An insect Konservat-Lagerstätte in the Late Kimmeridgian lagoon of Orbagnoux (Rhône valley, France)

The Late Kimmeridgian lithoraphic marine limestones of the area around Orbagnoux (Rhône, France), are well known for their fish fauna and terrestrial flora. Here we describe the first records of insects and insect activities (plant attacks and trails in sediments) from these layers, including the oldest record of the gerromorphan bugs, as a new genus and species Gallomesovelia grioti, attributable to the most basal family Mesoveliidae and subfamily Madeoveliinae. These new fossils suggest the presence of a complex terrestrial palaeoecosystem on the emerged lands near the lagoon where the limestones were deposited. The exquisite state of preservation of these fossils also suggests that these outcrops can become crucial Konservat-Lagerstättes for the Late Jurassic of Western Europe

For Peerj

An insect Konservat-Lagerstätte in the Late Kimmeridgian lagoon of Orbagnoux (Rhône valley, France)

André Nel[1]*, Patricia Nel[1], Régis Krieg-Jacquier[2], Jean-Marc Pouillon[3] and Romain Garrouste[1]*

[1] Muséum National d'Histoire Naturelle, Institut de Systématique, Evolution, Biodiversité, ISYEB, UMR 7205 CNRS UPMC EPHE, CP50, 45 rue Buffon, F-75005 Paris, France; e-mails: anel@mnhn.fr, pnel@mnhn.fr, garroust@mnhn.fr,

[2] 18 rue de la Maconne, F-73000 Barberaz, e-mail: regis.krieg.jacquier@gmail.com

[3] 178 rue des Plattieres, F-38300 Nivolas Vermelle, France, e-mail: jmpdb@wanadoo.fr

ABSTRACT

The Late Kimmeridgian lithoraphic marine limestones of the area around Orbagnoux (Rhône, France), are well known for their fish fauna and terrestrial flora. Here we describe the first records of insects and insect activities (plant attacks and trails in sediments) from these layers, including the oldest record of the gerromorphan bugs, as a new genus and species *Gallomesovelia grioti*, attributable to the most basal family Mesoveliidae and subfamily Madeoveliinae. These new fossils suggest the presence of a complex terrestrial palaeoecosystem on the emerged lands near the lagoon where the limestones were deposited. The exquisite state of preservation of these fossils also suggests that these outcrops can become crucial Konservat-Lagerstättes for the Late Jurassic of Western Europe.

Localities near Solnhofen and Eichstatt is early Tithonian, see Schweigert, G. 2007. Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany - first results and open questions. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 245 (1): 117-125. http://dx.doi.org/10.1127/0077-7749/2007/0245-0117

Subjects Entomology, Paleontology

Keywords Insecta, Heteroptera, Mesoveliidae, gen. et sp. nov., attacks on *Zamites* leaves, trails in sediment.

INTRODUCTION

If the Late Kimmeridgian Konservat-Lagerstätte of lithographic limestone of Bavaria is well known with the numerous discoveries of emblematic fossils (*Archaeopteryx*, etc.), clearly less fossils were obtained from the French equivalents of these rocks in the departments of Ain and Rhône. Only the lithographic limestone formation of Cerin has been the subject of significant scientific studies on taphonomy, flora, and ichnofossils (*Bernier et al., 1991*). The fauna is there essentially of marine origin (*Wenz et al., 1994; Gaillard et al., 2006*) if the presence of vertebrate trackways demonstrates that some terrestrial environments were very close to this place. Nevertheless no insect and no trace of the activity of these animals were discovered at Cerin, unlike the rich palaeoentomofauna of Solenhofen-Eichstätt. The sites around Orbagnoux were better candidates for the discovery of terrestrial arthropods because fossil plants are more frequent and frequently well preserved. Nevertheless if this area was investigated in 19th century and before the years 1990, no recent field researches were made and no insect has ever been discovered there.

During two field researches during 2012 and 2013, with the help of the Société des Naturalistes et Archéologues de l'Ain and the Groupe 'Sympetrum' (Recherche et Protection des Libellules), we could discover in the outcrops around Orbagnoux a small bug that represents the first Late Jurassic insect of France, plus plant attacks caused by insects, and probably track ways of aquatic fly larvae. These first discoveries suggest that more terrestrial arthropods are present in these layers. Also the quality of preservation of these fossils is superior to those of the fossil insects from the Bavarian lithographic limestone, suggesting that Orbagnoux can become in the next future one of the major insect outcrops for the Late Jurassic.

MATERIAL AND METHOD

The fossils were collected in the small valley of the river Dorches (a river Rhône tributary), situated on the territory of the Corbonod village, North West of Orbagnoux mine (Long. 5° 46’ 32.2” E, Lat. 45° 59’ 26.3” N, alt. 597 m), and in the newly recorded outcrop of the “Croix de Famban” (situated along the small road D123, alt. 1310-1313 m, Long. 5° 45’ 58.5” E, Lat. 45° 56’ 58.9” N, and along the eastern margin of the anticlinal surface, 200 m south of the road), situated south west of Orbagnoux, in lithographic and bituminous limestones of the same horizon. These levels are raised and follow the anticlinal of le Grand Colombier situated west parallel to the Rhône valley between Corbonod and Songieu (*Gudefin, 1968*). *Tribovillard et al. (1999)* considered that this formation is very poor in macroorganisms (“quasi-abiotic platy limestone accumulation”). The highly bituminous black shales inside of the Orbagnoux mine (*Chateauneuf et al., 1982*) contain few macrofossils (own observations: mainly rather poorly preserved ammonites and bivalves, foraminifers and ostracods). On the contrary, fossil plants, fishes and Crustaceae are well known in other layers outside of the mine (*Barale, 1981; Tejo Yuwono, 1987*) (see Figure 1). More precisely, plants remains (leaves, fruit cones, seeds, branches, pollen) are very frequent in the less bituminous dark brown levels outside of the mine in the Dorches valley. The flora comprises no less than 34 species (Pterydophytes, Pteridopsemales, Cycadales, Ginkgoales, Bennetitales, Coniferales). The most frequent leaves correspond to bennetitalle *Zamites*. Fossil fishes (*Sauvage, 1893; Wenz et al., 1994*), vertebrate coprolithes, marine Crustacea, oysters, small ammonite shells and aptyci (*Enay et al., 1994*) can be found in yellow lithographic layers situated more meter above the plant layers (*Barale et al., 1992*). An insect has been found in these layers; it is described below. The animals seem to be quite rare in the plant layers. A second small outcrop is situated 30 m (alt. 657 m, along a small forest road) south of the main one. It is very rich in plant remains, some with insect attacks, described below. The new outcrop of the "Croix de Famban" (unrecorded in *Barale, 1981*) has given also thick layers rich of large leaves of *Zamites* and delicate laminites with small fishes, Crustacea, and traces of animal activities in the sediment (some being herein attributed to fly larvae).

These lithographic and bituminous limestones (Late Kimmeridgian "calcaire en plaquettes" Formation) correspond to a marine shallow lagoonal environment. The formation of these carbonate deposits are due to the developments of microbial mats ("kopara" *Tribovillard et al., 1999, 2000*). The palaeoenvironment corresponds to a lagoon delimited by a reef barrier and to islands occupied by terrestrial organisms (plants and animals) coming into the lagoon. Some insects (fly larvae) could apparently live in the shallow brackish sediments (see below).

Specimen examinations have been made with an Olympus microscope SZX9 with digital camera Olympus E3 and drawings made with a drawing tube. Environmental SEM images have been made with Tescan Vega II LSU in variable pressure mode (SE, secondary electron).

SYSTEMATIC PALEONTOLOGY

1. Adult insect from Orbagnoux

This small fossil insect is clearly a Hemiptera Heteroptera: Gerromorpha, attributable to the relatively small family Mesoveliidae Douglas and Scott, 1867 (see discussion below). It represents the oldest record of the heteropteran infraorder Gerromorpha. If the Mesoveliidae is currently considered as the sister group of all other Gerromorpha (Damgaard et al., 2012), their absence in the Mesozoic remained surprising as the Gerridae, Hydrometridae, and Veliidae are known in the Early Cretaceous, while the Hebridae and Veliidae are recorded from the Cenozoic (*Damgaard, 2008a*). The immature gerromorphan nymph from the Mid Cretaceous French amber described by *Perrichot et al. (2005)* is now attributed to this family, while two other Mesoveliinae are also newly recorded from the same amber *(Solórzano Kraemer et al., pers. comm.)*. Nevertheless all the other Mesozoic taxa previously attributed to the Mesoveliidae are currently considered as Heteroptera incertae sedis (*Damgaard et al., 2012*). The Miocene *Mesovelia dominicana* Garrouste and Nel, 2010 remains the unique described Cenozoic Mesoveliidae.

Infraorder Gerromorpha Popov, 1971

Family Mesoveliidae Douglas and Scott, 1867

Subfamily Madeoveliinae Poisson, 1959

Included genera. *Madeovelia* Poisson, 1959, *Mesoveloidea* Hungerford, 1929, *Gallomesovelia* gen. nov.

Genus *Gallomesovelia* gen. nov.

Type species. *Gallomesovelia grioti* sp. nov.

Diagnosis. Adult macropterous characters. Large size (body 6.0 mm long); large rounded eyes; tegmen covered with setae; abdominal sternite 8 similar to sternite 7.

Etymology. Named after Gallia, ancient Latin name for France, and *Mesovelia*. Gender feminine.

Gallomesovelia grioti sp. nov.

(Figures 2-3)

Material. Holotype specimen MNHN.F.A51098 (print and counterprint of a nearly complete bug, fossilised in lateral view, legs and antennae not preserved).

Diagnosis. As for the genus

Etymology. Named after our friend and colleague Claire Griot, who rendered possible the field researches around Orbagnoux outcrop.

Remark. A rather large (ca. 60 mm long) shrimp is fossilised in the piece of rock 0.5 mm (three laminae) below the print of this bug. It was first detected by the presence of a depression in the sediment. Its presence was confirmed by an X-ray exam of the piece of rock (see Figure 4).

Description. Body 6.0 mm long; with wings and thorax covered with a distinct pile of microsetae; head 0.75 mm long, 0.87 mm high, deflected in front of eyes but without transverse constriction; compound eye rather large, rounded, 0.35 mm diameter; no ocelli; cephalic trichobothria not preserved; insertion of antenna visible below eye; labium elongate, reaching level of mid coxae, four-segmented, with segments 1 and 2 very short, segment 3 very long, 1.32 mm long, much longer than segment 4, 0.37 mm long; no pair of bucculae covering base of labium; thorax 2.2 mm long; prothorax 0.62 mm long 3.8 mm high, with a suture separating tergum and sternopleuron; pronotum short; mesoscutellum triangular exposed, 0.5 mm long; a small metanotal elevation; forewing 3.6 mm long, covered with microsetae, lacking claval commissure but with two basal cells and one apical cell and a "pterostigma"-like broadening of Sc+R; coxae inserted close to ventral midline of thorax, all oriented obliquely backward (especially for the posterior ones), distance between fore and mid coxae 0.54 mm, between mid and hind coxae 1.0 mm; abdomen 3.1 mm long, ca. 1.7 mm high, with seven sternites visible laterally, i.e. sternites 2 to 7 plus sternite 8 narrower than other sternites, and not divided in two parts (male).

Discussion. This fossil bug falls in the Gerromorpha because of the following characters, after *Schuh & Slater (1995)*: compound eyes large, rounded; head not constricted transversely; forewing lacking claval commissure, not divided into a corium-clavus-membrane; wings and part of body covered with a distinct pile of microsetae. Unfortunately the cephalic trichobothria, characteristic of the Gerromorpha, are not visible above the eye (*Andersen, 1982*). An attribution to the Mesoveliidae: Madeoveliinae would be supported by the following characters: macropterous; mesoscutellum triangular exposed; coxae inserted close to the ventral midline of thorax (plesiomorphy); no pair of bucculae covering base of labium; ocelli lacking; forewing with two basal cells and one apical cell (*Andersen, 1982, 1999; Schuh & Slater, 1995*).

better: "not detected"

The family Mesoveliidae is diagnosed on male genitalia and egg characters, unfortunately absent *Gallomesovelia* gen. nov. Nevertheless, the mesoscutellum present but relatively reduced and the metanotal elevation, are both apomorphic characters present in *Gallomesovelia*, the macropterous Mesoveliidae but also in the Hebridae (*Damgaard, 2008b: 454*).

The attribution of *Gallomesovelia* to the Madeoveliinae is supported by the following apomorphies (*Andersen & Polhemus, 1980; Andersen, 1999; Damgaard et al., 2012: 193*): head deflected in front of eyes; adults macropterous and without ocelli. More precisely, the absence of ocelli supports an attribution to the Madeoveliinae, as the reduction of ocelli in the macropterous morphs is convergent in the Mesoveliidae: Madeoveliinae, the Gerridae, plus some Veliidae and Hydrometridae (*Damgaard, 2008b; Damgaard et al., 2012*). The two modern madeoveliine genera *Madeovelia* and *Mesoveloidea* have the plesiomorphic presence of prothoracic suture separating tergum and sternopleuron (*Andersen, 1999: 13; Damgaard et al., 2012: 193*). *Gallomesovelia* has this character too. The shape of the pronotal lobe cannot be determined because of the fossilisation in lateral view; nevertheless, it seems that there is no anterior constriction as in winged Mesoveliinae (*Andersen & Polhemus, 1980*). The general shape of body and forewing venation of *Gallomesovelia* are similar to those of *Madeovelia* and *Mesoveloidea* in the large rounded eyes, shape of labium, tegmen covered with setae (*Poisson, 1959; Hungerford, 1929; Jaczewski, 1931; Moreira et al., 2006*). The main difference of *Gallomesovelia* with both the male and the female of *Mesoveloidea* is the abdominal sternite 8 as large and long as sternite 7. A further important difference is the greater size (body 6.0 mm long in *Gallomesovelia* instead of 2.9 mm in *Mesoveloidea peruviana* Drake, 1949, 2.9 to 3.8 mm in *Mesoveloidea williamsi* Hungerford, 1929, and 2.6 mm in *Madeovelia guineensis* Poisson, 1959). More generally *Gallomesovelia* is rather large compared to the modern and fossil Mesoveliidae.

considred by ...

The Mesoveliidae are consid *Damgaard, 2008; Weirauch & Schuh, 2012*ered the most basal lineage of Gerromorpha (), but not the oldest Gerromorpha + Panheteropera (Panheteroptera = Nepomorpha + Leptodomorpha + Cimicomorpha +Pentatomorpha) known. The oldest known Heteroptera are undescribed Nepomorpha from the Triassic (Late Carnian) of Virginia (*Fraser & Grimaldi, 1999*).

Gallomesovelia is the oldest known representative of the superfamily Gerromorpha. *Li et al. (2012)* placed the gerromorphan radiation during the Jurassic using molecular phylogeny and fossil calibration. Our fossil is a new landmark for dating the gerromorphan lineages and is congruent with all the current hypotheses.

2. Insect attacks on *Zamites* leaves

The first found fossil (specimen MNHN.F.A51100, A. Nel leg.) is the print and counterprint of a leaf of a *Zamites* species, 70.0 mm long, 75.0 mm wide, with 13 leaflets preserved, with several surface feeding traces. These structures are longitudinally oriented, generally situated along the margins of the leaflets, elongate, 5.0-16.0 mm long, 2.0-2.5 mm wide. The sides of the slots are straight and the ends are rounded. Their central parts are devoid of organic matter in the print but the surface of the leaflet cuticle is still present in the counterprint. They are surrounded by a darker zone that corresponds to a rim of reaction tissue 0.5-1.0 mm wide, darker than the organic matter of the main part of the leaflet (see Figures 5-6A-B). Except in one case, there is only one attack per leaflet and only seven of the 13 leaflets are attacked.

Two other *Zamites* leaves with traces of insect activities were found in the collection François Escuillié (Gannat, France), coming from the same outcrop and level. The second specimen is a large leave with all leaflets attacked by insects, some of them covering nearly all the surface of the leaflet. Nevertheless they are fundamentally identical to the traces on the first leaf (see Figure 5A). The third specimen is a unique small hyaline oval trace filled with carbon and looks slightly different from the traces on the first and second specimens (Figure 5B).

If the leaves of *Zamites* are very frequent in the outcrop of Orbagnoux, no other trace of insect activity was detected among ca. 100 leaves of *Zamites*. They can be considered as being quite rare. No other plant was found attacked.

If insect mines are rather frequent and diverse in the fossil record (Labandeira and Currano, 2013), few have been found on leaves of Mesozoic Bennettitales (*Jud et al., 2010*). *Pott et al. (2008)* described oviposition damages on foliage from the Upper Triassic of Australia. *Pott et al. (2012)* and *Edirisooriya & Dharmagunawardhane (2013)* described leaf-margin feedings on Middle Jurassic *Anomozamites villosus* and *Otozamites beanie* respectively. *Schweigert & Dietl (2010)* described rounded structures on *Zamites feneonis* as “probable prints of former galls” from the Late Kimmeridgian of Nusplinger lithographic limestone in Germany. *Harris (1942)* also described galls on the bennettitalean *Anomalozamites*. The insect attacks from Orbagnoux are completely different from these structures but nearly identical to those described on some Upper Triassic *Zamites* from the United States (*Ash, 1997: 242, figs 3-4, 2005*).

These structures could correspond to a surface feeding DT103 "elongate window feeding (sub)parallel to major venation" type (sensu *Labandeira et al., 2007*), rather than to mining activities as the surface of the leaflet cuticle is preserved at least on one side and no remain of coprolite was found.

The main differences with the attacks on Triassic *Zamites* described by *Ash (1997)* are as follows: those from Orbagnoux are broader, covering more than two veins of the leaflet; they are situated along the leaflet margin instead of being 1-3 mm from the margins. Thus they were probably caused by different insects. *Ash (1997)* supposed that the Triassic attacks could have been caused by "grazing insects". It is quite delicate to determine which type of insect could have caused the mines from Orbagnoux. Nevertheless, a holometabolous larva could have made such attacks. Similar attacks are frequent on modern angiosperm leaves, caused by larvae of Diptera, Lepidoptera, or Coleoptera. Because of the hardness of the *Zamites* leaflets, it is more likely a beetle larva (e.g. Chrysomelidae, a group known in the Jurassic) that could have caused these attacks.

3. Sinusoidal trails similar to trace fossil *Cochlichnus* Hirchock, 1858

These sinusoidal traces of an animal activity were found in thin yellow lithographic laminites in the outcrop of the "Croix de Famban" (specimen MNHN.F.A51099, Figure 6C-D). Small fishes, vertebrate coprolites, worms, and Crustacea (isopods and shrimps) are also present in the same layers. Plants are frequent in thicker layers just above these laminites but absent in the laminites. These traces are similar to grazing trails formed by stratiomyid or ceratopogonid fly larvae in shallow freshwater or brackish sediments (*Metz, 1987; Mángano et al., 1996*). Similar traces in marine environments have been interpreted of worm- or gastropod-origin (*Hakes, 1976*). Together with the other organisms found in this outcrop, they demonstrate that the corresponding palaeoenvironment was clearly not abiotic.

4. Palaeoenvironmental implications

If the main part of the fauna found in the Late Jurassic layers around Orbagnoux clearly correspond to marine environments (ammonites, bivalvia, shrimps, isopods, fishes, etc.), the present discoveries confirm the presence of a very close terrestrial biota, which was supposed after the presence of a rather diverse flora represented by leaves and reproductive organs (cones). The rarity of the insects together with the partly decayed state of the type specimen of *Gallomesovelia grioti* (legs and antennae missing), suggest a transport of these terrestrial organisms into a marine environment. Modern mesoveliids (water treaders) are predators, and strictly freshwater or terrestrial insects, living in humid places, but some are associated with marine habitats (intertidal). *Gallomesovelia grioti* could have lived very close to the sea margin or even in the brackish part of the lagoon itself, as some modern Mesoveliidae (*Andersen, 1982: 338*): it was maybe a surface skater because of the particular orientations of the coxae, directed backwards (*Andersen, 1982: 288-289*). Due to the preservation of the terrestrial insect bodies that is generally rather poor in the Bavarian Kimmeridgian, it would be nearly impossible to expect to find there such small and delicate insects similar to *Gallomesovelia grioti*. This situation renders very precious any new discovery of terrestrial arthropods in Orbagnoux outcrops. The discovery of an insect attack on a *Zamites* leave shows that the diversity of the terrestrial arthropods was probably significant there, the insect fauna not being reduced to few aquatic or subaquatic bugs, like in an simple atoll lagoon beaches or beach rock. Nevertheless future investigations shall be necessary to discover the palaeodiversity of this new insect world.

ACKNOWLEDGEMENTS

We sincerely thank the Société des Mines d'Orbagnoux for the kind authorization to collect fossils in their property. Special thanks to Torsten Wappler for information and references on insect attacks on *Zamites*. We also thank a lot the following colleagues for their kind help during the field researches in 2012 and 2013: MMr. Bernard Béreyziat, Michel Béreyziat, Guy Robert, Pierre Roncin, Jean-Marie Demaury, Thierry Virton, Bernard Janvier, and Daniel Grand. A special thank to Claire Griot because she rendered possible these investigations, inviting us in her wonderful country and home. Lastly we thank Mr. François Escuillié for the authorization to photograph the specimens in his collection. We thank Sylvain Pont from LMCM lab/ MNHN Direction des collections MEB Service for MEM-EDS Imaging.

REFERENCES

Andersen NM. 1982. The semiaquatic bugs (Hemiptera: Gerromorpha): phylogeny, adaptations, biogeography and classification. *Entomonograph* **3**:1-445.

Andersen NM. 1999. *Cryptovelia stysi* sp. n. from Borneo with a reanalysis of the phylogeny of the Mesoveliidae (Heteroptera: Gerromorpha). *Acta Societatis Zoologicae Bohemicae* **63**:5-18.

Andersen NM, Polhemus JT. 1980. Four new genera of Mesoveliidae (Hemiptera: Gerromorpha) and the phylogeny and classification of the family. *Entomologica Scandinavica* **11**:369-392.

Ash SR. 1997. Evidence of arthropod-plant interactions in the Upper Triassic of the Southwestern United States. *Lethaia* **29**:237-248.

Ash SR. 2005. Synopsis of the Upper Triassic flora of Petrified Forest National Mark and vicinity. *In*: Nesbitt SJ, Parker WG, Irmis RB (eds). Guidebook to the Triassic Formations of the Colodaro Plateau in Northern Arizona: Geology, Palaentology, and History. *Mesa Southwest Museum, Bulletin* **9**:53-61.

Barale G. 1981. La paléoflore jurassique du Jura français: étude systématique, aspects stratigraphiques et paléoécologiques. *Documents des Laboratoires de Géologie de Lyon* **81**:1-466.

Barale G, Philippe M, Thevenard F. 1992. Locality of Orbagnoux: Gully la Dorche. *4th International Organization of Palaeobotany Conference*: 60-69.

Bernier P. Gaillard C, Gall J-P, Barale G, Bourseau J-P, Buffetaut E, Wenz S. 1991. Morphogenetic impact of microbial mats on surface structure of Kimmeridgian micritic limestone (Cerin, France). *Sedimentology* **38**:127-136.

Chateauneuf JJ, Alabouvette B, Cautru JP, Feys R, Glintzboeckel C, Malatrait AM, Marteau, P. 1982. Evaluation des ressouces en schistes bitumineux de la France et esquisse de valorisation. *Rapport du Bureau de Recherches Géologiques et Minières*, 82 SGN 617 GEO: 202 pp.

Damgaard J. 2008a. Evolution of the semi-aquatic bugs (Hemiptera: Heteroptera: Gerromorpha) with a re-interpretation of the fossil record. *Acta Entomologica Musei Nationalis Pragae* **48**: 251-268.

Damgaard J. 2008b. Phylogeny of the semiaquatic bugs (Hemiptera-Heteroptera, **Gerromorpha).** *Insect Systematics & Evolution* **39:**431-460.

Damgaard J, Moreira FFF, Hayashi M, Weir TA, Zettel H. 2012. Molecular phylogeny of the pond treaders (Insecta: Hemiptera: Heteroptera: Mesoveliidae), discussion of the fossil record and a checklist of species assigned to the family. *Insect Systematics & Evolution* **43**:175-212.

Drake CJ. 1949. Two new Mesoveliidae, with check list of American species. *Boletín de Entomología Venezolana* **7**:145-147.

Enay R, Bernier P, Barale G, Bourseau J-P, Buffetaut, E., Gaillard C, Gall J-C, Wenz S. 1994. Les ammonites des calcaires lithographiques de Cerin (Ain, France): stratigraphie et taphonomie. *Geobios* **27** (Supplement 1):25-36.

Edirisooriya G, Dharmagunawardhane HA. 2013. Plant insect-interactions in Jurassic fossil flora from Sri Lanka. *International Journal of Scientific and Research Publications* **3**:1-12.

Fraser NC, Grimaldi DA. 1999. A significant late Triassic Lagerstätte from Virginia, U.S.A. *Rivista del Museo Civico di Scienze Naturale E. Caffi* **20**:79-84.

Gaillard C, Goy J, Bernier P, Bourseau J-P, Gall J-C, Barale G, Buffetaut E, Wenz S. 2006. New jellyfish taxa from the Upper Jurassic lithographic limestones of Cerin (France): taphonomy and ecology. *Palaeontology* **49**:1287-1302.

Garrouste R, Nel A. 2010. First semi-aquatic bugs Mesoveliidae and Hebridae (Hemiptera: Heteroptera: Gerromorpha) in Miocene Dominican amber. *Insect Systematics & Evolution* **41**:93-102.

Gudefin H. 1968. *Recherche des causes de la pollution organique constatée dans l'eau d'exhaure de la mine d'Orbagnoux (Ain).* Bureau de Recherches Géologiques et Minières, Lyon, février 1968:39 pp.

Hakes WG 1976. Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *The University of Kansas Paleontological Contributions* **63**:1-60.

Harris TM. 1942. *Wonnacottia*, a new bennettitalean microsporophyll. *Annals of Botany* New Series **6**:577-592.

Hungerford HB. 1929. A new genus of semi-aquatic Hemiptera. *Bulletin of the Brooklyn Entomological Society* **24**:288-290.

Jaczewski TL. 1931. The male of *Mesoveloidea williamsi* Hungerford (Hemiptera: Heteroptera). *Proceedings of the Entomological Society of Washington* **33**:64-66.

Jud NA, Rothwell GW, Stockey RA. 2010. Paleoecological and phylogenetic implications of *Saxicaulis meckertii* gen. et sp. nov.: a bennettitalean stem from the Upper Cretaceous of Western North America. *International Journal of Plant Science* **171**:915-925.

Labandeira CC, Currano E. 2013. The fossil record of plant-insect dynamics. *Annual Review of Earth and Planetary Sciences* **41**:287-311.

Labandeira CC, Wilf P, Johnson KR, Marsh F. 2007. Guide to insect (and other) damage types on compressed plant fossils (Version 3.0 - Spring 2007). Smithsonian Institution, Washington, DC.

Li Min, Tian Ying, Zhao Ying and Bu, Wenjun 2012. Higher level phylogeny and the first divergence time estimation of Heteroptera (Insecta: Hemiptera) based on multiple genes. *PLoS One*, **7** (2) pe32152:1-17.

Mángano MG, Buatois LA, Claps GL. 1996. Grazing trails formed by soldier fly larvae (Diptera: Stratiomyidae) and their paleoenvironemental and paleoecological implications for the fossil record. *Ichnos* **4**:163-167.

Metz R. 1987. Sinusoidal trail formed by a recent biting midge (family Ceratopogonidae): trace fossil implications. *Journal of Paleontology* **61**:312-314.

Perrichot V, Nel, A, Néraudeau D. 2005. Gerromorphan bugs in Early Cretaceous French amber (Insecta: Heteroptera): first representatives of Gerridae and their phylogenetic and palaeoecological implications. *Cretaceous Research* **26**:793-800.

Poisson RA. 1959. Sur un nouveau représentant africain de la faune terrestre commensale des biotopes hygropétriques: *Madeovelia guineensis* gen. n., sp. n. (Heteroptera). *Bulletin de l'Institut Français d'Afrique Noire* (A) **21**:658-663.

Pott C, Labandeira CC, Krings M, Kerp H. 2008. Fossil insect eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria. *Journal of Paleontology* **82**:778-789.

Pott C, McLoughlin S, Wu Shinqing, Friis EM. 2012. Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: mechanical defence against herbivorous arthropods. *Review of Palaeobotany and Palynology* **169**:48-60.

Moreira FFF, Ribeiro JRI, Nessimian JL. 2006. Description of the male and the southernmost record of *Mesoveloidea williamsi* Hungerford, 1929 (Hemiptera: Heteroptera: Mesoveliidae). *Zootaxa* **1269**:51-56.

Sauvage HE. 1893. Note sur quelques poissons du calcaire bitumineux d'Orbagnoux (Ain). *Bulletin de la Société d'Histoire Naturelle d'Autun* **6**:427-443.

Schuh RT, Slater JA. 1995. *True bugs of the World (Hemiptera: Heteroptera). Classification and natural history*. Comstock Publishing Associates, Cornell University Press, Ithaca and London:i-xii + 1-336.

Schweigert G, Dietl G. 2010. Miscellanea aus dem Nusplinger Plattenkalk (Ober-Kimmeridgium, Schwäbische Alb). 11. Ein Blattrest mit Abdrücken von Gallen. *Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins* (N.F.) **92**:35-40.

Tejo Yuwono N. 1987. *Lithostratigraphie, microfacies et analyse de la matière organique des formations géologiques (Kimméridgien à Berriasien du Jura méridional, région de Seyssel, Ain et Haute-Savoie*. Thèse Université de Savoie, Chambéry:120 pp.

Tribovillard N, Trichet J, Défarge C, Trentesaux A 1999. Jurassic lagoonal environments and quasi-abiotic platy limestone accumulation: microbial interventions. *Sedimentology* **46**:1183-1197.

Tribovillard N, Trentesaux A, Trichet J, Défarge C. 2000. A Jurassic counterpart for modern kopara of the Pacific atolls: lagoonal, organic matter-rich, laminated carbonate of Orbagnoux (Jura Mountains, France). *Palaeogeography, Palaeoclimatology, Palaeoecology* **156**:277-288.

Wenz S, Bernier P, Barale G, Bourseau J-P, Buffetaut E, Gaillard C, Gall J-C. 1994. L'ichthyofaune des calcaires lithographiques du kimméridgien supérieur de Cerin (Ain, France). *Geobios* **27** (supplément 1):61-70.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

• André Nel and Romain Garrouste analyzed the data, wrote the paper, prepared figures, reviewed drafts of the paper.

• Patricia Nel, Régis Krieg-Jacquier & Jean-Marc Pouillon participate to the field researches, reviewed drafts of the paper, contributed with iconography.

Figure 1. Some fossil organisms from Orbagnoux outcrop. (A) *Brachyphyllum elegans*, specimen JMP 455 (coll. J.-M. Pouillon); (B) Fern incertae sedis, specimen JMP 391 (coll. J.-M. Pouillon); (C) "fish" (coll J.-C. Demaury); (D) shrimp (coll J.-C. Demaury) (scale bars 10 mm).

Figure 2. Aquatic bug from Orbagnoux outcrop: *Gallomesovelia grioti* sp. nov. (Holotype MNHN.F.A51098). (A) reconstruction H: head, E: Eye, M: mesonotum, Pr : pronotum, As: abdominal segments Cx: coxae, Me: metanotum, Mee: metanotum elevation, Wv: wing veins,

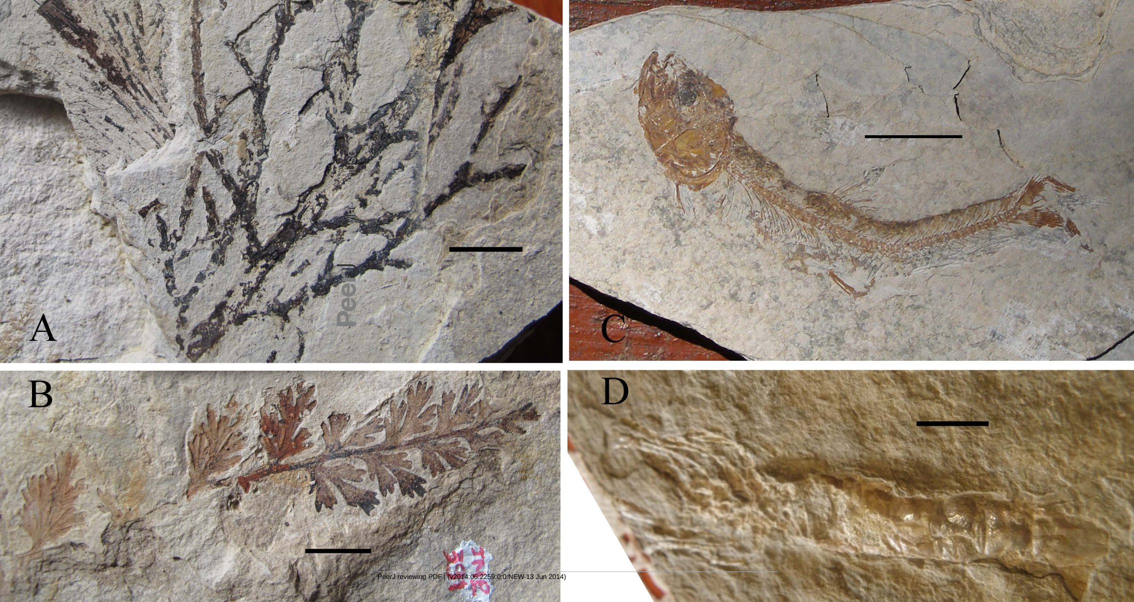
Gs: genital segment, Pt: pterostigma; (B) photograph without alcohol; (C) photograph under alcohol (scale bars 1 mm for A, B and C).

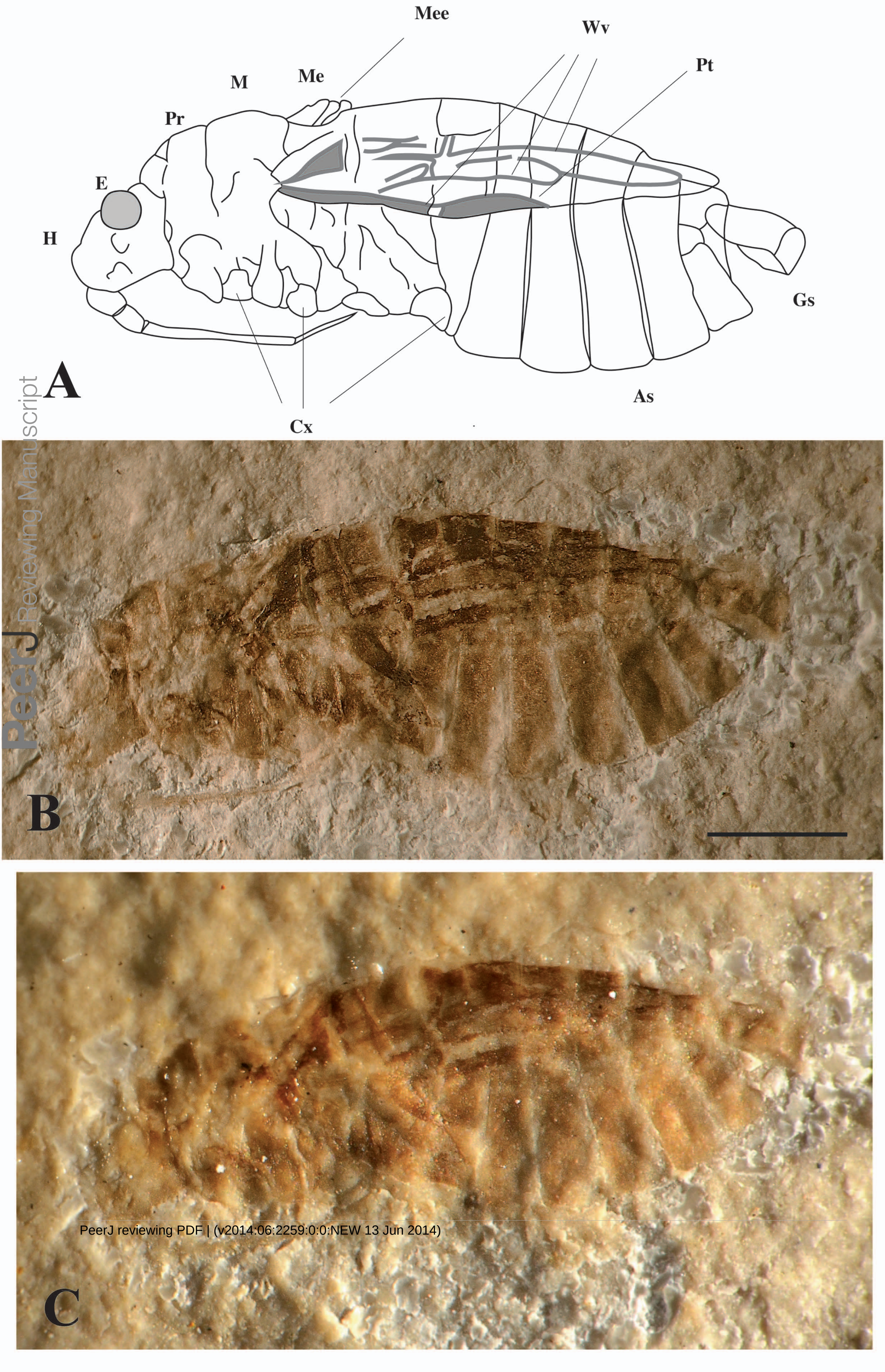
Figure 3. ***Gallomesovelia grioti*** **sp. nov.** (Holotype MNHN.F.A51098). Environmental MEB imaging. (A) complete fossil (scale bar 1 mm), square: location of figure B; (B) dorso-abdominal detail of wing veins (horizontal) covered with setae (scale bar 200 μm).

Figure 4. Shrimp (Crustacea indet., Malacostraca?). Specimen fossilised below holotype of *Gallomesovelia grioti* (scale bar 10 mm).

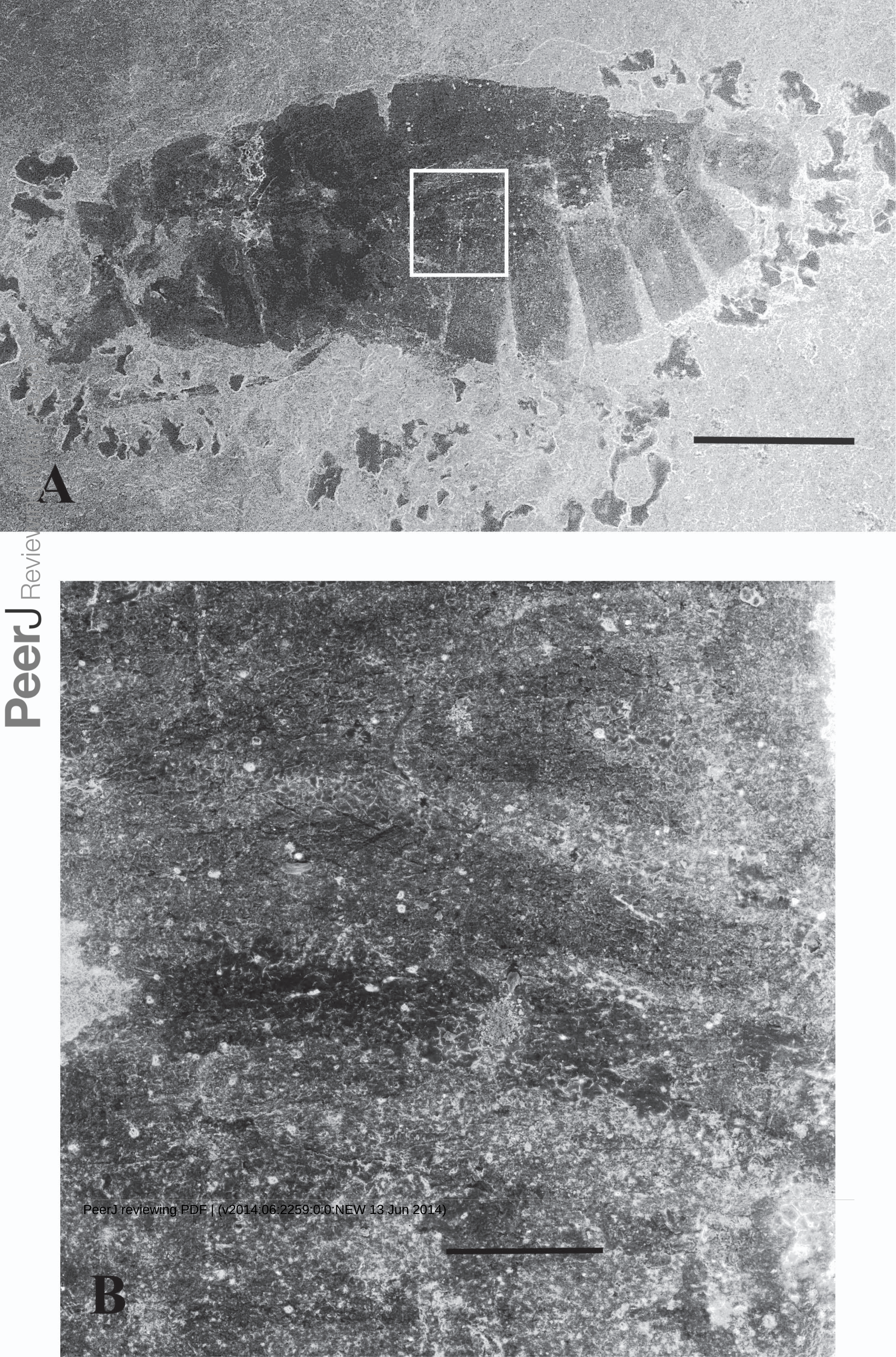
Figure 5. Attack on ***Zamites*** **leaves. (**A) specimen with nearly all leaflets attacked (scale bar 2 cm), (B) specimen with only one attack on a leaflet (scale bar 1cm).

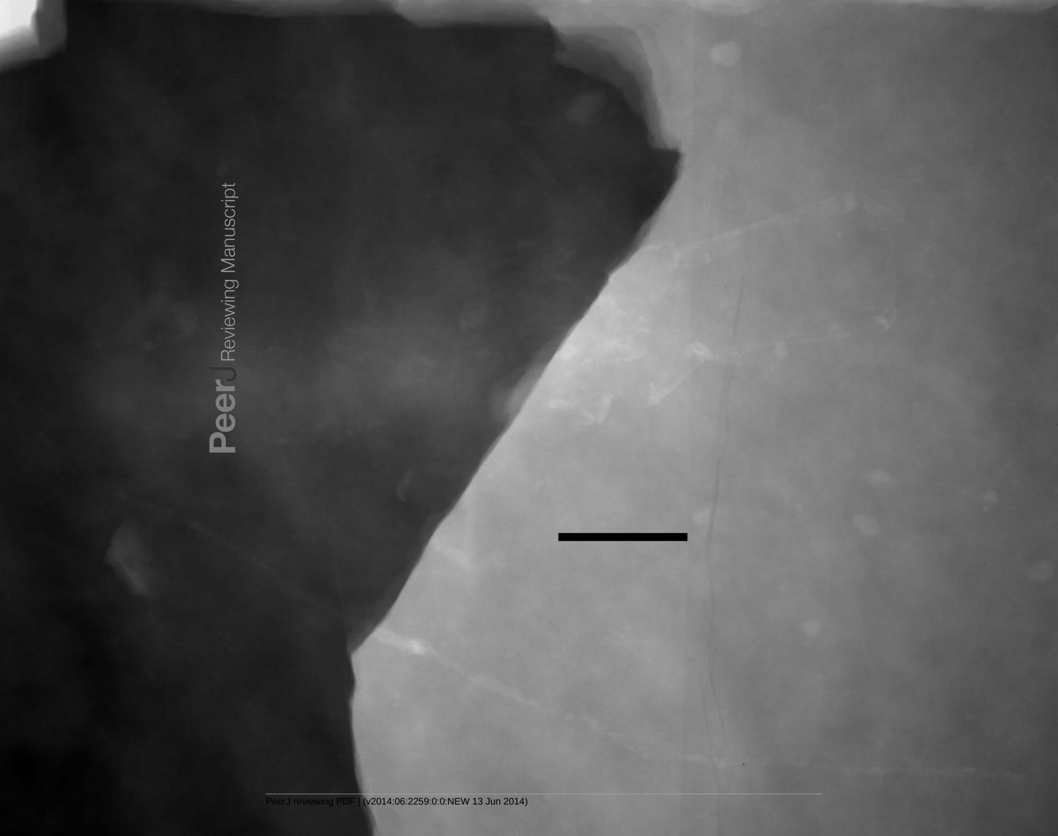
Figure 6. Traces of activities of insects. (A) Attacks on a *Zamites* leave (MNHN.F.A51100), print, Orbagnoux outcrop; (B) counterprint; (C) sinusoidal trails cf. *Cochlichnus* (MNHN.F.A51099)**,** print**,** Croix de Famban outcrop: (D) counterprint (scale bars 10 mm).


A
B
C
D

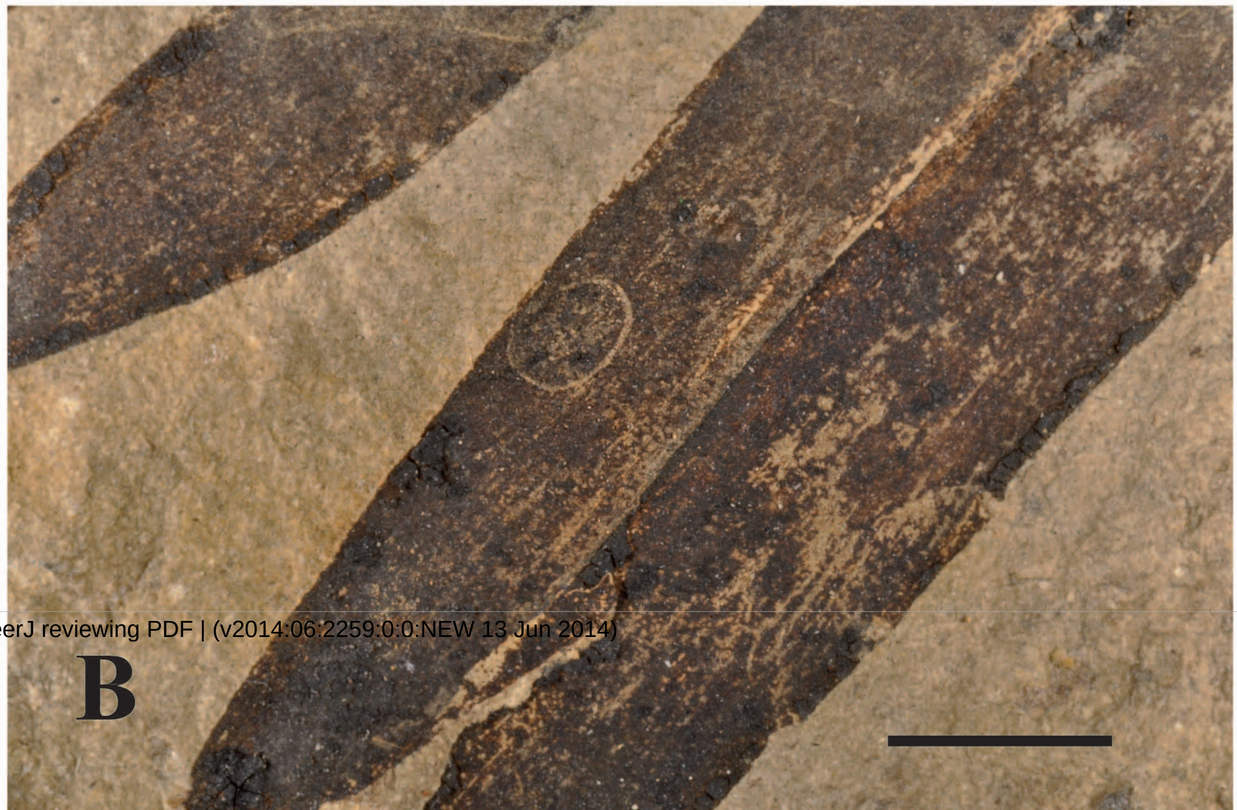


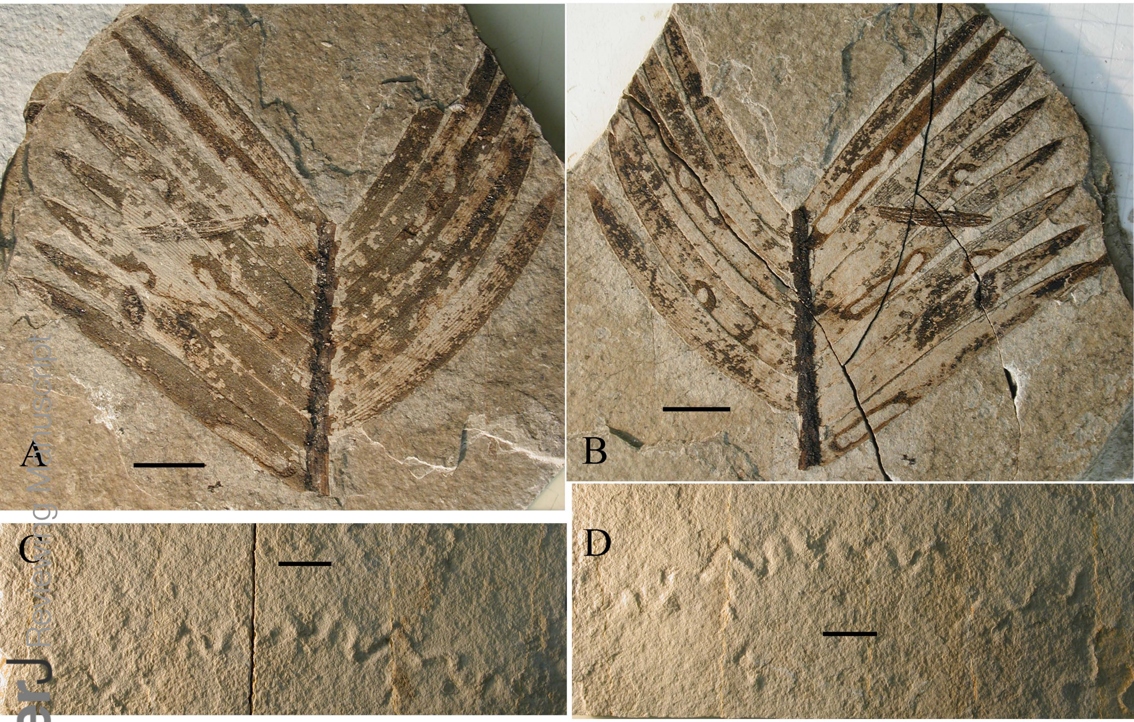
Mee
Wv
Pt
M
Me
Pr
E
H
Gs
As
Cx
A
B
C


A
B




A


B


A
B
C
D