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A peculiar large-eyed aposematic bug *Miropictopallium coloradmonens* n. gen., n. sp. (Heteroptera: Pentatomomorpha: Yuripopovinidae) from mid-Cretaceous Kachin amber

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ABSTRACT

Miropictopallium coloradmonens, a new genus and a new species are described and illustrated in the family Yuripopovinidae, based on two specimens from the mid-Cretaceous Kachin amber. The documented diversity of the Yuripopovinidae is thus increased to 15 species in 12 genera. The new genus possesses a number of distinct morphological characteristics for this family including very large eyes, intricate body colour pattern and enlarged scutellum. In addition, the new genus has unfused costal and subcostal veins on the tegmen, a character previously not reported from amber-preserved members of the family. The diagnostic characters of the family are discussed in light of the new descriptions. The newly discovered features prompt some implications towards understanding of the palaeoecology and palaeobiodiversity of the fossil Coreoidea.

KEYWORDS: Heteroptera, Pentatomomorpha, Yuripopovinidae, Cretaceous, Burmese amber, Kachin amber, fossil resin, new taxa, taxonomy.

INTRODUCTION

The Pentatomomorpha group exhibits hemimetabolous development and comprises almost 19,000 extant species that are distributed worldwide. Among the seven infraorders of Heteroptera (Insecta: Hemiptera), it ranks as the second most diverse in terms of species abundance. Currently, there are 940 genera and 40 recognized families organized into six superfamilies: Aradoidea, Coreoidea, Idiostoloidea, Lygaeoidea, Pentatomoidea, and Pyrrhocoroidea (Henry 2017; Liu *et al*. 2019; Weirauch *et al*. 2019; Schuh & Weirauch 2020).

Most pentatomorphan insects are terrestrial and primarily feed on plants, although some are predators and can be used as biocontrol agents (Schuh & Slater 1995; Weirauch & Schuh 2011; Schuh & Weirauch 2020).

Coreoidea, commonly known as leaf-footed bugs, is a diverse and agriculturally important insect group, representing a superfamily of true bugs within the infraorder Pentatomomorpha, encompassing 436 genera and approximately 3850 species, distributed extensively across all zoogeographical regions (Schuh & Weirauch 2020).

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Within Coreoidea, there are five recognized extant families: Alydidae Amyot & Audinet-Serville, 1843; Coreidae Leach, 1815; Hyocephalidae Bergroth, 1906; Rhopalidae Amyot & Audinet-Serville, 1843; Stenocephalidae Amyot & Audinet-Serville, 1843; and three extinct families: Trisegmentatidae Zhang, Sun & Zhang, 1994; Yuripopovinidae Azar, Nel, Engel, Garrouste & Matocq, 2011 (CoreoideaSF Team 2018) and Pachymeridiidae Handlirsch, 1906. However, Pachymeridiidae, while falling within Pentatomomorpha, might be related to Lygaeoidea (Dai 2022). Nevertheless, the phylogenetic relationships within Coreoidea remain contentious according to various studies (Schaefer 1993; Henry 1997; Azar *et al.* 2011; Du *et al*. 2017; Schuh & Weirauch 2020; Zhou *et al.* 2022).

Fossil coreoids have been documented from the Triassic to the Cenozoic with the earliest reported coreoid from the late Triassic of Toksun, China (Lin 1992). Coreoids are frequently described based on rock impressions that often do not preserve critical structures for precise identification. Amber offers exceptional preservation of minute structures in three dimensions, enabling precise study and identification of fossil entomofaunas (Grimaldi *et al.* 1994; Azar *et al.* 2011). Therefore, amber-preserved fossils hold significant promise for understanding the palaeobiodiversity and phylogenetic relationships within Coreoidea, together with modern research and development (Dong *et al*. 2022).

The Early Cenomanian age of 98.79 ± 0.62 Mya of Burmese amber was determined using U-Pb dating of zircon crystals from the amber-bearing horizon (Shi *et al.* 2012). This dating is supported by an ammonite fossil found in the amber, which confirms a Late Albian – Early Cenomanian origin (Yu *et al.* 2019). Notably, the Kachin amber has preserved the most diverse Mesozoic-aged amber palaeobiota recorded to date (Ross 2019, 2020, 2021, 2022, 2023, 2024; Shi *et al.* 2022; Beurel *et al.* 2024; Oskolski *et al.* 2024). The Kachin entomofauna suggests a range of microenvironments and niches within the amber producing forest.

The extinct family Yuripopovinidae was established by Azar *et al.* (2011) on the basis of a single specimen found in the Early Cretaceous Lebanese amber. Subsequently other representatives of the family have been described (Table 1). Yuripopovinidae was originally classified as part of Coreoidea. However, some subsequent studies refrained from classifying the family as Coreoidea, referring it more widely to Pentatomomorpha (Du *et al.* 2019; Shang *et al.* 2020; Zhou *et al.* 2022).

Recently, *Jinjupopovina eosahwae* Sohn & Nam, 2024 has been found in the upper Lower Cretaceous Jinju Formation in South Korea. This discovery prompted a discussion of the unique antennal morphology of *Jinjupopovina*, which provides a rare example of simultaneous enlargement in length and width of antennomeres in Heteroptera. The paper assesses its taxonomic status in the family and discusses the evolution of enlarged antennae within Coreoidea. It is suggested that *Jinjupopovina* may represent an evolutionary dead end in antenna morphology within the family Yuripopovinidae (Sohn & Nam 2024).

Table 1. Genera and species assigned to the family Yuripopovinidae.

Horizon	Locality	Taxon	Reference
Upper Albian – Lowermost Cenomanian, Cretaceous	Southeast Asia: Myanmar: Northern Myanmar	*Caulisoculus electrus*	Zhang & Chen 2020
		Caulisoculus monlyae	Zhuo *et al.* 2022
		Caulisoculus minutus	Shang *et al.* 2020
		Megaoptocoris punctatus	Zhuo *et al.* 2022
		Megaoptocoris similis	Zhuo *et al.* 2022
		Pseudocaulisoculus longicornis	Kóbor *et al.* 2021
		Reticulatitergum hui	Du *et al.* 2019
		Birmaniaespina robustispina	Yu *et al.* 2023
		Miropictopallium coloreadmonens gen. et n. sp.	Present paper
Upper Hauterivian – Barremian, Lower Cretaceous	East Asia: China: North East China: Liaoning	*Crassiantenninus minutus*	Du *et al.* 2017, 2019
		Dehiscensicoris sanctus	Du *et al.* 2017, 2019
		Minuticoris brunneus	Du *et al.* 2017, 2019
		Pingquanicoris punctatus	Du *et al.* 2017, 2019
Lower Barremian, Lower Cretaceous	West Asia: Lebanon: Central Lebanon	*Yuripopovina magnifica*	Azar *et al.* 2011
Lower Cretaceous, Jinju Formation	East Asia: South Korea: South Gyeongsang Prov.: Jinju City	*Jinjupopovina eosahwae*	Sohn & Nam 2024

The current study describes the fifteenth species belonging to the family. *Miropictopallium coloradmonens* n. gen., n. sp. presents unique characteristics not found in other members of the family, including intricate colour patterns, enlarged eyes and scutellum, and a prominent connexivum, further highlighting the wide disparity and diversity within the Yuripopovinidae in the Burmese amber and fossil Coreoidea as a whole.

MATERIALS AND METHODS

The fossil specimens described in the present study were quarried from the amber mine near Noije Bum, Tanaing town, Hukawng Valley (Kachin Province) in northern Myanmar. The amber specimens were legally purchased from the trader ‘burmite_ miner' on the Internet trading platform eBay and fully comply with International Paleoentomological Society guidelines (Szwedo *et al.* 2020). The specimens are now deposited in the insect collection of the Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel Aviv University, Israel (SMNHTAU-I.) as SMNHTAU-I.442144 (holotype) and SMNHTAU-I.442145 (paratype).

To enable a clear and undistorted visual inspection, the amber was ground down and polished using silicon carbide sandpaper of increasing grit sizes. Special care was taken to preserve the integrity of the specimen with minimum necessary removal or amber. The specimens were examined and photographed using a Nikon AZ100 stereomicroscope equipped with a Nikon DS-Fi1 camera and Nikon AZ Plan Apo 1× objective lens. The resulting images were digitally stitched together using Helicon Focus 8.2.2 (HeliconSoft (RRID: SCR_014462)). Drawings were created using Procreate 5.3.4 (Procreate 5.3.4, Savage interactive) based on photographs and observations made with the stereomicroscope. The measurements were taken from the images using ImageJ Software (Schneider 2012). Body length was measured along the midline from the head apex to the abdomen apex. Body width was measured at the maximum width of body. The length of the tegmina was measured from the base to its apex. All measurements are given in millimetres (mm).

The terminology used follows Azar *et al.* (2011), Du *et al.* (2017, 2019) and Zhou *et al.* (2022). The preserved colour patterns are described using four main tones: white, which designates very light pigmentation, light brown, brown, and black, designating progressively darker pigmentation.

TAXONOMY

Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Pentatomomorpha Leston, Pendergrast & Southwood, 1954
Superfamily Coreoidea Reuter, 1910
Family Yuripopovinidae Azar, Nel, Engel, Garrouste & Matocq, 2011

Genus *Miropictopallium* n. gen.

LSID: urn:lsid:zoobank.org:act:03C58037-EF0C-4540-9BAE-F281551754EA.

Etymology: The genus name is a combination of the Latin *mirus* (wonderful), *pictus* (painted), and *pallium* (cloak) referring to the intricate colour pattern of the insect's body. The gender is neuter.

Type species: *Miropictopallium coloradmonens* n. sp.

Diagnosis: In the key of Zhou *et al.* (2022), *Miropictopallium* n. gen. runs to *Megaoptocoris* Zhou, Luo, Xie & Li, 2016, from which it differs in several important aspects, including larger eye size, antenna shorter than half of body length, more elongate scutellum, and tegmen with unfused costal and subcostal veins. These characteristics further distinguish the new genus from *Birmaniaspina* Yu, Chen & An, 2024, and *Jinjupopovina* Sohn & Nam, 2024.

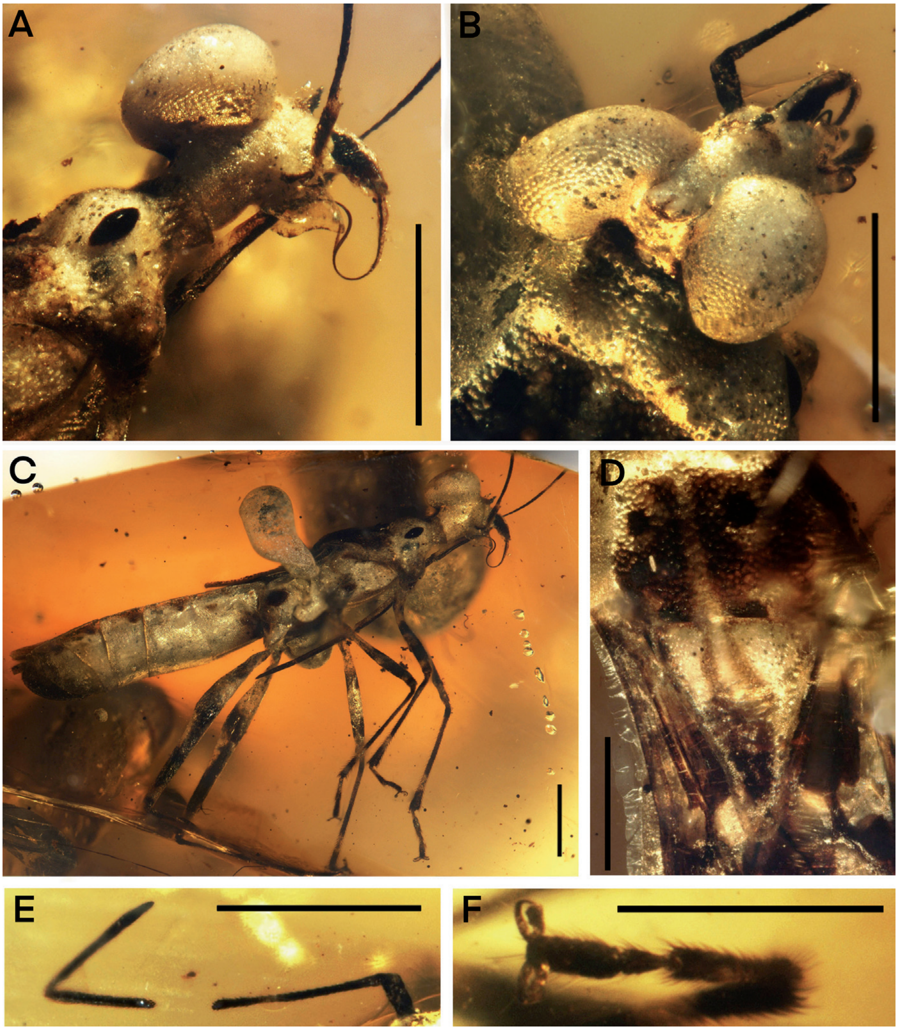

Fig. 1. Holotype of *Miropictopallium coloradmonens* n. sp., scale = 1 mm: (A) head and pronotum, lateral view; (B) head, dorsal view; (C) right lateral view of specimen; (D) posterior part of pronotum and scutellum; (E) left antenna; (F) left mid tarsus (scale = 0.5 mm).

Remarks: The new genus can be confidently assigned to the Yuripopovinidae based on the unique combination of tegmen characters among Coreidae: corium hyaline with two large cells and longitudinal veins reduced in number, apically thickened costal margin forming the pterostigma-like structure, crossvein on corium-membrane boundary not joined to claval suture, claval commissure absent, in addition to four-segmented antennae, ocelli present, pronotum wide trilobed with sinuous flank, and well-developed collar and callus (Azar *et al.* 2011; Du *et al.* 2017).

Miropictopallium coloradmonens **n. sp.**

(Figs 1–6)

LSID: urn:lsid:zoobank.org:act:250C0B94-5126-4FD9-AD6B-E8EE83EDD236.

Etymology: The species name combines the Latin *color* (colour) and *admonens* (warning) referring to the presumed aposematic function of the colouration.

Description: *Colouration*. *Head* (Figs 1A, 1B): Head white, clypeus black with thin longitudinal white line dorsally; labrum brown: rostral segments I and II light brown, with external edge black; segments III and IV black; stylet black. Antennifers black ventrally. Frons anteriorly brown, anterior frons spine black, posterior frons spine white. Eyes white, ocellar tubercle brown posteriorly; prominent black spot posterior to each compound eye. Antennae black except for light brown apex of segments I and II.

Thorax (Figs 1A, 2A, 2B): Collar light brown with dorsal side white. Pronotum: pronotal calli white, with light brown spot in anterior side of each prominence;

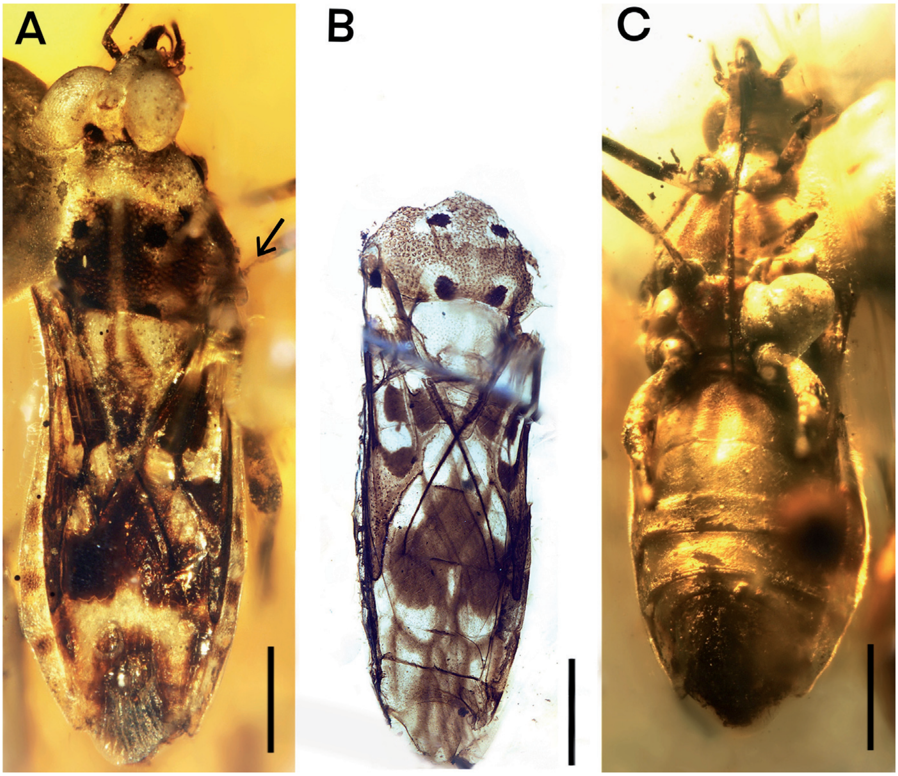

Fig. 2. Habitus of *Miropictopallium coloradmonens* sp.nov, scale = 1 mm: (A) holotype, dorsal view; (B) paratype, dorsal view; (C) holotype, ventral view.

anteroposteriorly keeled oval protuberance, laterally black; ventral extensions of middle pronotal lobe light brown; posterior lobe of pronotum brown with two curving white lateral lines on anterior ¾; longitudinal middle line light brown; two pairs of round black spots, annulated with white margin distally as thick as diameter of each spot, narrowing proximally closer to middle line; anterior spots with white margin touching middle pronotal lobe, posterior spots touching posterior pronotal margin with white margin posteriorly vanishing; lateroposterior pronotal laminae light brown.

Scutellum white; basal humerus light brown: rhombus-shaped brown spot in the middle with longitudinal white line, not reaching its apical margin; apical margin of scutellum white.

Pleurites white, mesosternum white, bearing four evenly spaced longitudinal brown lines. Metasternum brown; brown spot on anterolateral side of mid coxae; black oval spot on distal metapleuron, dorsolateral to hind coxae; brown spot on lateroposterior part of hind coxae.

Abdomen (Figs 4A, 4D): White. Middle anterior half of sternite III brown; brown triangular spots on sternite III, near lateral edge, and another spots immediately posterior to hind coxae and anterior of lateral margin of each sternite and tergite; sternite VII and genitalia black.

Legs (Figs 1C, 1F): Fore and mid femora basal ¼ white, medially black, with two lateroventral white spots and black apex. Hind femora white at basal ⅓ with black spot near base, apical ⅔ black with white line on posterior-median section and black spot near apex. All tibiae of similar colouration, light brown with three black bands: basal band, middle band (longest), and apical band. Tarsi black, apart to basal half of first tarsomere.

Tegmina (Figs 2A, 2B, 3A, 3B): Holotype: Tegminal surface white; corium veins and coriaceous region light brown; basal veins of membrane brown, apical veins light brown. Anterior large corium cell bears three irregular brown spots, at apex, at middle and at base; posterior large corium cell with brown semi-square spot apically. Anterior base of membrane with round brown spot surrounded by a white margin. Large rectangular cell on membrane white at its basal ⅓, otherwise light brown, longitudinally bounded by brown veins. Clavus light brown. Anterior membrane apex light brown. Anal vein black, basally dark brown.

Paratype: As in holotype, except for more developed middle brown spot on anterior cell of corium. Prominent brown spot on anterior base of membrane, apically with brown margin, posterolaterally attaching, two brown lines extending apically from rounded margin, posterior line bifurcate. Large rectangular cell brow, white on its basal ⅓.

Structure. Head: Not porrect anteriorly, nearly triangular, nearly as high as long, distinctly narrower and shorter than pronotum, narrower than middle lobe of pronotum; base of head forming neck, hidden from dorsal view by collar (Figs 1A, 1B).

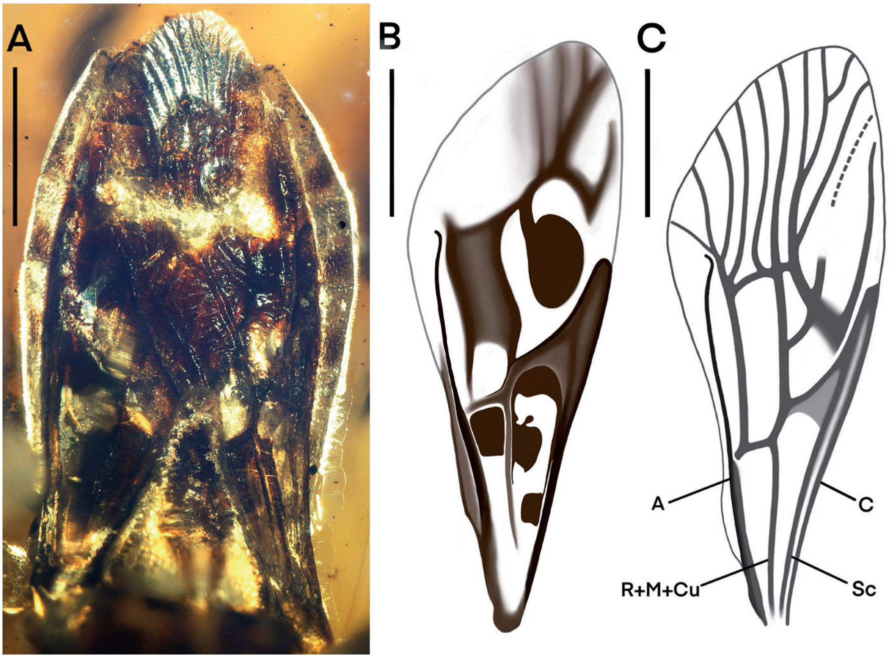

Fig. 3. Tegmen of *Miropictopallium coloradmonens* n. sp., scale = 1 mm: (A) holotype; (B) paratype, drawing of tegmen colouration; (C) holotype, tegmen venation.

Eyes large, reniform in dorsal view, ovoid in lateral view, not covering apices of antennifers; closely spaced anteriorly, spreading obliquely posteriorly and protruding backwards, reaching callus; borne on stout eyestalks oriented obliquely upwards. Posterior margin of eyes overhanging collar, reaching callus (Figs 1A, 1B).

Single pair of contiguous ocelli on prominent tubercle (Fig. 1B), closer to occiput; posterior margin of ocelli at midline of compound eyes; clypeus well-developed (Figs 1A, 1B), tapering, unarmed, setose, strongly protruding beyond mandibular plates, longer than first antennal segment, slightly curved down. Labrum narrow, elongated (Figs 1A, 1B). Bucculae prominent, triangular, exceeding edge of maxillary plate, tapering, sharply pointed apically, posterior margin sinuous; extending anteriorly to compound eyes, in line with anterior edge of maxillary plate and base of antenna, posterior to base of labium, leaving it uncovered; frons slightly bulging anteriorly, anterior margin triangular and carinate, armed with pair of pointing forward spines, placed antero-posteriorly; not covering antennal bases, lightly setose, bearing faint transverse carinae and apically tapering into blunt point; vertex smooth, widening posteriorly encroaching onto eyes; maxillary plate smooth.

Antennifers laterally protruding under the first antennomere (Figs 1A, 1B).

Antennae short, four-segmented, all segments cylindrical, covered with short

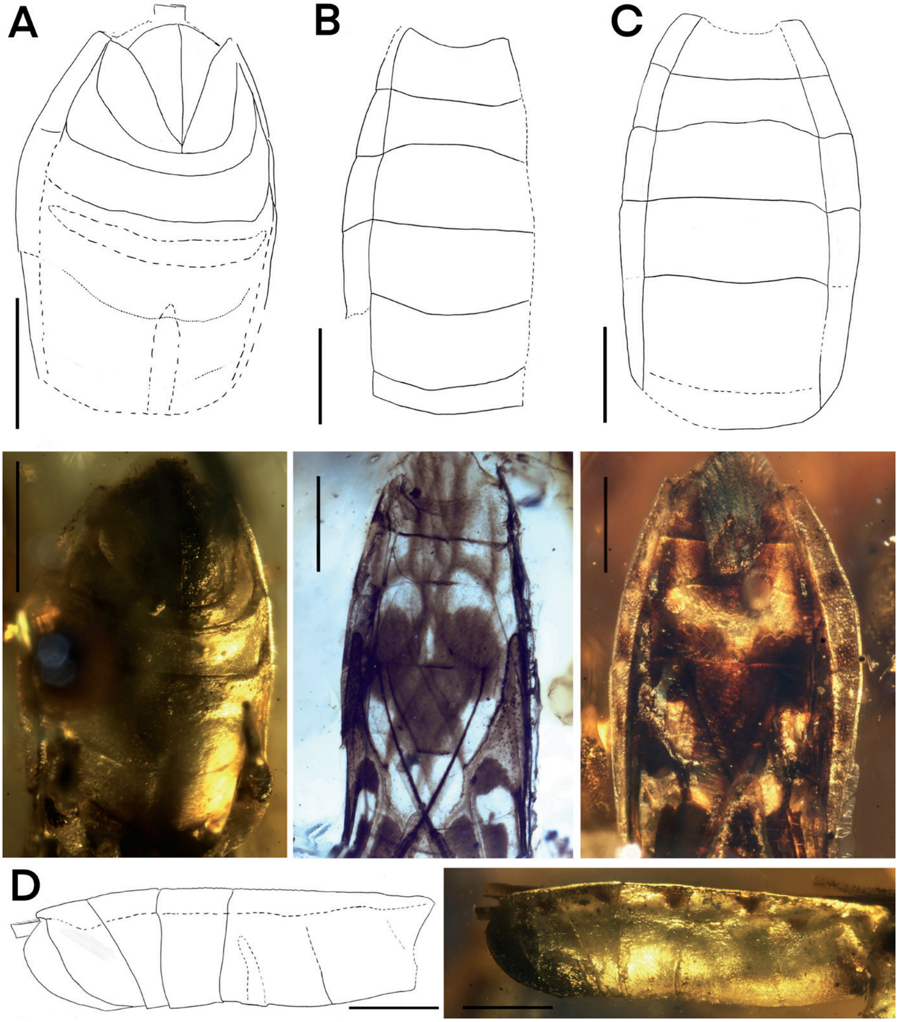

Fig. 4. Abdomen of *Miropictopallium coloradmonens* n. sp., scales = 1 mm: (A) holotype, ventral view; (B) paratype, dorsal view; (C) holotype, dorsal view; (D) holotype, lateral view.

setae; first segment very short and thickest; segment II subequal in length to segment IV; segment III longest; third and fourth segments slightly inflated apically; segment IV fusiform (Fig. 1E).

Rostrum long, straight and slender; adpressed to body, slightly curved following body contour; reaching into anterior quarter or sternite IV. Segment I lightly setose, segments I and II laterally compressed, providing thicker appearance in lateral view, segments III and IV cylindrical. First and third segments are subequal in length; segment II longest; segment IV shortest, tapering; stylet adpressed to the external surface (Fig. 1C).

Thorax: Pronotum nearly trapeziform, wider then long, with sinuous flanks; somewhat trilobed with boundaries of lobes demarcated by grooves. Integument sparsely setose, densely tuberculated and punctured (Figs 1A, 1D). Punctures irregularly shaped with single seta in middle of each; located in grooves between tubercles forming a mesh-like pattern. Callus laterally bearing pair of longitudinally keeled protuberances; each protuberance and adjacent ventral surface smooth (Figs 1A, 1C, 6).

Collar (anterior lobe) well developed ventrally and laterally, but poorly divided from callus region (middle lobe) dorsally. Anterior margin slightly curving up and straight in dorsal view; slightly depressed dorsoventrally; oval in frontal view, ~0.5× as high as wide (Fig. 1B).

Callus (middle lobe) well developed, much longer than collar in dorsal view; about 2.6× wider than collar; bearing two transverse prominences divided by medial groove, each bearing distinct distal anteroposteriorly keeled oval protuberance (Fig. 1A). Callus lacking lateral lamella, smoothly curving down body sides. Posterior lobe of pronotum nearly hexagonal in shape, about twice as wide as long; dorsally bulbous; anterolateral margin slightly convex; posterolateral margin convex and laminate; lamina forming a prominent process laterally surpassing humerus; posterior margin slightly concave (Fig. 1D).

Scutellum surface sparsely setose and densely sculptured with fine tubercles and minute punctures; relatively large, triangular, longer than wide; relatively wide at ⅔ of pronotum width measured at humeri; equal to pronotum length at midline (Fig. 1D). Level with pronotum anteromedially; slightly bulbous, flattening posteriorly. Posterior margin expanded and laminate, ending apically in laterally compressed rounded lobe. Apex raised above tegmina; margin bounded by downward pointing setae. Basal humerus sharp. Anterior margin slightly convex; lateral margins slightly concave (Fig. 1D).

Ventrally thorax lightly setose with semi-erect short setae, smooth, punctate distally. Metathoracic scent gland conspicuous, partly obscured by bubbles on both sides. Prosternum, mesosternum and metasternum with longitudinal middle groove. Mesosternum nearly trapezoid, metasternum nearly hexagonal, posterior part of mesosternum extending to midline of mid coxae (Fig. 2C).

Abdomen: Sclerotized, with small sparse setae, medially smooth and laterally rough; not flattened, rounded apically, extends laterally, exposing laterotergites from below tegmina to form prominent connexivum. Dorsal side of abdomen smooth and flat, tergites unfused, tergites III to V subequal in length, margins straight. Tergites VI and VI shorter. Anterior margin of tergite VI concave posterior margin straight, posterior margin of tergite VII concave (Figs 2B, 2C).

Ventral side of abdomen convex, median groove extending from the anterior of abdomen to the first quarters of sternite IV. Lateral edges of longitudinal groove

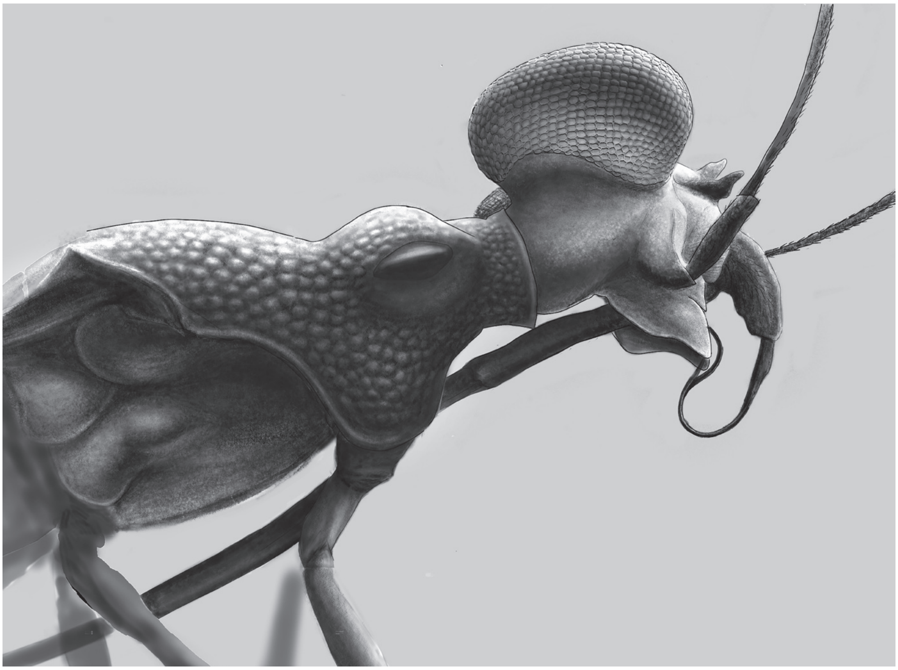

Fig. 5. Holotype of *Miropictopallium coloradmonens* n. sp., head and thorax, lateral view.

not forming a sharp edge but smoothly transiting to sternite surface. Sternites II, III, and IV fused, divided by transverse depressions (Figs 2C, 4A, 4D). Rest of the sternites telescopic: sternite II narrow; sternites III and IV large, roughly rectangular in ventral view, sternite IV longest, sternite III second widest; sternites IV and V widest laterally; sternites IV and V well delimited; sternite IV bearing transverse carina at about ⅓ of its length from posterior margin, not extending to lateral margins; sternite III not bulged; sternites V to VII progressively more concave (Figs 2C, 4A). Posterior margin of sternite VII entirely medially cleft.

Ovipositor long and curved up. Valvifers VIII paired, subtriangular and longitudinally elongated. Laterotergites and valvulae invisible.

Legs: Slender, not flattened, mid legs slightly longer than fore legs, hind leg about 1.5× longer than mid leg; trochanters small, triangular; subequal in dimensions; coxae stout, coniform, slightly rounded (Fig. 2C). Distance between fore coxae about half the distance between mid coxae and between hind coxae; distance between fore, mid and hind coxae subequal. All femora lightly setose; fore femora fusiform, slightly constricted before somewhat rounded apex (Fig. 1C). Fore femora slightly thinner than mid femora, while hind femora about twice as thick as mid femora. Fore femora subequal in length to mid femora; hind femora about 1.8× longer. Hind femora fusiform, slightly curved inward. Proximal part of hind femora expanded laterally with abrupt narrowing at about 0.4 of its length distally, forming angle; expanded portion bears longitudinal carinae proximally (Fig. 1C).

Tibiae covered with long setae; apices densely setose; subequal in length to femora, but distinctly narrower, slender, antero-posteriorly expanded at apex to about twice mid width. Fore tibiae subequal in length to mid tibiae, hind tibiae about 1.8× as long as fore or mid tibiae (Fig. 2C).

All tarsi are subequal in size, three-segmented, densely covered with fine setae, third tarsomere bearing several longer setae (Fig. 2C). Tarsomere I longest, tarsomere II shortest. Basal tarsomere subequal in length to middle and apical tarsomeres combined. Apical tarsomere thickest, slightly thicker than basal tarsomere. Tarsomere II narrowing proximally until insertion into tarsomere I (Fig. 1F). Tarsi with a pair of equally sized claws and pulvilli. Claws sharp, slender, hook like. Pulvilli geniculate medially, apically pad-like, arising from between claws (Fig. 1F).

Tegmina: Macropterous, membranous and well developed, reaching abdominal apex, ~3.4× as long as wide. Wing apex rounded, costal margin basally slightly concave or nearly straight, apically distinctly convex (Figs 2A, 2B, 3A). Claval margin thickened basally; claval commissure absent. Embolium with C and Sc veins nearly adhering but separate, apically fusing form narrow sclerotized edge. Coriaceous thickening extends posteriorly along crossvein to form elongate triangular pterostigma-like structure with anterior edge slightly convex, nearly straight, posterior edge concave. Corium membranous, hyaline, ~0.6× as long as tegmen, with three longitudinal veins forming two large cells and faint narrow cell, being part of thickened anterior wing edge (Figs 3A, 3C). Corium veins and sclerotized region are weakly punctate and sparsely covered with closely adhering setae. Crossvein on corium membrane boundary not joined with claval suture. Clavus reduced, lanceolate, apices concealed, slightly shorter than side of scutellum, and ~⅓ of wing length. Anal vein thickened. Membrane hyaline, lacking setae, bearing numerous weakly defined and longitudinal veins (Fig. 3A, 3C). Basal membrane with large rectangular cell and two smaller irregular cells. Two prominent crossveins on membrane base-apex boundary, apical veins bifurcating. At least 10 veins reaching outer margin. Membrane ornamented with some wide transverse wrinkles at its base and with denser not parallel wrinkles posterior to apex of anal vein, forming wavy texture.

Hindwings: Lanceolate with rounded apex, ⅘ as long as tegmen (Fig. 2B).

Measurements: See Table 2.

Holotype (SMNHTAU-I.442144): Macropterous female with subparallel body sides. Body almost completely preserved apart from: right III and IV antennomeres, part of the left antennomere III, and the left margin of the thorax. *Locality and horizon*: The Upper Albian–Lower Cenomanian Kachin amber yielding the described specimens originates from Northern Myanmar, Kachin Province, Hukawng Valley, Tanaing (near Noije Bum).

Paratype (SMNHTAU-I.442145): Macropterous, sex indeterminable with subparallel body sides. Partially preserved including only the abdominal tergites, tegmina, apices of hind wings, mid tibiae, mid tarsi, and posterior lobe of pronotum. The paratype exhibits minor structural and colour pattern differences from the holotype. The hindwing is longer. The pronotum texture is less pronounced, displaying reduced tubercles between the punctures. For differences in colouration refer to the description.

Table 2. Measurements and ratios of the holotype and paratype *M. coloradmonens* n. sp.

Meristic features	**Holotype**			**Paratype**		
	Length	**Width**	**L/W Ratio**	**Length**	**Width**	**L/W Ratio**
Body	6.42	2.05	3.13		2.02	
Head	0.89	1.33	0.67			
Eyes	0.79	0.38				
Interocular distance (center)	0.27					
Interocular distance (min)	0.18					
Distance between ocelli centers	0.11					
Compound eye to ocellus	0.04					
Clypeus	0.45	0.16				
Labrum	0.72	0.01				
Labium (total)	3.46					
Segment I	0.82	0.10				
Segment II	1.33	0.10				
Segment III	0.79	0.07				
Segment IV	0.52	0.07				
Labium segments length ratio	1:1.62:0.96:0.63					
Antennae to body length ratio				0.4		
Antennae	2.65					
Antennomere I	0.27	0.09				
Antennomere II	0.67	0.04				
Antennomere III	1.02	0.05				
Antennomere IV	1.69	0.07				
Antennomeres length ratio	1:2.48:3.78:2.56					
Pronotum	1.56	2.05	0.76			
Pronotum width at humerus		1.8				
Pronotum width at callus		1.52				
Collar (dorsal, medially)	0.1	0.59				
Collar height	0.29					
Scutellum	1.53	1.07	1.43	1.39	1.08	1.28
Tegmen attachment to scutellum apex	4.19			4.44		
Abdomen	3.08	2.02		3.04	1.67	1.82
Tegmen	4.49	1.34		4.97	1.37	3.63
Clavus	1.36			1.79		
Hind wing				3.57	0.97	
Fore leg	3.51					
Fore femur	1.39					
Fore tibia	1.45					
Fore tarsus	0.67					
Tarsomere I	0.31					

Table 2: Measurements and ratios of *M. coloradmonens* n. sp. *(continued)*

Meristic features	**Holotype**			**Paratype**		
	Length	**Width**	**L/W Ratio**	**Length**	**Width**	**L/W Ratio**
Tarsomere III	0.2					
Mid leg	3.74					
Mid femur	1.52					
Mid tibia	1.56					
Mid tarsus	0.66					
Tarsomere I	0.31					
Tarsomere II	0.09					
Tarsomere III	0.22					
Hind leg	5.84					
Hind femur	2.55					
Hind tibia	2.65				2.43	
Hind tarsus	0.64				0.67	
Tarsomere I	0.31				0.35	
Tarsomere II	0.1				0.15	
Tarsomere III	0.21				0.28	
Claw	0.16				0.16	

TAPHONOMY

Holotype. The amber is clear yellow, with sparse syninclusions which include branched plant trichomes, some lepidopteran scales, and boring Pholadidae bivalves (Smith & Ross 2018). The bug's hind tibiae are adhered to a slightly darkened amber flow. This surface is likely to have been hardened by the time the bug arrived as no part of it penetrated this surface. The bug was likely adhered to the old flow and covered by a new prolific flow while still alive as evidenced by its completeness. A trail of bubbles is leading to its head from the anterior, which would have formed it the new flow coming from the posterior; the bug was attached at its hind legs, thus while flowing around the bug the different fluid flows would have joined together over the head, allowing the formation of bubbles. The amber did not undergo significant compression as evidenced by spherical bubbles immediately adjoining the specimen, however local deformation is visible in the eye region, possibly as a result of the intersecting pholadid burrow disturbing the amber when it was not fully hardened.

Paratype. The amber is clear yellow, with unidentifiable plant matter syninclusions. Only the dorsal portion of the bug is preserved. It is dorsally attached to an amber flow showing some darkening and cracking, which indicates that a significant time passed before the covering of the second flow. It is likely that the bug had stuck to the first resin flow and was subsequently pulled off of the still sticky resin with

Fig. 6. Reconstruction of *Miropictopallium coloradmonens* n. sp. on a gymnosperm.

its back portion remaining behind by a predator, before a secondary flow covered it fully. The first flow bears a nematoceran Diptera and a pair of detached wings of *Burmacompsocus perreaui* Nel & Waller, 2007 (Psocodea: Compsocidae), which were probably left behind via a similar process.

DISCUSSION

Zhou *et al*. (2022) proposed three diagnostic characters for Yuripopovinidae as follow: (1) clavus of tegmen reduced, long and triangular or linear, claval commissure absent; (2) the tegminal veins R+M+Cu fused, together with A and C+Sc as three longitudinal veins on the corium+clavus; (3) abdominal sternites II, III and IV fused, and delimited by transverse depressions. The present specimens fulfil completely the first and third characters. Hence, the complete fusion of tegmen veins C and Sc does not constitute a synapomorphy of Yuripopovinidae. As such the second character is proposed to be modified to: (2) Corium+clavus with two separate longitudinal veins and C with Sc adhering or fused forming a thickened pterostigma-like structure on the anterior wing edge. Previous studies of Yuripopovinidae identified the anteriormost vein on the corium as the costal vein, however the identity of this vein as C or Sc in Heteroptera is contentious (Betts *et al.* 1986). In addition, the identity of the other vein on the corium has not been clearly established, R+M+Cu proposed by Zhou *et al*. (2022). This discussion, however, is beyond the scope of the study and thus the established convention for Yuripopovinidae will be followed.

This is the first observation of separate C and Sc veins in amber-preserved Yuripopovinidae. The C and Sc veins together form the thickened costal margin of the wing like in the impression fossils where this character state is reported, namely in *Dehiscensicoris sanctus* Yao & Ren, 2016 and *Pingquanicoris punctatus* Yao & Ren, 2016.

Zhou *et al*. (2022) proposed that the fusion between sternites II, III, and IV may be a diagnostic character for all of Yuripopovinidae. As the authors did not have access to the specimens of the other described species in the family their assumption could not be fully confirmed. The current specimen possesses this feature, strengthening the conclusion that it may indeed be a synapomorphy. It is still to be determined whether the character is synapomorphic to Yuripopovinidae, with only three genera so far confirmed to possess it (*Yuripopovina* Azar, Nel, Engel, Garrouste & Matocq, 2011, *Megaoptocoris* and *Miropictopallium* n. gen.).

All Yuripopovinidae from Lebanese and Kachin amber share an enlarged head with large stylate compound eyes and trilobate pronotum. These unique characters were proposed to hint at their close evolutionary relationship separating them from the other yuripopovinid taxa (Kóbor & Roca-Cusachs 2021).

Variable proportions of the rostrum and antennomeres within the genera of *Caulisculus* Zhang & Chen, 2020 and *Megaoptocoris* indicate that this character may not be very useful for genus level diagnosis but may still be diagnostic at the species level. The yuripopovinids from the Yixian formation described by Du *et al*. (2017) further strengthen this conclusion with specimens of a single species showing variable lengths or rostral segments but conserved general proportions.

It is noteworthy that holotype of *Miropictopallium coloradmonens* n. sp. is the first specimen of Yuripopovinidae that allows a clear view of the abdominal tergites. It shows that the fusion of sternites and laterotergites II, III, and IV does not extend to the tergites, which appear unfused.

Miropictopallium n. gen. shows multiple characters which are unique for the family. The new genus is distinct from the other genera of Yuripopovinidae in the following:

The body is 6.5-mm long and is the largest among the Yuripopovinidae from both Lebanese and Kachin ambers.

Head: The compound eyes are of significant size relatively to the head. The ratio the eye width to the head width in dorsal view is ~0.15 (Fig. 1B), while all other described species in the family possess a ratio equal to or higher than 0.3. The eyes are arranged closely together at the front and expanded diagonally backward (Fig. 1B). The eyes are protruding posteriorly to reach the callus of the pronotum (Fig. 1B). The anterior margin of the frons is carinate and apically armed with a pair of spines as in Figs 1A, 1B. The pair of contiguous ocelli (Fig. 1B) are borne on the protrusion unlike in *Caulisoculus* Zhuo & Chen, 2022 and *Pseudocaulisoculus* Kóbor & Roca-Cusachs, 2021. The antennae are shorter than half the length of the body. The clypeus is well developed and protruding, longer than the first antennal segment, which is unique among the yuripopovinid genera where the character state is known (*Reticulatitergum* Du, Hu & Yao, 2019, *Megaoptocoris*, *Caulisoculus*, *Yuripopovina*, *Birmaniaespina* Yu, Chen & An, 2024) (Fig. 1A). The bucculae are prominent, triangular, facing downward and away from the maxillary plates, unique among the yuripopovinid genera for which the character state is observable (*Megaoptocoris*, *Yuripopovina*, *Reticulatitergum*, *Caulisoculus*, *Birmaniaespina*) (Fig. 1A). The rostrum reaches the anterior quarter of the abdominal sternite IV (Fig. 1C), similar to *Megaoptocoris*, but different from *Reticulatitergum*, *Caulisoculus*, *Pseudocaulisoculus*, *Yuripopovina* and *Birmaniaespina*. The combination of the rostrum segments' length: the segments I & III subequal and the segment II longer than I (Fig. 1C), distinguishes *Miropictopallium* n. gen. from all yuripopovinid genera, apart from *Reticulatitergum* and *Crassiantenninus* Yao & Ren, 2016.

Thorax: The collar (Fig. 1A) is depressed dorsoventrally, unique for Yuripopovinidae for which the character state is known (*Reticulatitergum*, *Yuripopovina*, *Megaoptocoris*, *Caulisoculus*, *Pseudocaulisoculus*). In the dorsal view, the collar is indistinctly developed and poorly separated from the callus (Fig. 1B). The surface of the pronotum and the scutellum is uniformly and distinctly sculptured with round tubercles bumps and fine punctures among them (Figs 1B, 1C), in contrast with the punctate texture in other Yuripopovinidae genera. The callus of the pronotum is tuberculated bumpy and punctate, bearing a pair of smooth laterally keeled protuberances (Fig. 1A). These protuberances are reminiscent of the bulbous callus of *Megaoptocoris*, however, the smooth protrusion is limited to the lateral surface and is black in colour. The posterolateral margin of the pronotum is laminate, with lamina forming a process that laterally surpasses the humerus and the tegmen base. A similar process is observed in *Megaoptocoris*, but is less developed in *Miropictopallium* as in Figs 1D, 2A. The relative size of the scutellum is larger than in other yuripopovinids; the scutellum equal to the pronotum in length, and is ⅔ times as long as the width of the pronotum at the humeri (Figs 1D, 2A). The scutellum differs in shape from the rest of Yuripopovinidae by the lateral edges being slightly concave, the lateral margins expanded posteriorly and laminate, bounded by downward pointing setae, and by the apex raised above the tegmina (Fig. 1D). The anterior margin of the mesosternum does not extend to the anterior margin of the mid coxae, unlike in *Megaoptocoris* (Figs 1F, 2C).

Abdomen: The longitudinal groove extends to the sternite IV and smoothly joins the sternite surface in *Miropictopallium* n. gen., but has distinct lateral ridges in *Megaoptocoris*. The sternite IV is the longest; the sternites III and IV are subequal in *Megaoptocoris* (Fig. 4A). The abdomen extends laterally over the tegmina to form a prominent connexivum as in Figs 2A, 3A and 4C. The abdomen is convex (Figs 1C, 4D), similar to *Reticulatitergum* and *Yuripopovina*, and in contrast with *Caulisoculus* and *Megaoptocoris.* (The shape of the abdomen is not observable in other Yuripopovinidae.) The posterior margin of the tergite VII is concave, unlike straight posterior margin in *Megaoptocoris* (Fig. 4C).

Legs: The hind femora laterally bulging and bearing proximal longitudinal carinae (Fig. 1C).

Tegmina: with costal and subcostal veins are not fully fused, and the coriaceous pterostigma-like structure is elongated, apically tapering, and with concave posterior margin. Basal membrane possesses a large rectangular cell and two smaller irregular cells (Figs 3A, 3C).

PALAEOECOLOGICAL CONSIDERATIONS

The Burmese amber likely formed in the vicinity of fully marine conditions by the seashore as indicated by numerous inclusions of marine organisms (Mao *et al.* 2018; Smith & Ross 2018; Salamon *et al.* 2019; Yu *et al.* 2019). The amber producing palaeoenvironment is often interpreted as a wet tropical forest dominated by gymnosperms (Xing *et al.* 2018; Grimaldi 2002; Li *et al.* 2020; Feldberg 2021). This environment would have provided many microhabitats for the diverse entomofauna. Both the large eyes and colour pattern may help to elucidate the behaviour of *Miropictopallium coloradmonens* n. sp.

Miropictopallium coloradmonens n. sp. possesses eyes which are much larger than in the rest of Yuripopovinidae. The eyes are notably longitudinally elongated and extend backwards. It is likely that this is an adaptation for increased visual acuity. One of the main determinants of the resolution in the compound eyes, such as those of insects is the value of the interommatidial angle which represents the ratio of the ommatidium (=lens) diameter to the local radius of the eye $\Phi = D / r$. The smaller is the interommatidial angle, the greater is the eyes resolution. Thus, the increase of the local radius of the eye, or flattening of its surface would facilitate an increase in resolution. As such, the longitudinal elongation and flattening of lateral surfaces of the eyes of *Miropictopallium coloradmonens* n. sp. would have given it increased spatial resolution in this plane of vision (Land 1997). Variation of the resolution across different regions of the insect eye is commonly encountered. For example, the males of many fly species possess a so-called love spot, which is a dorsal extension of the eyes that is thought to allow greater resolution for mate detection (Perry *et al.* 2016).

Predatory insects, such as mantids, tend to exhibit an increase in resolution in the anterior facing portion of the eyes which facilitates prey tracking, a pattern unlike to that seen in *Miropictopallium coloradmonens* n. sp. (Land 1997). The shape of the eyes of *M. coloradmonens* n. sp. should permit higher resolution in the dorsal and lateral directions. The dorsal ommatidia appear to be larger than lateral ones, which would have allowed increased sensitivity, coupled with increased resolution due to reduced local curvature and the expansion of dorsal eye area in place of head cuticle (Pichaud *et al.* 2022). It is unlikely that *Miropictopallium coloradmonens* was carnivorous, as its rostrum is very elongated, while the common adaptation for predation among carnivorous Heteroptera is a stout rostrum, used for prey capture (Elson *et al.* 1937; Wang *et al.* 2020). Therefore, its well-developed eyes would represent an adaptation to something other than search for prey, and likely functioned for predator or mate detection. Further research is needed to determine the extent of variation in the mouthparts among the pentatomid groups with the diverse feeding behaviour.

Miropictopallium colouraedmonens n. sp. showcases a strikingly intricate colouration pattern of stripes and spots on its dorsal and lateral surfaces (Figs 2A, B, 3A, B), a stark departure from the previously documented genera, characterized by their low-contrast colouring. The described specimen is a female, which should indicate that the highly ornate colouration pattern is not related in this species to sexual selection (Resh & Cardé 2009). Alternative explanations for the striking patterns are camouflage and aposematism. Aposematic colouration is an evolutionary strategy in which an organism intentionally makes itself conspicuous in contrast to the background signalling predators about the unpalatability of the organism (Prudic *et al.* 2007; Resh & Cardé 2009). This effect is primarily achieved through vibrant red or yellow colours that contrast with black patches. This draws attention twice, both through the bright colours and strong contrast (Resh & Cardé 2009; Stevens & Ruxton 2012). Disruptive colouration is a type of camouflage, which breaks the visible outline of the organism through contrasting colours that form false edges or blur existing ones thus disrupting the predator's cognitive prey recognition mechanisms. On the other hand, cryptic camouflage exploits the predators' ability to detect prey on specific backgrounds (Schaefer *et al.* 2006).

As a rule, the occurrence of bright colours in fossils cannot be unequivocally confirmed, because amber and sedimentary environments tend not to preserve much pigmentation apart from shades of light and dark. A notable exception to this rule is the preservation of iridescent structural colour which is not present or hinted upon in the specimens, since they lack the characteristic silver appearance imparted by its degradation (Cai *et al.* 2020). However, bright pigmentation is expected to occur on otherwise lighter pigmented areas, which would be visible on fossils. Independently from pigments, as strong contrast is an important aspect in aposematism, stark light and dark pigmentation could be taken to indicate possible aposematic colouration (Stevens & Ruxton 2012; Ruxton *et al.* 2019).

Larger patches of starkly contrasting patterns that would draw a predator's attention at a distance, are a common feature of many aposematic patterns. These are likely used to reduce the incidence of accidental attacks by giving the predator time to act (Tullberg *et al.* 2005; Stevens & Ruxton 2012).

The colour pattern of *Miropictopallium coloradmonens* n. sp. suggests a likely use as aposematism. The body of the bug has clearly defined light- and dark-coloured patches next to each other to produce a high contrast pattern. Similar patterns can be observed in aposematic members of Lygaeidae (Burdfield-Steel & Shuker 2014). Another notable feature are the rows of black dots on the dorsal and lateral surfaces (pronotum, metathorax, connexivum), when the occurring on a darker background (dorsal pronotum) the dots are surrounded by a light-coloured ring, increasing contrast. The rows of dots produce an outstanding repeating geometric pattern. It is possible that these insects lived in more open and well-lit environments than other yuripopovinid species leading to selective pressure favouring improved ability for predator detection and aposematism.

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