

## Horseflies and Athericids (Diptera: Tabanidae, Athericidae) from the Lower Cretaceous of England and Transbaikalia

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**Abstract**—New taxa of tabanids and athericids are described from the Lower Cretaceous deposits of England and Transbaikalia. The relationships of new genera to the Recent Athericidae and Recent and fossil Rhagionidae are discussed. *Atherix sauneri* Théobald, 1937 from the Oligocene of France is removed from the family Athericidae.

**Key words:** Horseflies, athericids, Lower Cretaceous, England, Transbaikalia.

### INTRODUCTION

Horseflies (tabanids) and athericids are rather scarce in the fossil record (Evenhuis, 1994). However, any finds of these flies are especially interesting in relation to the appearance of bloodsucking in dipterous insects (Lukashevich and Mostovski, 2003). Females of the majority of horseflies and athericids are bloodsuckers of mammals and birds; additionally, horseflies are known as bloodsuckers of reptiles and athericids are recorded as parasites of amphibians. It is interesting to note that the appearance of horseflies (Martins-Neto, Kucera-Santos, 1994; Coram *et al.*, 1995; Ren, 1998) occurs in the Early Cretaceous, i.e., the same time as the appearance of other dipteran families with hematophagous representatives (e.g., Kalugina, 1991; Borkent, 2001; Hennig, 1972; Szadziewski, 1996; Szadziewski and Arillo, 1998). Horseflies are recorded as a family in the Upper Cretaceous of Gondwana (McKay and Rayner, 1986), but the only impression from the South African locality of Orapa is still undescribed, and its affinity cannot be clarified from the published figure. So far, athericids have been recorded only from the Cenozoic (Cockerell, 1914; Stuckenberg, 1974), being most abundant in Baltic amber. Judging from the original description and wing drawing by Théobald (1937), *Atherix sauneri* from the Oligocene of France should not be referred to the Athericidae. Contradictory characters include, among others, a very long vein  $R_{2+3}$  that terminates well beyond a short  $R_1$  (near the wing apex) and an enlarged and distally shifted discal cell. For the same reasons, this species cannot be referred to the family Rhagionidae, in which the genus *Atherix* was previously placed. Generally speaking, the combination of characters of this species as mentioned by Théobald is quite unusual and placement among

Recent families is not possible without reexamination of the type material; however, the chances of finding truly aberrant dipterans in the Cenozoic are slim.

The new finds extend the geographical and stratigraphical range of both Tabanidae and Athericidae. The Lower Cretaceous of England has provided the most diverse material. In addition to a horsefly wing previously recorded from the Upper Berriasian Durlston Formation (Coram *et al.*, 1995), described below as *Eotabanoid lordi* sp. nov., a wing of the athericid *Athericites sellwoodi* sp. nov. was found in the Lower Berriasian Lulworth Formation and *A. kensmithi* sp. nov., *A. gordonii* sp. nov., and *A. finchi* sp. nov. were found in the Hauterivian/Barremian Weald Clay. Geological reviews of insect-bearing Wealden deposits were published earlier (Jarzembowski, 1991; Ross and Cook, 1995), and the Purbeck geology was reviewed by Clements (1993). A single wing of an athericid, *A. zazicola* sp. nov., and a nearly complete horsefly, *Baissomyia redita* sp. nov., were found in the exceptionally fossiliferous Transbaikalian locality of Baissa. A detailed description of the Zaza Formation, exposed at the left bank of the upper reaches of the Vitim River is still unpublished; general accounts are, however, given by Martinson (1961) and Zherikhin *et al.* (1999).

The climate in Europe was variable during the Early Cretaceous (Allen, 1998) so it is not surprising that the rare athericids from the Purbeck and Wealden belong at the very least to different species. A generic assignment of species is difficult based solely on wing venation, and we therefore describe all the species within the formal genus *Athericites* gen. nov. It should be noted, however, that *A. sellwoodi* sp. nov. from the Lulworth Formation differs substantially from all other known Early Cretaceous species and most probably belongs to

a separate natural genus. The climate was also variable in the Early Cretaceous of Transbaikalia (Zherikhin *et al.*, 1999), but no conclusions concerning the climate can be drawn using the new dipteran material due to its rarity. The characters preserved in the new fossil tabanids do not permit a full taxonomic comparison with Recent horseflies. Nevertheless, the general appearance of the body and (or) wing venation places them firmly in the Tabanidae.

Venational features characteristic of athericiform genera were considered in detail by Stuckenberg (1973), and these are reviewed here in relation to the new Mesozoic material. First, the close terminal convergence of veins  $R_{2+3}$  and  $R_1$ , considered by Stuckenberg to be characteristic of athericids, is seen in *Athericites*. Second, in athericids, veins  $R_4$  and  $R_5$  diverge at much less of an angle than in rhagionids and tabanids. In the latter, divergence occurs by the apomorphic elongation of the apical part of the wing. Among the *Athericites* species, both states of this character are recorded. *A. sellwoodi* sp. nov., *A. gordonii* sp. nov., and *A. finchi* sp. nov. have a fork, which particularly resembles that of Recent athericids, whereas in *A. kensmithi* sp. nov. and *A. zazicola* sp. nov., vein  $R_4$  starts at a steeper angle. This is especially pronounced in the latter species, where it is obviously a secondary feature due to the apparent narrowing of the apical portion of the wing. It should be noted that, in some Jurassic rhagionids, such as *Palaeobolbomyia* (Mostovski, 2000) and a series of undescribed rhagionids with four branches of M, this fork is often narrowed basally. It is quite possible that this character was unstable at the time of separation of the athericid–tabanid stem from rhagionids.

Third, vein  $R_4$  normally terminates before the wing apex in athericids, whereas in rhagionids, it often terminates at the apex. There are exceptions among Recent members of both families; in Jurassic rhagionids,  $R_4$  often enters the margin of the wing before the apex. In all species of *Athericites*, this vein also terminates short of the apex.

Fourth, in athericids, the third posterior cell is broadened apically, since veins  $M_3$  and  $M_4$  are convergent, sometimes leading to closure of the fourth posterior cell. Among Recent rhagionids,  $M_3$  and  $M_4$  are much less convergent and are often parallel; exceptions occur among athericids as well. The third posterior cell also happens to be somewhat broadened apically in the type species and undescribed species of the genus *Protorhagio* Rohdendorf, 1938 and some other Jurassic rhagionids. This cell is distinctly broad in all species of *Athericites* gen. nov., although this is poorly pronounced in *A. zazicola* sp. nov.

Fifth, the basal cell tends to be elongate in athericids, which correlates with a displacement of the discal cell towards the wing margin and a corresponding shortening of the second and third posterior cells. Again, there are exceptions. Thus, the basal cells are relatively short and the discal cell is not shifted distally

in the genus *Dasyomma*. However, this genus is distinctive within the family Athericidae and has even been placed in a separate subfamily (Stuckenberg, 1973). In Recent and fossil rhagionids, the basal cells are short and species of *Athericites* gen. nov. are closer to rhagionids in this respect, but in *Athericites* gen. nov., the discal cell is elongate and the posterior cells are correspondingly shortened, which is atypical of rhagionids.

Sixth, as a rule, the transverse rm meets the discal cell farther from its basal end and is often distad of the basal section of  $M_4$ . In Recent rhagionids and tabanids, rm is usually nearer the base of the discal cell, but in *Eostratiomyia avia* Rohdendorf, 1964, some *Protorhagio*, and a number of other fossil rhagionids, the transverse rm is evidently shifted distally, sometimes to the very middle of the discal cell. Among the species of the new genus, such a shift is recorded in only *A. gordonii* sp. nov., but its absence from other species merely supports the close position of this group to the ancestral stalk.

Finally, seventh, in athericids,  $M_1$  is more gently arched near its base; this character is common in many fossil rhagionids, although this vein can often be strongly arched near its base. Only in *A. kensmithi* sp. nov. and most likely *A. zazicola* sp. nov., this vein is more or less sharply arched after the separation of  $M_2$ ; it is evidently gently arched in other species of *Athericites* gen. nov.

Several tentative apomorphies of Recent athericids seen to varying degrees in *Athericites* gen. nov. place the new genus within the Athericidae. These characters include  $R_{2+3}$  and  $R_1$  close together,  $R_4$  entering the wing margin before the wing apex, third posterior cell broadened distally, third and fourth posterior cells shortened, and transverse rm displaced distally. Regarding the presence of these characters in Jurassic rhagionids, this highlights the need for their complete revision and the recognition of groups that might be ancestral to athericids and tabanids.

The type material is deposited in the following museums and institutions: Paleontological Institute, Russian Academy of Sciences (PIN), Booth Museum, Brighton, United Kingdom (BMB), Maidstone Museum and Bentlif Art Gallery, Kent, UK (MNEMG), Natural History Museum, London (NHM).

## SYSTEMATIC PALEONTOLOGY

### Family Tabanidae Latreille, 1802

#### Genus *Baissomyia* Mostovski, Jarzembowski et Coram, gen. nov.

*E t y m o l o g y.* From the locality of Baissa and the Greek *myia* (fly).

*T y p e s p e c i e s.* *B. redita* sp. nov.

*D i a g n o s i s.* Female. Large fly with compact abdomen, closely fitting head, and slender legs. Pedicel small and nearly quadrate in side view; stylus thin, rather long, and not subdivided into rings. Proboscis elongate, nearly as long as height of head capsule, mouthparts well developed. Labium and syntrophium



**Fig. 1.** *Baissomyia redita* sp. nov., holotype PIN, no. 4210/3152,  $\times 6.2$ .

equal in size. Clypeus weakly swollen.  $R_1$  and  $R_{2+3}$  not convergent, costal section of  $R_{2+3}$ – $R_4$  twice as long as  $R_1$ – $R_{2+3}$ . Basal cells almost equal in length, rather short. Transverse *rm* in basal third of discoidal cell. Discoidal cell apparently weakly broadened apically. Alula and thoracic squama well developed. Abdomen apparently not flattened dorsoventrally, not telescopic, evenly narrowing towards apex, and consisting of seven visible segments; seventh segment shortest and perhaps partially extended. First abdominal tergite with small incision at anterior margin. Cerci one-segmented, short, conical.

**Species composition.** Type species.

**Comparison.** The new genus differs from Recent horseflies by having a nearly entire anterior margin of the first abdominal tergite that has only a weak incision, an elongated and undivided stylus, and by a more or less conical rather than flattened abdomen.

**Remarks.** Unfortunately, the wing of the only representative of the genus is poorly preserved, so some characters that would place it unequivocally within the horseflies are not visible. In particular, it is unclear whether or not the  $R_{4+5}$  fork was broad, and the shape of the anal cell is unknown. On the basis of some preserved features, this genus may be allocated to the Rhagionidae, Athericidae, or Tabanidae. However, it differs from athericids in that  $R_1$  and  $R_{2+3}$  are not closed distally and in the equally short basal cells. A stout body with a compact abdomen consisting of non extendable

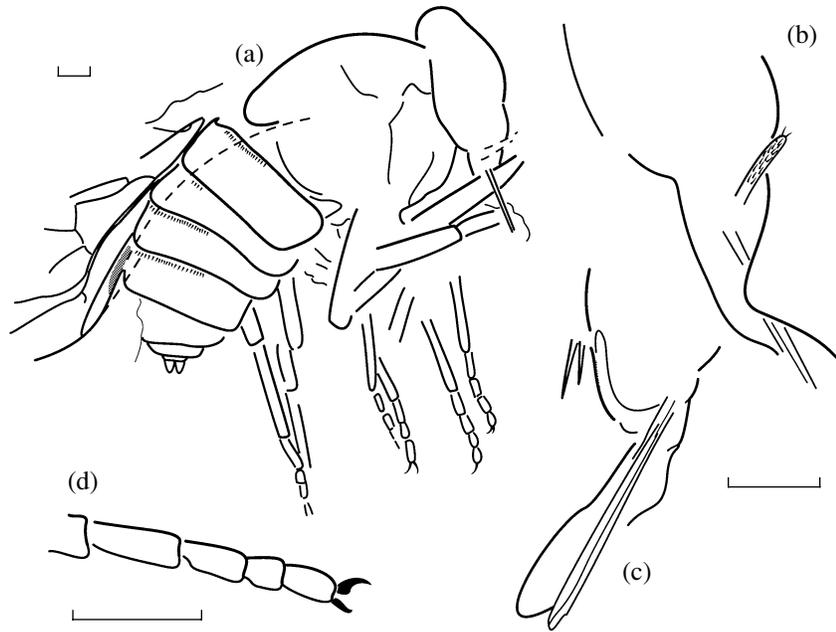
segments and comparatively slender legs, an elongate proboscis with strong stilettes, and one-segmented conical cerci deny its closeness to rhagionids.

*Baissomyia redita* sp. nov.

**Etymology.** From the Latin *redita* (returned).

**Holotype.** PIN, no. 4210/3152, part and counterpart of a well preserved complete female; Buryat Republic, Sosnovoozersk District, left bank of the Vitim River downstream of the Sololi Creek mouth, Baissa locality; Lower Cretaceous, Zaza Formation, bed 22 (Martinson, 1961).

**Description** (Figs. 1, 2). The body and all femora are dark; the tibiae are pale; the tarsi, especially their tips, are dark; basal halves of the first tarsomeres are somewhat paler. The whole body is densely covered with short, fine, and appressed hairs, which are longer on the dorsal side and along the posterior margin of tergites. The maxillary palps are rather slender, slightly curved, and covered with short hairs, which are directed forward. Vein  $R_1$  bears a row of fine setae at least in its visible apical portion. A dark stigma is developed as a narrow patch beneath  $R_1$ . Vein  $R_{2+3}$  is straight at least in its apical half, curving forward just before reaching the wing margin. The knob of the halteres is round. The claws are weakly curved, with a blunt tubercle at the base. Small, elongate pigmented dots are present along the anterior margins of tergites 1–4.



**Fig. 2.** *Baissomyia redita* sp. nov., holotype PIN, no. 4210/3152: (a) complete insect, (b, c) part and counterpart of lower portion of head capsule and proboscis, and (d) tarsus apex and claws. Scale bars, 1 mm in all figures.

**Measurements**, mm: body length, 15.3.

**Material.** Holotype.

**Genus *Eotabanoid* Mostovski,  
Jarzembowski et Coram, gen. nov.**

**Etymology.** From the generic name *Tabanus*.

**Type species.** *E. lordi* sp. nov.

**Diagnosis.** Wing somewhat narrowed and attenuated apically. Costal vein base much thickened. Costal section  $R_1$ – $R_{2+3}$  almost twice as long as sections  $Sc$ – $R_1$  and  $R_{2+3}$ – $R_4$ . Fork  $R_{4+5}$  broad, both free veins entering wing margin far from its apex. Basal cells short, transverse  $rm$  dividing anterior margin of discal cell 1:5. Vein  $M_1$  weakly arched basally. Fourth posterior cell slightly narrowed distally.  $CuA$  with row of very short setae before transverse  $mcu$ . Anal cell closed.

**Species composition.** Type species.

**Comparison.** Comparison with Recent taxa is difficult due to the few, relatively uninformative preserved characters; however, this genus differs from *Baissomyia* by a longer costal section of  $R_1$ – $R_{2+3}$ .

**Remarks.** The general shape of the wing, the much thickened basal costal vein, the long and nearly straight  $R_{2+3}$ , and the broad  $R_{4+5}$  fork unequivocally place the new genus in the Tabanidae. The presence of setae on  $CuA$  in *E. lordi* is unusual; this character occurs in some athericids and tabanids (Stuckenberg, 2000); however, it is hardly important enough to relate the new genus closely to these taxa.

***Eotabanoid lordi* sp. nov.**

**Etymology.** The species is named after Prof. A.R. Lord.

**Holotype.** BMB, no. 019617(019618), part and counterpart of wing; England, Dorset, Durlston Bay; Lower Cretaceous, Purbeck Limestone Group, Upper Berriasian, Durlston Formation, bed DB175 (Clements, 1993).

**Description** (Fig. 3). Vein  $R_{2+3}$  is weakly sinuous. Vein  $R_{4+5}$  bears several fine setae immediately before the transverse vein  $rm$ . Vein  $R_4$  is rather sharply curved forward in its distal third. The basal cells are equally long; the posterior cell is distinctly broad. The discal cell is slightly broadened distally.  $CuA$  and  $CuP$  are fused at the wing margin.

**Measurements**, mm: wing length, 8.6.

**Material.** Holotype.

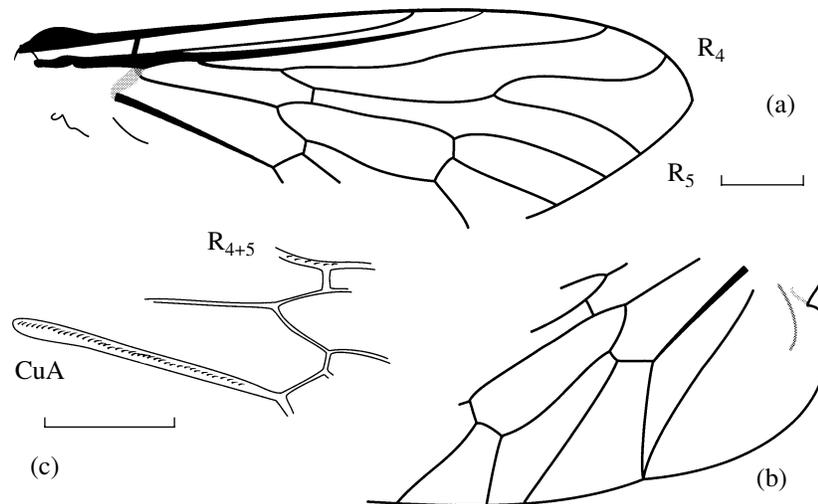
**Family Athericidae Stuckenberg, 1973**

**Genus *Athericites* Mostovski,  
Jarzembowski et Coram, gen. nov.**

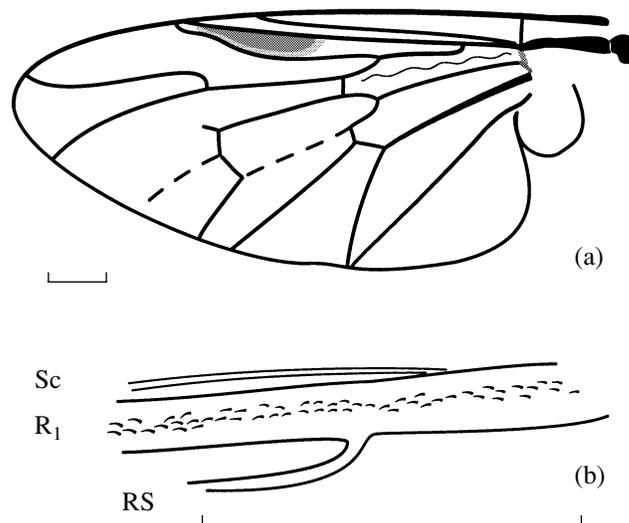
**Type species.** *A. gordonii* sp. nov.

**Diagnosis.**  $R_{2+3}$  and  $R_1$  vein tips very close. Vein  $R_4$  terminated before wing apex. Basal cells comparatively short, their distal ends not extending as far as the level of  $Sc$  termination. Vein  $M_1$  usually weakly arched basally. Fourth posterior cell narrowed distally; veins  $M_3$  and  $M_4$  convergent. Anal cell closed or very narrowly opened. Stigma very dark, well developed beneath vein  $R_1$ .

**Species composition.** Five new species.



**Fig. 3.** *Eotabanoid lordi* sp. nov., holotype BMB, no. 019 617 (019 618): (a, b) wing venation details visible on part and counterpart and (c) setation pattern of wing veins.



**Fig. 4.** *Athericites zazicola* sp. nov., holotype PIN, no. 4210/5215: (a) general appearance and (b) setation pattern of R<sub>1</sub>.

*Athericites zazicola* sp. nov.

**E t y m o l o g y.** From the Zaza Formation and the Latin *cola* (dweller).

**H o l o t y p e.** PIN, no. 4210/5215, excellently preserved wing; Buryat Republic, Sosnovoozersk District, left bank of the Vitim River downstream of the Sololi Creek mouth, Baissa locality; Lower Cretaceous, Zaza Formation, bed 31 (Martinson, 1961).

**D e s c r i p t i o n** (Fig. 4). The wing is rather broad, lanceolate, slightly tapering toward the apex, and has a well-developed anal lobe. Vein R<sub>1</sub> bears an irregular double row of very fine setae on its upper margin. R<sub>2+3</sub> is characteristically strongly sinuous before entering the costal vein and smoothly curved beneath the end of

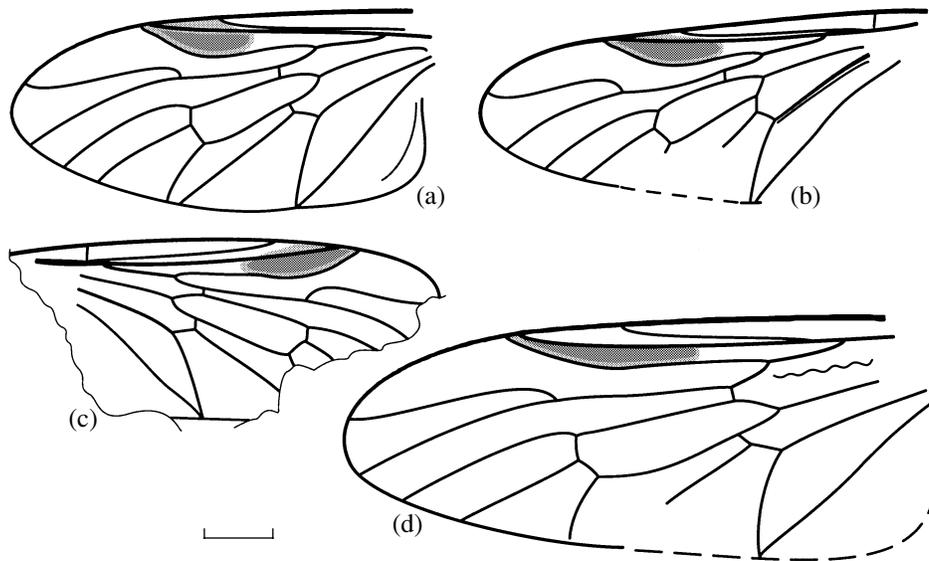
Sc. The R<sub>4+5</sub> fork is broad, the R<sub>4</sub> vein deviates at a right angle and then abruptly turns towards the wing apex. The basal cells are equally long, the posterior basal cell is just a little wider than the anterior one. Veins M<sub>3</sub> and M<sub>4</sub> are weakly convergent. The anal cell is not broad and narrowly opened. The stigma is dark, with rather sharp margins, developed only beneath R<sub>1</sub>.

**M e a s u r e m e n t s,** mm: wing length, 11.1; wing width, 4.9.

**M a t e r i a l.** Holotype.

*Athericites kensmithi* sp. nov.

**E t y m o l o g y.** This species is named in honor of the English dipterologist K.G.V. Smith.



**Fig. 5.** Wings of new athericids of the genus *Athericites* from the Lower Cretaceous of England: (a) *A. kensmithi* sp. nov., holotype NHM, no. In 64655, (b) *A. gordonii* sp. nov., holotype BMB, no. 023835, (c) *A. finchi* sp. nov., holotype BMB, no. 023836, and (d) *A. sellwoodi* sp. nov., holotype MNEMG, no. 2001.47.

**Holotype.** NHM, no. In 64655, wing impression; England, Surrey, Ockley, Smokejacks Brickworks; Lower Cretaceous, Upper Weald Clay, Lower Barremian.

**Description** (Fig. 5a). The wing is moderately broad, not tapering, but evenly rounded around the apex; the anal lobe is weakly developed.  $R_{2+3}$  is characteristically sinuous before entering the costa and strongly curved beneath the Sc termination. The  $R_{4+5}$  fork is not broad,  $R_4$  starting nearly at a right angle and then turning smoothly towards the wing apex. The basal cells are equally long, the posterior basal cell being just a little wider than the anterior one.  $M_1$  is remarkably arched at its base.  $M_3$  and  $M_4$  are strongly convergent. The anal cell is not broad, with a point-petiole. The stigma has somewhat indistinct margins; it is dark beneath  $R_1$  and noticeably paler above this vein.

**Measurements**, mm: wing length, 8.9; wing width, 4.2.

**Comparison.** It differs from *A. zazicola* sp. nov. by a narrower  $R_{4+5}$  fork, evenly curved  $R_4$ , weakly developed anal lobe, and a wider wing apex.

**Material.** Holotype.

*Athericites gordonii* sp. nov.

**Etymology.** This species is named in honor of William Gordon, collector.

**Holotype.** BMB, no. 023835, wing impression; England, Surrey, Ockley, Smokejacks Brickworks; Lower Cretaceous, Upper Weald Clay, Lower Barremian.

**Description** (Fig. 5b). The wing is moderately broad, narrowly rounded at the apex.  $R_{2+3}$  is very

weakly sinuous before entering the costa, evenly curved beneath the Sc termination. The  $R_{4+5}$  fork is moderately broad, vein  $R_4$  starting at an acute angle and smoothly sinuous. The anterior basal cell is noticeable longer than the posterior one, which is twice as broad as the former. Vein  $M_1$  is weakly arched at its base. The anal cell is rather narrow, nearly parallel sided proximad of transverse mcv, and narrowly opened. The stigma is slightly elongate, with somewhat indistinct margins, dark beneath  $R_1$  and notably paler above this vein.

**Measurements**, mm: wing length, 6.7; wing width, 2.5.

**Comparison.** This species differs from *A. zazicola* and *A. kensmithi* by its smoothly sinuous  $R_4$  and very unequal basal cells.

**Material.** Holotype.

*Athericites finchi* sp. nov.

**Etymology.** This species is named in honor of Tom Finch, collector.

**Holotype.** BMB, no. 023836 (023837), part and counterpart of wing; England, Surrey, Capel, Clockhouse Brickworks; Lower Cretaceous, Lower Weald Clay, Upper Hauterivian.

**Description** (Fig. 5c). The wing is moderately broad.  $R_{2+3}$  is more or less evenly arched posteriorly, but is not sinuous before entering the costa. The  $R_{4+5}$  fork is not broad; vein  $R_4$  starts at an acute angle and is smoothly sinuous. The basal cells are equally long, the posterior basal cell is only a little broader than the anterior one. Vein  $M_1$  is weakly arched at the base. Veins  $M_3$  and  $M_4$  are strongly convergent. The anal cell is not

broad and has a point petiole. The stigma has somewhat indistinct margins; it is dark beneath  $R_1$  and notably paler above this vein.

**Measurements**, mm: wing length, 6.5; wing width, 2.7.

**Comparison.** This species is especially close to *A. kensmithi*, from which it differs by a more smoothly curved vein  $R_4$ , vein  $R_{2+3}$  not being sinuous before its end, and by  $M_1$  being less curved basally.

**Remarks.** It is not improbable that *A. finchi* and *A. kensmithi* are the same species, the differences between them being due to belonging to different populations.

**Material.** Holotype.

*Athericites sellwoodi* sp. nov.

**Etymology.** This species is named after Prof. B. Sellwood, sedimentologist at the University of Reading.

**Holotype.** MNEMG, no. 2001.47, wing impression; England, Dorset, Durlston Bay; Lower Cretaceous, Purbeck Limestone Group, Lower Berriasian, Lulworth Formation, beds DB65–69 (Clements, 1993).

**Description** (Fig. 5d). The wing is rather narrow, narrowing towards its apex; the anal lobe is weakly developed.  $R_{2+3}$  is very weakly arched posteriorly, nearly parallel to  $R_1$ , and not sinuous before entering the costa. The  $R_{4+5}$  fork is narrow, the  $R_4$  vein starting at an acute angle and weakly sinuous. The basal cells are equally long, the posterior basal cell being a little narrower than the anterior one. Vein  $M_1$  is weakly arched basally. Veins  $M_3$  and  $M_4$  are strongly convergent. The anal cell is rather broad and has a point stalk. The stigma is distinctly elongate, developed only beneath  $R_1$  and evenly darkened.

**Measurements**, mm: wing length, 9.1; wing width, 3.7.

**Comparison.** This species differs from all other species of the genus by an extremely weakly arched vein  $R_{2+3}$ , the narrow  $R_{4+5}$  fork, weakly sinuous  $R_4$ , a broader anterior basal cell, and very broad anal cell.

**Material.** Holotype.

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