26	0.33-0.35
metapraetarsus	0.18	0.29-0.31	0.22	0.28-0.30
Fore wing				
length	3.81	4.35-4.70	3.95	4.43-5.06
width	0.83	0.92-0.94	0.96	0.94-0.97
Hind wing				
length	3.52	n/a	2.78	n/a
width	0.90 (?)	n/a	1.00 (?)	n/a

Waterfall (camp) / 11.02.2012 780 m, at light / gallery forests, savanna / leg. R. Dobosz & G. Kopij; 1♂, 1♀ – NAMIBIA, Kaokoland / 17°24'23,8''S 14°13'02,6''E / Ruacana Waterfall (camp) / 22-23.02.2012 780 m / gallery forests, savanna/ leg. R. Dobosz & G. Kopij. All paratypes have an additional red label: PARATYPE / *Afrocranus ujotdensis* / gen. & sp. nov. / Gębicki, Walczak & Świerczewski 2025.

**E t y m o l o g y.** The specific epithet comes from the latinised acronym UJD (pronounced ‘ujotde’) referring to Uniwersytet Jana Długosza (Jan Długosz University), the university located in Southern Poland associated with the study of the recent and fossil planthoppers and leafhoppers fauna.

***Afrocranus mixtus* sp. nov.**  
Walczak, Gębicki & Świerczewski

(Figs 4-11)

urn:lsid:zoobank.org:act:5291A665-EB72-458C-8938-F8ECA30542A2

**D i a g n o s i s.** The species differs from *Afrocranus ujotdensis* sp. nov. according to the following characteristics: vertex medially about four times longer than the compound eye width, in the dorsal view; wings – M vein length from the *r-m* transverse veinlet to the *M<sub>1</sub>* and *M<sub>2</sub>* fork shorter than the *M<sub>2</sub>* vein length; transverse veinlets *r-m* and *m-cu* at the same level; male terminalia – pygofer posterior margin curved; the longest appendage of the phallotheca almost straight, in the ventral view; subanal process with two distinct apical teeth.

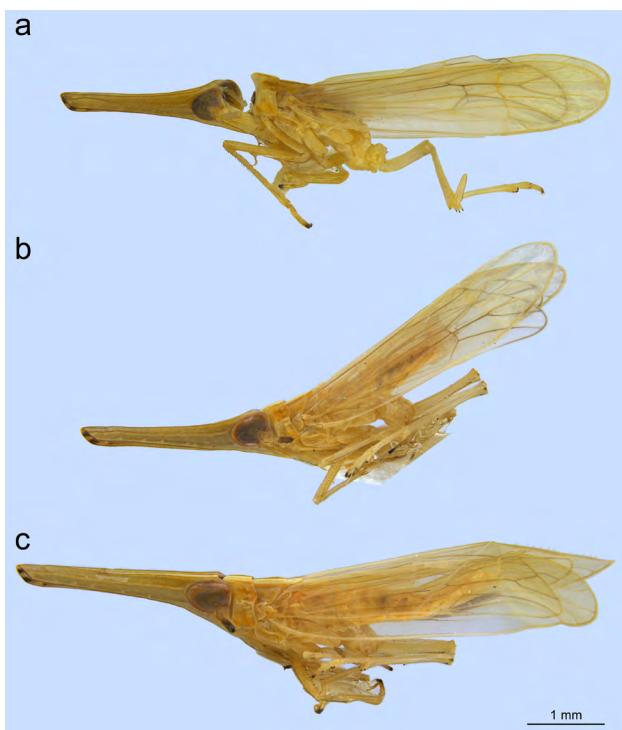


Fig. 4. *Afrocranus mixtus* gen. et sp. nov., habitus: a – male, holotype, lateral view; habitus, paratypes, lateral view: b – male; c – female.



Fig. 5. *Afrocranus mixtus* gen. et sp. nov., habitus, paratypes, dorsal view: a – male; b – female.

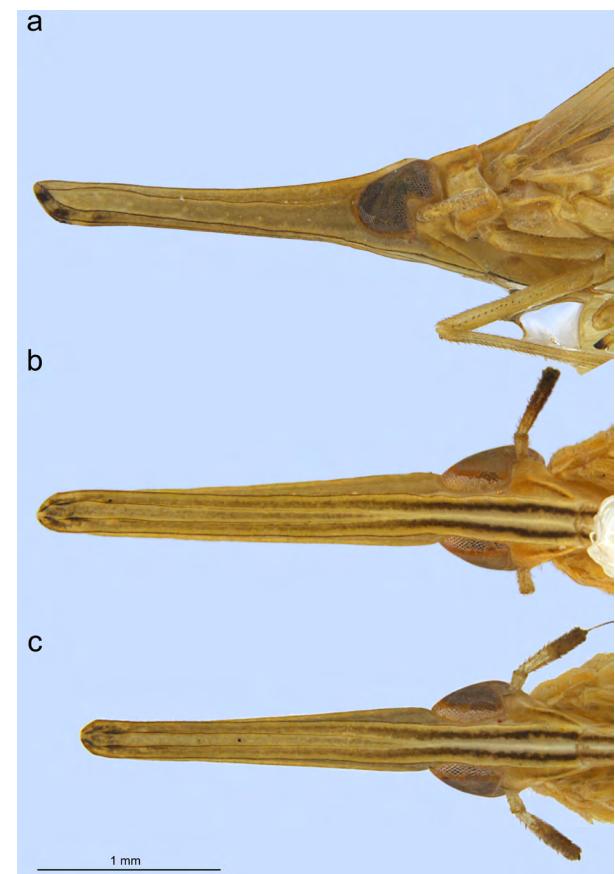


Fig. 6. *Afrocranus mixtus* gen. et sp. nov., head, paratypes: a – female, lateral view; b – frons, female; c – same, male.

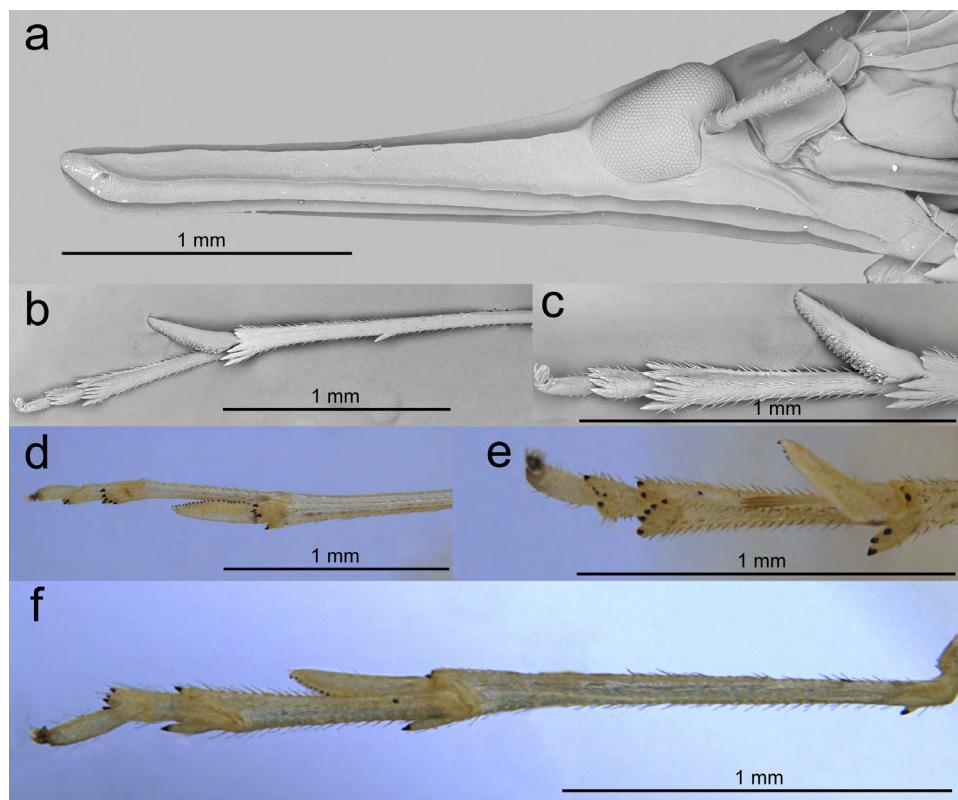


Fig. 7. *Afrocranus mixtus* gen. et sp. nov., male, paratype: a – head, lateral view, SEM; b – metatibia and metatarsus, lateral view, SEM; c – metatarsus, lateral view, SEM; d – same, ventral view; e – same, ventral view; f – metatibia and metatarsus, dorsal view.

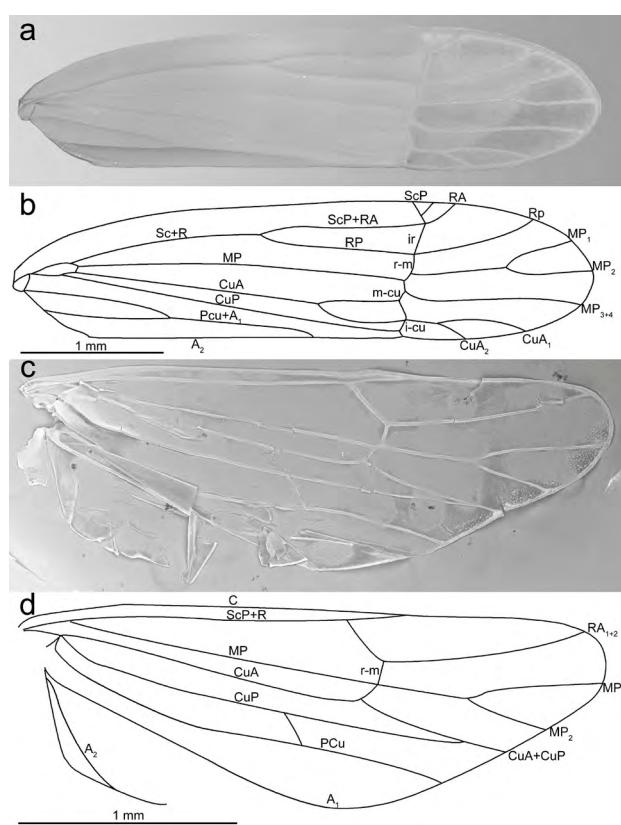


Fig. 8. *Afrocranus mixtus* gen. et sp. nov., wings, male, paratype: a – right forewing, SEM; b – same, scheme of venation; c – right hindwing, SEM; d – same, scheme of venation.

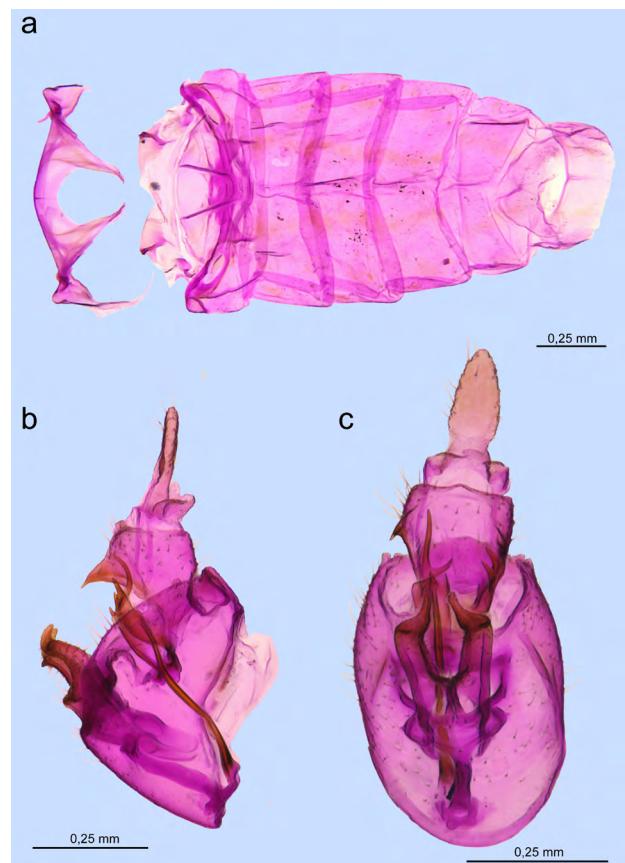


Fig. 9. *Afrocranus mixtus* gen. et sp. nov., male abdomen and terminalia, paratype: a – abdomen with apodemes, ventral view; b – male terminalia, lateral view; c – same, frontal view.

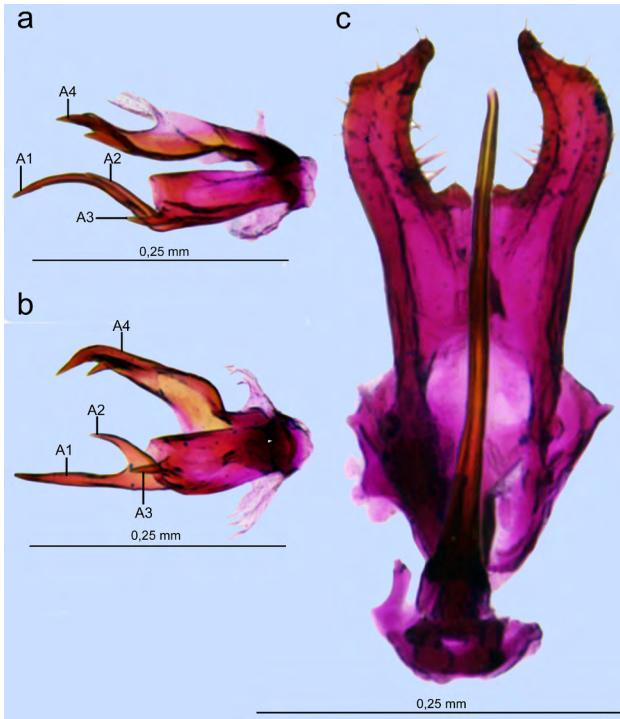


Fig. 10. *Afrocranus mixtus* gen. et sp. nov., male genitalia, holotype: a – phalloteca with subanal appendages, lateral view; b – same, ventral view; c – aedeagus with styles, dorsal view.

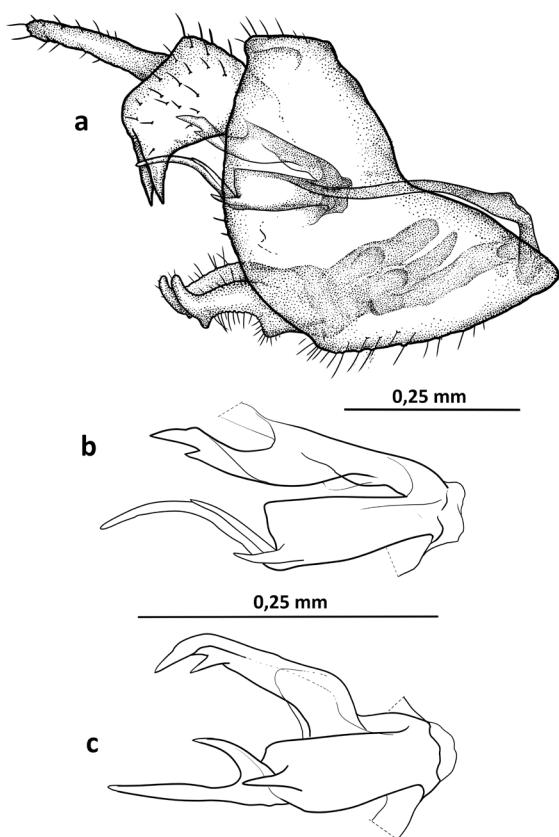


Fig. 11. *Afrocranus mixtus* gen. et sp. nov., male genitalia, hand drawing: a – terminalia, lateral view; b – phalloteca with subanal appendages, ventral view; c – same, lateral view.

**Measurements.** Total length (with tegmina): (holotype) – 6.48 mm, females (paratypes) – 6.95–7.90 mm (n = 10). Additional measurements are indicated in Table 2.

**Description.** Vertex medially about 4 times longer than the compound eye width, in the dorsal view (Figs 5a-b). Lateral carinae of the frons curved at the apex of the head, in the lateral view, connected with the lateral carinae of the vertex just below the top of the fastigium. Hind wings – M vein length from the *r-m* transverse veinlet to the  $M_1$  and  $M_2$  fork shorter than the  $M_2$  vein length; transverse veinlets *r-m* and *m-cu* at the same level (Figs 8c-d). Male apodemes of abdomen base as in Fig. 9a.

**Male terminalia** – pygofer posterior margin curved (Fig. 9b, 11a); the longest appendage of the phallotheca almost straight, in the ventral view (Figs 10b, 11c); subanal process with two distinct apical teeth (Figs 10a, 11b).

**Colouration.** The examined dried specimen were similar in colouration to *Afrocranus ujodensis* sp. nov. (Figs 4a-c, 5a-b) but the top of fastigium was with two pairs of dark brown spots (third pair blurred), located alongside the frontal lateral carinae (Figs 5a-b).

**Habitat.** Gallery forest, edge of dry forest – pasture, wetlands, wetlands near villages, rice fields, 73–332 m a.s.l.

**Distribution.** Western Madagascar: Toliara Province (Makay Massif), Boeny region – Mahajanga – Tsingy de Namoroka, Ambalamanga Mangoky River.

**Material (MNHN).** Holotype, ♂: 1<sup>st</sup> label (white) – “Madagascar / province de Toliara / massif du Makay, 159 m / S21°40'29.4'' E44°59'36.2''”, 2<sup>nd</sup> label (white) – “MUSEUM PARIS / ft Ambalamanga rv Mangoky / PL, 19-I-2011 / D. Ouvrard rec”, 3<sup>rd</sup> label (white) – “MNHN Paris EH25912”, 4<sup>th</sup> label (red) – “HOLOTYPE ♂ / *Afrocranus mixtus* / gen. & sp. nov. / Walczak, Gębicki & Świerczewski 2025”.

**Paratype series,** 21♂♂, 24♀♀: 1♀ – Madagascar / province de Toliara / riviere Mangoky / S21°41'001'' E45°08'777'' // MUSEUM PARIS / 08-I-2011 / A. Soulier-Perkins rec. // MNHM Paris EH25874; 2♀♀ – Madagascar / province de Toliara / massif du Makay / S21°37'16'' E45°09'59'' // MUSEUM PARIS / forêt sèche, PL / 09-I-2011 / A. Soulier-Perkins Rec. // MNHM Paris EH25836, EH25837; 1♂, 3♀♀ – Madagascar / province de Toliara / massif du Makay, 301 m / S21°36'236''

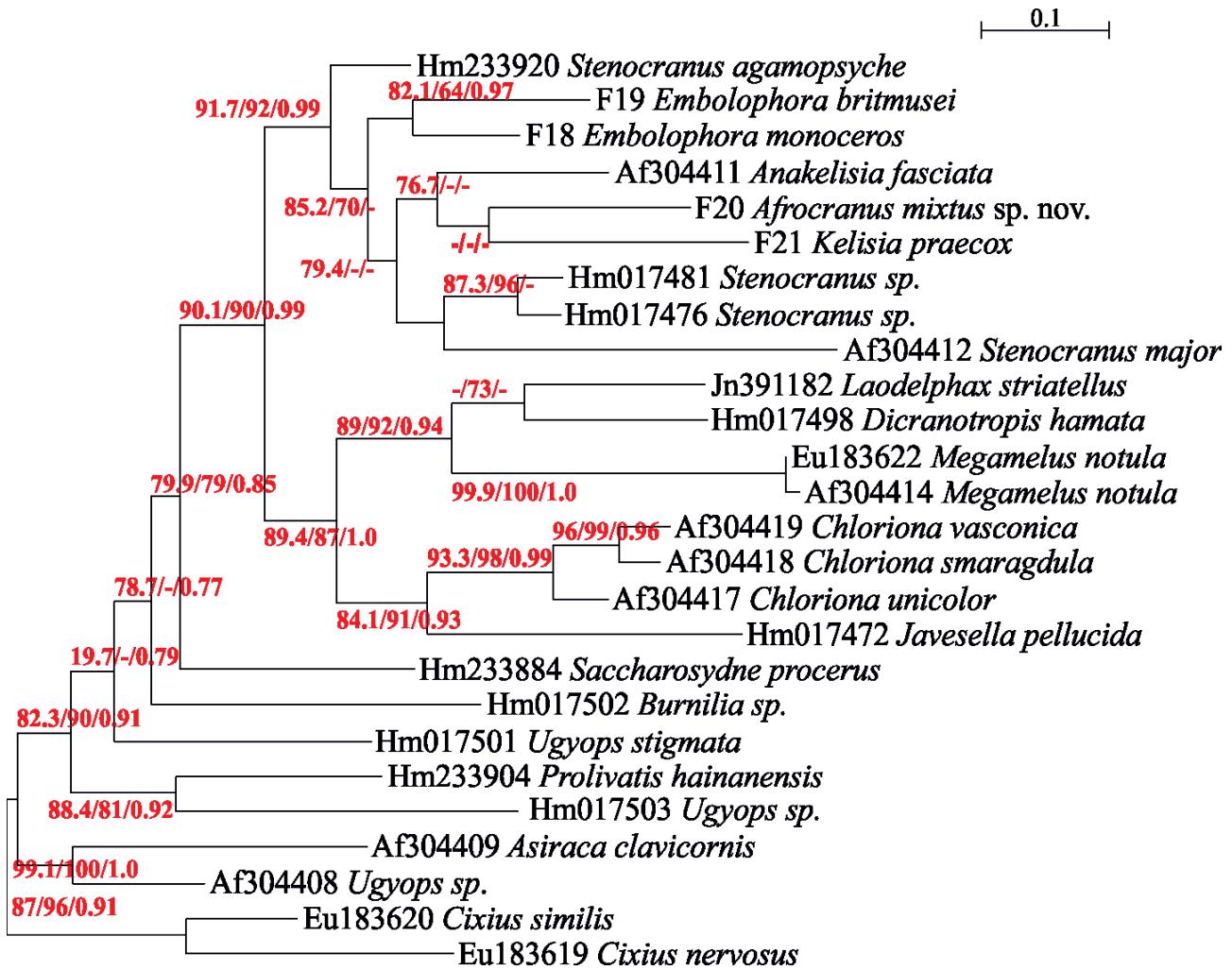


Fig. 12. Phylogenetic tree showing the position of *Afrocranus mixtus* sp. nov. among representatives of the Delphacidae family, inferred from a maximum likelihood (ML) and Bayesian Inference (BI) analysis based on cytochrome oxidase I (COI) gene sequences. The first number on the branch is an SH-aLRT support (%), the second is an ultrafast bootstrap support (%) from IQ-TREE and the third is the posterior probabilities from MrBayes. – support, bootstrap and posterior probability values below 60% and 0.6. Scale bar: expected substitutions per site.

E45°06'464'' // MUSEUM PARIS / croisée des rivières, PL / 14-I-2011 / D. Ouvrard rec. // MNHM Paris EH26001, EH26003, EH25994, EH25999; 3♂♂, 3♀♀ – Madagascar / province de Toliara / massif du Makay, 316 m / S21°34'06.2'' E45°04'31.9'' // MUSEUM PARIS / plateau / 14-I-2011 / A. Soulier-Perkins rec. // MNHM Paris EH25885, EH25887, EH25889, EH25890, EH25891, EH25892; 1♂, 1♀ – Madagascar / province de Toliara / massif du Makay, 332 m / S21°34'007'' E45°04'257'' // MUSEUM PARIS / Forêt galerie, fond canyon / 14-I-2011 / D. Ouvrard rec // MNHM Paris EH25833, EH25828; 1♂, 2♀♀ – Madagascar / province de Toliara / massif du Makay, 301 / S32°34'07,5'' E45°04'32,1'' // MUSEUM PARIS / croisée des rivières, PL / 16-I-2011 / A. Souli-

er-Perkins Rec. // MNHM Paris EH25850, EH25854, EH25855; 1♂ – Madagascar / province de Toliara / massif du Makay 159 m / S21°40'29.4'' E44°59'36.2'' // MUSEUM PARIS / ft Ambalamanga rv Mangoky / PL, 18-I-2011 / D. Ouvrard rec // MNHM Paris EH25993; 1♀ – Madagascar / province de Toliara / massif du Makay 153 m / S21°40'27.6'' E44°59'45.3'' // MUSEUM PARIS / forêt sèche Ambalamanga / 19-I-2011 / A. Soulier-Perkins rec. // MNHM Paris EH25808; 5♂♂, 2♀♀ – Madagascar / province de Toliara / massif du Makay 159 m / S21°40'29.4'' E44°59'36.2'' // MUSEUM PARIS / ft Ambalamanga rv Mangoky / PL, 19-I-2011 / D. Ouvrard rec // MNHM Paris EH25805, EH25897, EH25898, EH25895, EH25914, EH25902, EH25903; 2♂♂, 1♀ – Madagascar / province

de Toliara / massif du Makay 159 m / S21°40'29.4'' E44°59'36.2'' // MUSEUM PARIS / rv Mangoky / PL, 19-I-2011 / A. Soulier-Perkins rec. // MNHM Paris EH25805, EH25813, EH25897; 1♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / edge dry forest-pasture / S16°24'04'' E45°17'47'' // MUSEUM PARIS / 21-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26076; 3♂♂, 2♀♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / edge dry forest-pasture / S16°24'04'' E45°17'47'' // MUSEUM PARIS / 22-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26067, EH26069, EH26070, EH26075, EH26076; 1♂ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / PL / S16°24'44.9'' E45°17'42.8''' // MUSEUM PARIS / 24-X-2016, 92 m / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26156; 1♂ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / between camp & wetland / S16°24' E45°17' // MUSEUM PARIS / 25-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26011; 1♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / wet canyon / S16°24'36.1'' E45°18'19.5'' // MUSEUM PARIS / 26-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26159; 1♂ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / between camp & wetland / S16°24' E45°17' // MUSEUM PARIS / 27-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26010; 1♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / edge dry forest-pasture / S16°24'04'' E45°17'47'' // MUSEUM PARIS / 28-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26014; 1♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / wetland near willage / S16°23'50'' E45°17'12''' // MUSEUM PARIS / 29-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26117; 1♂, 1♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / wetland near willage / S16°23'50'' E45°17'12''' // MUSEUM PARIS / 29-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26122, EH26123; 1♀ – Madagascar, Mahajanga / P.N. Tsingy de Namoroka / wetland near willage / S16°23'50'' E45°17'12''' // MUSEUM PARIS / 30-X-2016, PL / T. Bourgoin, G. Kunz & A. Soulier-Perkins rec. // MNHM Paris EH26128. All paratypes have additional red label: PARATYPE / Afrocranus mixtus / gen. & sp. nov. / Walczak, Gębicki & Świerczewski 2025.

**E t y m o l o g y.** The specific epithet comes from the Latin word *mixtus*, meaning mixed, and refers to the presence of the feature of Kelisiinae in the species representing Stenocraninae. The characteristic of this phenomenon can be found in the Discussion section.

## Molecular phylogenetic analyses

The studied species form two clearly separate clades in the phylogram: Stenocraninae + Kelisiinae and Delphacinae (Fig. 12). Moreover, within the first clade, three subclades can be distinguished. The first one is formed of *Stenocranus agamopsyche* Kirkaldy, 1906 from South-Eastern Asia and Central Australia, together with *Embolophora britmusei* and *E. monoceros* from Southern Africa. *Afrocranus ujodensis* sp. nov. and probably other species belonging to this genus and the representative of Kelisiinae i.e. *Anakelia fasciata* Kirschbaum, 1868 and *Kelisia praecox*, belong to the second sub-clade. The third subclade consists of the Palaearctic species of the genus *Stenocranus*.

Other representatives of the family Delphacidae form the group of Asiracinae, such as *Saccharosydne procerus* Matsumura, 1931, *Burnilia* sp., *Ugyops stigmatus* (Crawford, 1914), *Prolivatis hainanensis* (Chen & Hou, 2012) sister to species *Ugyops* sp., *Asiraca clavicornis* (Fabricius, 1794) and *Ugyops* sp.

Among the analysed taxa, the pairwise comparison based on the partial COI sequence *Afrocranus mixtus* sp. nov. differs from the subset of the species for Stenocraninae on average by 14.18%, and from Kelisiinae on average by 14.5%. Furthermore, Stenocraninae and Kelisiinae have an average of 13% and 14% intrageneric variability, respectively.

## Discussion

The newly described genus *Afrocranus* features all the taxonomical characteristics typical for Stenocraninae, which are especially the shape of the calcar, sclerotised sperm-conducting tube connected with the phallotheca, the presence of phallotheca appendages, lack of flagellum, phallothrema with a smooth margin, and the lack of double subanal processes characteristic for Kelisiinae. The unique feature distinguishing both species from other representatives of Stenocraninae, especially the closely related genus *Embolophora*, and all other Delphacidae is the presence of single, massive and prolonged

subanal process. A similar structure in the form of an elongated, weakly sclerotised spine can be also observed in *Kelisicranus arundiniphagus* Bartlett, 2006, which was also classified by Bartlett (2006) to Stenocraninae. On the other hand, this single characteristic is not sufficient to classify *Afrocranus* gen. nov. as belonging to Kelisiinae, in which the subanal process is not present or has a rudimentary form.

According to Bartlett (2006), the presence of subanal processes is an important autapomorphic characteristic for Kelisiinae. In this subfamily, subanal processes of the 10<sup>th</sup> segment are symmetrical and differently elongated, with the exception of *Kelisia monoceros* Ribaut, 1934, in which a single process is of a secondary origin taking into account its symmetrical base (Ribaut 1934). In Kelisiinae, there is a small unique group of species having three subanal processes, i.e. apart from two elongated, symmetrical processes we can observe an additional, more or less shortened, median single process. This process, being rudimental in *Kelisia curvata* Beamer, 1945 and clearly elongated in *K. ribauti* Wagner, 1938 and *K. riboceros* Asche, 1986 (Wagner 1938; Beamer 1945; Asche 1986), is not homologous, in our view, with other the subanal processes present in Kelisiinae, but refers to a single subanal process of *Kelisicranus* and *Afrocranus* gen. nov. The three abovementioned genera *Kelisicranus*, *Terauchiana* and *Afrocranus* probably represent a separate taxonomic group, which can be contrasted with other representatives of Stenocraninae, which do not have a subanal process. Taking into account the head hypertrophy, *Afrocranus* is the most closely related to the African genus *Embolophora*, especially *E. britmusei*. It is also similar to the Neotropical *Tanycranus elongatus* and species belonging to the genus *Frameus*, but differs from the latter with a widened and bluntly rounded fastigium.

Regarding the structure of the pro- and mesonotum, *Afrocranus* is closely related to *Terauchiana singularis* and the species of *Embolophora*. The tegmina venation of *Afrocranus* is similar to *Embolophora* and some *Stenocranus*, or even to *Plesiodelphacinae* Asche, 1985. It refers especially to the three median veins ( $M_1$ ,  $M_2$  and  $M_{3+4}$ ) and the short common stem  $CuA_1 + CuA_2$ , which is the result of an icua reduction (Asche 1983, 1985b). The morphology of the hind legs in *Afrocranus* is close to that of *Embolophora* and *Terauchiana singularis*, especially in the aspect of 5 apical teeth in the second metatarsus.

Both the newly described species seem to be endemic. *Afrocranus ujotdensis* is known only from one locality in Namibia. This is the driest country

in sub-Saharan Africa, but it is well known for its richness in species and sustainable natural resource utilisation. The animal world in Namibia is rich and diverse, and its preservation is supported by several national parks and reserves (Schalkwyk *et al.* 2010). *Afrocranus mixtus* is confined exclusively to Madagascar, where it was collected exclusively in Makay Massif and Tsingy de Namoroka National Park. Madagascar, being the fourth largest island in the world, is one of the top biodiversity hotspots on Earth (Fritz-Vietta *et al.* 2011). The vertebrate taxa show between circa 50 and 100% of endemism in a particular group. Invertebrates are far from being described to the extent that would allow any definite statement. Still, the degree of endemism is expected to be at least as high as that in vertebrates (Goodman & Benstead 2005; Chłond *et al.* 2018; Masłowski *et al.* 2023).

Our molecular analysis, based only on one segment of the COI gene, provides preliminary confirmation that *Afrocranus* seems indeed to be a different genus, and this is also congruent with our morphological observations. Moreover, it also indicates a close relationship among the Kelisiinae and Stenocraninae planthoppers. This view has been widely presented by different authors (Dijkstra *et al.* 2003, 2006; Urban *et al.* 2010; Bucher *et al.* 2023; Luo *et al.* 2024). Both groups represent evolutionary old lineages, probably formed in the early Crataceous, about 100 Mya (Bucher *et al.* 2023). According to the latest research, Kelisiinae and Stenocraninae form monophyletic sister groups, forming one clade, which is against the second phylogenetic lineage, consisting of three tribes (Saccharosydmini + Tropiduchini Stål 1866 + Delphacini) of the Delphacinae subfamily (Bucher *et al.* 2023). These three subfamilies, together with Vizcayinae Asche, 1990, are treated as a monophyletic group of 'higher' Delphacidae (Asche 1990; Luo *et al.* 2024). Taking into account the low number of the studied representatives of Kelisiinae and Stenocraninae, both genetically and even morphologically, their phylogenetic relationship requires further detailed studies.

## Acknowledgements

We would like to thank our three anonymous reviewers for their insightful comments and suggestions, which greatly strengthened the overall manuscript. We are also grateful to Dr Adeline Soulier-Perkins (MNHN) and Dr Roland Dobosz (USM) for the loan of the specimens used in this study. Additional thanks to Łukasz Junkert for making the

drawings and to Marzena Zmarzły and Krzysztof Kudła (University of Silesia in Katowice, Institute of Biology, Biotechnology and Environmental Protection) for the graphic design.

## Author Contributions

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

## Conflict of Interest

The authors declare no conflict of interest.

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