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New Palaeontinidae (Cicadomorpha) from the Triassic of Central Asia: the earliest intimidating eyespots in Hemiptera

Новые Palaeontinidae (Cicadomorpha) из триаса Средней Азии: древнейшие отпугивающие глазчатые пятна у Hemiptera

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KEY WORDS: Homoptera, Auchenorrhyncha, Palaeontinoidea, Madygen, morphology, evolution, anti-predator mechanisms, predator mimicry.

КЛЮЧЕВЫЕ СЛОВА: Homoptera, Auchenorrhyncha, Palaeontinoidea, Мадыген, морфология, эволюция, способы защиты от хищников, имитация хищника.

ABSTRACT. Large cicadas *Papiliontina dracomima* **gen.** et **sp.n.**, *P. spectans* **sp.n.** and *P. machaon* **sp.n.** are described from the Middle to Late Triassic of Madygen, Kyrgyzstan. These are the oldest finds of the Mesozoic family Palaeontinidae. Two of the three species show a pair of large, concentric eyespots on their forewings, providing the earliest evidence for this anti-predator mechanism in Hemiptera. *Fletcheriana magna* Riek, 1976 from the Late Triassic of South Africa is singled out into *Karoontina* **gen.n.**: *Karoontina magna* (Riek, 1976), **comb.n.**

РЕЗЮМЕ. Крупные цикады *Papiliontina dracomima* **gen.** et **sp.n.**, *P. spectans* **sp.n.** и *P. machaon* **sp.n.** описаны из среднего–позднего триаса Мадыгена в Киргизии. Это древнейшие находки мезозойского семейства Palaeontinidae. У двух из трёх видов на передних крыльях видна пара больших, концентрических глазчатых пятен — это самое раннее свидетельство подобного способа защиты от хищников у Hemiptera. *Fletcheriana magna* Riek, 1976 из позднего триаса Южной Африки выделена в род *Karoontina* **gen.n.**: *Karoontina magna* (Riek, 1976), **comb.n.**

Palaeontinidae are large moth-like cicadas known from the Jurassic and Early Cretaceous worldwide [Menon *et al*., 2005; Wang *et al*., 2009]. Only two species of Palaeontinidae were recorded from the Triassic [Nam *et al*., 2017]. A new palaeontinid genus with three new species is described below from the Middle to Late Triassic of Madygen, Kyrgyzstan, and these are the oldest finds of the family. Two of the three species bear a pair of large concentric eyespots on their forewings, a colour pattern known in some Lepidoptera, but not in other Palaeontinidae and Hemiptera.

The famous fossil site near the village of Madygen in Kyrgyzstan has yielded the world's richest Triassic insect fauna, unusual tetrapods, fishes, crustaceans, bivalves, plants *etc*. [Voigt *et al*., 2017]. Twenty insect orders and more than one hundred families (including twenty families of Hemiptera) have been reported, and more than half a thousand species described from Madygen [Shcherbakov, 2008, 2011, 2021, 2022]. The Madygen Formation crops out in five areas, and the area richest in insects is Dzhailoucho. The clayey rock matrix at Dzhailoucho is linearly distorted, so that some specimens are extended lengthwise and others crosswise. Therefore, the length-to-width ratios are not diagnostic of the Dzhailoucho fossils, and the best estimate for their size is the square root of length x width (√LW).

All three specimens described below were collected together with ~3000 other insects in 1965 by a field party of the Paleontological Institute, USSR Academy of Sciences headed by Alexander G. Sharov. In search of such large insects as Orthoptera and Titanoptera, and small flying reptiles [Sharov, 1968, 1970, 1971], he undertook large-scale excavations, which yielded many unique finds not repeated by several subsequent expeditions.

The material is deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). The specimens were photographed with a Nikon D800 camera mounted with a Nikon AF-S ED Micro Nikkor 60 mm f/2.8G lens. Images were z-stacked with Helicon Focus Pro 6.7. Furthermore, a Leica DFC425 camera coupled to Leica M165C stereo-

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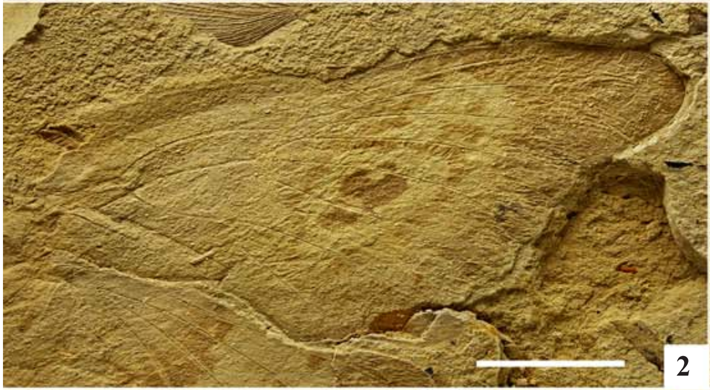
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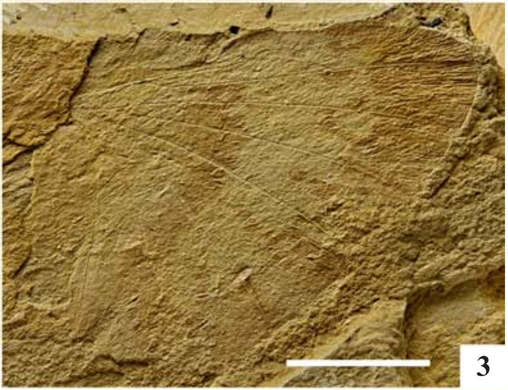
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microscope was used. The vein nomenclature follows Shcherbakov [1984, 1996].

Family Palaeontinidae Handlirsch, 1906

Papiliontina Shcherbakov, **gen.n.**

TYPE SPECIES. *Papiliontina dracomima* Shcherbakov, **sp.n.**

DIAGNOSIS. Forewing subtriangular; costal margin moderately arched; apical margin concave, festooned; well-developed tornus much projecting beyond line continuing commissural margin. Costal area with shallow depression along midline. Pterostigmal area wider than interradial area, with one slanting RA branch. Basal cell narrow, CuA stem abruptly bent at its apex and arched beyond it. Sc adjacent to R (except base) up to R fork. R forked distally (not earlier than 2/3 way from basal cell to nodal line), R fork narrow, RP nearly straight at nodal line. Prenodal *m-cu* weak, Y-shaped; nodal *m-cu* feebly arched or nearly straight. CuA2 straight beyond nodal line. Commissural margin with high carina. Basal cell closed with X-junction of M and CuA, and/or large eyespot on M branches. Hind wing subtriangular with radiating veins; R and CuA forks and long oblique *r-m* and *m-cu* close to wing base, M 3-branched near basal cell. Fore and hind wing membrane minutely granulate, near apical margin finely striate. Marginal membrane very narrow.

COMPOSITION. Three new species described below.

COMPARISON. The Triassic genus *Hallakkungis* is similar to *Papiliontina* **gen.n.** in the R stem forked distally, the wide pterostigmal area with a slanting RA branch ('RA1'), and the tornus projecting beyond continuation of the commissural margin, to *P. dracomima* **sp.n.** in the clavus truncate, and to *P. machaon* **sp.n.** in the nodal *m-cu* connecting MP and CuA stems before their forks. However, in *Hallakkungis* the costal margin is deeply arched near base, the apical margin is straight, the basal cell is wider and closed with rather long arculus, R bifurcates at the nodal line, CuA stem is not bent at the nodal line, and CuA2 is arched forwards beyond it. The new genus differs from Jurassic and Cretaceous genera in the structure of the basal cell and the CuA stem, and in the distal R bifurcation in the forewing, and 3-branched M in the hind wing.

ETYMOLOGY. From generic names *Papilio* and *Palaeontina*; gender feminine.

Papiliontina dracomima Shcherbakov, **sp.n.**
Figs 1–4, 8–9, 12–13.

MATERIAL. Holotype PIN 2555/2136, insect with one forewing and both hind wings spread (positive impression); Dzhailoucho (Madygen, northern area), Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Forewing 45 mm long, 19 mm wide (√LW = 29.3 mm; different length to width ratios in the holotype forewings of three new species are not diagnostic due to rock distortion); wingspan ~10 cm. At least 4 weak oblique veins in costal area; slanting postnodal R branch arising well beyond nodus. R forked 2/3 way from basal cell to nodal line. Basal cell closed with X-junction of M and CuA. MP stem more than twice shorter than MA stem. Nodal *m-cu* connecting MP2 near base and CuA bifurcation. Clavus obliquely truncate at apex. Prenodal part slightly darkened, anterior margin mostly dark, postnodal part with dark apical band and ocellate spot; the eyespot with dark and inner light rings complete, and outer light ring extended up to RA; dark central part not reaching MA2 and extended posterior to MP2, with two light flecks at MP1 and MP2. Hind wing 29 mm long (2/3 forewing length), 22 mm wide, costal area projecting crescent-like, anterior margin with more than ten close-set hooks before coupling lobe and deeply sinuate at lobe; anal area small, CuP and Pcu rather short; membrane light with dark narrow transverse band before midlength, broader apical band, and several radial streaks arising from inner margin of apical band. Pronotum 15 mm wide, 6 mm long, convex, shield-like, transverse oval with humeral angles triangularly projecting, covered with sparse transverse wrinkles. Meso- and metanotum very short, their posterior margins bisinuate with small triangular medial projections (rudimentary meso- and metascutellum). First abdominal tergites very short (1st–3rd preserved).

ETYMOLOGY. From Greek *drakon* (fabulous lizardlike animal) and *mimos* (imitator, actor).

Papiliontina spectans Shcherbakov, **sp.n.**
Figs 5–6, 10.

MATERIAL. Holotype forewing PIN 2555/2137± (very base and apex and most of clavus missing); Dzhailoucho (Madygen, northern area), Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Forewing 38 mm long, 21 mm wide as preserved, reconstructed length ~42 mm and width ~23 mm (√LW ~31 mm). At least 3 weak oblique veins in costal area; slanting postnodal R branch arising just beyond nodus. R forked just before nodal line. Basal cell closed with very short arculus. MP stem longer than MA stem. Nodal *m-cu* connecting MP2 near base and CuA stem before fork. Clavus acute at apex. Prenodal part dark, anterior margin mostly light, postnodal part with dark apical band and ocellate spot; the eyespot with dark and inner light rings developed only on outer side, and inner light ring with extension up to RA; dark central part stretching from MA2 up to MP2, in inner half with 7 light flecks in two transverse rows.

COMPARISON. Differs from the type species in the longer MP stem, more distal R bifurcation, acute apex of the clavus, and the colour pattern, including the structure of ocellate spot.

ETYMOLOGY. Latin *spectans* (watching).

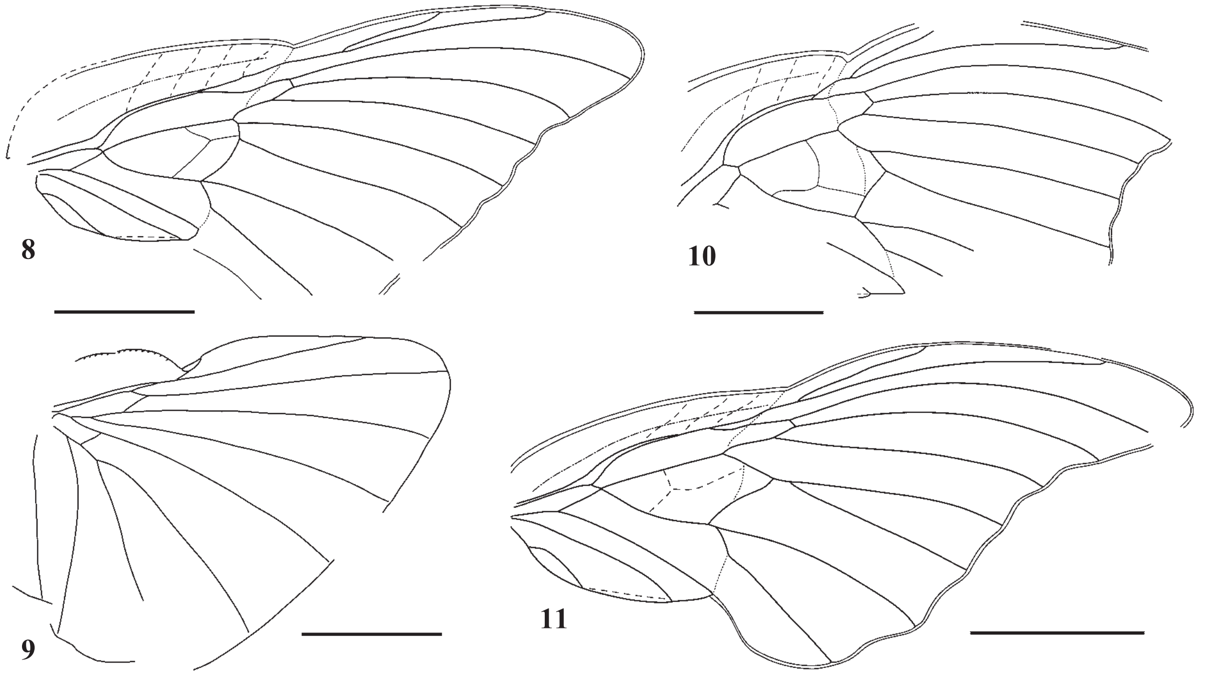
Papiliontina machaon Shcherbakov, **sp.n.**
Figs 7, 11.

MATERIAL. Holotype forewing PIN 2555/2314±; Dzhailoucho (Madygen, northern area), Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Forewing 41 mm long, 17 mm wide (√LW = 26.4 mm). At least 3 weak oblique veins in costal area; slanting postnodal R branch arising just beyond nodus. R forked 3/4 way from basal cell to nodal line. Basal cell closed with X-junction of M and CuA. MP stem longer than MA stem. Nodal *m-cu* connecting MP and CuA stems before

Figs 1–7. *Papiliontina* spp., holotypes, Madygen, Triassic: 1–4 — *P. dracomima* **sp.n.**: 1 — whole specimen; 2 — forewing (mirrored); 3 — hind wing; 4 — forewing eyespot (increased contrast; mirrored); 5–6 — *P. spectans* **sp.n.**: 5 — forewing; 6 — forewing eyespot (increased contrast); 7 — *P. machaon* **sp.n.**, forewing. Scale bars: 1 cm.

Рис. 1–7. *Papiliontina* spp., голотипы, Мадыген, триас: 1–4 — *P. dracomima* **sp.n.**: 1 — образец целиком; 2 — переднее крыло (перевернуто зеркально); 3 — заднее крыло; 4 — глазчатое пятно переднего крыла (контраст увеличен; перевернуто зеркально); 5–6 — *P. spectans* **sp.n.**: 5 — переднее крыло; 6 — глазчатое пятно переднего крыла (контраст увеличен); 7 — *P. machaon* **sp.n.**, переднее крыло. Длина масштабных линеек: 1 см.



Figs 8–11. *Papiliontina* spp., Madygen, Triassic, venation: 8–9 — *P. dracomima* **sp.n.**: 8 —forewing; 9 — hind wing; 10 — *P. spectans* **sp.n.**, forewing; 11 — *P. machaon* **sp.n.**, forewing. Scale bars: 1 cm.

Рис. 8–11. *Papiliontina* spp., Мадыген, триас, жилкование: 8–9 — *P. dracomima* **sp.n.**: 8 — переднее крыло; 9 — заднее крыло; 10 — *P. spectans* **sp.n.**, переднее крыло; 11 — *P. machaon* **sp.n.**, переднее крыло. Длина масштабных линеек: 1 см.

their forks. Clavus acuminate at apex. Forewing unevenly darkened, more so in posterior and discal areas, without distinct dark pattern.

COMPARISON. Similar to *P. spectans* **sp.n.** in the MP stem longer than MA stem, distal R bifurcation, and the clavus not truncate, but differs from it and the type species in the nodal *m-cu* joining MP stem and the absence of the ocellate spot.

ETYMOLOGY. After the type species of the genus *Papilio*.

Karoontina Shcherbakov, **gen.n.**

TYPE SPECIES. *Fletcheriana magna* Riek, 1976.

DIAGNOSIS. Forewing triangular oval; costal margin moderately arched, costal area with few oblique veins. Basal cell rather narrow, closed with arculus. R fork narrow, distal (level with M fork), RP nearly straight at nodal line. CuA stem bent at apex of basal cell and arched beyond it. Nodal *m-cu* bent inwards. CuA2 straight beyond nodal line. Pterostigmal area wide. Forewing dark, postnodal part with rows of small light spots.

COMPOSITION. Monobasic: *Karoontina magna* (Riek, 1976), **comb.n.**

COMPARISON. Similar to *Papiliontina* **gen.n.** in the R stem forked distally, the CuA stem bent at the apex of the narrow basal cell, and the costal margin moderately arched, but in the latter genus the nodal *m-cu* is feebly arched or nearly straight, and the postnodal part is more triangular, with concave festooned apical margin, without rows of light spots. In *Fletcheriana triassica* Evans, 1956, the type species of the genus *Fletcheriana* (Dunstaniidae), the costal area is wider, with more numerous Sc branches, the R is forked much earlier (halfway from basal cell to nodal line, before M fork), the R fork and radial area are much wider, and the RP is bent stepwise at the nodal line.

ETYMOLOGY. From Karoo Supergroup and the genus *Palaeontina*; gender feminine.

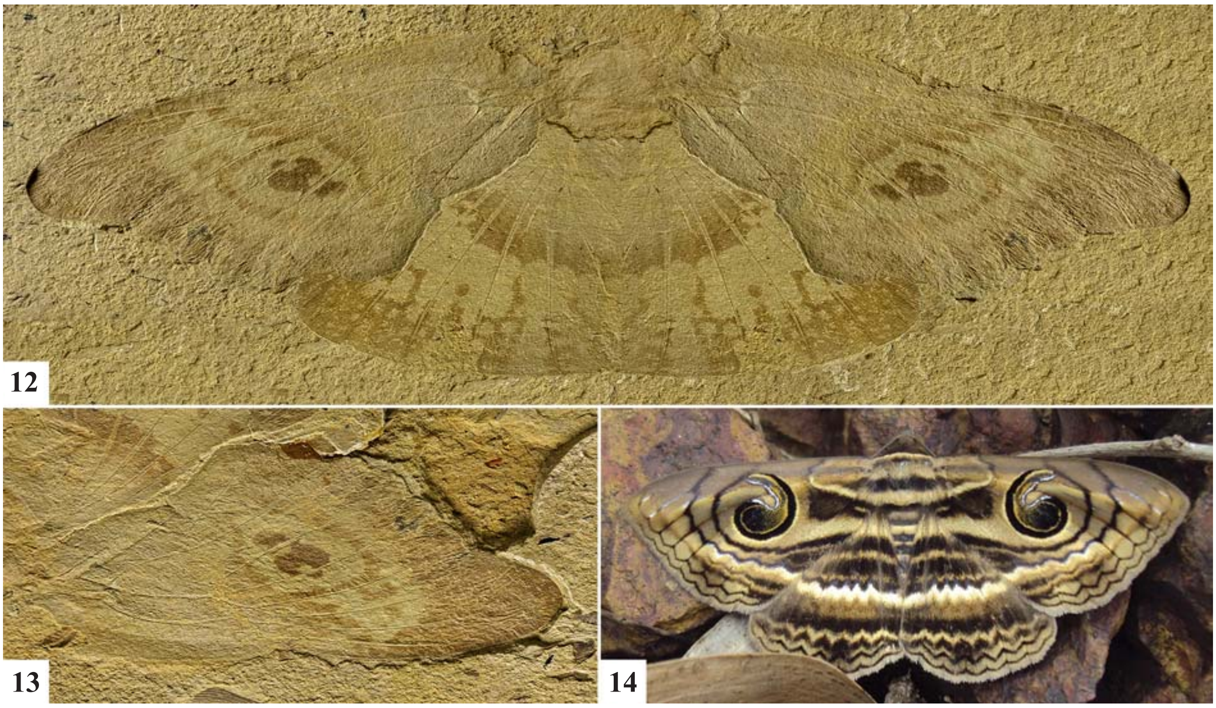
Discussion

Palaeontinids were initially considered butterflies or moths [Westwood, 1854; Butler, 1873; Oppenheim, 1885] and placed in a separate family [Handlirsch, 1906–1908] and suborder of Lepidoptera [Tillyard, 1919], but then reinterpreted as cicada-like Homoptera [Scudder, 1875; Brauer *et al.*, 1889; Martynov, 1927, 1931]. Tillyard [1916, 1918, 1921] described the families Dunstaniidae and Mesogereonidae from the Triassic of Australia and considered palaeontinids and mesogereonids related to Cicadoidea, and dunstaniids at first to Lepidoptera, and then to Heteroptera. Becker-Migdisova [1949: 45] united all three families into a superfamily Palaeontinoidea. Considering *Palaeontina* Butler, 1873 to be a lepidopteran, Evans [1956] proposed the family Cicadomorphidae for some of allied genera, but Becker-Migdisova [1962] synonimized Cicadomorphidae under Palaeontinidae.

Evans [1956] assigned the monotypic genus *Fletcheriana* Evans, 1956 from the Middle Triassic (Anisian) of Australia to Cicadomorphidae. Riek [1976] described *Fletcheriana magna* Riek, 1976 from the Late Triassic (Carnian) of South Africa and transferred this genus to Dunstaniidae. Nam *et al.* [2017] assigned to Palaeontinidae the monotypic genus *Hallakkungis* Nam *et al.*, 2017 from the Late Triassic (Norian) of Korea. Becker-Migdisova and Wootton [1965] described two genera of Dunstaniidae from the Ladinian–Carnian of Madygen and pointed out that Dunstaniidae differ from Palaeontinidae in the R and M forks more proximal and the RA, RP and MA sharply curved at the nodal line in the forewing. Accordingly *'F.' magna* Riek, 1976 (not assigned to any genus) was moved to Palaeontinidae, and it was noted that the most primitive palaeontinids are still similar to Dunstaniidae in the forewing shape and hind wing venation [Shcherbakov, 1984, 1985]. Three Jurassic species known from isolated hind wings were assigned to *Fletcheriana*, but Wang *et al*. [2009] removed two of them to two palaeontinid genera and considered this genus transitional between Dunstaniidae and Palaeontinidae. The genera *Karoontina* **gen.n.** with one Carnian species, *K. magna* (Riek, 1976), **comb.n.** and *Papiliontina* **gen.n.** with three Ladinian–Carnian species are similar in many respects and represent the most primitive palaeontinids known so far. The latter genus is more primitive in the structure of the basal cell, but more specialized in the wing shape and presence of eyespots.

Eyespots evolved independently in many insects and vertebrates as anti-predator devices. Small spots, located near the rear end or the wing margin of the insect, deflect predator attacks away from vital parts of the body [Stevens, 2005; Kodandaramaiah, 2011]. Several pairs of dark spots may be part of the spider-like pattern on the tegmina of living and fossil planthoppers, which is an example of predator (or evasive prey) mimicry [Shcherbakov, 2007]. A pair of much larger eyespots with concentric dark and light elements mimics the eyes of a large vertebrate predator and intimidates other predators [De Bona *et al*., 2015; Mukherjee, Kodandaramaiah, 2015]. Some moths and planthoppers, which have several pairs of eyespots of different sizes, can use both deflection and intimidation mechanisms [Kodandaramaiah *et al*., 2015; Jiang *et al*., 2023]. The effectiveness of intimidating and deflective eyespots has been experimentally proven, including when lizards attack butterflies [Halali *et al*., 2019; Radford *et al*., 2020].

Intimidating eyespots on insect wings are nearly as ancient as the winged insects themselves. The oldest record of such anti-predator device is a pair of large transverse oval light rings (with a dark centre) on the dark forewings of a large protorthopteran *Protodiamphipnoa gaudryi* (Brongniart, 1885) (= *P. tertrini* Brongniart, 1894) from the latest Carboniferous of France [Nel, Poschmann, 2021]. Large concentric eyespots were widespread and diverse in Mesozoic lacewings of the family Kalligrammatidae (Jurassic–mid-Cretaceous), convergently similar to Cenozoic butterflies [Labandeira *et al*., 2016]. The eyespots of *Papiliontina* spp. are no less intricate than the most complex kalligrammatid eyespots, with a dark center ("pupil") highlighted by light flecks (so-called "ocules") and



Figs 12–14. Intimidating eyespots: 12–13 — *Papiliontina dracomima* **sp.n.**, Madygen, Triassic: 12 — reconstruction of the holotype with spread forewings (photomontage); 13 – forewing (costal margin looking down); 14 — *Spirama retorta* (Clerck, 1764) (Erebidae), female, India, recent; image by Vinayaraj, 2013, licence CC BY-SA 3.0. https://en.wikipedia.org/wiki/Spirama#/media/File:Spirama_retorta_13.jpg

Рис. 12–14. Устрашающие глазчатые пятна: 12–13 — *Papiliontina dracomima* **sp.n.**, Мадыген, триас: 12 — реконструкция голотипа с отведенными в стороны передними крыльями (фотомонтаж); 13 – переднее крыло (костальный край обращен вниз); 14 — *Spirama retorta* (Clerck, 1764) (Erebidae), самка, Индия, современная; фото Vinayaraj, 2013, licence CC BY-SA 3.0. https://en.wikipedia.org/wiki/Spirama#/media/File:Spirama_retorta_13.jpg surrounded with one light, one dark, and another light ring. This means that already by the mid-Triassic, some insects perfectly imitated a pair of eyes of vertebrate predators (probably reptiles).

Various modern moths and some katydids and lanternflies [Goemans, 2006] have a pair of intimidating eyespots only on their hind wings, which are hidden under the cryptically coloured forewings at rest, and display them when disturbed, which startles the predator and enhances the effect. In *Papiliontina dracomima* **sp.n.** (and probably also *P. spectans* **sp.n.**) a pair of large eyespots is developed only on the forewings, as in many kalligrammatids, some modern mantises (*Pseudocreobotra*), grasshoppers, beetles [Cott, 1940], and moths. *Pseudocreobotra* spreads its forewings displaying eyespots to startle predators, and *Protodiamphipnoa* may have done the same. Some Oriental and Australian owl moths (Erebidae) have large ocellate spots on their forewings, held flat in repose. In *Speiredonia* spp., the large spots on forewings look like eyes, and small spots on the hind wings like the nostrils of a large reptile [Herbison-Evans *et al.*, 2022]. Even more similar to *P. dracomima* **sp.n.** are decorated several species of another erebid genus, *Spirama* Guenée, 1852: these moths resemble a frontal view of a snake's face with its slightly opened mouth, imitated by the light bands of the hind wings (Figs 12, 14) [Wikipedia, 2022]. If *Papiliontina* species held their wings flat and sideways at rest (and this is quite likely, judged by the poor development of the mesoscutellum), or spread their forewings to show the hind wings when startled, the light bands on the hind wings looked like an open mouth with protruding teeth (dark streaks). Otherwise, if *Papiliontina* species held the forewings rooflike in repose, then in the side view their concave, uneven apical margins and protruding apices complemented the illusion of a lizard's head (Fig. 13). In this case, the light areas of their hind wings were probably vividly coloured and only seen when in flight, as in various modern grasshoppers and some Cicadidae (*Platypleura* spp.) with bright hind wings hidden under cryptically coloured forewings at rest (so-called flash behaviour [Drinkwater *et al.*, 2022]).

Eyespots are not known in other palaeontinids. Most Jurassic and some Cretaceous Palaeontinidae bear dark and light transverse bands (or rows of spots) on their wings, and this disruptive colour pattern camouflaged them on host plants. Some Jurassic and many Cretaceous forms lack such transverse banding [Menon *et al.*, 2005; Ueda, 2008]. This shift in predominant dark patterns in palaeontinids (eyespots – transverse bands – no bands) is possibly related to the development of the visual perception abilities in their predators, arboreal reptiles and early birds.

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