The first Mesozoic Derbidae (Homoptera: Fulgoroidea) from Cretaceous Burmese amber

Первые мезозойские Derbidae (Homoptera: Fulgoroidea) из мелового бирманского янтаря

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ABSTRACT. Derbachile hochae gen. et sp.n., D. aschei sp.n. and Achiderbe obrienae gen. et sp.n. from mid-Cretaceous Burmese amber described in Derbachilini trib.n. are the first Mesozoic and the earliest fossil Derbidae. D. hochae sp.n., with 2.6 mm tegmina, is one of the smallest derbids known. Like their modern relatives, Burmite derbids could feed on monocots and woody dicots, and their nymphs could dwell in rotting wood and plant debris. Transformation of achilid-like ancestors into typical derbids is discussed. The new tribe combines achilid facies of primitive derbids with some characters of more advanced tribes, such as sensory pits on the costal vein in tegmen, narrow face, flattened antennae and subantenal carina. The tribe is assigned to the primitive subfamily, which is renamed Breddiniolinae Eenhof, 1950, stat.n. (= Cedusinae Emeljanov, 1992, syn.n.) by priority.

REZIOME. Derbachile hochae gen. et sp.n., D. aschei sp.n. и Achiderbe obrienae gen. et sp.n. из среднечемового бирманского янтаря описаны в подсемействе Derbachilini trib.n. Это первые мезозойские и древнейшие ископаемые семейства Derbidae. D. hochae sp.n. с передними крыльями 2.6 мм — одна из мельчайших известных дербид. Подобно современным дербидам, меловые могли питаться на однодольных и древесных двулиных, а их личинки — обитать в гниющей древесине и растительном опаде. Обсуждается преобразование подобных ахиллами предков в типичных дербид. Новая триба сочетает ахиллидные черты примитивных дербид с некоторыми признаками более продвинутых триб, такими как сенсорные ямки на костальной жилке переднего крыла, узкое лицо, уплощённые усики и подсушковый киль. Эта триба отнесена к примитивному подсемейству, название которого, согласно приоритету, изменено на Breddiniolinae Eenhof, 1950, stat.n. (= Cedusinae Emeljanov, 1992, syn.n.).

Derbidae, with more than 160 described genera and almost 1,700 species, is the third most diverse planthopper family after Cixiidae and Delphacidae [Bourgoin, 2020], having a higher proportion of diversity in the tropics than the latter two families. The family is currently divided into three subfamilies and 21 tribes [Bourgoin, 2020]. Derbids are structurally diverse: the higher tribes are easily recognizable by their peculiar appearance, while the most primitive ones often look like Achilidae, so that the assignment of three tribes to Derbidae has yet to be confirmed by studying their male genitalia.

The fossil record of Derbidae is rather scarce, and until now has been limited to the Cenozoic. Currently only five of the extant tribes are recorded from ambers and sedimentary rocks (Cedusini, Cenchreini, Derbini, Otocerinii, Zoraidini) [Emeljanov, 1994, 2002, 2008a; Emeljanov, Shcherbakov, 2000; Storeshi, Szweda, 2002; Szweda, 2004a, 2005, 2006]. The extinct tribe Ptychoptilini from Eocene Baltic amber, described in Achilidae [Emeljanov, 1990], was related to the derbid tribes Ipsnolini and Vinatini by Szwedo and Stroi [2001], and therefore moved to Derbidae [Bourgoin, 2020]. The alleged Triassic find does not belong to the family [Emeljanov, 1994].

Mid-Cretaceous Burmese amber, formed on an island in the tropical ocean Tethys between Gondwana and Laurasia [Westerweel et al., 2019], contains a rich insect
fauna. This amber was dated to the early Cenomanian (~99 Ma) [Shi et al., 2012], but it has recently been shown that ambers from some mines are much older or younger (from early Albian to late Campanian, ~110–72 Ma) [Xing, Qiu, 2020]. Among diverse Burmite Fulgoroidea, there are four endemic families (Dorytocidae, Yektakatiidae, Jubisentinidae, Katlasitidae) [Emeljanov, Shcherbakov, 2018; Song et al., 2019; Zhang et al., 2019; Luo et al., 2020b], three widespread Cretaceous families (Perirossidae, Mimarachnidae, Neazoniidae) [Shcherbakov, 2007a, b, 2017; Zhang et al., 2017; Jiang et al., 2018; Luo et al., 2020a; etc.], and a few extant families, such as Cixiidae and Achilidae [Shcherbakov, 2000; Szvedo, 2004b]. Upon closer inspection, some of Burmite achilid-like fossils turned out to be very primitive derbids. They are described below as a new tribe.

The type specimens are deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera and z-stacked with Helicon Focus 7.0. The type specimens are deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera and z-stacked with Helicon Focus 7.0. The specimens were also examined under a Zeiss Axioskop 2 microscope with a Zeiss AxioCAM 105 digital camera. Nomenclature of the plant hopper cranium is given after Anufriev and Emeljanov [1988].

**Family Derbidae Spinola, 1839**

Subfamily Breddiniolinae Fennah, 1950, stat.n.

**TYPE GENUS:** *Breddiniola* Muir, 1934.

**COMPOSITION.** Breddiniolini Fennah, 1950; Ptychoptilini Emeljanov, 1990; Vinatini Emeljanov, 1992; Cedusini Emeljanov, 1992; Ipsololini Emeljanov, 1995; Goneokarelini Emeljanov, 1995; Phrygimi Emeljanov, 1995; Derbachilini trib.n.

*Tribe Derbachilini Emeljanov et Shcherbakov, trib.n.*

**DIAGNOSIS.** Tegmina long (tegmen length greater than body length), shallowly testiform in repose, with achilid-like venation, shallowly convex costal margin, longitudinal branches of *M* and *CuA*, *CuA2* terminating on apical margin, apically truncate clavus about 1/2 wing length, and sensory pits on *C*. Hind wing with *Sc* and *M* forking before crossveins, 3-branched *CuA*. Pedicel somewhat enlarged and flattened. Subantennal ridge low or absent. Apical segment of rostrum long.

**REMARKS.** The new tribe combines the primitive structure of the hind wing and rostrum with a few characters of moderately derived Derbidae (sensory pits on *C*, enlarged flattened antennae). The type genus shows also the narrowed metope and primitive structure of pronotum and hind legs, and its type species, a rudimentary subantennal ridge. Such a character combination is unknown in other Derbidae (see Discussion).

**Genus Derbachilus Emeljanov et Shcherbakov, gen.n.**

**TYPE SPECIES:** *Derbachilus hocha* Emeljanov et Shcherbakov, sp.n.

**DIAGNOSIS.** Small, slender. Tegmen with slight, elongated, much widened distally, clavus less than 1/2 wing length. *C* with sensory pits at base and along anterior margin; *Sc* and *M* forming short stalk beyond basal cell; *Sc* forking earlier than *CuA*; stigmal cell darkened; *RA2* with short fork, *RA2a* recurrent, *RP* simple; *M* with 4 terminations, MA forking much earlier than MP, medial cell narrow, medial apical cells long; *CuA1* and *CuA2* connected by crossvein *icua* distal to 2*m*-*cu*, *CuA1* bent at 2*m*-*cu* and *icua*, 1st procubital cell long and wide distally; *CuA2* distant from posterior margin and reaching apical margin; crossvein on clavus between *CuP* and *Pcu*. Hind wing broad, *RP* simple, *M* forking before crossveins *r*-*m* and *m*-*cu*, *CuA* with 3 terminations. Pedicel enlarged, more or less flattened. Metoep narrow dorsally. Lateral ocelli present. Subantennal ridge low or absent. Rostrum surpassing mid coxae, apical segment more than three times longer than wide. Pronotum with strongly elevated, long, triangular, triradiate disc occupying almost 1/2 width. Mesonotum with lateral discal carinae strongly converging anteriorly, median carinae weak or absent. Legs long, slender. Hind tibia with 2–3 lateral teeth (1st minute, at base) and 8–11 apical teeth, tarsomere 1 with 6–9, II with 4–6 apical teeth, without discernible subapical setae.

**COMPOSITION.** Type species and *D. ashei* sp.n., gender feminine.

**Derbachilus hocha** Emeljanov et Shcherbakov, sp.n.

**Figs 1–10, 27.**

**MATERIAL.** Holotype PIN 5608/134, — Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous (probably Albian–Cenomanian).

**DIAGNOSIS.** Wings hyaline; body pale, disc of mesonotum dark; legs pale with dark streaks; median carina of mesonotum absent; hind tibia with 2 lateral teeth.

**DESCRIPTION.** Tegmen 2.6 mm long, ca. 1.0 mm wide, elongate, much widened distally, 2.5:1, hyaline, slightly infuscated anterior margin, veins and stigmal cells fuscos. Anterior margin shallowly convex, with slight concavity at nodus; apical margin rounded. Costal vein turning flat, transversely corrugate distal of *Sc*; *Cu* and *C* and ambient vein with sensory pits up to apex of tegmen. *Sc* and *Cu* fork distal of, and union of claval veins. Nodal *r*-distal to nodal *m-cu*. *MA* fork about halfway from nodal *r*- to *2r*-*m*. Medial cell long and narrow, about as large as cell distal to it and twice larger than cell anterodistal to it. Crossvein on clavus between *CuP* and *Pcu* before middle. Clavus truncate at apex. Hind wing 2.2 mm long, 1.1 mm wide, relatively large, 0.8 as long as tegmen, and moderately broad, 2.0:1, apex distinctly not reaching apex of tegmen in repose; membrane transparent, veins infuscated. Costal margin convex, coupling lobe in concavity before wing midlength. *Sc* apex level with *M* fork. *M* fork 1.2 times as long as *CuA1* fork. Body 2.2 mm long; body and appendages pale fuscos, disc of mesonotum brown, femora and tibiae with brown longitudinal streaks. Head 1/2 as wide as pronotum; eyes large, hemispherical, emarginate below; head and corypee deeply arcuately excavate posteriorly; posterior angles of corypee at eye midlength. Cephalic plate, anteriorly less than 1/3 head width and as wide as long in middle, depressed between high lateral carinae converging anteriorly, with strong median carina; corypee curved into, and median carina continued onto, metoep. Metoep triradiate, narrow and more depressed dorsally, more than twice widened ventrally; epistomal suture depressed. Scape elongate, obliquely produced anterodorsally, pedicel twice longer than scape, oval, ear-shaped, flattened dorsally, scapes, pedicel 2/3 as long as head width. Pedicel covered with cuticular denticles, with more than ten plaque organs on each side. Low subantennal ridge running from epistomal suture to below antennal base.
Figs 1–10. *Derbachile hochae* gen. et sp. n., holotype male, Burmese amber: 1 — habitus, dorsal; 2 — habitus, ventral; 3 — head and thorax, dorsal; 4 — head and thorax, ventral (arrows, subantennal ridges); 5 — tegmen, anterodorsal; 6–7 — C and stigmal cell: 6 — right, 7 — left tegmen; 8 — hind legs; 9 — genitalia, ventral; 10 — genitalia, dorsal. Scale bars: 0.5 mm.

Рис. 1–10. *Derbachile hochae* gen. et sp. n., голотип, самец, бирманский янтарь: 1 — общий вид, сверху; 2 — общий вид, снизу; 3 — голова и грудь, сверху; 4 — голова и грудь, снизу (стрелки — подусиковые кили); 5 — переднее крыло, спереди-сверху; 6–7 — C и стигмальная ячейка: 6 — правое переднее крыло, 7 — левое переднее крыло; 8 — задние ноги; 9 — гениталии, снизу; 10 — гениталии, сверху. Длина масштабной линейки: 0.5 мм.
nate, strongly narrowed towards uncinaricate, laterally compressed anteclypeus. Rostrum reaching hind coxae, apical segment at least 4 times as long as wide. Pronotum 0.85 as wide as mesonotum, 1.3 as long in middle as wide, inverted V-shaped, lateral margins acute, posterior margin sinuate medi- ally; strongly elevated triangular tricarinicate disc 1.4 as wide as long in middle, almost 1/2 pronotum width. Mesonotum with nearly diamond-shaped disc, lateral carinae less than 1/2 disc strongly converging anteriorly, median carina absent. Legs very slender, femora and tibiae carinate. Hind tarsus nearly 2/3 as long as tibia, tarsomere I and II widely at apices; tibia with minute lateral tooth near base and larger one before midlength, and 8 apical teeth in uneven pecten; tarsomere 1 with 6, II with 4 apical teeth. Claws slender. Male genital block small, anal tube rather short, styles directed caudally, with slender processes.

ETYMOLOGY. Named in honour of Prof. Hannelore Hoch, a brilliant entomologist, specialist on Cixiidae and other Fulgoroidea.

*Derbachile aschei* Emeljanov et Shcherbakov, sp. n.

Figs 11–20, 25, 26.

MATERIAL. Holotype PIN 5608/123a, ♂, head and thorax dorsally eaten by some arthropod scavenger; paratypes: PIN 5608/123b, male (?), in same amber piece as holotype, oxidized, antennae detached; 5608/129, sex unknown, fore legs malformed, most of head, hind legs and abdomen eaten away; 5608/130, female — Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous (probably Albian–Cenomanian).

DIAGNOSIS. Wings fuscous with darker shade along vein apices and pale at and near crossveins; body and legs fuscous; median carina of mesonotum incomplete; hind tibia with 3 lateral teeth.

DESCRIPTION. Tegmen 2.9 (paratype 5608/130) –3.6 mm long (paratype 5608/129), elongate, much widened distal- ly, 2.3:1; membrane fuscous, finely transversely corrugate; veins darker, apical vein sections margins with darker shade; stigmatic cell brown; pale: ScR1, RA2a, RA2b, ir and RP near it, 2r-m, ima, MP2 base, 2m-cu, CuA1 from 2m-cu to icua, icua and CuA2 shortly beyond it, postclaval crossvein, and truncate claval apex. Anterior margin almost straight near base and shallowly convex below; apical margin broadly rounded. Costal vein turning flat, eccentric distad of ScR fork. C and ambient vein with minute sensory pits from base to apex of tegmen. ScR fork slightly distad of, and CuA fork more distad of, union of claval veins. Nodal r–m distal to, or sometimes level with, nodal m–cua. MA fork much closer to nodal r–m than to 2r–m. Medial cell long and narrow, about as large as cell anterodistal or cell distal to it. Crossvein on clavus between CuP and middle of Pcu. Claval furrow continued beyond truncate claval apex; CuP+Pcu+1A running close to posterior margin slightly beyond postclaval crossvein. Hind wing very large, almost 0.9 as long as tegmen, and very broad, 1:7:1, apex slightly not reaching apex of tegmen in repose; membrane pale fuscous, finely wrinkled; apical vein sections margins with darker shade, veins and coupling lobe brown, medial and claval folds pale. Costal margin biconvex, coupling lobe in concavity before wing midlength. ScRA apex proximal of level of M fork. M fork 1.3 times as long as CuA1 fork. Body 2.3 (paratype 5608/130) –2.9 mm long (paratype 5608/123b); body and appendages various shades of brown. Head 1/2 as wide as pronotum; eyes large, ovoid, emarginate below; head and coryphe aracutely excavate posteriorly; posterior angles of coryphe close to eye midlength. Coryphe narrow trapezoidal, anteriorly less than 1/5 head width and less than 1/2 as wide as long in middle, slightly depressed between high lateral carinae markedly converging anteriorly, median carina obsolete; cory- phe steeply curved into metope. Metope tricarinicate, narrow and depressed between high lateral carinae, more than twice widened ventrally. Lateral ocellus anterior to eye. Scape rather short, not produced, pedicel 2.5 as long as scape, enlarged and slightly flattened, scape + pedicel 3/4 as long as head width. Pedicel covered with cuticular denticles, with many plaque organs. Subpentamid ridge absent. Postclypeus tricarinicate, strongly narrowed towards uncinaricate, laterally flattened ante- clypeus. Rostrum reaching hind coxae, apical segment dark, 4 times as long as wide. Pronotum 0.9 as wide as mesonotum, 0.4 as long in middle as wide, inverted V-shaped, lateral margins acute, posterior margin sinuate medially; strongly elevated triangular tricarinicate disc as wide as long in middle, almost 0.4 pronotum width. Mesonotum with nearly diamond- shaped disc, lateral carinae of disc obsolete, converging ante- riorly, weak median carina in anterior part. Legs slender, femora and tibiae carinate. Hind tarsus 2/3 as long as tibia, tarsomere I longer than II+III; tibia and tarsomeres I and II markedly widened at apices; tibia with minute lateral tooth near base and two larger ones before 1/3 and 2/3 length, and 11 apical teeth in uneven pecten; tarsomere I with 9, II with 6 apical teeth. Claws slender. Male genital block rather large, anal tube long, with lateral lobes, styles long, upcurved. Fe- male genital block subtriangular in ventral aspect.

REMARKS. The specimens assigned to this species share the same general structure and colour pattern, but show significant size variation, indicating that they may belong to more than one closely related species, distinguishable only by the charac- ters of male genitalia, as in the genus *CEDUSA* Fowler, 1904.

ETYMOLOGY. Named in honour of Dr Manfred Asche, an eminent entomologist, specialist on Delphacidae and other Fulgoroidea.

Genus *Achiderbe* Emeljanov et Shcherbakov, gen. n.

TYPE SPECIES: *Achiderbe obrienae* Emeljanov et Shcherbakov, sp. n.

ETYMOLOGY. Free combination of generic names *Achil- us* and *Derbe*; gender feminine.
First Mesozoic Derbidae from Burmese amber
**Achiderbe obrienae** Emeljanov et Shcherbakov, **sp.n.** Figs 21–24, 28.

**MATERIAL.** Holotype PIN 5608/126, ♀, most of head and dorsal part of thorax eaten by some arthropod scavenger, distal parts of hind legs polished away; syninculations: 2 Empidoidea — Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous (probably Albian–Cenomanian).

**DESCRIPTION.** Tegmen 3.9 mm long, elongate, 2.8:1, fuscous with pale: irregular transverse bands proximally, crossveins and vein apices distally; stigmal cell pale at nodus, distally of same shade of brown as adjacent cells. Anterior margin shallowly convex near base and at nodus, almost straight between; apical margin obliquely rounded. Costal vein thickened near base, turning flat, slender distad of ScR+M stalk; C and ambient vein with sensory pits, better developed at base, traceable up to apex of tegmen. ScR fork much distad of, and CuA fork distad of, union of claval veins. Nodal r-m level with nodal m-cu. MA fork about halfway from nodal r-m to 2r-m. Medial cell long and broad, much larger than cell distal to it or cell anterodistal to it. Clavus truncate at apex, without crossvein. Hind wing ca. 2.9 mm long, 1.2 mm wide, not large, 0.75 as long as tegmen, and narrow, 2.4:1, apex considerably not reaching apex of tegmen in repose; membrane fuscous, veins brown. Costal margin biconvex, coupling lobe in concavity beyond wing midlength. ScRA apex proximad of level of M fork. M fork twice as long as CuA1 fork. Body 3.6 mm long; body and appendages various shades of brown. Antero- dorsal part of head not preserved. Scape elongate, obliquely produced anterodorsally, pedicel thricre longer than scape, paddle-shaped, flattened, scape + pedicel about as long as clypeus. Pedicel covered with cuticular denticles, with many plaque organs. Subantennal ridge absent. Postclypeus strongly narrowed towards unicarinate, laterally flattened anteclypeus. Rostrum reaching hind coxae, apical segment dark, about 4 times as long as wide. Pronotum not preserved. Mesonotum with lateral discal carinae strong, subparallel, median carina well-developed. Legs rather short and stout, tibiae tetrahedral, somewhat flattened, hind tibiae without lateral teeth in proximal half (their distal half and hind tarsi not preserved), claws strong. Abdomen slightly inflated, laterotergites rectangular. Male genital block rather small; pygofer ventrally sinuate with median depression between two oblique carinae; anal tube rather long, with posteralateral lobes; styles short and broad, their apices bent mediad.

**ETYMOLOGY.** Named in honour of Dr Lois B. O’Brien, a worldwide known entomologist, specialist on Fulgoroidea.

**Discussion**

On the classification of Derbidae. Frederick Muir [1913] divided Derbidae into six groups and subgroups based almost exclusively on the venation and relative size of wings: I, *Cenchrea* group; II, *Otiocerus* group; III,
with Sikaiana and Zoraida subgroups; IV, with Derbe + Mysidia and Rhotana subgroups. Later he created four subfamilies and two tribes, Cenchreinae, Otiocerinae, Derbinae (Derbini including Zoraida, Sikaianini) and Rhotaninae [Muir, 1917], and then rearranged these taxa as six tribes of two subfamilies, Zoraidinae (Zoraidini, Sikaianini) [Muir, 1918a] and Derbinae (Derbini, Rhotanini, Cenchreini, Otiocerini) [Muir, 1918b]. Fennah [1952] revised Derbidae into the same six tribes without grouping them into subfamilies. Emeljanov [1992, 1995] revised the family classification using additional characters, first of all sensory pits on the body and tegmina, and reconstructed phylogeny for the family. He divided Derbidae into three subfamilies, including Otiocerinae (= Zoraidinae) and the new subfamily Cedusinae, and proposed a series of new tribes and subtribes: Ipsinolini, Gonoekarellini, Phrygini, Vinatini, Cedusini (including subtribe Ecenchreina), Cedochoereni, Dawnario- idini, Nicertini, Kamandakini, Patarini, Noracrococarini and Phenicini, sinking Mysidiini (created by Broomfield [1985]) under Derbini as a subtribe. The Eocene tribe Ptychoptilini, described in Achilidae by Emeljanov [1990], was later moved to Derbidae [Bourgoíne, 2020]. Emeljanov and Fletcher [2004] transferred the tribe Breddiniolino from Achilida to Derbidae Cedusinae based on the structure of male genitalia, and by priority, the name of the subfamily should be changed to Breddinioinae Fennah, 1950, stat.n. (= Cedusinae Emeljanov, 1992, syn.n.). Banaszkiewicz and Szwedo [2005] added one more tribe, Aquaelliciini.

The subfamily Derbinae was separated from Cedusinae by a single character, namely the presence of sensory pits in adult [Emeljanov, 1995]. Giving such a great taxonomic value to sensory pits is unique among Fulgoroidea. Development of sensory pits was used as the principal character to diagnose tribes in Orgeriinae and Caliscelinae [Emeljanov, 1969, 2008b] and (in conjunction with other characters) subfamilies in Meenodinae [Muir, 1930]. The presence of sensory pits on the head and on the C and clavus in the tegmen was the only criterion for distinguishing Cedochoereni and Cenchreini (Derbinae) from Cedusini (Cedusinae): the pits are absent in Cedusini, present only on the basal part of C in Cedococherini, and on the head, C and Pcu in Cenchreini [Emeljanov, 1992, 1995]. However, there are exceptions: in some Cedochoereni the pits are developed also at the scutellar margin of clavus (Cedochoerus Emeljanov, 2008) [Emeljanov, 2008a, fig. 12], and vice versa, the pits on tegmen are restricted to the basal part of C also in some Cenchreini (Dawnaria giraldestoni Muir, 1913), Nicertini (Leptaleocera cocinea Muir, 1913) and Otio- cerini (Paralyricen jepsoni Muir, 1913; Platocera annulipes Muir, 1913, Pyrrhoneura immaculata Muir, 1913, etc.) [Muir, 1913, pl. 3].

Another important set of character changes at the transition from the basal derbid tribes to Derbinae is associated with the apex of clavus, postclaval area and postclaval crossvein. Achilidae and the most primitive, still achilid-like derbids (grade A) have tegmina not as long as the body, their postnodal parts overlapping in repose (often short) and sometimes with extra folding, apex of clavus transversely or obliquely truncate, CuP sharply bent posteriorly near the apex, Pcu+1A joining CuP there, CuA2 reaching apical margin, claval furrow continued into long and wide postclaval area, and postclaval crossvein long and transverse. Somewhat more derived derbids that had lost the achilid habitus (grade B), have the tegmina longer than the body length, steeply tectiform in repose, CuP nearly straight apically, and Pcu+1A joining either CuP near apex (Cedusini Ecenchreina, Cedochoereni, some Cenchreini — e.g. Gone- okara Muir, 1913, Agoo Bahder et Bartlett, 2019), or 2A or their junction (cixti condition restored: Cedusina, Dawnarioidiini, other Cenchreini — e.g. Basileocephalus Kirkaldy, 1906, Dwnaria Distant, 1911). Further transformations of the claval region occur in still more derived derbids: CuP after junction with Pcu+1A running along posterior margin up to postclaval crossvein, clavus open, postclaval area short and narrow, CuA2 joining posterior margin, postclaval crossvein short and oblique. This condition, recorded already in a few Cenchreini (some Phaciocephalus Kirkaldy, 1906, Herps Stål, 1862), is further developed in higher Derbidae [Fennah, 1952].

The characters that unite all Derbidae are the fusion of tergite IX with the anal tube in males, and probably also peculiar wax pores on the abdomen. In the evolution of Derbidae, there was a transformation of the basal, achilid-like forms into higher derbids through accumulation of derived characters. Accordingly, the tribes of Derbidae were arranged in a phylogenetic sequence [Emeljanov, 1995]. The character changes that have occurred from primitive tribes to typical derbids are as follows:

1. Shortening of the apical segment of rostrum — at least thrice as long as wide in Breddinioini, Ipsinolini, Gonoekarellini, Vinatini, Ptychoptilini, Derbachilini trib.n.; at most twice in other derbids (except for Archara Metcalf, 1945 of Otio- cerini) [Fennah, 1952];
2. Reduction of lateral teeth on hind tibia — four or three teeth in Breddinioini; three or two in Derbachile gen.n.; two in Vinatini; one tooth in Ipsinolini, Gono- ekarellini, Phrygini and Ecenchrea Muir, 1913 (Cedusini Ecenchreina); no teeth in other derbids, except Zoraidini and Sikaianini;
3. Reduction of subapical setae on apical pectens of hind tarsomeres — setae present in Breddinioini and Ipsinolini; absent in Derbachile gen.n. and other derbids;
4. Medial shortening of pronotum and reduction of its disc — pronotal disc elevated, tricarinate, triangular, nearly as long as wide in Ipsinolini, Vinatini, Pty- choptilini, Derbachile gen.n.; much shorter in Gono- ekarellini, Phrygini, some Cenchreini; not elevated, ecarinate in other derbids;
5. Reduction of M fork in hind wing — M forked before r-m in Breddinioini, Derbachilini trib.n.; beyond r-m in Ipsinolini, Phrygini, Cedochoereni; simple in other primitive derbids;
6. Reduction of CuA1 fork in hind wing — CuA1 forked before m-cu in Breddinioini; beyond m-cu in Ipsinolini, Gonoekarellini, Phrygini, Derbachilini trib.n.; simple in other derbids.
(7) modification of antenna — enlarged and somewhat flattened in Derbachilini trib.n.; enlarged in Vina-
tini, Derbini, and flattened in some Otiocerinae;
(8) development of subantennal lobe — ridge at lorogenous boundary in Phrygiini [Emeljanov, 1995];
    low ridge in Derbachile hochae sp.n.; lobe in Cedusini,
    Cedochreini, Cenchreini, most Otiocerinae;
(9) shortening of ScRA in hind wing — in Cedusini
    (except Emelianovedusa Szwedo, 2006 from Baltic
    amber) and higher tribes;
(10) increase of wing/body size ratio — tegmen
    length greater than body length in Breddiniolini,
    Derbachilini trib.n., and in Cedusini and higher tribes;
(11) loss of tegminal overlap and truncate apex
    of clavus — tegmina overlapping, clavus truncate in Bred-
diniolini, Ipsnolini, Goneokarellini, Phrygiini, Vinatini,
    Pychoptilini and Derbachilini trib.n.; tegmina not over-
lapping, clavus more acute or open in Cedusini and
    higher tribes;
(12) development of sensory pits in adults — on C
    in tegmen (sometimes on its base only) in Derbachilini
    trib.n., Dawnarioidini, and some Cedochreini, Cen-
chreini, Niceritini and Otiocerini; on C and/or other
    veins and/or head in higher tribes.

Therefore, the transformation of achilid-like ancestors
into typical derbids was rather gradual. This process may
be termed ‘derbization of achilids’, by analogy with other
-izations [Shcherbakov, 2007a, 2012; Gnezdilov, 2013].

The tribe Cedusini is transitional from Breddiniolini
to Derbinae. This tribe is similar to Cenchreini and other
Derbinae in most of the above characters, except the
absence of sensory pits in adult, and in some genera the
long ScRA in hind wing or one lateral tooth on hind tibia
[Szwedo, 2006]. The sensory pits appear in adults due to
retention of the nymphal pits, so they are especially
susceptible to reversals in the evolution. The degree of
development of sensory pits on the tegmen is quite vari-
able in Cenchreini, and e.g. in Dawnaria they are restrict-
ed to the basal part of C, so there is only one step to their
loss. Hence, it seems possible that sensory pits were
secondarily lost in adult Cedusini, or even that their
appearance and loss in adult Derbidae occurred more
than once. The new Cretaceous tribe represents another
plausible transition from achilid-like basal derbids to the
higher tribes (see below).

**Systematic position of the new tribe.** The new taxa
from Burmese amber are recognized as derbids based on
the small size of body relative to wings, modified anten-
ae, presence of sensory pits on the C of tegmen, venation
achilid-like (but without bends on R and CuA branches or
a transverse fold at the nodus in tegmen, characteristic of
Achilidae), and also the enlarged 1st procubital cell,
darkened stigmal cell, RA2 with short fork and recurrent
RA2a in Derbachile gen.n., rudimentary subantennal
ridge in D. hochae sp.n., and fuscous colouration of
tegmina with pale crossveins in D. aschei sp.n. Each of
these characters taken alone is found also outside Der-
biae, but in such a combination they occur only in this
family. The fuscous colouration of tegmina with pale
crossveins and a dark stigmal cell is found e.g. in the
subtribe Cedusina, and short recurrent RA2a in some
Cedusina, Kamendakini, Patarini and Aquaeliciini.

In the venation of tegmen (including a long postnod-
al part and longitudinal branches of M and CuA) and
sensory pits on the base of C, the new tribe is similar to
the Central American tribe Cenchreini, but differs in
the more complete hind wing venation, long apical
segment of rostrum, and hind tibia with lateral teeth.
These latter characters place the new tribe among the
most primitive derbids.

Figs 25–28. Venation of Derbachilini: 25–26 — Derbachile aschei sp.n.; 25 — tegmen; 26 — hind wing; 27 — Derbachile hochae gen.
et sp.n., tegmen; 28 — Achiderbe obrienae gen. et sp.n., tegmen. Scale bars: 1.0 mm.
Рис. 25–28. Жилкование Derbachilini: 25–26 — Derbachile aschei sp.n.; 25 — переднее крыло; 26 — заднее крыло; 27 —
Derbachile hochae gen. et sp.n., переднее крыло; 28 — Achiderbe obrienae gen. et sp.n., переднее крыло. Масштабные линейки: 1,0 мм.
In the presence of the cup-pcu crossvein on clavus, Derbachile gen.n. is more primitive than all other derbids and similar to some Cixiidae, Delphacidae and Kinnaridae and primitive Fulgoridae [Emeljanov, 2013].

Derbachile gen.n. is distinct from all other derbids also in the crossvein icua shifted much distal to 2m-cu, and the 1st procubital cell markedly widened distally. The icua is shifted slightly distal to 2m-cu (but 1st procubital cell narrow) in some species of the genus Anticedusa (Costa Rican A. loisae Emeljanov, 2008) and some specimens of New Zealandian Eoecnchrea maorica (Kirkaldy, 1909) [Synave, 1973: 146] (both of Cedusini Eoecnchrea), whereas in the other species or specimens it is proximal or interstitial [Muir, 1913: pl. 3; Emeljanov, 2008: 913]. The icua is interstitial to 2m-cu in both genera of the tribe Cedocheini.

In the primitive, achilid-like hind wing venation, the new tribe is similar to, and more primitive than, the South American tribes Ipsnolini and Phrygini (in these latter the M is forked distal to crossveins).

In the enlarged and more or less flattened pedicel and sometimes also obliquely produced scape, Derbanchilini trib.n. are similar to Otiocteriini. Microscopic cuticular denticles densely covering pedicel in the new genera are similar to those found in Cixiidae, Meenoplopidae, Kinnaridae, Achilixiidae and some Derbidae [Li-ang, 2001: 222, fig. 6].

In the long apical segment of rostrum, the new tribe is similar to the tribes Bredinniolini (Afro-Australo-Melanesian), Ipsnolini and Gnonekarellini (Chilean), Vinatini (Oriental), and Ptychoptilini from Baltic amber.

Derbachile gen.n. is similar to Bredinniolini and Vinatini in the presence of 2–3 lateral teeth on the hind tibia, to Ipsnolini, Vinatini and Ptychoptilini in the elevated, long, tricarinate disc of pronotum, and to Phrygini in the ridge under antenna.

In the CuP+Pcu+1A continued along posterior margin and joining it beyond postclaval crossvein in the tegmen, D. aschei sp.n. is similar to some Cenchreini (e.g. Herpis) and Nicertini.

Thus, in nine of the above-mentioned 12 characters the tribe Derbanchilini trib.n. agrees with achilid-like tribes of Bredinniolinae, in the increased wing/body size ratio rather with higher tribes, in the presence of sensory pits on C with some Derbinae, and in the enlarged flattened antennae with Otiocteriinae. The new tribe is among the most primitive Derbidae, though its type genus shows some similarity (possibly homoplasic) to the basal tribe Cedocheini of the moderately advanced subfamily Derbinae. In shallowly tectiform discus of pronotum, and to Vinatini in the presence of 2–3 lateral teeth on the hind tibia, to Ipsnolini, Vinatini and Ptychoptilini in the elevated, long, tricarinate disc of pronotum, and to Phrygini in the ridge under antenna.

The second new genus, Achiderbe gen.n. is incompletely known and lacks some salient characters of Derbachile gen.n., although in general it is similar to the latter in venation and body structure. Therefore, it is assigned to the new tribe tentatively.

On biology of Burmese amber Derbidae. The Burmite derbids are tiny insects, like many other members of the family that are usually small planthoppers, including the primitive tribes, most Cenchreini and especially Rhotanini, while some Derbini and Zoraidini are much larger. D. hochae sp.n. with tegmen 2.6 mm long is at the lower size limit for the family, along with some Rhotanini [Zelazny, Webb, 2011].

Modern adult Derbidae feed mainly on monocots, especially palms, and woody dicots, rarely on ferns, and most species were reported from only one host plant genus [Wilson et al., 1994]. Their nymphs feed on fungi in rotting wood and decaying organic debris [Yang, Yeh, 1994; Wheeler, Wilson, 1996; Howard et al., 2001]. A similar lifestyle was possible for the Burmite derbids, which were not uncommon in a Cretaceous tropical forest. Some twenty angiosperm species are recorded from Burmese amber, including trees and monocots [Liu et al., 2018; Paleobiota of Burmese amber. 2020]. Palms and other monocots are discovered in the Early Cretaceous of Gondwana [Martinez et al., 2016; Coiffard et al., 2019]. Therefore, it is possible that the earliest Derbidae already enjoyed their favourite hosts 100 Ma ago.

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