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Redescription of *Megalomus densistriatus* Henriksen, 1922 (Neuroptera: Hemerobiidae) from the earliest Eocene Fur Formation, Denmark

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Abstract

Megalomus densistriatus Henriksen, 1922 (Neuroptera: Hemerobiidae) from the earliest Eocene Fur Formation (Denmark) is redescribed based on the holotype and 57 additional forewings. The assignation of the species to the Eocene genus *Archibaldia* Makarkin, 2023 is confirmed, as *A. densistriata*; it possesses all diagnostic character states of this genus. This species is one of most abundant Neuroptera in this formation occurring mainly in positive ash layers (younger) of the lower horizons of the Silstrup Member, but two specimens are found in the negative layers (older) of the lower to upper horizons of the Knudeklint Member. *Archibaldia densistriata* likely preferred upper microthermal to lower mesothermal mesic climate conditions similar to those estimated for *A. wehri* (Makarkin *et al*., 2003) from the early Eocene of western North America.

Key words: Neuroptera, Hemerobiidae, *Archibaldia*, earliest Eocene, Fur Formation

Introduction

The Hemerobiidae comprise more than 550 extant species distributed worldwide (Oswald & Machado 2018). The fossils are rather numerous, and to date 38 fossil species have been described (see list in Li *et al*. 2023, and Makarkin & Wedmann 2023; Makarkin 2023, 2024; Chen *et al*. 2024a, b).

In the Eocene, the family is represented by 18 fossil species from Europe, North America and the Far Eastern Asia (Pictet-Baraban & Hagen 1856; Henriksen 1922; Krüger 1922, 1923; Jarzembowski 1980; Makarkin *et al*. 2003; Makarkin & Wedmann 2009; Jepson *et al*. 2010; Makarkin *et al*. 2019; Nel & Jarzembowski 2019; Makarkin & Perkovsky 2020; Perkovsky & Makarkin 2020; Makarkin 2023, 2024; Chen *et al*. 2024a; Makarkin & Wedmann 2024). They occur in the latest Eocene Bembridge Marls (England), the late Eocene Baltic and Rovno ambers, the early/middle Eocene Tadushi Formation in the Russian Far East, the middle Eocene Kishenehn Formation (Montana, USA), the early Eocene Green River Formation (Colorado, USA), the Okanagan Highland (British Columbia, Canada, and Washington, USA) and particularly the Danish Fur Formation.

The Hemerobiidae are the commonest Neuroptera in the Fur Formation. The Henrik Madsen collection alone contains around 500 specimens, and more than 50 specimens are deposited in the Fur Museum (pers. data). However, the only species of the family described from the formation to date is *Megalomus densistriatus* Henriksen, 1922. Its systematic position has been discussed earlier (*e.g*., Oswald 1993; Makarkin *et al*. 2016). Unfortunately, the only specimen assigned to the species by Henriksen (1922) was partially inadequately described, making it difficult to correctly determine its generic affinity. Recently, it was tentatively transferred to the Eocene genus *Archibaldia* Makarkin, 2023 based on the original description and preliminary examination of few specimens (Makarkin 2023, 2024: Makarkin & Wedmann 2024).

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Here, we re-describe the species based on the holotype and numerous additional specimens, and confirm its position in *Archibaldia*.

Materials and methods

We examined fifty-eight presumed *Megalomus densistriatus* specimens including the holotype from the Fur Formation in northern Jutland, Denmark. This formation is one of the best-known early Eocene Lagerstätte, with overviews provided by *e.g.*, Larsson (1975); Pedersen & Surlyk (1983), Archibald & Makarkin (2006), Pedersen *et al*. (2012), and Madsen & Rasmussen (2021).

The specimens were found at the best known localities of the Fur Formation: northern Mors Island (Ejerslev: Cliff and Mo-clay pit; Gullerup; Klitgaard; Klovbakker; Svalklit; Hanklit; Sundby; Skærbæk; and Skarrehage); Fur Island (East Cliff); Salling Peninsula (Junget); and the Thy District (Vildsund).

The Fur Formation is divided into the Knudeklint Member (lower horizons; negative ash layers from -1 to -33), and Silstrup Member (upper horizons; positive ash layers from +1 to +140) (Rasmussen *et al*. 2016). The vast majority of the specimens of this species were found in the positive ash layers. When precise data are available, these are from the lower horizons of the Silstrup Member (ash layers +15 and +25 to +30). Two specimens are collected from negative ash layers, -11 to -13 at Ejerslev Mo-clay pit (upper horizons of the Knudeklint Member), and -24 to -29 at East Cliff (lower horizons of the Knudeklint Member).

Specimens were photographed using a Canon EOS 5D II camera, either with a Canon EF 100 f2.8 USM macro lens or in conjunction with an Olympus SZ60 stereo microscope. The line drawings were prepared from camera images using Adobe Photoshop CS3.

Venational terminology follows Breitkreuz *et al*. (2017), except for details (*e.g.*, spaces, veinlets, traces, oblique radial branches' ("ORB") concept) that follow Oswald (1993). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, *e.g.*, 1r-m, crossvein in first gradate series between R and M.

Abbreviations: A1–A3, first to third anal veins; cf, claval flexion line/fold; CuA, anterior cubitus; CuP, posterior cubitus; CuA1, proximal-most branch of CuA; hv, humeral veinlet; M, media; MA, anterior media; MP, posterior media; mf, medial flexion line/fold; ORB1–ORB3, first (proximal-most) to third oblique radial branches; RA, anterior radius; RP, posterior radius; Sc, subcosta.

Institutional abbreviations: FUM, Fur Museum (Museum Salling), Nederby, Denmark; HM, Henrik Madsen collection in Museum Mors (Fossil and Moclay Museum), Denmark; NHMD, Natural History Museum of Denmark, University of Copenhagen.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Hemerobiidae Leach, 1815

Subfamily Drepanepteryginae Krüger, 1922

Genus *Archibaldia* Makarkin, 2023

Type species. *Cretomerobius wehri* Makarkin *et al*., 2003, by original designation.

Revised diagnosis. Relatively large hemerobiids (forewing 10–16 mm long), which may be distinguished from other genera of the family by possession of the following forewing character states: basal crossveins present between R and M (1r-m) [1] and between RA and ORB1 (or ORB2) [2]; ORB1 with several anteriorly-directed pectinate branches [3]; M dichotomously branched with three or more long branches originating proximad third gradate series [4]; CuP deeply forked proximad first gradate series (often dichotomous) [5]; crossveins between branches of CuA in third gradate series present [6]; crossveins present between branches of CuP in first gradate series [7].

Species included. *A. wehri* (Makarkin *et al*., 2003) from the early Eocene of western North America (USA: Washington: Republic locality); *A. densistriata* from the early Eocene Fur Formation, Denmark; *A. aristovi* Makarkin, 2023 from the early/middle Eocene of the Russian Far East (Tadushi Formation); *Archibaldia? gradata* (Makarkin *et al*., 2016) from the late Eocene Baltic amber (preliminarily).

Remarks. *Proneuronema gradatum* is assigned to the genus *Archibaldia* preliminarily as it lacks character states [1], [2], and [6]. On the other hand, the forewing venation of this species differs significantly from that of all known species of *Proneuronema* Makarkin *et al*., 2016 (*i.e*., *P. minor* Makarkin *et al*., 2016 from Baltic amber; *P. sidorchukae* Makarkin & Perkovsky, 2020 and *Proneuronema damzeni* Makarkin & Wedmann, 2024 from Rovno amber) by the configuration of M and CuP (see Makarkin 2023 and Makarkin & Wedmann 2024).

Archibaldia densistriata (Henriksen, 1922)

Figs 1–13

Megalomus densistriatus Henriksen, 1922: 14–16, Fig. 4; Larsson 1975: 196, 203; Willmann 1990: 7; Makarkin 1991: 60; Oswald 1993: 262; Ansorge 1997: 162; Engel & Grimaldi 2007: 22; Makarkin *et al*. 2016: 362; Yang *et al*. 2018: 147 (Tabl. 1); Makarkin 2023: 116; Makarkin 2024: 167.

Archibaldia densistriata: Makarkin & Wedmann 2024: 595, 599.

Type material. Holotype: MGUH 1821 (part), deposited in NHMD; a nearly complete, poorly preserved forewing (Fig. 1).

Type locality and horizon. Denmark: northern Jutland: Fur Island (precise locality unknown); Fur Formation (label says "concretion"; examination of the stone with the fossil shows that the concretion is from the ash-layer +15 or above); earliest Eocene (early Ypresian).

Additional material examined. Fifty-one specimens from the Fur Formation collected at the following localities in northern Jutland: Mors Island, **Ejerslev**: FUM N 10525 (Fig. 6A) (part), collected by Jan and Elly Verkleij; a complete forewing; a concretion (from a positive ash layer); FUM N 10526 (Fig. 6B) (part), collected by Jan and Elly Verkleij; a complete forewing; a concretion (from a positive ash layer); FUM N 10527 (Fig. 3) (part), collected by Jan and Elly Verkleij; an incomplete forewing; a concretion (from a 'positive ash layer); HM 14M-3027 (Fig. 9H) (part), collected by H. Madsen on 01.02.1992; an incomplete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-3105 (Fig. 9A) (part), collected by H. Madsen on 29.02.1992; an incomplete forewing; Ejerslev Mo-clay pit (a positive ash layer); HM 14-3361 (Fig. 10D) (part and counterpart), collected by H. Madsen on 21.06.1992; an incomplete forewing; Ejerslev Cliff (a positive ash layer); HM 14-A2706 (Fig. 6E) (part and counterpart), collected by H. Madsen on 19.11.1993; a complete, rather well-preserved forewing; Ejerslev Cliff (ash layer +15); HM 14M-3744 (Fig. 8C) (part), collected by H. Madsen on 13.09.1992; a nearly complete forewing; Ejerslev Mo-clay pit (ash layer ≤+19); HM 14M-3795 (Fig. 10C) (part and counterpart), collected by H. Madsen on 02.10.1992; a nearly complete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-4073 (Fig. 6F) (part and counterpart), collected by H. Madsen on 02.01.1993; a nearly complete forewing; Ejerslev Cliff (ash layer +15); HM 14M-B2314 (Fig. 10E) (part and counterpart), collected by H. Madsen on 11.04.1995; an incomplete forewing; Ejerslev Mo-clay pit (ash layer +15); HM 14M-B2983 (Fig. 5) (part and counterpart), collected by H. Madsen on 06.08.1995; an incomplete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-B4041 (Fig. 9F) (part and counterpart), collected by H. Madsen on 17.02.1996; an incomplete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-B4264 (Fig. 10B) (part), collected by H. Madsen on 01.03.1996; a nearly complete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-2519 (Fig. 11B) (part and counterpart), collected by H. Madsen on 22.08.1991; an incomplete, rather well-preserved forewing; Ejerslev Mo-clay pit (a positive ash layer); HM 14M-2480 (Fig. 11C) (part and counterpart), collected by H. Madsen on 04.08.1991; an incomplete, poorly-preserved forewing; Ejerslev Mo-clay pit (a positive ash layer); HM 14M-B3899 (Fig. 11D) (part and counterpart), collected by H. Madsen on 02.02.1996; an incomplete, poorly-preserved forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-A4605 (Fig. 11E) (part and counterpart), collected by H. Madsen on 25.11.1994; an incomplete, poorly-preserved forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-B3907 (Fig.11F) (part and counterpart), collected by H. Madsen on 02.02.1996; an incomplete, poorly-preserved forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-C3498 (Fig. 11H) (part and counterpart), collected by H. Madsen 14.03.1997; an incomplete, poorly-preserved forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30). Mors Island: **Gullerup**: FUM

N 11102 (Fig. 8H) (part and counterpart), collected by E. Rettig; an incomplete forewing; a concretion (from a positive ash layer); FUM N 11104 (Fig. 8G) (part and counterpart), collected by E. Rettig; an incomplete forewing; a concretion (from a positive ash layer); FUM N 13894 (Fig. 6H) (part and counterpart), collected by E. Rettig; a nearly complete forewing; a concretion (from a positive ash layer); FUM N 16656 (Fig. 8E) (part and counterpart), collected by Jan & Elly Verkleij; an incomplete forewing; a concretion (from a positive ash layer); FUM N 13895 (Fig. 11A) (part and counterpart), collected by E. Rettig; an incomplete, very poorly preserved forewing; a concretion (from a positive ash layer). Mors Island: **Klitgaard**: FUM N 13883 (Fig. 6D) (part and counterpart), collected by E. Rettig; a nearly complete forewing; Klitgaard Cliff, a concretion (from a positive ash layer); FUM N 13904 (Fig. 7H) (part and counterpart), collected by E. Rettig; an incomplete forewing; Klitgaard Cliff, a concretion (from a positive ash layer); FUM N 16965 (Fig. 7D) (part and counterpart), collected by E. Rettig; a nearly complete forewing; Klitgaard Cliff, a concretion (from a positive ash layer); HM 6M-2205 (Fig. 6G) (part), collected by H. Madsen in 1990; a nearly complete forewing; Klitgaard Mo-clay pit, a concretion (from a positive ash layer); HM 6M-2258 (Fig. 9C) (part and counterpart), collected by H. Madsen in 1990; an incomplete forewing; Klitgaard Mo-clay pit, a concretion (from a positive ash layer). Mors Island: **Klovbakker**: HM 4-2003 (Fig. 8A) (part and counterpart), collected by H. Madsen in 1990; a nearly complete forewing; a concretion (from a positive ash layer). Mors Island: **Svalklit**: FUM N 13898 (Fig. 7A) (part and counterpart), collected by E. Rettig; a complete forewing; a concretion (from a positive ash layer); FUM N 13899 (Fig. 9D) (part and counterpart), collected by E. Rettig; an incomplete forewing; a concretion (from a positive ash layer); FUM N 17009 (Fig. 7B) (part and counterpart), collected by E. Rettig; a nearly complete forewing; a concretion (from a positive ash layer). Mors Island: **Hanklit**: FUM N 13900 (Fig. 9G) (part and counterpart), collected by E. Rettig; a complete forewing; a concretion (from a positive ash layer). Mors Island: **Sundby**: HM 5-4334 (Fig. 7F) (part and counterpart), collected by H. Madsen on 08.02.1993; an ash layer between +25 and +30. Mors Island: **Skærbæk**: HM 10-B3138 (Fig. 9E) (part and counterpart), collected by H. Madsen on 26.08.1995; an incomplete forewing; an ash layer between +25 and +30. Mors Island: **Skarrehage**: HM 11-3942 (Fig. 10A) (part and counterpart), collected by H. Madsen on 01.12.1992; an incomplete forewing; an ash layer between +25 and +30; HM 11-A4485 (Fig. 9B) (part and counterpart), collected by H. Madsen on 29.10.1994; an incomplete forewing; an ash layer between +25 and +30; HM 11-A4705 (Fig. 8D) (part and counterpart), collected by H. Madsen on 22.12.1994; a complete forewing; ash layer +15; HM 11-A4706 (Fig. 4) (part and counterpart), collected by H. Madsen on 22.12.1994; a nearly complete forewing; ash layer +15; HM 11-3165 (Fig. 11G) (part and counterpart), collected by H. Madsen on 11.04.1992; an incomplete, poorly preserved forewing; a concretion (from a positive ash layer). Fur Island: **East Cliff**: FUM N 13474 (Fig. 8B) (part), collected by Jan & Elly Verkleij; an incomplete forewing; an ash layer between -24 and -29; HM 17-C3223 (Fig. 10H) (part and counterpart), collected by H. Madsen on 02.02.1997; a nearly complete forewing; an ash layer between +25 and +30. **Fur Island** (precise locality unknown): FUM N 13909 (Fig. 8F) (part), collected by Jan & Elly Verkleij; a nearly complete poorly-preserved forewing; a concretion (from a positive ash layers); FUM N 16783 (Fig. 7E) (part), collected by Jan & Elly Verkleij; a complete, rather poorly-preserved forewing; a concretion (from a positive ash layer). Salling Peninsula: **Junget**: HM 21-2011 (Fig. 10F) (part and counterpart), collected by H. Madsen in 1990; an incomplete forewing; a concretion (from a positive ash layer). Thy District: **Vildsund**: HM VSK-2238 (Fig. 2) (part and counterpart), collected by H. Madsen in 1990; a nearly complete well-preserved forewing; a concretion (from a positive ash layer). **Precise localities unknown**: FUM N 16746 (Fig. 7G) (part), collected by O. Burholt; a complete well-preserved forewing; a concretion (from a positive ash layer); FUM N 17006 (Fig. 7C) (part), a nearly complete, poorly-preserved forewing; a concretion (from a positive ash layer); FUM N 17008 (Fig. 6C) (part and counterpart); an incomplete, well-preserved forewing; a concretion (from a positive ash layer); TJS 0123 (Fig. 10G) (part), collected by E. Rettig; an incomplete, rather poorly-preserved forewing; a concretion (from a positive ash layer).

Forewings of presumed *Archibaldia densistriata*: HM 14M-B4970 (Fig. 12A) (part and counterpart), collected by H. Madsen on 28.06.1996; an incomplete forewing; **Ejerslev** Mo-clay pit (ash layer +15); HM 14M-B4731 (Fig. 12B) (part and counterpart), collected by H. Madsen on 27.05.1996; an incomplete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 14M-B3312 (Fig. 12C) (part), collected by H. Madsen on 16.09.1995; an incomplete forewing; Ejerslev Mo-clay pit (an ash layer between +25 and +30); HM 8-2193 (Fig. 12D) (part and counterpart), collected by H. Madsen in 1990; an incomplete forewing; **Klitgaard** Cliff, a concretion (from a positive ash-layer); HM 14M-C2203 (Fig. 12E) (part), collected by H. Madsen on 26.07.1996; an incomplete forewing; **Ejerslev** Mo-clay pit (an ash layer between +25 and +30).

Hind wing of presumed *Archibaldia densistriata*: HM 14M-B3268 (Fig. 13) (part and counterpart), collected by Henrik Madsen on 16.09.1995; a poorly preserved hind wing; **Ejerslev** Mo-clay pit (an ash layer between +25 and +30).

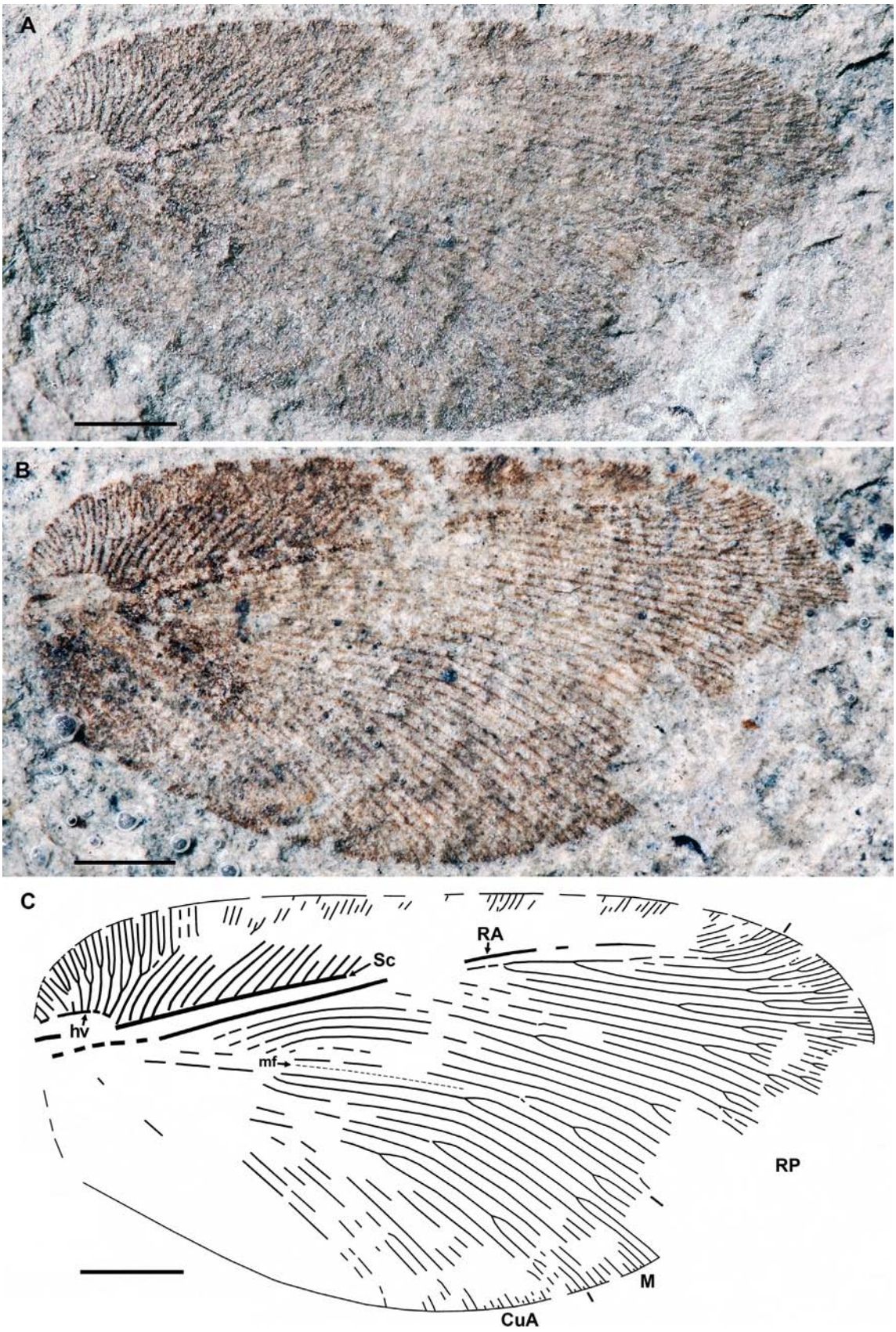

FIGURE 1. *Archibaldia densistriata* (Henriksen, 1922), holotype MGUH 1821. A, dry; B, wetted with alcohol; C, drawing of forewing venation. Scale bars 2 mm.

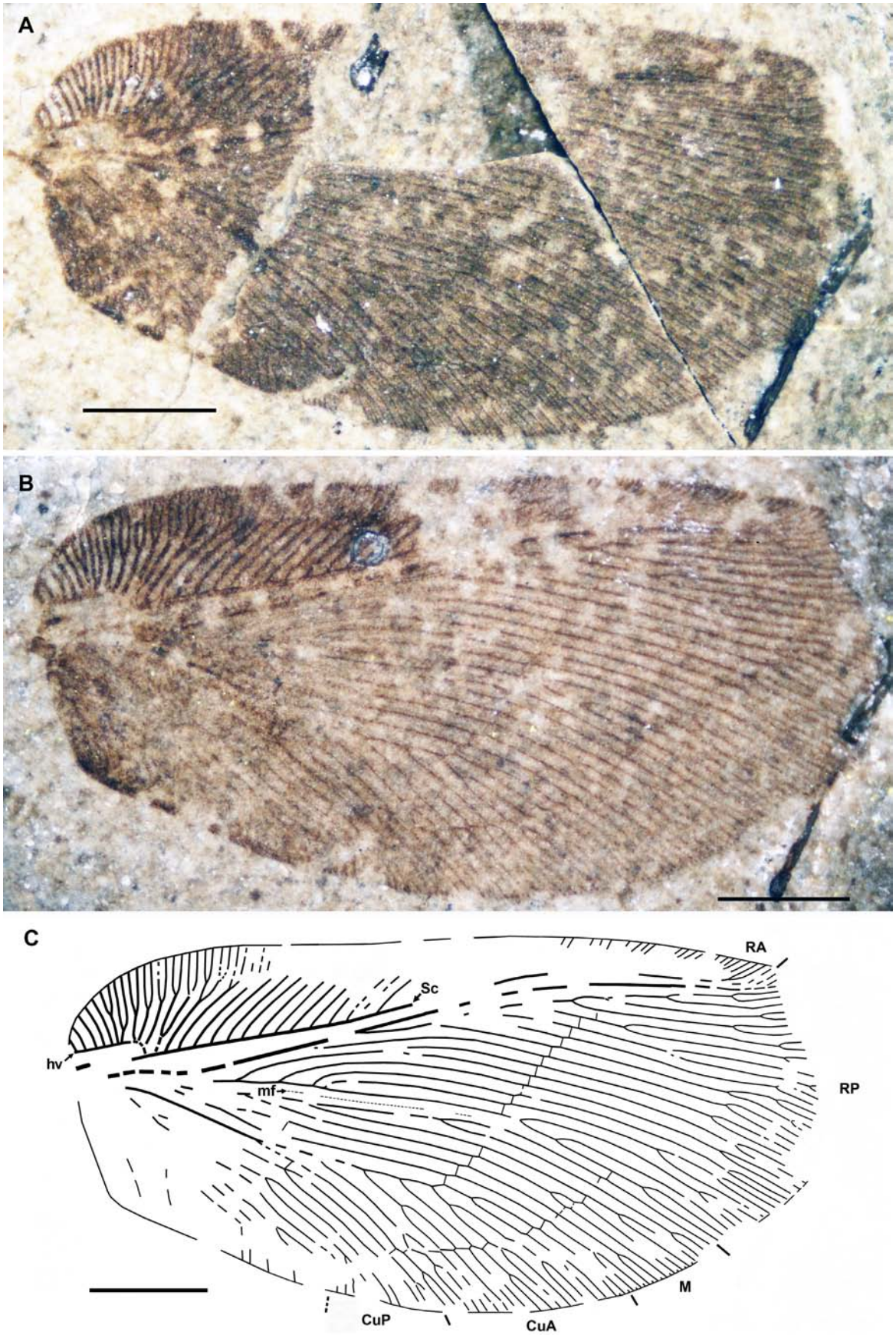

FIGURE 2. *Archibaldia densistriata* (Henriksen, 1922), specimen HM VSK-2238. A, part; B, counterpart (both wetted with alcohol; converted to standard right view C); drawing of forewing venation. Scale bars 2 mm.

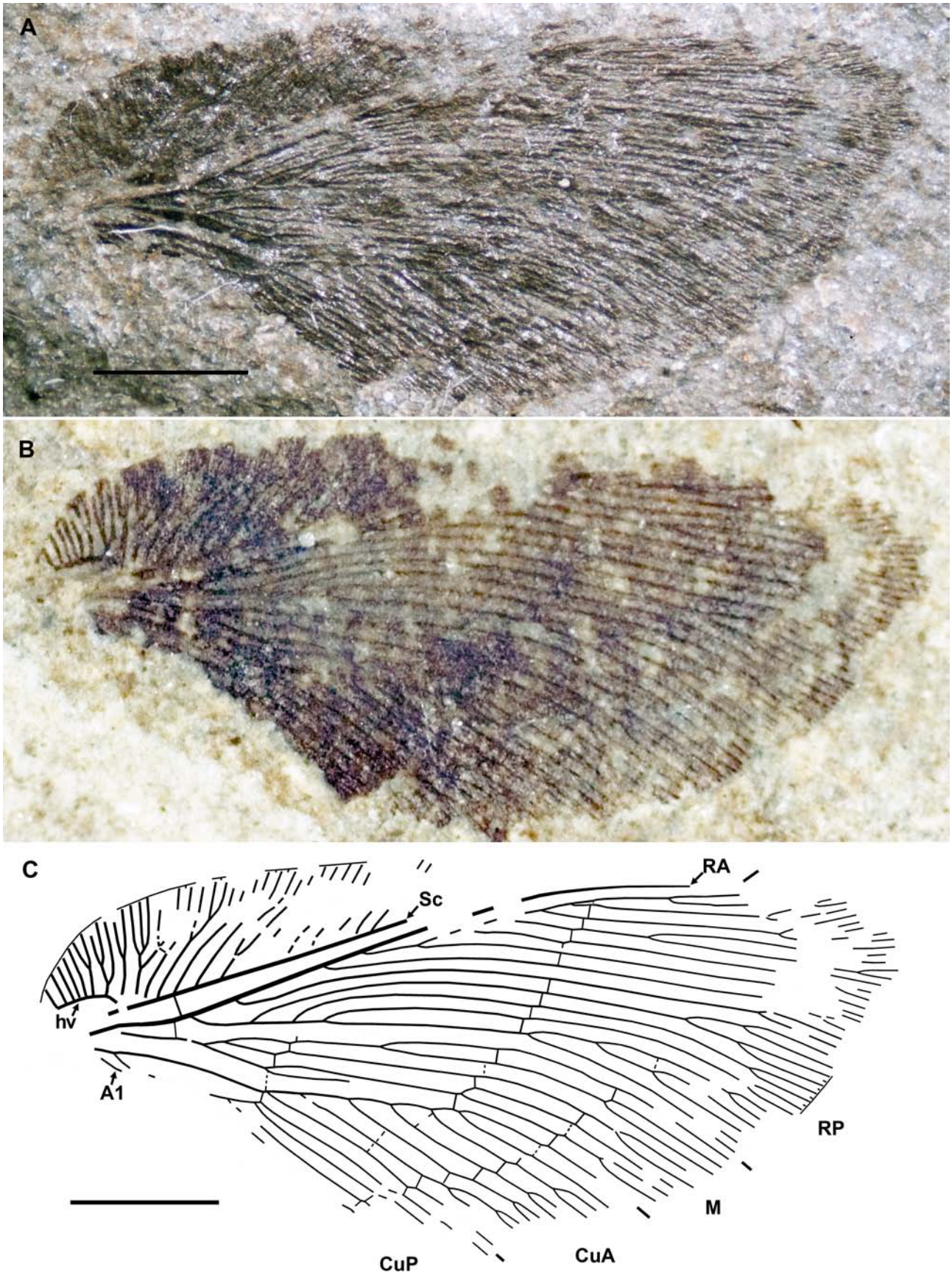

FIGURE 3. *Archibaldia densistriata* (Henriksen, 1922), specimen FUM N 10527. A, part (dry); B, same (wetted with alcohol); C, drawing of forewing venation. Scale bars 2 mm (A, B to same scale).

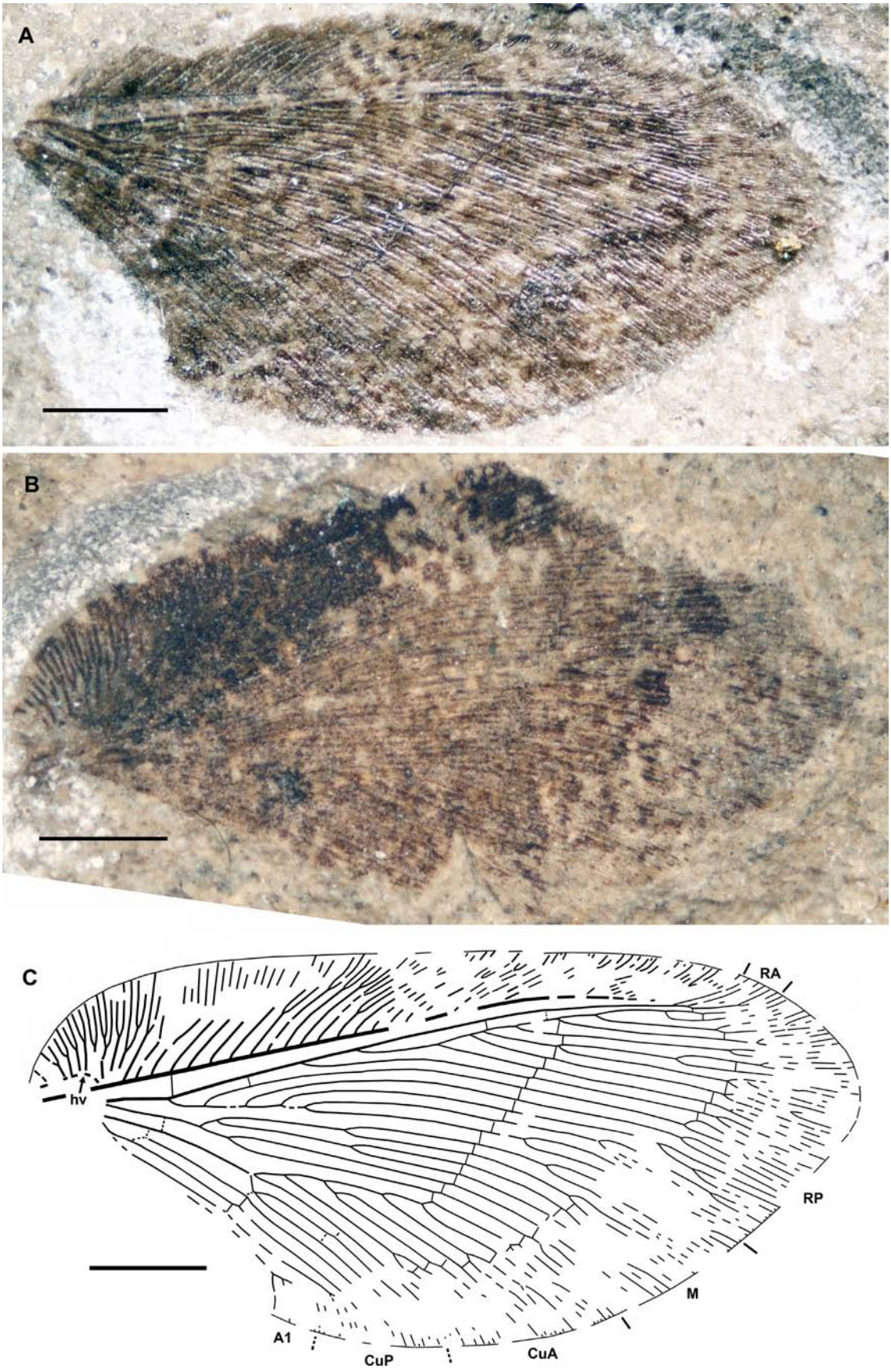

FIGURE 4. *Archibaldia densistriata* (Henriksen, 1922), specimen HM 11-A4706. A, part (dry); B, counterpart (wetted with alcohol; converted to standard right view); C, drawing of forewing venation combined from the part and counterpart. Scale bars 2 mm.

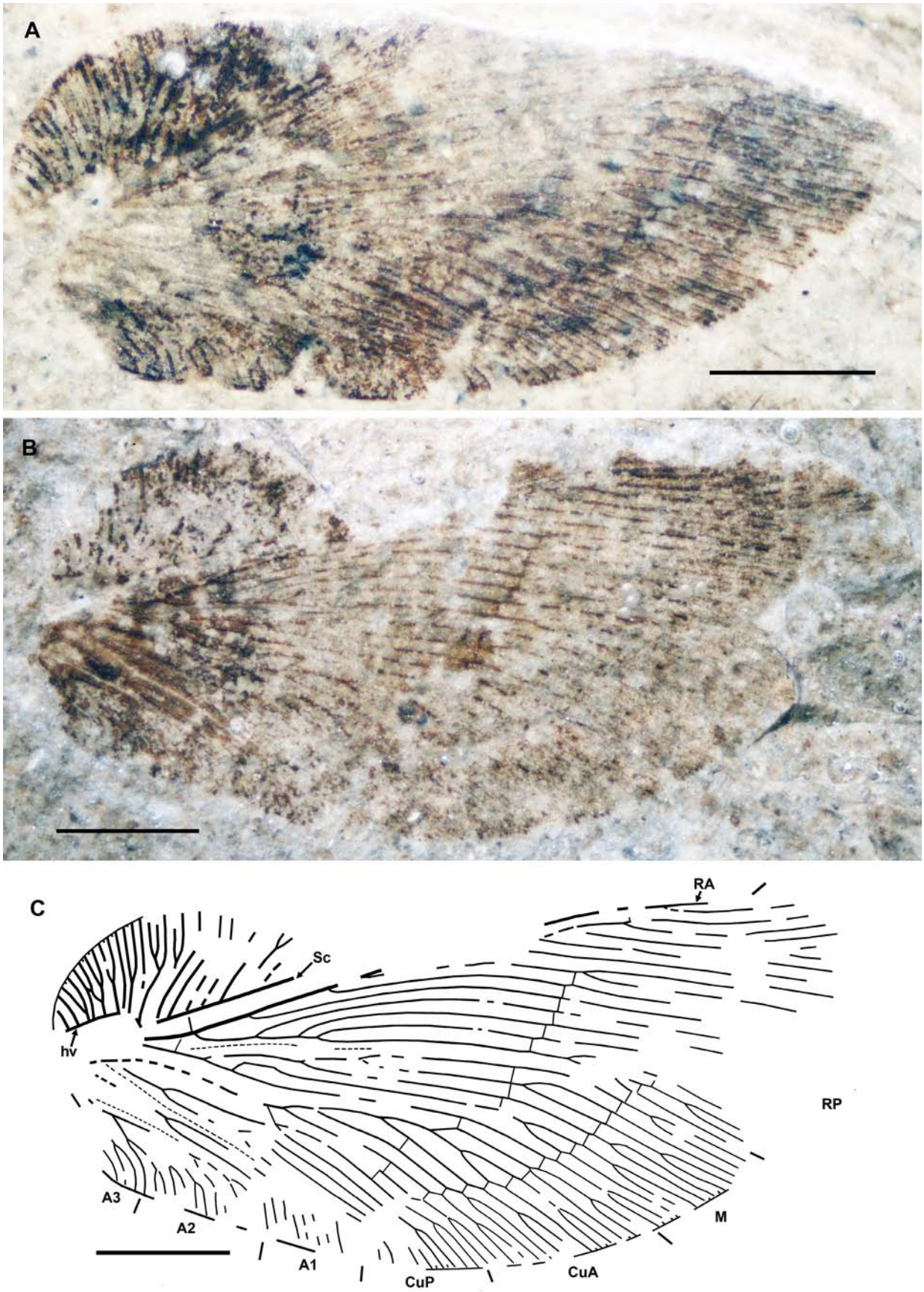

FIGURE 5. *Archibaldia densistriata* (Henriksen, 1922), specimen HM 14M-B2983. A, part (converted to standard right view); B, counterpart (both wetted with alcohol); C, drawing of forewing venation. Scale bars 2 mm.

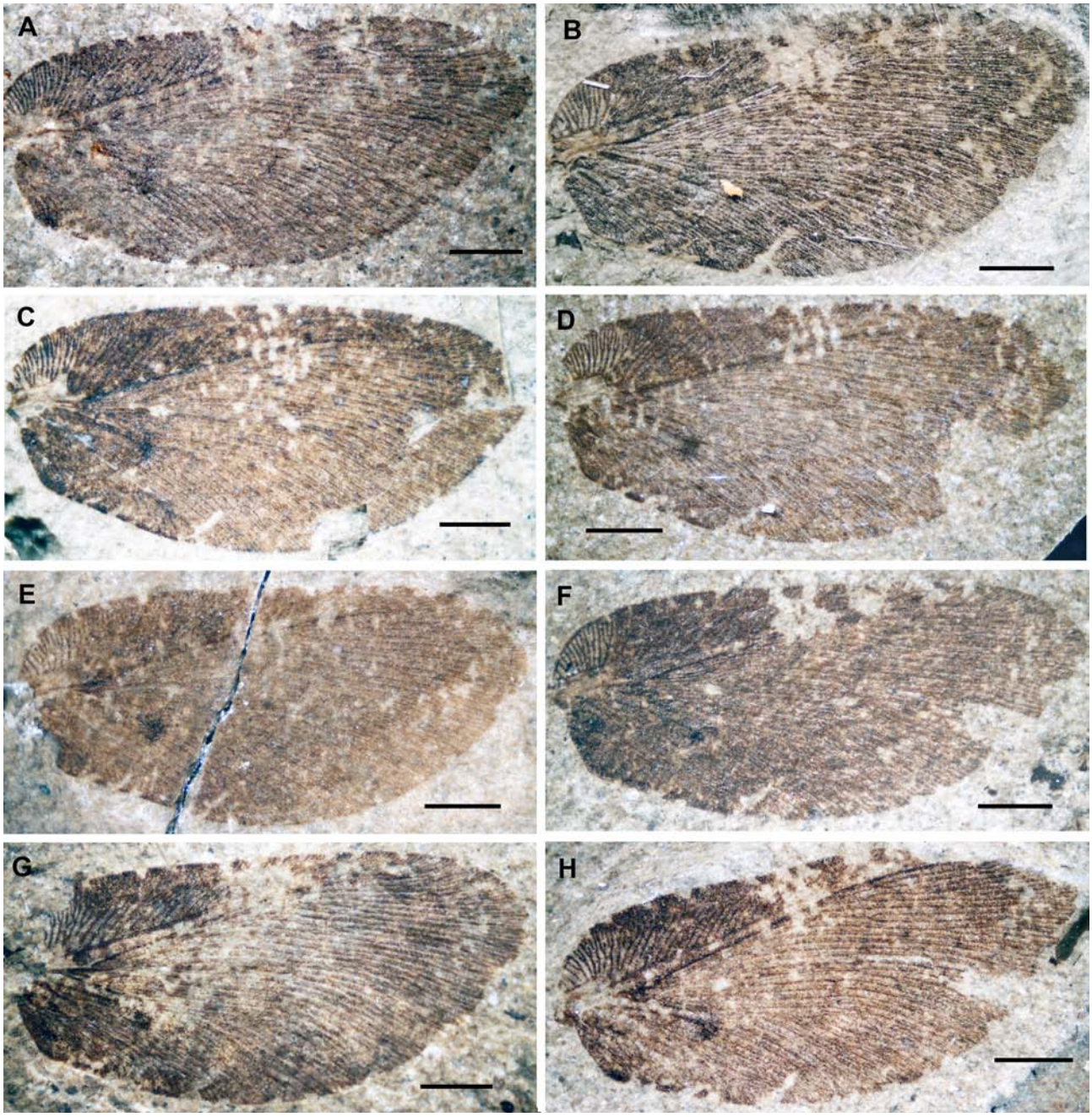

FIGURE 6. *Archibaldia densistriata* (Henriksen, 1922), forewings. A, FUM N 10525; B, FUM N 10526; C, FUM N 17008; D, FUM N 13883; E, HM 14-A2706; F, HM 14M-4073; G, HM 6M-2205; H, FUM N 13894. All wetted with alcohol; converted to standard right view. Scale bars 2 mm.

Diagnosis. May be distinguished from other species of the genus by the following forewing character states: crossveins between subcostal veinlets absent [present in *A. wheri*, *A.? gradata*]; ORB2 originates much distad (or at level of) basal branch of ORB1 [much proximad basal branch of ORB1 in *A. aristovi*].

Description based on all available specimens. Forewing 12.3–15.8 mm long (N = 24), 6.1–8.0 mm wide (N = 21). Costal space broad, gradually narrowing towards wing apex, but distally quite wide. Subcostal veinlets in proximal half of wing very stout and oblique; distal veinlets generally poorly preserved; crossveins not detected between these. Humeral veinlet strongly recurrent with 7–11 branches; of these, two to five (mostly proximal) simple, others forked one to three times. Subcostal space moderately broad, narrowing towards wing apex; basal crossvein located approximately at level of origin of ORB1; intermediate and distal crossveins not detected due to

poor preservation. Sc and RA distally not fused. RA terminates at margin well before wing apex, with few veinlets. RA space (between RA and distal ORB) narrow, usually with three crossveins (of these one located proximad third series of gradate crossveins) (Fig. 4C). RP with three to four ORBs. ORB1 with three to five anteriorly-directed branches proximad third gradate series of crossveins. Distal ORB with six to eight branches. ORBs between ORB1 and distal ORB (ORB2 or ORB2 and ORB3) shallowly forked. M dichotomously forked, four to six times proximad third gradate series. Cu divided into CuA, CuP near wing base. CuA pectinately forked, with four to six branches proximad third gradate series. CuP generally dichotomously forked, three to four times (proximal-most fork deep, proximad (or at) first gradate series of crossveins). A1 deeply forked, both branches distally forked several times. A2 pectinately branched with several forked branches. A3 relatively short, with few branches. Three distinct flexion lines (folds): between RP, M (radiomedial (=medial) flexion line); between CuP, A1 (cubitoanal (=claval) flexion line); between A1, A2 (intraanal flexion line). Continuous first (basal) gradate series of crossveins includes at least four crossveins from Sc to CuP. Continuous second gradate series contains seven to eight crossveins from ORB1 to posterior branch of CuP, and one between anterior branch of ORB1 and R. Continuous third gradate series includes up to 20 crossveins from RA to CuA, and several irregular crossveins between branches of CuA. Fourth (outer) series continuous, up to 38 crossveins from RA to at least posterior branch of CuP.

Color pattern. Most of wing brownish, except membrane between branches of humeral veinlet significantly lighter; dark brown area present in proximal part of costal space, and blackish spot approximately at origin of CuA1. Membrane surrounding crossveins in the third and fourth gradate series occasionally dark brown forming two transverse fasciae.

Hind wing (based only on HM 14M-B3268: Fig. 13) *ca*. 12 mm long, 5.5 mm wide. Costal space relatively narrow. Sc and RA widely separated distally. RA space appears very broad proximally. Other details very poorly preserved.

Re-description of the holotype and description of best-preserved specimens. *Holotype MGUH 1821* (Fig. 1). Forewing 15.8 mm long, 8.0 mm wide (length/width ratio 1.98). hv with 11 branches (five distal branches forked once or twice, others simple). ORB1 with five anteriorly-directed branches; distal ORB with up to eight branches. M probably forked five to six times proximad third gradate series. Medial flexion line (fold) rather distinct. CuA with several long branches. Other details of the venation poorly discernible. Coloration: wing slightly brownish almost throughout except dark brown areas in proximal costal space and surrounding area approximately at the origin of CuA1, and in anal area; membrane between the branches of humeral veinlets remarkably lighter.

Specimen HM VSK-2238 (Fig. 2). Forewing 12.6 mm long as preserved (estimated complete length *ca*. 13.5 mm), 6.4 mm wide (length/width ratio 2.11). RP with three ORBs. ORB1 with four anteriorly-directed branches proximad third gradate series of crossveins. ORB2 shallowly forked. ORB3 with seven branches, two of which are forked proximad fourth gradate series of crossveins. M forked five times proximad third gradate series of crossveins. Medial flexion line (fold) rather distinct. CuA pectinate, with six branches; two of which forked proximad third gradate series of crossveins; branches zigzag curved at fourth (outer) gradate series of crossveins. CuP forked three times proximad fourth gradate series of crossveins. Anal veins preserved fragmentarily. Crossveins of first (basal) gradate series not preserved. In second series, two crossveins preserved: between branches of M and between CuA, CuP. Third series nearly complete, 15 crossveins from fifth branches of ORB3 to CuA. Fourth (outer) series incomplete, with 12 preserved crossveins from ORB1 to CuP. Coloration generally as in the holotype.

Specimen FUM N 10527 (Fig. 3). Forewing *ca*. 11.6 mm long as preserved (estimated complete length *ca*. 12 mm), *ca*. 5.4 mm wide as preserved (estimated complete width *ca*. 5.6 mm) (length/width ratio 2.14). rv with eight branches (three distal branches forked once to twice, other simple). RP with four ORBs. ORB1 with three anteriorly-directed branches proximad third gradate series of crossveins. ORB2, ORB3 shallowly forked (at or distad fourth (outer) gradate series). ORB4 (distal) with six branches, one of which is deeply forked. M forked five times proximad third gradate series of crossveins; one (posterior) branch abnormally incomplete, terminating proximad third gradate series of crossveins. CuA pectinate, with six branches. CuP incomplete, probably with four long branches. Basal part of A1 preserved fragmentarily. First (basal) gradate series of crossveins with two preserved crossveins: between Sc, R and R, M. Second series represented by five preserved crossveins from ORB1 to CuP. Third series nearly complete, with 17 crossveins from stem of ORB4 to posterior branch of CuA. Fourth (outer) series incomplete, with 13 preserved crossveins from ORB1 to one of posterior branches of CuP. Color pattern in general as in the holotype, but much darker.

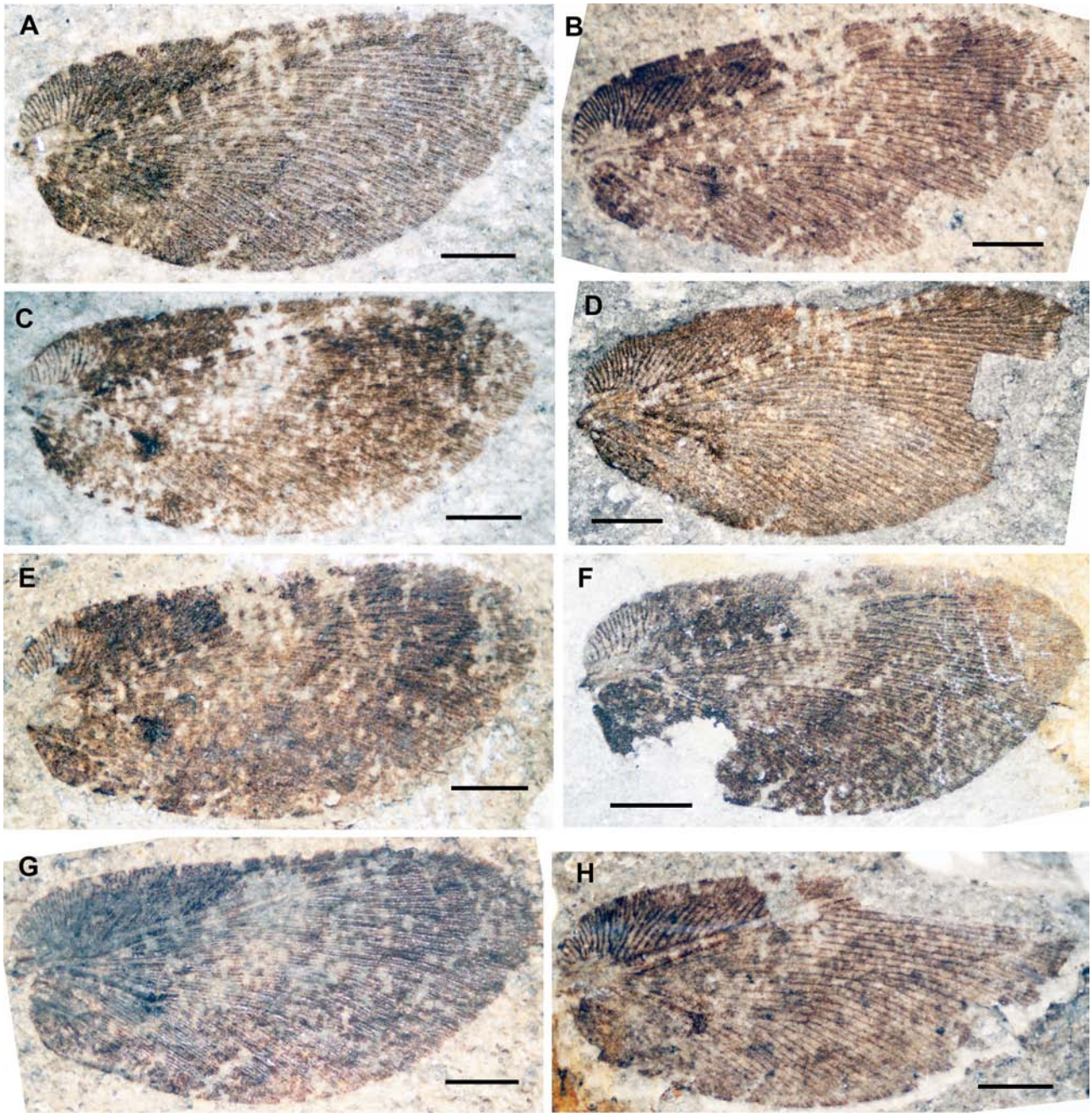

FIGURE 7. *Archibaldia densistriata* (Henriksen, 1922), forewings. A, FUM N 13898; B, FUM N 17009; C, FUM N 17006; D, FUM N 16965; E, FUM N 16783; F, HM 5-4334; G, FUM N 16746; H, FUM N 13904. All wetted with alcohol; converted to standard right view. Scale bars 2 mm.

Specimen HM 11-A4706 (Fig. 4). Forewing 14.3 mm long, 6.9 mm wide (length/width ratio 2.07). rv with seven branches (five distal branches forked once, others simple). RP with three ORBs. ORB1 with four branches directed anteriorly proximad third gradate series of crossveins. ORB2 shallowly forked. ORB3 (distal) with seven branches, one of branches forked twice proximad fourth (outer) gradate series of crossveins. M nearly dichotomously forked five times proximad third gradate series; proximal-most fork located distad origin of ORB1. Cu divided into CuA, CuP near wing base. CuA pectinate, with five branches, one of which is deeply forked. CuP dichotomously forked, with fine long branches; its most-proximal fork located near its origin. A1 preserved fragmentarily, with probably three distal pectinate branches. First (basal) gradate series of crossveins with three preserved crossveins: between Sc, R; M, CuA; and CuA, CuP. In second series, three preserved crossveins between the branches of CuP. Third

series complete, with 18 crossveins from the stem of RA to CuA and two poorly preserved crossveins between branches of CuA. Fourth (outer) series partially preserved, with 19 crossveins from RA to CuP. Two additional crossveins: between RA and ORB3 proximad third gradate series; between RA and ORB1 (possibly belonging to second gradate series). Color pattern: wing generally brownish; costal space (except basal portion), basal part of wing and distally in area of fourth gradate series dark brown; area approximately at the origin of CuA1 blackish; membrane surrounding crossveins in third gradate series dark brown forming transverse fascia (color patterns of part and counterpart differ significantly).

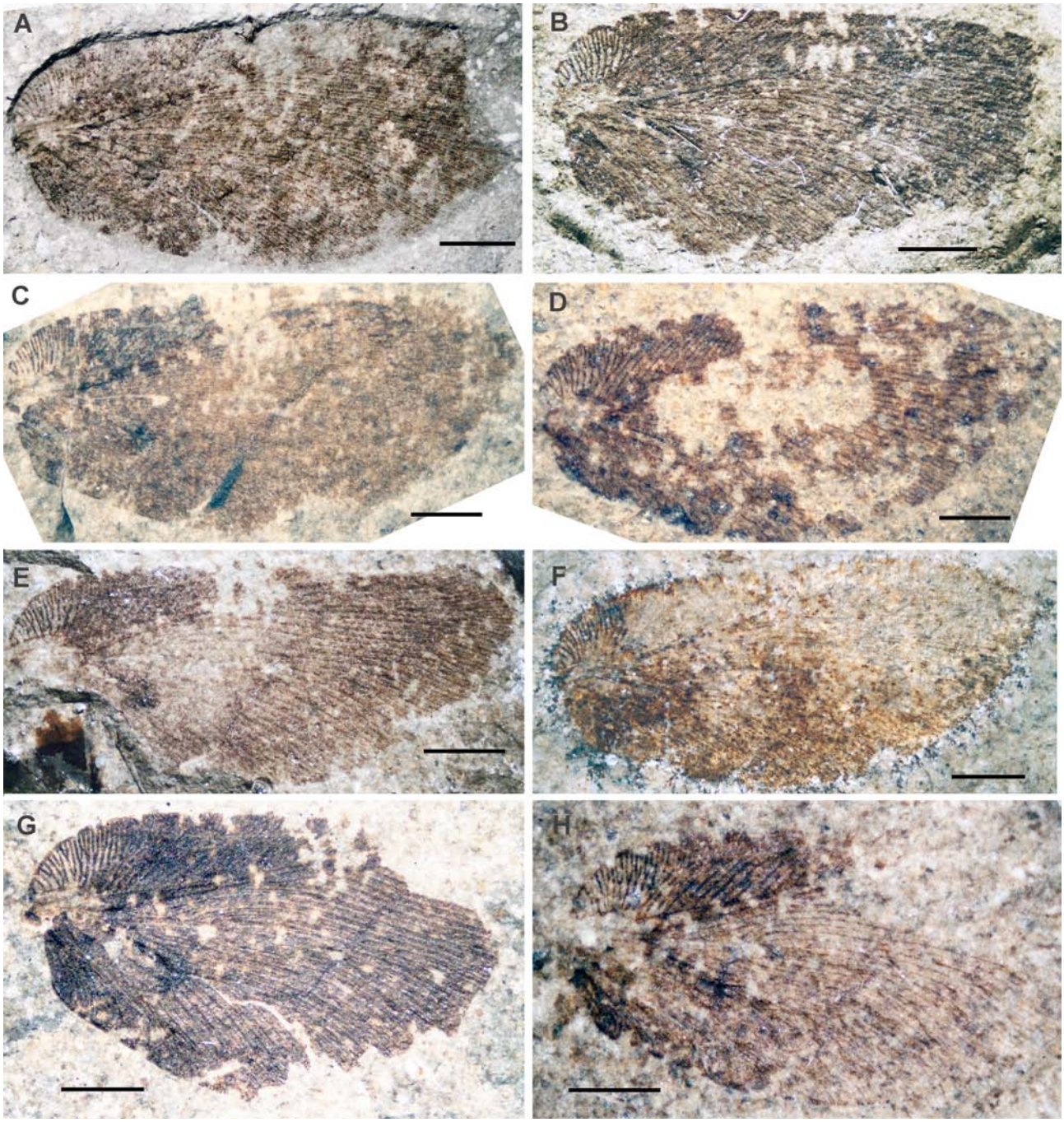

FIGURE 8. *Archibaldia densistriata* (Henriksen, 1922), forewings. A, HM 4-2003; B, FUM N 13474; C, HM 14M-3744; D, HM 11-A4705; E, FUM N 16656; F, FUM N 13909; G, FUM N 11104; H, FUM N 11102. All wetted with alcohol; converted to standard right dorsal view. Scale bars 2 mm.

Specimen HM 14M-B2983 (Fig. 5). Forewing 13 mm long (as preserved; estimated complete length *ca*. 14 mm), 6.4 mm wide (length/width ratio 2.19). hv with nine branches (four simple, others forked once to three times). RP

with five ORBs. ORB1 with three anteriorly-directed branches proximad third gradate series of crossveins. ORB2, ORB3 shallowly forked. ORB4 with five branches (one of these deeply forked); ORB5 probably shallowly forked (its presence is abnormal). M forked four times proximad third gradate series. CuA with four branches proximad fourth gradate series of crossveins (two deeply forked). CuP probably five-forked proximad fourth gradate series. A1 long, deeply forked, both branches distally forked several times (branching type unclear). A2 long, pectinately forked, all branches forked. A3 relatively short, weakly branched. Two preserved crossveins in first (basal) gradate series: between Sc and R, and between R and M. Second series: only one preserved crossvein (between CuA, CuP) long, oblique. Third series incomplete, with 14 preserved crossveins from RA to CuP. Fourth (outer) series incomplete, with 16 preserved crossveins from ORB1 to CuP. Coloration generally as in the holotype, but much darker; also, membrane surrounding crossveins in third and fourth gradate series dark brown forming two transverse narrow fasciae.

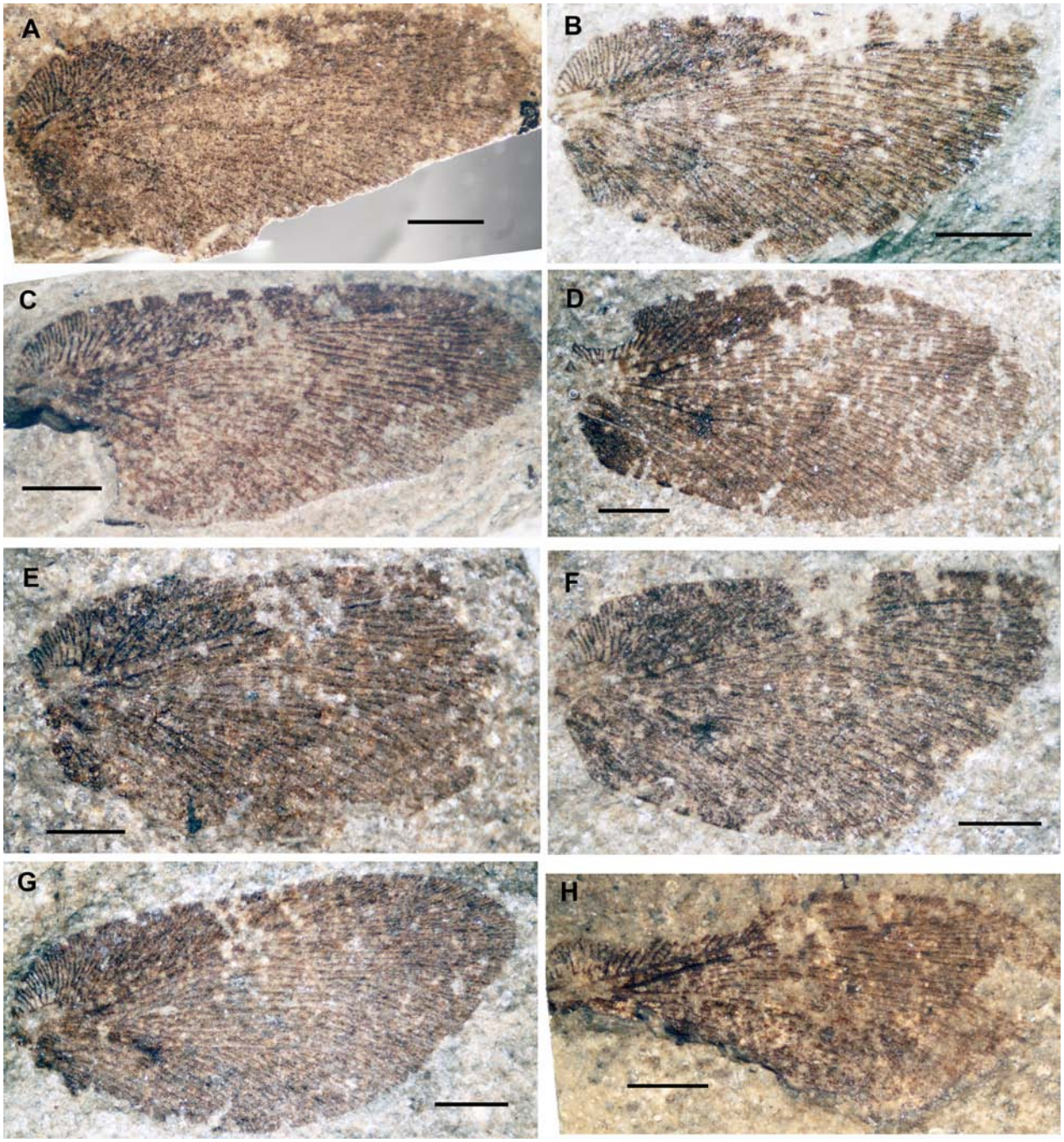

FIGURE 9. *Archibaldia densistriata* (Henriksen, 1922), forewings. A, HM 14M-3105; B, HM 11-A4485; C, HM 6M-2258; D, FUM N 13899; E, HM 10-B3138; F, HM 14M-B4041; G, FUM N 13900; H, HM 14M-3027. All wetted with alcohol; converted to standard right view. Scale bars 2 mm.

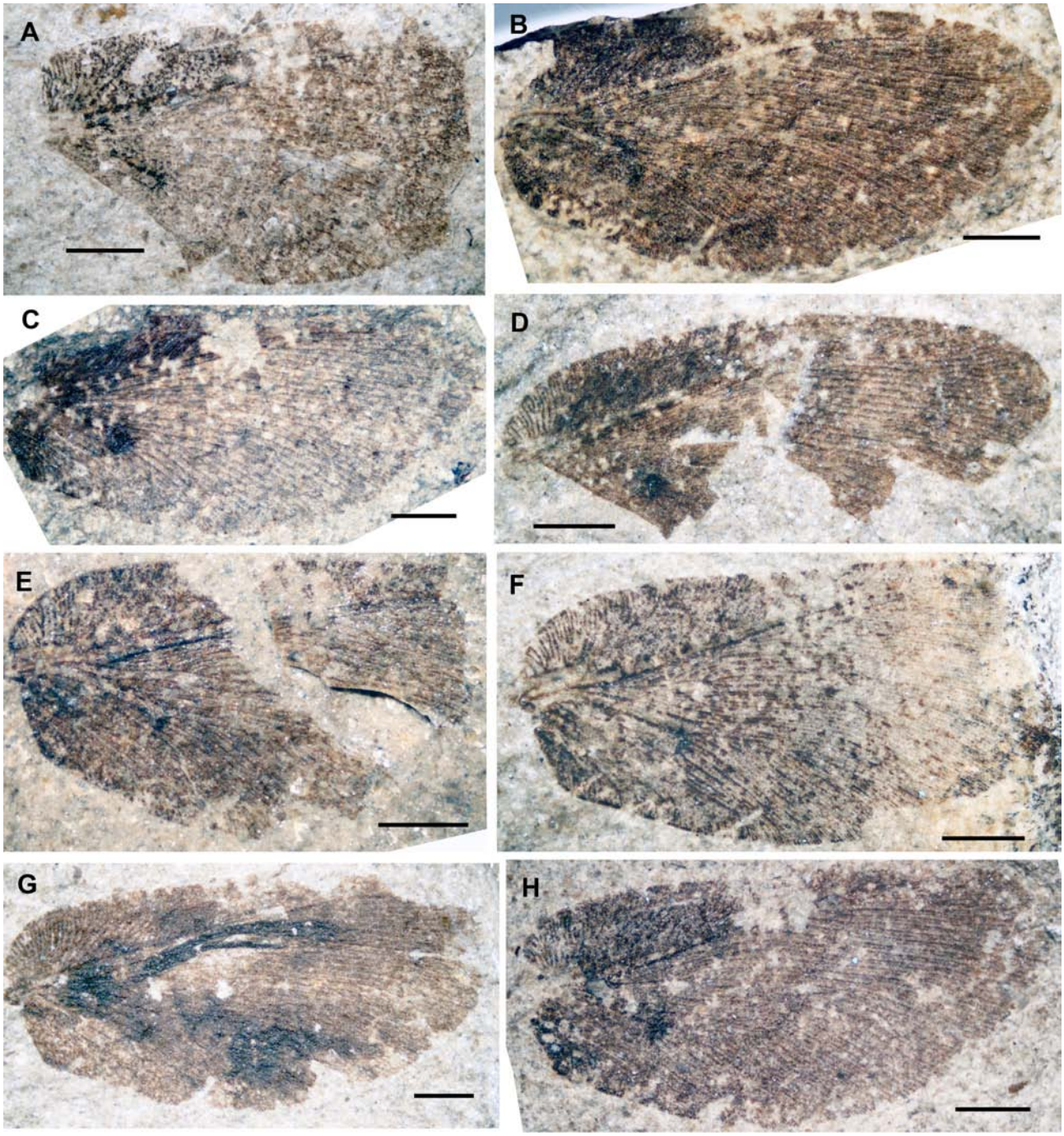

FIGURE 10. *Archibaldia densistriata* (Henriksen, 1922), forewings. A, HM 11-3942; B, HM 14M-B4264; C, HM 14M-3795; D, HM 14-3361; E, HM 14M-B2314; F, HM 21-2011; G, TJS 0123; H, HM 17-C3223. All wetted with alcohol; converted to standard right dorsal view. Scale bars 2 mm.

Remarks. No complete specimens of the species have been found to our knowledge and therefore the assignment of the hind wing HM 14M-B3268 to it is speculative, based on the following arguments. This hind wing belongs to Hemerobiidae: its shape is characteristic of the family; Sc and RA are widely spaced distally (fused in Polystoechotidae and Osmylidae); the preserved venation in the postero-distal part of the wing excludes Chrysopidae and Mantispidae, and is characteristic of Hemerobiidae; the long CuA parallel to the hind margin is not traced (present in Berothidae). Its length (*ca*. 12 mm) is corresponding to length of forewings of *Archibaldia densistriata* (12.3–15.8 mm). Other numerous hemerobiids from the Fur Formation are smaller and their hind wings are shorter, *ca*. 5–10 mm. Unfortunately, the only hind wing is very poorly preserved, and few details are discernible.

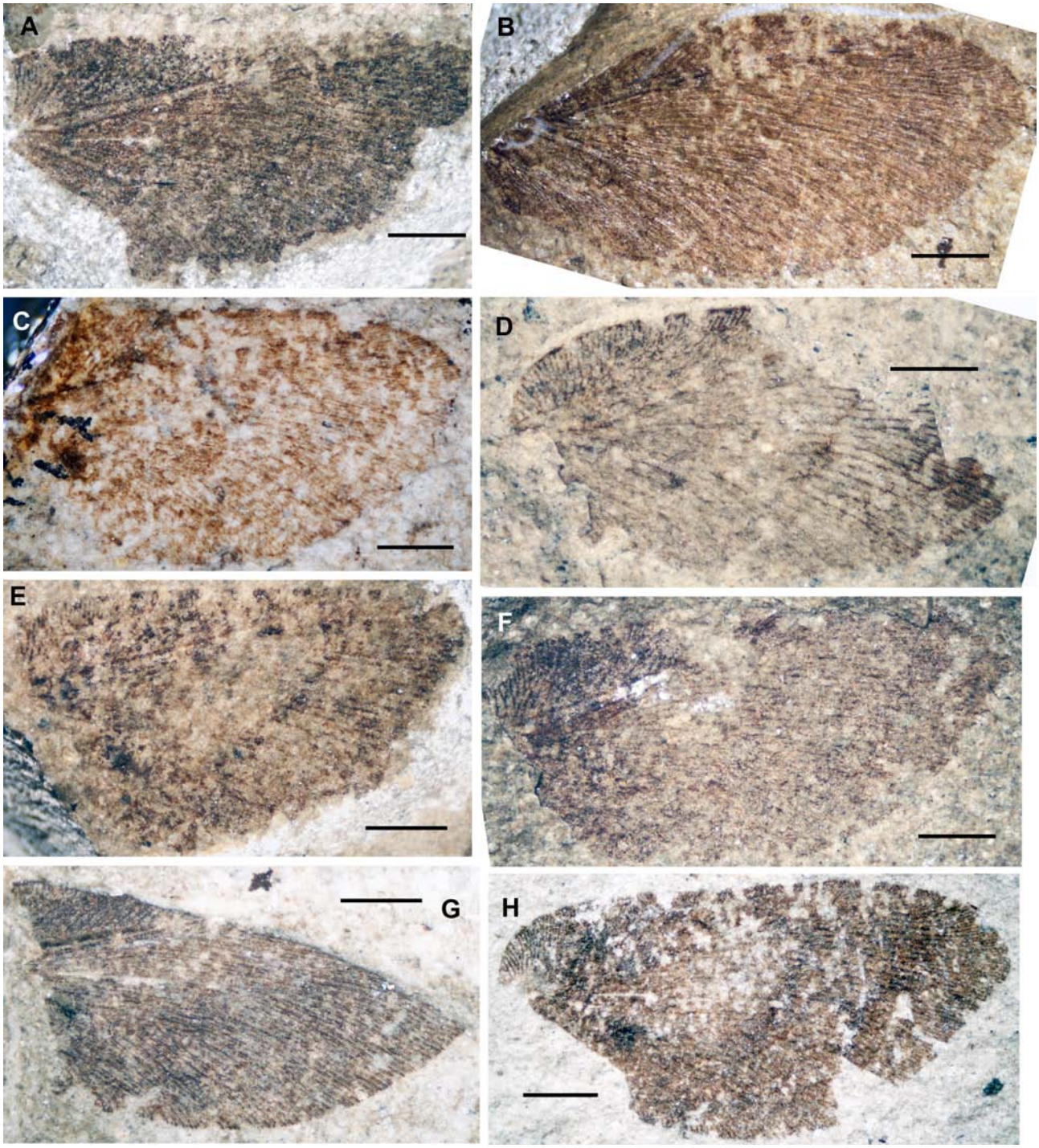

FIGURE 11. *Archibaldia densistriata* (Henriksen, 1922), poorly-preserved forewings. A, FUM N 13895; B, HM 14M-B4970; C, HM 14M-2480; D, HM 14M-B3899; E, HM 14M-A4605; F, HM 14M-B3907; G, HM 11-3165; H, HM 14M-C3498. All wetted with alcohol; converted to standard right view. Scale bars 2 mm.

The poorly preserved and incomplete forewings shown in Figure 11 have some coloration characteristic of *A. densistriata* and are assigned to that species. The very poorly-preserved and incomplete forewings shown in Figure 12 have some venation features of *Archibaldia*, but does not have the coloration of *A. densistriata*, and they are assigned to this species only preliminarily.

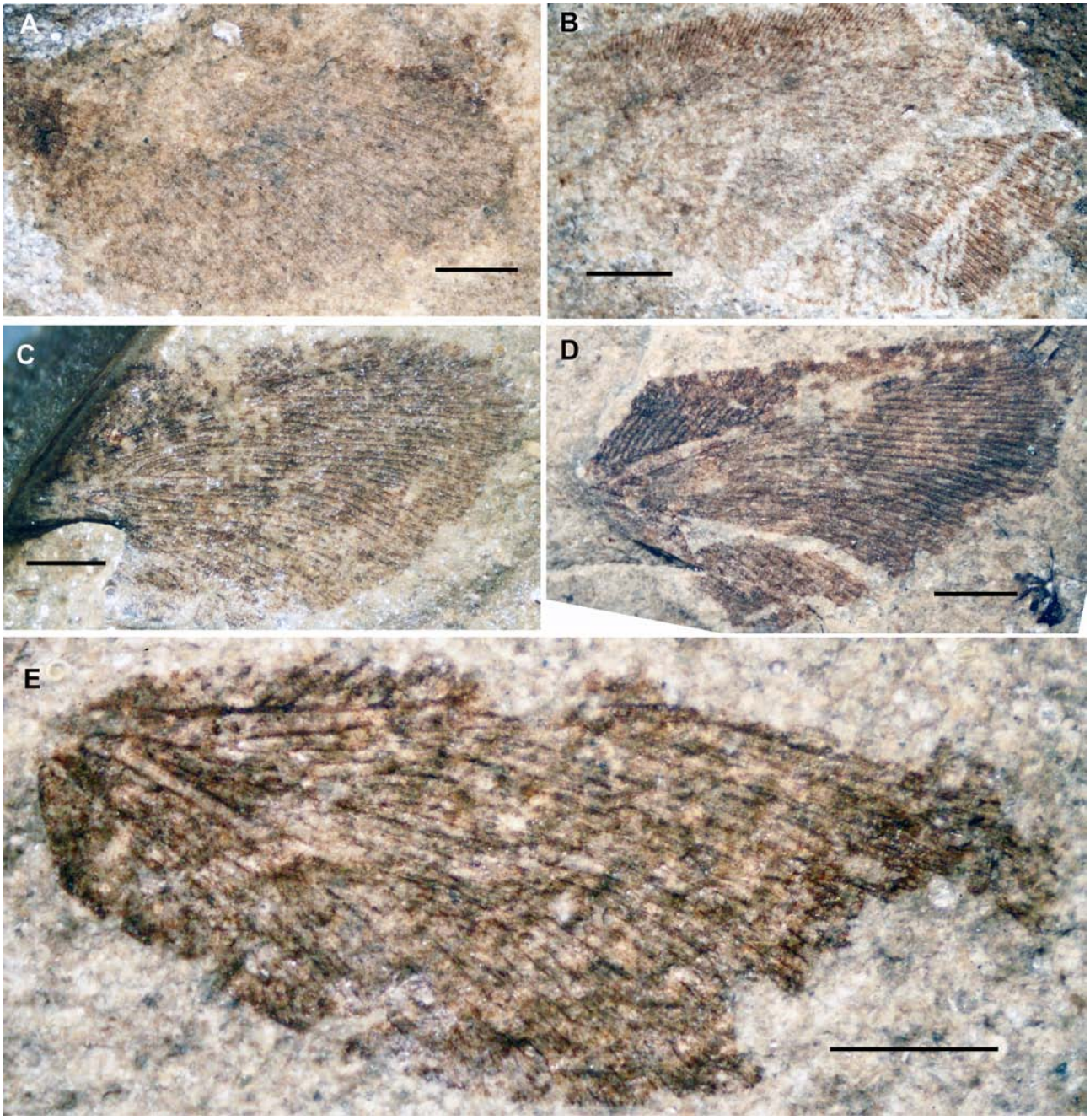

FIGURE 12. Forewings of presumed *Archibaldia densistriata* (Henriksen, 1922). A, HM 14M-2519; B, HM 14M-B4731; C, HM 14M-B3312; D, HM 8-2193; E, HM 8-2193. All wetted with alcohol; converted to standard right view. Scale bars 2 mm.

Discussion

Genus affinity of *Megalomus densistriatus*

The examined material shows that the characters of *Megalomus densistriatus* fully correspond to the diagnosis of the genus *Archibaldia* (see Diagnosis). Unfortunately, the membrane of this species is mostly dense and brownish. Due to this, the venation of most specimens is not clearly discernible, like that of extant species of *Drepanepteryx* Leach, 1815. All diagnostic character states of *Archibaldia* are preserved only in the few best-preserved specimens. In particular, the basal crossvein 1r-m is detected only in FUM N 10527 and HM 14M-B2983 (Figs 3, 5); crossvein between ORB1 and RA is well preserved only in HM 11-A4706 (Fig. 4).

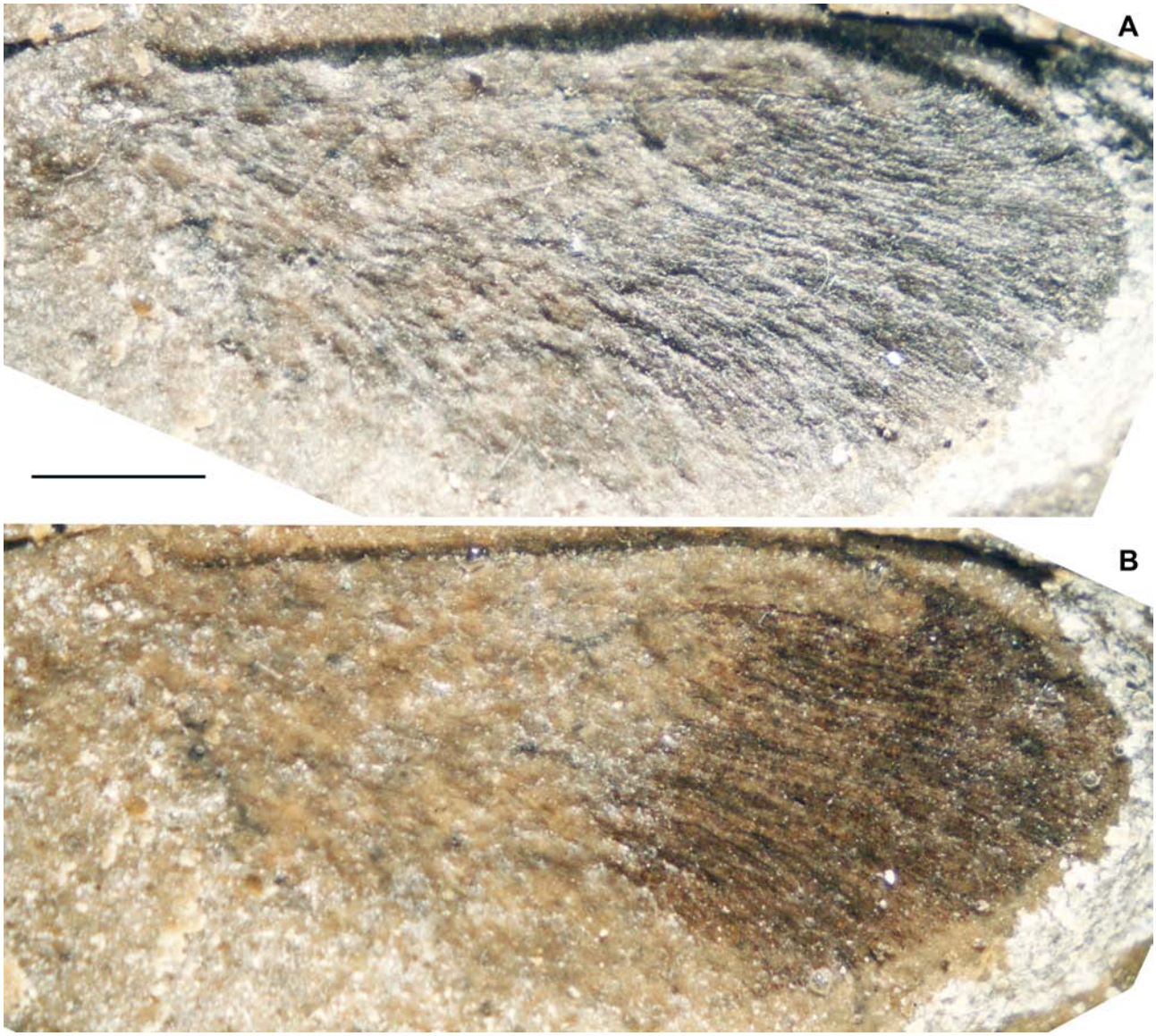

FIGURE 13. Hind wing of presumed *Archibaldia densistriata* (Henriksen, 1922). HM 14M-B3268. A, part, dry; B, part, wetted with alcohol (both converted to standard right view). Scale bar 2 mm (both to same scale).

We add a character [#6] to the genus diagnosis of Makarkin (2023). Crossveins between branches of CuA in the third gradate series are present in two species of *Archibaldia* (*i.e.*, *A. densistriata* and *A. wehri*: Makarkin *et al*. 2003: Fig. 4), and not detected in *A. aristovi* because of incomplete preservation (Makarkin 2023: Fig. 2). These crossveins occur only in few species of Hemerobiidae, all belonging to *Megalomus*-like genera: the extant *Austromegalomus insulanus* Oswald, 1988, *Drepanepteryx phalaenoides* (Linnaeus, 1758), and *Megalomus moestus* Banks, 1895 (Oswald 1993: Figs 140, 182; Monserrat 1997: Fig. 99).

Crossveins between branches of CuP in the first gradate series [#7] are not detected in *A. densistriata* due to poor preservation of this area in all specimens examined.

Characteristics of *Archibaldia densistriata*

Unfortunately, the body of the species is not preserved in any specimens, and only one presumed poorly-preserved hind wing is identified. Thus, it is known exclusively by its forewings. Additionally, the bodies and hind wings of other species of the genus are not preserved either (except for the pterothorax of *Archibaldia? gradata*, but this species is preliminarily assigned to the genus).

The forewing venation of *A. densistriata* is very similar to those of *A. wehri* and *A. aristovi*, especially given its variability. The venation of two undescribed specimens of the genus from the early Eocene Republic locality (USA), the type locality of *A. wehri*, is more similar to that of *A. densistriata* than to the holotype of *A. wehri*. The presence of crossveins in the costal space of these specimens is the only reliable difference from *A. densistriata*. *Archibaldia aristovi* is known by the basal portion of a forewing, and differs from *A. densistriata* only by the RP branching (see Diagnosis) and color pattern (*A. aristovi* possesses numerous small brown spots).

The rather high variability of *A. densistriata*'s venation is normal for all species of Drepanepteryginae. Such an anomaly as observed in FUM N 10527, *i.e*., the incomplete branch of M (Fig. 3), is also normal for the family. However, an anomaly found in HM 14M-B2983, *i.e*., the extra distal ORB5 (Fig. 5), has never been seen before in Hemerobiidae.

The forewings of *A. densistriata* are clearly different in shape. In general, the length/width forewing ratio differs between males and females of most examined Hemerobiidae (Makarkin & Kholin 1995). The greatest sexual differences in this ratio are observed in *Hemerobius tristriatus* Kuwayama, 1954: 2.38±0.01 in males and 2.51±0.02 in females, *i.e*., the ratio of the female forewing is on average 0.95 of that of the male forewing. This is significantly lower than for *A. densistriata*; differences between extreme values in its length/width forewing ratio are 0.84, *i.e*., the forewing shape of *A. densistriata* is more variable. Apparently, representatives of both sexes are present among the specimens examined.

The more or less stable elements of the color pattern of *A. densistriata* include a pale membrane between branches of the humeral veinlet, dark brown area in the proximal costal space, and a blackish spot approximately near the origin of CuA1. An undescribed specimen of the genus from Republic has a color pattern particularly similar to that of *A. densistriata* possessing these stable elements. The brown membrane around crossveins of the third and (rarely) fourth gradate series is probably not present in every forewing or is poorly preserved in most forewings of both *A. densistriata* and *A. wehri*.

Probable climatic parameters of *Archibaldia densistriata*

The Fur Formation was deposited during an approximately 650-thousand-year period, from -33 ash layers (lowest depositions of the formation) to +140 (uppermost) (Jones *et al*. 2025: Fig. 7). But *A. densistriata* is known to occur in a much shorter period. Most specimens of *Archibaldia densistriata* are found in positive ash layers (younger), mainly from +25 to +30, rarer in +15, but two specimens are from negative layers (older), from -11 to -13 and -24 to -29. The color pattern and discernable venation of these specimens from negative layers do not differ from those from positive layers, including the holotype. Therefore, they surely belong to *A. densistriata*. The age of +19 layer is estimated to be 55.331 Ma; the age of the lowest depositions of the formation is approximately 55.785 Ma (Charles *et al*. 2011; Stokke *et al*. 2020; Jones *et al.* 2025).

Therefore, the species is documented in no more than a 250,000-year period, but it likely existed during most of the Fur Formation deposition. We assume that the environmental conditions in the older layers were unfavorable for it. In upper horizons of the formation (positive layers) the climate was cooler than in lower horizons, although the lowest layers were deposited during a period of sharp, relatively short-term cooling (the so called "recovery phase") (Jones *et al*. 2019; Stokke *et al*. 2020). This may be why the positive layers lack some cryophobic taxa that occur in negative layers, *e.g*., the recently described Drepanicinae and possibly Calomantispinae (Neuroptera: Mantispidae), syncompressed *Ropronia* Provancher, 1886 (Hymenoptera: Roproniidae) and Mantodea (Makarkin *et al*. 2025a, b; Shcherbakov *et al*. 2025; Makarkin & Perkovsky 2026; Perkovsky & Rasnitsyn 2026). Upper horizons (layers +25 to +30) are those where the highest number of aphids are found, which is a good indicator of this cooling (Rust 1999; Prokin *et al*. 2024; Makarkin *et al*. 2025b). The larvae and adults of *A. densistriata* undoubtedly fed mainly on aphids like most living representatives of Hemerobiidae. In general, the climatic parameters of *Archibaldia* species were likely similar to those of the morphologically resemble *Neuronema* McLachlan, 1869, species of which live today mainly in eastern Palearctic. At least two species of *Archibaldia* (*A. densistriata* and *A. wehri*) probably preferred the upper microthermal to lower mesothermal mesic climatic conditions, similar to those of modern coastal southern British Columbia (climatic parameters of *A. wehri* after Greenwood *et al.* 2005).

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