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Palaeoentomological study of the lacustrine oil-shales of the lower Miocene San Chils locality (Ribesalbes-Alcora Basin, Castellón province, Spain)

Sergio ÁLVAREZ-PARRA[1*] *& Enrique PEÑALVER*[2]

[1] Departament de Dinàmica de la Terra i de l'Oceà and Institut de Recerca de la Biodiversitat (IRBio), Facultat de Ciències de la Terra, Universitat de Barcelona, c/ Martí i Franquès s/n, 08028 Barcelona, Spain; sergio.alvarez-parra@ub.edu.
[2] Instituto Geológico y Minero de España (Museo Geominero), c/Cirilo Amorós 42 entreplanta, 46004 Valencia, Spain; e.penalver@igme.es.

*Corresponding author

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ABSTRACT

For the first time, the study of the fossil record present in laminated bituminous dolostones from the San Chils locality, lower Miocene in age (ca. 19 Ma), located at the Ribesalbes-Alcora Basin, is addressed. The identification of 11 families and three genera belonging to six insect orders (Orthoptera, Thysanoptera, Hemiptera, Coleoptera, Hymenoptera, and Diptera) has been carried out. Furthermore, ephippia of cladoceran crustaceans, one bird feather, vertebrate coprolites and plant remains have been found. The San Chils palaeodiversity has been compared to that of La Rinconada, a similar outcrop in the same basin and depositional unit. Both localities correspond to lacustrine deposits and were mined during the past two centuries. This work has increased the palaeontological richness of the Ribesalbes-Alcora Basin with new findings such as specimens of the subfamily Corixinae (Hemiptera: Corixidae), some ant workers (Hymenoptera: Formicidae), a specimen assigned to the genus *Exechia* (Diptera: Mycetophilidae), ephippia of *Daphnia* (*Ctenodapnia*) sp. (Branchiopoda: Cladocera),

RESUMEN

Este estudio aborda por primera vez el registro fósil presente en dolomías bituminosas laminadas/tableadas del yacimiento de San Chils (Cuenca de Ribesalbes-Alcora, Castellón) de edad Mioceno inferior (unos 19 millones de años). Se han identificado 11 familias y tres géneros pertenecientes a seis órdenes de insectos (Orthoptera, Thysanoptera, Hemiptera, Coleoptera, Hymenoptera y Diptera). Además, se han hallado efipios de crustáceos cladóceros, una pluma de ave, coprolitos de vertebrados y restos paleobotánicos. Dicha paleodiversidad se ha comparado con la de La Rinconada, un yacimiento de la misma cuenca y misma unidad sedimentaria. Ambas localidades corresponden a depósitos lacustres y fueron explotados mediante minería durante los dos últimos siglos. Con este estudio se ha incrementado la riqueza paleontológica de la Cuenca de Ribesalbes-Alcora, ya que se han hallado los primeros fósiles de la subfamilia Corixinae (Hemiptera: Corixidae), de hormigas de la casta obrera (Hymenoptera: Formicidae), del género *Exechia* (Diptera: Mycetophilidae) y de efipios de *Daphnia* (*Ctenodaphnia*), además de la familia

the possible first report of the genus *Sciocoris* (Hemiptera: Pentatomidae) for the Neogene fossil record and the possible presence of the family Aeolothripidae (Thysanoptera). The current collection of fossil specimens from San Chils is small, but shows that it shared similar palaeoenvironmental conditions to that of La Rinconada, both in the lake waters and in the surroundings. The preservation of the specimens is poor due to the weathering they suffered during more than a century exposed outside the mine, but the presence of delicate structures has enabled to classify the outcrop as a Konservat-Lagerstätte, like La Rinconada.

Keywords: Insects, crustaceans, palaeolake, taphonomy, palaeoecology.

de hemípteros Pentatomidae con el posible primer ejemplar del género *Sciocoris* en el registro fósil del Neógeno y la posible presencia de la familia de tisanópteros Aeolothripidae. La colección actual de ejemplares fósiles de San Chils es pequeña, pero muestra que compartió unas condiciones paleoambientales similares a las de La Rinconada tanto en las aguas del lago como en sus alrededores. Aunque la preservación de las muestras estudiadas de San Chils es deficiente debido a la meteorización física de la roca durante más de un siglo en el exterior de las minas, esta localidad se puede considerar un *Konservat-Lagerstätte* al igual que La Rinconada, ya que se ha constatado la conservación excepcional de estructuras orgánicas lábiles.

Palabras clave: Insectos, crustáceos, paleolago, tafonomía, paleoecología.

1. INTRODUCTION

The Ribesalbes-Alcora Basin is located east of the Iberian Peninsula, in Castellón Province. Mining of the Miocene lacustrine oil-shales and laminated bituminous dolomicrites was one of the most important economic activities of the area since the end of the XIXth century until 1914. The rock was extracted from mines in La Rinconada (Ribesalbes) and San Chils (Alcora), and accumulated outdoors before their processing to obtain hydrocarbons (Peñalver *et al*., 2016).

The prominent geologist and palaeontologist Royo y Gómez was the first promoter of the study of the Miocene fossils from the basin. The fossils collected from La Rinconada during the mining activity were later studied by Gil Collado, Hernández Sampelayo and Cincúnegui (Gil Collado, 1926; Hernández Sampelayo & Cincúnegui, 1926). Three insect species were described: *Hilara royoi*, *Nomochirus sampelayoi* (both of the order Diptera) and *Platycnemis*? *cincuneguii* (Odonata). Moreover, up to six insect orders were identified: Odonata, Homoptera, Heteroptera, Coleoptera, Hymenoptera, and Diptera. Since the end of XXth century, the fossil collection from La Rinconada increased and the palaeoentomological study of the basin continued (*e.g.*, Peñalver *et al*., 1996a; Peñalver & Martínez-Delclòs, 2000). In recent times, the exceptional preservation of salamander musculature from La Rinconada due to the action of microbial mats and the chemical conditions of burial was analysed by McNamara *et al*. (2010). Later, several palaeoecological inferences based on the plant remains from this locality were published (Barrón & Postigo-Mijarra, 2011; Postigo-Mijarra & Barrón, 2013).

Currently, the palaeontological record from La Rinconada includes 13 insect orders: Odonata, Orthoptera, Isoptera, Psocoptera, Thysanoptera, Hemiptera, Neuroptera, Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera, and Lepidoptera. Moreover, crustaceans (Ostracoda), arachnids (Araneae), gastropods (Pulmonata), amphibians (Anura and Caudata), and bird feathers and coprolites of different morphologies have been found. No fishes are known from the La Rinconada fossil record. The palaeobotanical record is abundant and outstanding. Evidences of plant-insect associations occur in several leaves (Peñalver *et al*., 2016).

Furthermore, several mammalian fossil localities, rich in micromammalian remains, have been described in the Ribesalbes-Alcora Basin. The first description of mammals was published by Agustí *et al*. (1988). Recently, new studies have enabled to discover 45 fossiliferous levels with mammalian record in the Araya/Mas de Antolino area (Crespo, 2017; Crespo *et al*., 2019). The mammalian fauna of the basin corresponds to the biozone C of the MN4, early Aragonian in age (see Agustí *et al*., 1988; Crespo *et al*., 2019).

The aim of this work is to study the poorly-known San Chils fossil record and to infer the taphonomic conditions and the general palaeoenvironmental characteristics for this locality. Moreover, its comparison with La Rinconada fossil record is especially relevant because this locality corresponds to a different area of a lower Miocene palaeolake of the Ribesalbes-Alcora Basin. Both assemblages could be coetaneous or of similar age, maybe only separated by thousands of years. Also, a comparison with the lower Miocene Rubielos de Mora outcrop in the basin of the same name (Teruel Province) is interesting based on its abundant insect fossil record, geographical proximity and similar age.

2. GEOLOGICAL SETTING

The Ribesalbes-Alcora Basin is a Neogene complex graben located in the SE Iberian Range and limited by ENE-WSW to NNE-SSW trending normal faults covering an area of approximately 150 km^2, with a Jurassic-Cretaceous carbonate-dominated sequence surrounding the basin (Anadón *et al*., 1989) (Fig. 1a). The alluvial and lacustrine deposits include two sequences (Agustí *et al*., 1988; Anadón *et al*., 1989; Anadón, 1994): the lower to middle Miocene Ribesalbes sequence and the upper Miocene Alcora sequence, up to 600 m and 200 m thick, respectively. The Ribesalbes sequence consists of five depositional units (A to E from the bottom to the top), but only two of them are rich in fossils, the units B and C (Fig. 1b).

The unit B is composed of dolostones (including oil-shales and laminated bituminous dolomicrites) with interbedded layers of mudstones and sandstones, and Cretaceous olistoliths. Remains of plants, insects, amphibians, feathers, and coprolites are well preserved due to the rock lamination and the taphonomic conditions that occurred in the palaeolake bottom. This unit outcrops in La Rinconada and San Chils mines (Anadón *et al*., 1989). The mammalian localities correspond to the unit C that outcrops in the Araya/Mas de Antolino area (Crespo *et al*., 2019). Recently, a synthetic stratigraphic column of the Campisano ravine deposits from the Araya/Mas de Antolino outcrop, with a total thickness of 140 m, has been published (Crespo *et al*., 2019).

The estimated age for the Ribesalbes sequence was first Oligocene (Hernández Sampelayo & Cincúnegui, 1926; Fernández Marrón & Álvarez Ramis, 1967), but later Fernández Marrón (1971) noted that the plant remains from La Rinconada better correspond to the early Miocene. New palaeobotanical and mammalian data support an early Miocene age for the fossiliferous levels in the basin (Ruiz-Sánchez *et al*., 2010; Postigo-Mijarra & Barrón, 2013). The mammalian fossils from the unit C have been placed on the biozone MN4 (Agustí *et al*., 1988; Crespo *et al*., 2019). Stratigraphically, the unit B is immediately below the unit C, so it could be ca. 19 My old (Peñalver *et al*., 2016), maybe one or two million years younger.

3. PALAEOLAKE TAPHONOMY

The lacustrine deposits of the unit B in the Ribesalbes sequence correspond to a meromictic lake with an anoxic monimolimnion permanently separated from an oxic mixolimnion (Anadón *et al*., 1989; de las Heras *et al*., 2003). Moreover, the endorheic origin of the lake could explain the lack of fish remains (Peñalver *et al*., 2016).

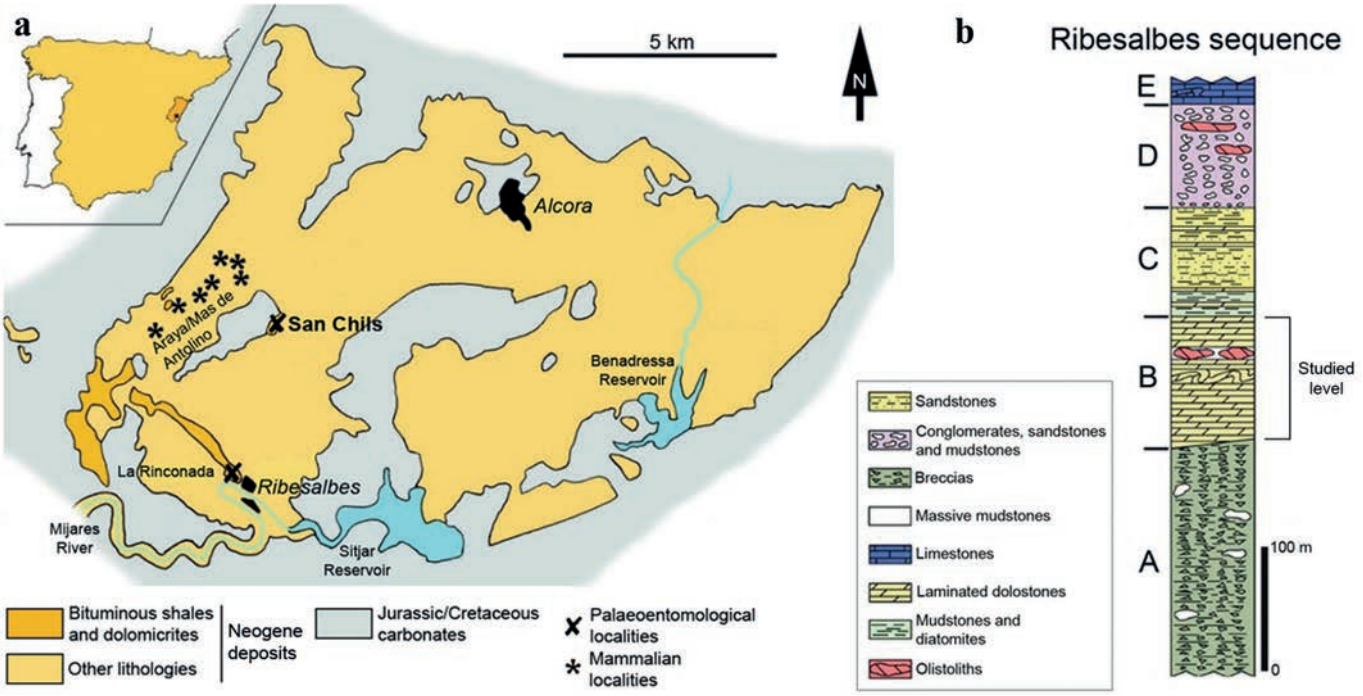


Figure 1. a) Geological map of the Ribesalbes-Alcora Basin showing the known palaeoentomological and the mammalian localities. Modified from Peñalver *et al*. (2016). **b)** Stratigraphic column of the Ribelsalbes sequence with the indication of the units A to E. Modified from Anadón *et al*. (1989), Barrón & Postigo-Mijarra (2011) and Crespo *et al*. (2019).

The presence of hydrocarbons in the laminated dolostones of the palaeolake is due to the abundance of cyanobacteria, freshwater diatoms and chlorophyte *Botryococcus braunii*. When favourable conditions occurred in the lake, these microorganisms most likely formed blooms that were related to eutrophication processes (Cabrera, 1999). The main characteristics of the water were a basic pH, high sulphate content and oligosaline to mesosaline conditions. The warm subtropical climate and the salinity levels influenced the persistent stratification of the water column. Sulphate reduction and methanogenesis processes occurred in the anoxic bottom (Cabrera, 1999; de las Heras *et al*., 2003).

La Rinconada locality is a typical Konservat-Lagerstätte. The absence of benthic fauna and bioturbation due to the anoxic environment of the lake bottom and the rock lamination caused by the growth of microbial mats and the sedimentation of fine-grained particles are the taphonomic conditions that explain the exceptional preservation in this locality (Peñalver *et al*., 2016).

4. MATERIALS AND METHODS

The studied fossils are present in oil-shales and laminated bituminous dolomicrites from the San Chils locality (Alcora, Castellón Province) in the Ribesalbes-Alcora Basin, where the lower Miocene unit B of the Ribesalbes sequence outcrops. We examined rock samples that were accumulated outdoors by mining companies around a century ago for incineration. All the fossils from this locality are deposited in the Museo de Ciencias Naturales de Valencia.

The outer, weathered parts of the rock samples were removed. The rock samples were observed with Kyowa SZM and Leica EZ4 stereomicroscopes in search of fossil remains. The fossils were identified and the best-preserved ones were anatomically described. Photographs were taken with an Olympus C-5050 digital camera attached to an Olympus SZX9 stereomicroscope and a Leica DMS1000 stereomicroscope with a digital camera attached. Canon EOS 650D and Macrofotografía 1.1.0.5 software were used to stack images. Drawings were made using drawing tubes attached to an Olympus SZX9 stereomicroscope, and Olympus BX51 and Olympus U-CTR30-2 compound microscopes. Photographs and drawings were adjusted using Photoshop CS2 software.

The coprolite SC-22 was isolated in a preparation using epoxy FETADIT 55/63. An Olympus BX51 with an attached ColorView Illu Soft Imaging System digital camera was used to observe potential identifiable remains as components of its content.

5. SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758

Order ORTHOPTERA Olivier, 1789

Suborder Caelifera Ander, 1936

Family **Acrididae** MacLeay, 1821

Acrididae indet.
(Figs. 2a-b)

Material. SC-85.

Description. A distal fragment of hindwing. The width is 3.50 mm. The apex is rounded and 10 longitudinal veins can be observed. Longitudinal veins go towards the apex and correspond to the posterior radial veins. Transversal veins delimit small cells. Transverse veins emerge from longitudinal veins. A stain colouration can be seen in the most distal portion.

Remarks. The wing specimen is incomplete, but its wing venation, as observed, is typical of Acrididae; the longitudinal and transversal veins that delimit small cells are characteristic. The preserved portion is identical to the distal areas of the hindwings abundantly found as isolated wings or present in complete adults of Acrididae, from both La Rinconada (Peñalver *et al*., 1996a) and Rubielos de Mora (Peñalver, 1998) outcrops [*e.g.*, the isolated hindwing MPZ-98/159 (Acrididae: Oedipodinae) from Rubielos de Mora, in regard to the width, veins pattern and rounded apex with a stain colouration].

Order THYSANOPTERA Haliday, 1836

Suborder Terebrantia Haliday, 1836

Family **Thripidae** Stevens, 1829

Thripidae? indet.
(Fig. 2c)

Material. SC-1A/SC-1B (part and counterpart), SC-96, SC-102, SC-103 and SC-109.

Description. All of these specimens lack wings and they are incomplete with the exceptions of SC-96 and SC-103. Their general morphologies are elongate, but only a few structures can be differentiated due to the poor preservation. Specimens SC-96 and SC-103 have the following body measurements: 0.85 mm and 1.07 mm length and 0.21 mm and 0.27 mm width, respectively. The head is round and small. In several specimens antennal fragments can be observed. Thorax is highly sclerotised;

SC-96 preserves the femur and tibia of one of the legs and SC-103 preserved the left wing with a marked longitudinal vein. The abdomen is divided in seven segments (visible in SC-103). A long, cylindrical, distal segment is not present in these specimens.

Remarks. The preservation of the specimens is poor, but the general morphology or habitus of all of them and the absence of a cylindrical, distal segment indicate that they belong to the suborder Terebrantia (Mound *et al*., 1976). Thripidae is the most abundant thysanopteran family in Rubielos de Mora and La Rinconada fossil records (Peñalver, 1998; Peñalver *et al*., 2016). These specimens can be considered of the same morphotype of Thripidae abundantly present in these two localities. Furthermore, their size is similar, so we tentatively identify them as Thripidae in spite of the absence of preserved wings. Some isolated abdomens from San Chils could also belong to the family Thripidae too.

Family **Aeolothripidae** Uzel, 1895

Aeolothripidae? indet.
(Figs. 2d-f)

Material. SC-33A/SC-33B (part and counterpart).

Description. Body elongate. Head, thorax and abdomen well-preserved and easily differentiable. Body measurements: 2.10 mm long, 0.43 mm wide. The antennal scapes are elongate and appear very close to each other at the anteriormost area of the head. Thorax is highly sclerotised and several disarticulated legs can be observed. Wings are not preserved. Abdomen has seven segments, and the intersegmental membranes are visible. Additional segments might have not been preserved due to the poor preservation in the posteriormost area, but this specimen lacks a long, cylindrical, distal abdominal segment.

Remarks. The habitus is typical of Thysanoptera and reminds to that of representatives of the family Aeolothripidae preserved in some Neogene compression deposits (Peñalver, 1998). The lack of a long, cylindrical, distal segment in the abdomen discards its identification as a member of the suborder Tubulifera, so this specimen belongs to the suborder Terebrantia (Mound *et al*., 1976). The La Rinconada fossil record contains representatives of the family Thripidae (Peñalver *et al*., 2016), but the Rubielos de Mora record also includes the family Aeolothripidae (Peñalver, 1998). The average length for Thripidae and Aeolothripidae specimens in Rubielos de Mora is 1.21 mm and 1.95 mm, respectively, the San Chils specimen (2.10 mm long) might belong to the latter. The body characteristics are similar in these families and their main differences occur in the wing venation; thus, the absence of wings in this specimen prevents its reliable identification as Aeolothripidae.

Order HEMIPTERA Linnaeus, 1758

Suborder Heteroptera Latreille, 1810

Family **Corixidae** Leach, 1815

Subfamily Corixinae Enderlein, 1915

Corixinae indet.
(Figs. 2g-h)

Material. SC-119.

Description. Isolated, incomplete hemelytron with a pattern of irregular transversal stripes that is 3 mm in length and 1.20 mm in width. It lacks its proximal portion and the preservation is poor.

Remarks. The characteristic transversal irregular stripes pattern is typical of the subfamily Corixinae. The wing patterns in the other subfamilies of the family Corixidae, Cymatiainae and Micronectinae, are regular stripes and stains patterns respectively (Dethier, 1986). The preservation of this specimen is poor and the Cenozoic corixids have been scarcely studied, but Martínez-Delclòs *et al*. (1991) proposed the genus *Corixa* for the specimens from Rubielos de Mora, very similar to the San Chils specimen (see also Peñalver, 1998).

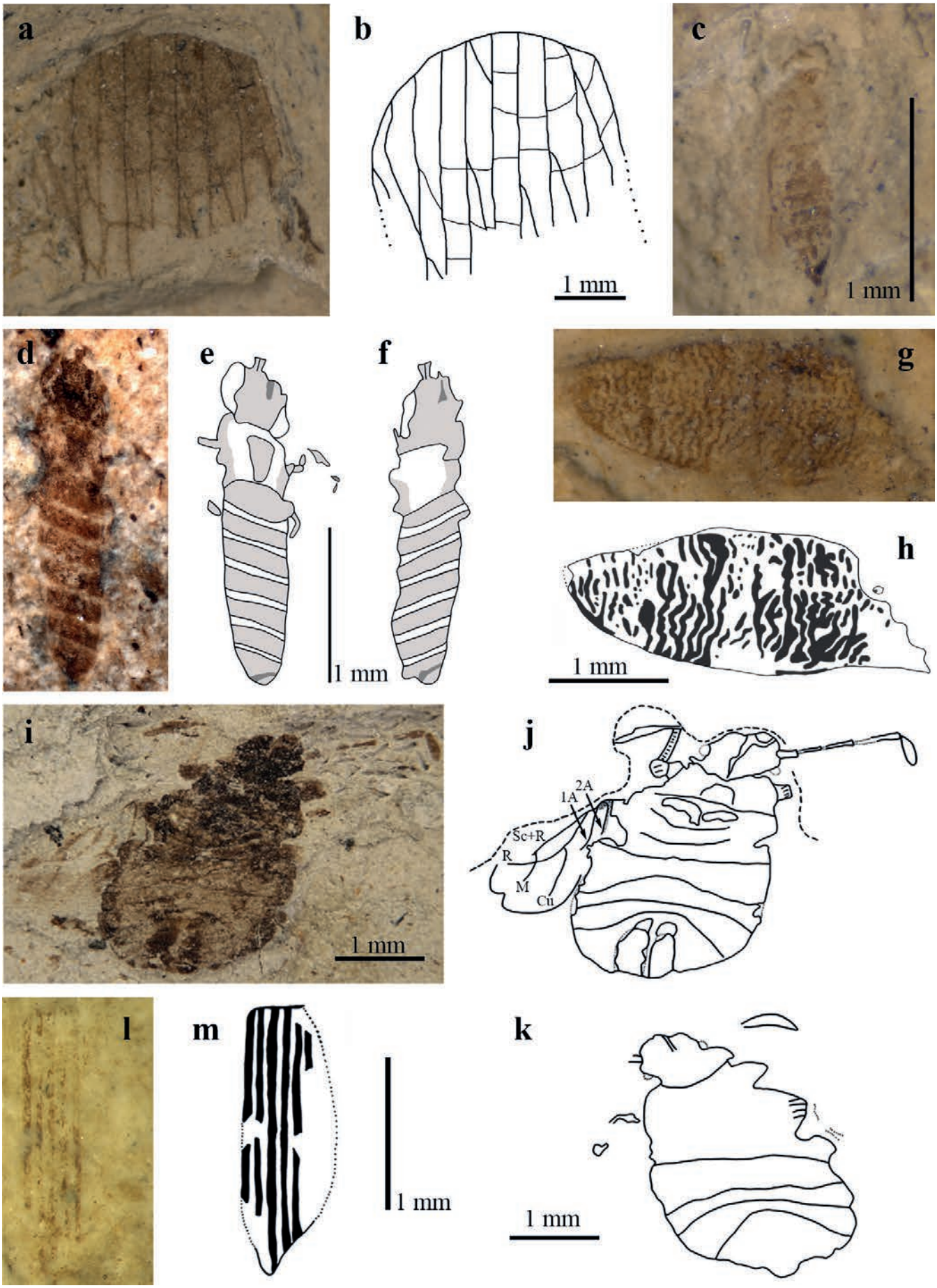
Family **Pentatomidae** Leach, 1815

Genus *Sciocoris* Fallén, 1829

Sciocoris sp.?
(Figs. 2i-k)

Material. SC-8A/SC-8B (part and counterpart).

Description. Body length is 3.03 mm, but it is slightly deformed. The head is wider than long. Rostrum and eyes are not preserved, but the relative size of the eyes can be inferred. The right antenna is deformed and disarticulated, but the left antenna is complete and is 1.77 mm long; the scape, three flagellomeres and a distal mace-shaped flagellomere can be seen in the left antenna. Two coxae and several legs fragments are visible in the thorax, which is highly sclerotised. Right hindwing is preserved; the apical area and a sclerotised proximal area with punctures can be observed. Venation includes Sc+R, R, M, Cu, 1A and 2A veins. Abdomen segmented in five sternites whose medial area is anteriorly directed. Genitalia is visible in the distal area of the abdomen.


a
b
1 mm
c
1 mm
d
e
f
1 mm
g
h
1 mm
i
1 mm
j
2A
1A
Sc+R
R
M
Cu
l
m
1 mm
k
1 mm

Remarks. The specimen can be assigned to the family Pentatomidae (Cassis & Gross, 2002) based on the presence of five antennal flagellomeres and its trapezoidal body shape. Although preservation is poor, several characteristics suggest that the specimen belongs to the genus *Sciocoris*: total length shorter than 4 mm, the antenna/body lenght proportion, round head with low prognathism, eyes of inferred small size and widest body area in the anterior abdominal portion (Salini & Viraktamath, 2015). The morphology of the genitalia suggests that this specimen is a female. It would be the first fossil record of the genus *Sciocoris* for the Neogene.

Order COLEOPTERA Linnaeus, 1758

Coleoptera indet.
(Figs. 2l-m)

Material. SC-26.

Description. Poorly preserved isolated elytron 1.76 mm in length. The costal area is not preserved and the apex is acuminate. Six longitudinal ribs can be observed, but only two of them are complete along the elytron.

Remarks. The general shape corresponds to a coleopteran elytron, but a more detailed taxonomical identification is not possible due to the lack of suitable characters considering the high variability of this type of elytra among coleopterans.

Order HYMENOPTERA Linnaeus, 1758

Suborder Apocrita Gerstäcker, 1867

Family **Braconidae** Nees, 1812

Braconidae indet.
(Figs. 3a-b)

Material. SC-6.

Description. The specimen suffered an intense deformation that chiefly affected the head and thorax. Its length is 2.10 mm. Eyes are laterally and close to one of them there is an undetermined, elongated structure that most likely corresponds to the remains of a leg. A deformed wing is preserved showing two veins (probably Rs and M) and a costal, large, marked pterostigma. Pterostigma is triangular in shape and extends towards to the wing apex. A petiole joins the thorax and the segmented gaster.

Remarks. The specimen is deformed and poorly preserved, but its habitus and the presence of a petiole enable to identify it as a Hymenoptera. The identification of this specimen within Braconidae is based on the size and morphology of its pterostigma. The pterostigma is similar to the ones present in braconid specimens from the close La Rinconada outcrop (Peñalver & Martínez-Delclòs, 2000) and from the extant representatives of the family Braconidae (see Achterberg, 1976).

Family **Formicidae** Latreille, 1809

Formicidae indet.
(Figs. 3c-d)

Material. SC-34 and SC-35.

Description. Their preservation is poor and they are slightly disarticulated, but head, thorax and gaster can be observed in anatomical positions. Wings are lacking and antennae are not preserved. Specimen SC-34 preserves the eyes, a deformed thorax and several legs fragments. Its petiole is hidden below a leg and the gaster, differentiated in four or five segments, and lacks a constriction at its base. Specimen SC-35 is smaller and shows a more intense deformation. Its scapes are distinguishable in the head. A thin thorax, possible legs fragments and the gaster are poorly preserved. The petiole can be observed.

Remarks. The two specimens are separated by 3.35 mm. Their general body morphologies correspond to the family Formicidae (Bolton, 2003). The small size, body morphology, thin thorax and absence of wings indicate that SC-34 and SC-35 belong to the worker caste. The identification of genera and species of fossil Formicidae in laminated rocks is challenging and the poor preservation of these specimens prevents a more accurate identification.

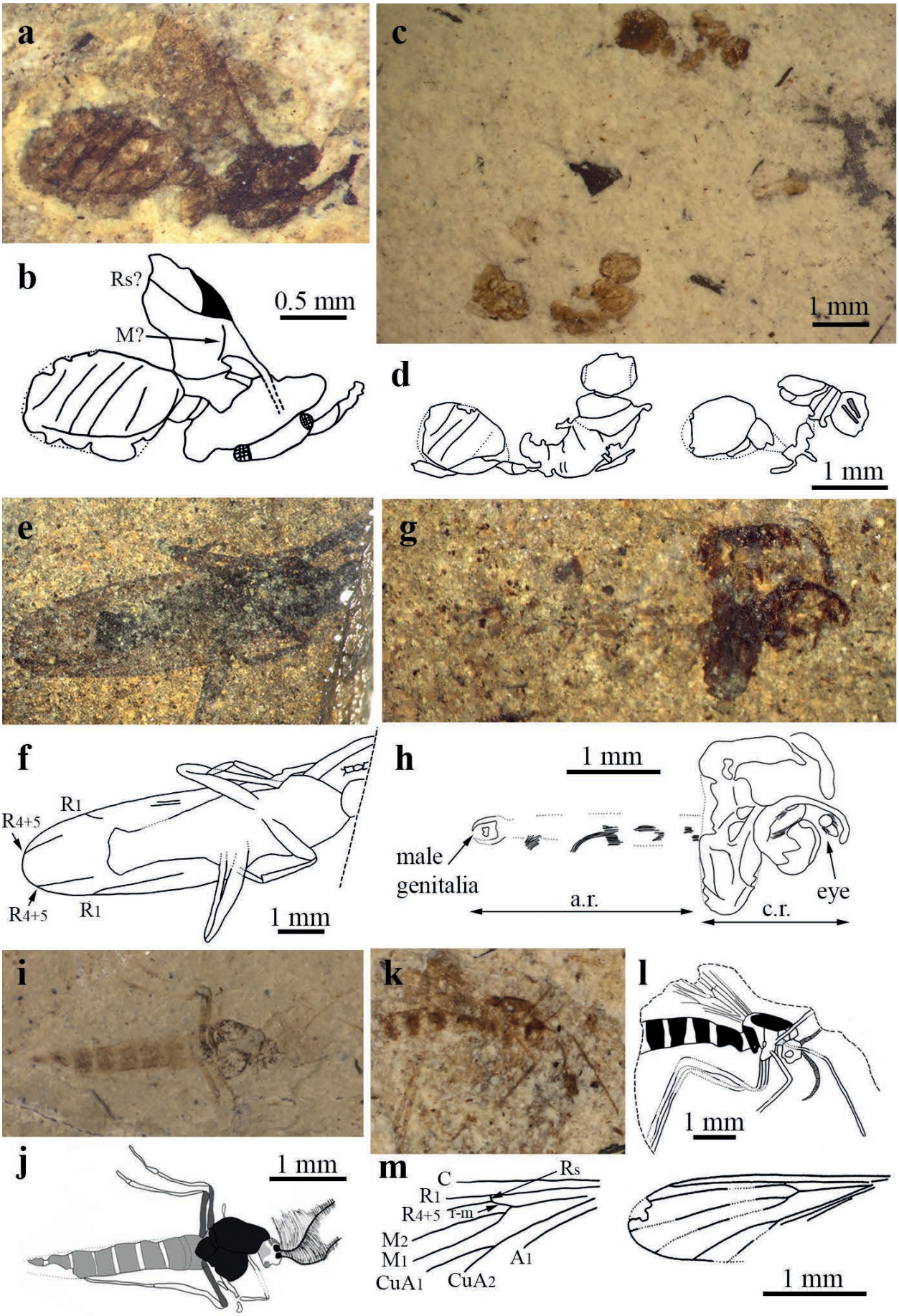
Order DIPTERA Linnaeus, 1758

Suborder Nematocera Latreille, 1825

Family **Bibionidae** Fleming, 1821

Genus *Bibio* Geoffroy, 1762

Figure 2. Photographs and drawings of San Chils insects. **a-b)** Acrididae indet., SC-85. **c)** Thripidae? indet., SC-103. **d-f)** Aeolothripidae? indet.; **(d-e)**, SC-33A, **(f)**, SC-33B. **g-h)** Corixinae indet., SC-119. **i-k)** *Sciocoris* sp.?; **(i-j)** SC-8A, **(k)** SC-8B. **l-m)** Coleoptera indet., SC-26. Each pair of photograph and drawing in a-b, d-e, g-h, i-k and l-m is at the same scale.


a
b
Rs?
M?
0.5 mm
c
1 mm
d
1 mm
e
g
f
R1
R4+5
R4+5
R1
1 mm
h
1 mm
male
genitalia
a.r.
c.r.
eye
i
k
l
1 mm
j
1 mm
m
C
Rs
R1
R4+5
r-m
M2
M1
A1
CuA1
CuA2
1 mm

Bibio sp.?
(Figs. 3e-f)

Material. SC-29.

Description. The anteriormost area of the head is not preserved. Only three legs showing femora and tibiae emerge from the thorax. Moreover, three tarsomeres and two claws are visible next to the head. Wings are folded and present a highly sclerotised venation in the costal area. Veins R_1 and R_{4+5} can be observed in both wings, but vein R_{2+3} is absent. The abdomen is deformed and compressed in its longitudinal axis.

Remarks. The habitus of this specimen and its wing venation correspond to the family Bibionidae (Hardy, 1981). The record of bibionids from La Rinconada includes the genera *Bibio*, *Plecia*, and *Penthetria*, but only *Bibio* lacks the vein R_{2+3} (Peñalver *et al*., 2016). So, we identified the San Chils specimen as a *Bibio* sp.? although the characteristic tibial spines cannot be observed. The identification to species level is not possible due to the poor preservation of the specimen and the questionable justification of the diverse fossil *Bibio* species.

Family **Chaoboridae** Edwards, 1912

Chaoboridae indet.
(Figs. 3g-h)

Material. SC-19, SC-43, SC-92, SC-95, SC-100A/SC-100B (part and counterpart) and SC-127.

Description. The remains found are pupal exuviae. The best-preserved one corresponds to the exuvium SC-43, which has a total length of 0.60 mm and 1.64 mm of cephalothoracic length. The cephalothoracic region is voluminous and preserves an eye. Siphonal tubes are not preserved. Abdominal region has longitudinal pilosity that is oriented laterodistally. A cercus and the male genitalia can be seen in the distal abdominal region of this specimen.

Remarks. The record of pupal exuviae in La Rinconada includes the dipteran families Chaoboridae and Chironomidae (Peñalver, 2002); they can be differentiated due to their characteristic morphology (Cook, 1981; Oliver, 1981). In Chironomidae, the cephalothoracic region is less voluminous and its proportional length when compared to the body is short; the herein described exuvium has the opposite characteristics and so it has been determined as a Chaoboridae exuvium.

Family **Chironomidae** Macquart, 1838

Chironomidae indet.
(Figs. 3i-j)

Material. SC-88 and SC-111.

Description. The specimen SC-111 is well preserved, but it is incomplete, lacking the apical abdominal portion. Its body length is 3.30 mm, as preserved. Antennae are plumose and filiform, with undetermined flagellomeres and marked, round (globose) scapes. Eyes are partially preserved and embrace the antennae. Thorax is gibbous and includes mesonotum and metanotum; between them, a small, elongate scutellum can be observed. Wings are not preserved, but a fusiform structure could correspond to a haltere. Three complete legs and several fragments can be observed; they have femora and tibiae apparently without pilosity. Abdomen with parallel margins constituted by seven segments. Genitalia is not preserved.

Remarks. The described specimens have the typical morphology of Chironomidae and show similarities with the fossil species *Nomochirus sampelayoi* described from the La Rinconada outcrop, such as the antennal length and plumose constitution, the gibbous thorax and the abdomen with parallel margins. This species is very abundant in La Rinconada (Peñalver, 2002; Peñalver *et al*., 2016); it is assumed that it lived in the palaeolake, at least during long annual periods, so most likely it is also present in the fossil record of San Chils. Nonetheless, the specimens found in San Chils lack some important anatomical structures to accurately classify them in *N. sampelayoi*: wings are not preserved, legs lack pilosity and it is not possible to determine the number of antennal flagellomeres. The genitalia is not preserved in the specimen SC-111, but it could be considered a male due to its conspicuous plumose antennae.

Family **Mycetophilidae** Newman, 1834

Genus *Exechia* Winnertz, 1863

Figure 3. Photographs and drawings of San Chils insects. **a-b)** Braconidae indet., SC-6. **c-d)** Formicidae indet., SC-34 and SC-35. **e-f)** *Bibio* sp.?, SC-29. **g-h)** Chaoboridae indet., SC-43. **i-j)** Chironomidae indet., SC-111. **k-m)** *Exechia* sp.; **(l)**, SC-12, **(m)**, wing venation of SC-12 and wing venation of MPZ-98/430 extracted from Peñalver (2002). a.r. = abdominal region; c.r. = cephalothoracic region. Each pair of photograph and drawing in a-b, e-f, g-h, i-j and k-l is at the same scale.

Exechia sp.
(Figs. 3k-m)

Material. SC-12.

Description. The specimen is covered by a sedimentary film in the distal portions of the abdomen and wings. Antennae are filiform with, at least, seven differentiable flagellomeres in a round head. Abdomen gibbous and voluminous. Five legs with abundant pilosity in femora and tibiae are preserved. Wings are overlapped. Wing venation includes: presence of veins C, R_1 and A, absence of vein R_{2+3}, vein R_{4+5} straight, CuA bifurcation more distal than that of M, and vein Rs located at roughly the same distance that the M bifurcation. Abdomen shows a marked segmentation.

Remarks. The habitus of this specimen is typical of the family Mycetophilidae. Its body morphology and the absence of the vein R_{2+3} enable to classify it in the subfamily Mycetophilinae (Peñalver, 1998). The classification in the genus *Exechia* is based on the following: straight vein R_{4+5}, CuA bifurcation more distal than that of vein M, and vein Rs located at the same distance than bifurcation of vein M (Vockeroth, 1981). Furthermore, the comparison between the San Chils specimen and the Rubielos de Mora specimen MPZ-98/430 confirms that they correspond to the same morphotype based on size, morphology and location of wing veins.

Class BRANCHIOPODA Latreille, 1817

Order CLADOCERA Latreille, 1829

Suborder Anomopoda Sars, 1865

Family **Daphniidae** Straus, 1820

Genus *Daphnia* Müller, 1785

Subgenus *Daphnia* (*Ctenodaphnia*) Dybowski & Grochowski, 1895

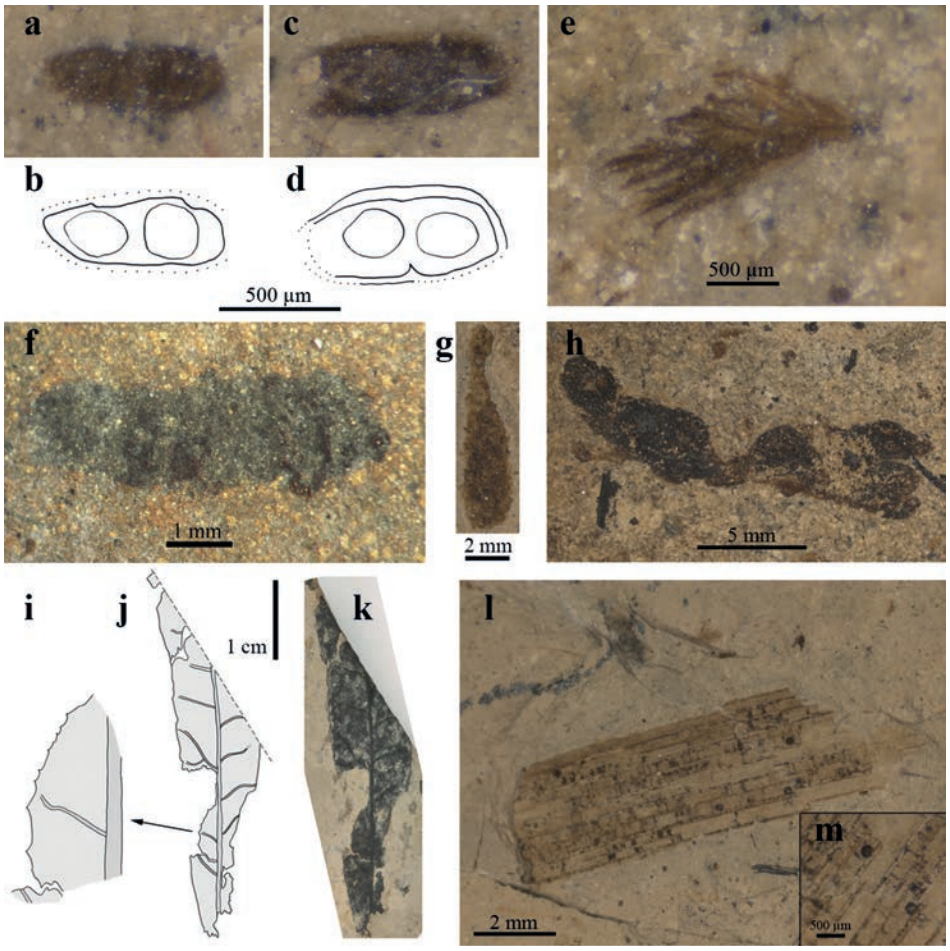


Figure 4. Photographs and drawings of San Chils fossils. **a-d)** *Daphnia* (*Ctenodaphnia*) sp. ephippia; **(a-b)**, SC-114A, **(c-d)**, SC-115A. **e)** Bird feather indet., SC-99A. **f-h)** Coprolites; **(f)**, SC-28, **(g)**, SC-101B, **(h)**, SC-116. **i-k)** *Myrica* sp. leaf with margin feeding, SC-7. **l-m)** Monocotyledon leaf with possible piercing/sucking marks, SC-110. Each pair of photograph and drawing in a-b, c-d and j-k is at the same scale.

Daphnia (*Ctenodaphnia*) sp.
(Figs. 4a-d)

Material. SC-114A/SC-114B (part and counterpart) and SC-115A/SC-115B (part and counterpart).

Description. They are poorly preserved but its high original sclerotisation enables to observe the ovoid general shape and the valve and eggs' margins. Specimen lengths are 0.75 mm (SC-114) and 0.87 mm (SC-115). Specimen SC-115 is better preserved than SC-114, thus the outer valve margin is partially visible and the straight dorsal margin can be observed. Two round eggs can be observed inside each ephippium.

Remarks. Two ephippia are separated by 3.60 mm, but their orientation in the slab is different. Ephippia of *Daphnia* (*Ctenodaphnia*) sp. have been abundantly found in Rubielos de Mora (Peñalver *et al*., 1996b). The San Chils ephippia correspond to the same morphotype as the ones from Rubielos de Mora.

6. ADDITIONAL TAXA RECORDED

Apart from the fossil arthropods described above, several plant remains and a few additional animal remains have been found in the bituminous slabs of San Chils.

6.1. Vertebrates remains

A tiny bird feather of 1.15 mm length is the only direct record of vertebrates in the bituminous slabs of San Chils (Fig. 4e). It has a central rachis with several long, oriented barbs, some of them branched in perpendicular barbules. This feather does not correspond to down feather due to the presence of well-developed rachis and oriented barbs but its taxonomical identification could not be carried out based on the lack of characters (Robertson *et al*., 1984). Bird feathers have been abundantly found in La Rinconada and Rubielos de Mora (Peñalver *et al*., 2016), being their presence common in lacustrine deposits (Davis & Briggs, 1995).

Furthermore, vertebrates are represented in San Chils as trace fossils. The San Chils fossil record includes 16 coprolites, and this type of remain is also abundant in Rubielos de Mora and La Rinconada outcrops (Peñalver, 2002; Peñalver *et al*., 2016). Most of the new records have a similar elongate, rectangular morphology and measure around 5.50 mm in length (Fig. 4f). They could correspond to the morphotype A7 of Rubielos de Mora, which has been associated to larval salamanders (Peñalver, 2002). The coprolites SC-101 and SC-116 have different morphologies (Figs. 4g-h). Specimen SC-101 is elongate with rounded edges and 9.25 mm in length; it is similar to the morphotype A1 of Rubielos de Mora, which has been related to adult salamanders. Specimen SC-116 is elongate (18.60 mm in length) and irregular in shape; it could correspond to the morphotype A6 of Rubielos de Mora, which has been related to adult salamanders or birds.

Lastly, the find of a laminated dolomicrite slab with an accumulation of nine coprolites of the morphotype A7 (SC-20, SC-21, SC-22, SC-23, SC-24, SC-25, SC-73, SC-82 and SC-83) and one Thysanoptera (SC-74) is remarkable. The content of the well-preserved coprolite SC-22 has been analysed. Results are inconclusive, as insect or vertebrate remains have not been found. However, colonial algae that could correspond to the genus *Botryococcus* and fungal ascospores can be observed in association with the abundant amorphous organic matter (Figs. 5a-e).

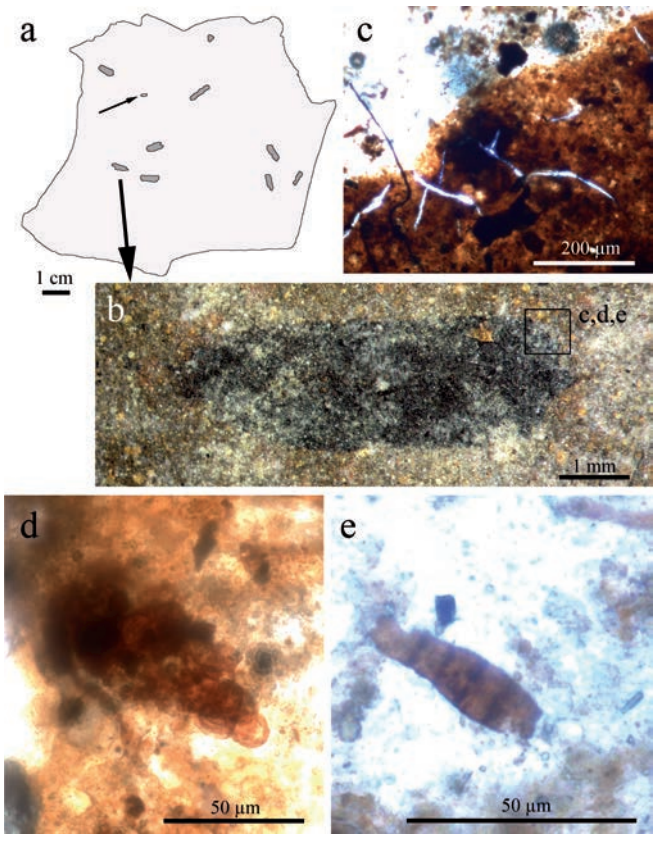


Figure 5. a) Drawing of a laminated bituminous dolomicrite with a coprolite accumulation (SC-20, SC-21, SC-22, SC-23, SC-24, SC-25, SC-73, SC-82 and SC-83; Thysanoptera SC-74 is indicated with a small arrow). **b)** Coprolite SC-22. **c)** Organic matter of the coprolite content. **d)** Colonial algae *Botryococcus* sp.? **e)** Fungic ascospores. Microphotographs c-e taken from the preparation for optic microscope of the coprolite in photograph b.

6.2. Plants and plant-insect interactions

Plant remains are abundant in San Chils. Their preservation is poor, but several specimens have been identified. The monocotyledons include one remain of the aquatic plant *Potamogeton* sp., six cf. Cyperaceae seeds, and bracts, inflorescences and seeds of Commelinidae. Furthermore, several fragments of monocotyledonous leaves with straight margins and parallel veins have been found; they could correspond to families Poaceae, Cyperaceae, Sparganiaceae or Juncaceae (Barrón & Diéguez, 2001). The dicotyledonous assemblage contains leaves of *Dicotylophyllum* sp., *Myrica* sp., and *Myrica lignitum* Saporta, 1865. Several slab surfaces with abundant remains of burned plants (fusinite) have been detected, indicating that the forests close to the ancient lake were affected by wildfires as described from the fossil record of La Rinconada (Peñalver *et al*., 2016).

Plant-insect interactions or associations can be observed in two leaves (SC-7 and SC-110). An elongate leaf (SC-7), elliptic in shape and having margin feeding traces, has been identified as *Myrica* sp. based on its pinnate, craspedodromous venation and serrate margin; the primary, secondary and tertiary veins are easily differentiable (Barrón & Postigo-Mijarra, 2011). The margin feeding consists of several semicircular marks in the left area that corresponds to a continuous marginal trace morphotype DT14 (Scott, 1992; Labandeira *et al*., 2007) (Figs. 4i-k). This margin feeding could be related to lepidopteran caterpillars, and similar records have been found in Rubielos de Mora and La Rinconada (Peñalver, 2002; Peñalver & Delclòs, 2004). The second plant-insect interaction is present in a monocotyledon leaf (SC-110) as piercing/sucking marks (Figs. 4l-m). Round and ellipsoidal scars, 0.18 mm in diameter, occur between parallel, straight veins, so this association corresponds to the morphotype DT132 (Labandeira *et al*., 2007).

7. DISCUSSION

7.1. Taphonomy

The specimens studied herein are incomplete, deformed or disarticulated; in general, their preservation is poor. Nonetheless, delicate structures, as wing venations, pupal exuviae and pilosity have been observed. The preservation of these delicate structures is typical of outcrops of exceptional preservation, or Konservat-Lagerstätten (Allison, 1988), such as of the La Rinconada locality in the same depositional unit. Furthermore, the San Chils rocks show infra-millimetric lamination due to the alternation of growths of microbial mats and sedimentation of fine-grained particles, as occurs in La Rinconada rocks. The evidence of microbial mats (see Peñalver, 2002) supports that the inferred early stages of fossilization occurred in the anoxic bottom of a meromictic palaeolake without bioturbation (Anadón *et al*., 1989; de las Heras *et al*., 2003). It should be noted that the microbial mats could influence the preservation of delicate structures (*e.g.*, Gall, 1990; Gall *et al*., 1990; Peñalver, 2002; Iniesto Rodríguez, 2016). The weathering of the examined San Chils slabs due to their accumulation outdoors for more than a century explains the poor preservation of the fossils they contain.

7.2. San Chils fossil record

The studied fossils come from the unit B of the Ribesalbes sequence in Ribesalbes-Alcora Basin, which consists of lower Miocene lacustrine deposits, and currently include a total of 127 specimens. These are adult (imaginal) insects, insect pupae/pupal exuviae, crustacean remains, an isolated bird feather, several coprolites and plant remains (some of them charcoalified). The most abundant fossils are plants and adult insect remains, representing the 33% and 31% of the total respectively (Fig. 6a).

The fossil insects found in San Chils are represented by adult insects and pupal exuviae in six orders: Orthoptera, Thysanoptera, Hemiptera, Coleoptera, Hymenoptera, and Diptera. The most abundant adult insects are Thysanoptera, accounting for 41% of the total (Fig. 6b). Diptera is the second most abundant insect order.

The exuviae from San Chils correspond to aquatic preimaginal stages of Diptera, both as isolated remains and exuvial accumulations. Isolated exuviae are incomplete, so the identification is challenging, but the presence of a voluminous cephalothoracic region suggests that they belong to family Chaoboridae. Several undetermined exuviae could correspond to the family Chironomidae based on their small cephalothoracic region. The exuvial accumulations are chitinous stains of undetermined number of specimens. Finally, the distinction of body fossils of pupae from their exuviae is difficult to stablish due to their poor preservation.

The six insect orders found in San Chils are very common in palaeoentomological localities around the world (Grimaldi & Engel, 2005). La Rinconada and San Chils share the abundance of pupae/pupal exuviae and the presence of vertebrate coprolites, bird feathers and levels with mass record of burned plant fibres. However, La Rinconada has a more diverse record of insect and plant remains, although most likely this difference is due to the comparatively smaller sample obtained to date from San Chils. Furthermore, the most abundant insect order in San Chils is Thysanoptera (Fig. 6b), but only 18 thrips specimens have been found in La Rinconada, probably

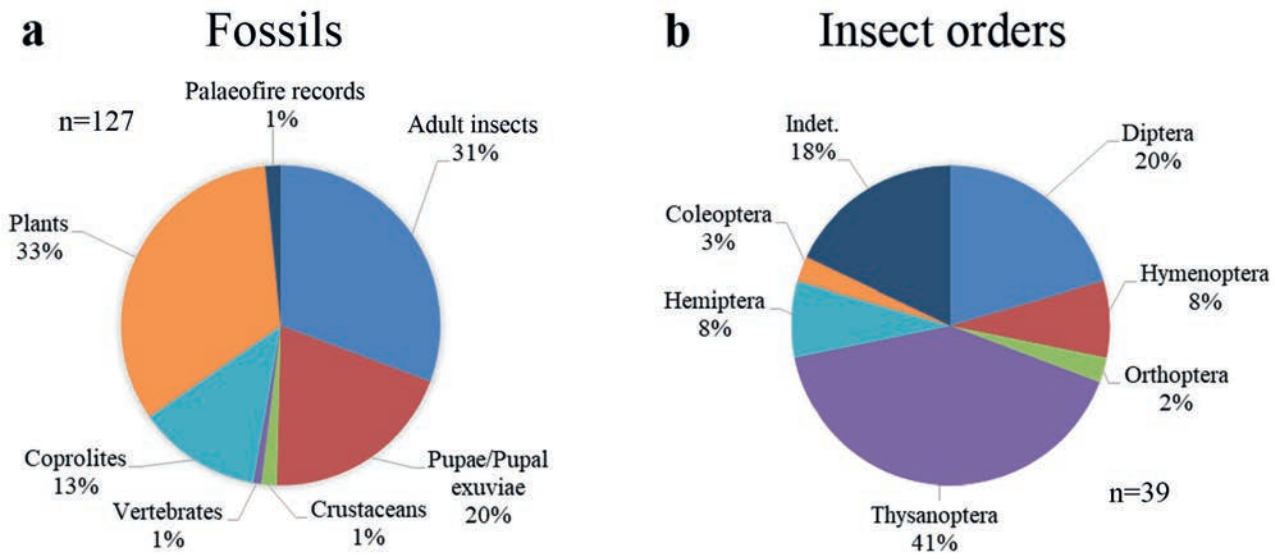


Figure 6. a) Representation of the percentage of types of fossils recorded in San Chils. **b)** Representation of the percentage of insect orders in San Chils fossil record.

due to a sampling bias related to their small size (Peñalver *et al*., 2016).

Several taxa from San Chils are new contributions to the Ribesalbes-Alcora Basin fossil record. These are: the specimen classified in the subfamily Corixinae (Hemiptera: Corixidae), the specimen assigned to the family Pentatomidae (Hemiptera), two ant specimens of the worker caste (Hymenoptera: Formicidae), the specimen classified within the genus *Exechia* (Diptera: Mycetophilidae), and two ephippia of the crustacean subgenus *Daphnia* (*Ctenodaphnia*). The possible presence of the family Aeolothripidae (Thysanoptera) could be added to this list. More interestingly, the discovery of a virtually complete and well-preserved specimen of *Sciocoris* sp. (Hemiptera: Pentatomidae) would correspond to the first report of the genus in the Neogene fossil record.

Other lower Miocene palaeoentomological localities in the Iberian Peninsula are Izarra (Álava), Vilobí del Penedès (Barcelona) and Rubielos de Mora (Teruel) (Peñalver *et al*., 1999). The insect fossil record from Izarra includes several uncommon taxa, but it shares with San Chils the families Acrididae (Orthoptera), Pentatomidae (Hemiptera), and Formicidae (Hymenoptera) (Arillo & Ortuño, 1997; Barrón *et al*., 1997; Peñalver *et al*., 1999). The fossils found in Vilobí del Penedès are abundant fishes and two specimens within the genus *Plecia* (Diptera: Bibionidae) (Peñalver *et al*., 1999). Finally, the lower Miocene locality of Rubielos de Mora yielded a rich and diverse insect fossil record of exceptional preservation (Peñalver, 1998). All the families found in San Chils have appeared in Rubielos de Mora (see Montoya *et al*., 1996).

7.3. Palaeoecology

The insect communities in lakes and palaeolakes are diverse and represented by a similar abundance among orders, but Diptera is usually slightly more abundant than others (Schowalter, 2011). These kinds of communities are present in Rubielos de Mora and La Rinconada fossil records (Peñalver, 2002). The palaeocommunity of San Chils was heterogeneous, with a dominance of Thysanoptera among the terrestrial adult insects according to the material hitherto studied. In any case, the presence of numerous isolated Diptera pupal exuviae and exuvial accumulations confirms the abundance of the order in this area of the palaeolake. The presence of pupal exuviae is an indicator of stagnant water areas and few predators. The difference between the record of exuviae and adult Diptera, with only eight adult specimens found, has been also observed in Rubielos de Mora (Peñalver, 1998). This circumstance can be explained due to taphonomic biases, because the preimaginal stages are most abundant and live in the aquatic environment of burial.

The San Chils aquatic insects are represented by Corixidae (Hemiptera) and abundant Chironomidae and Chaoboridae (Diptera) pupae. The rest of insect remains correspond to terrestrial insects that lived in or around the riparian areas. The lack of fishes in San Chils fossil record supports the hypothesis of an endorheic origin for the palaeolake and thus the impossibility of colonization, although it could also be due to unfavourable aquatic environmental conditions.

The producers in the food chain according to the current San Chils lacustrine fossil record were *Botryococcus* sp. algae and the aquatic plant *Potamogeton* sp. Phytophagous

Chironomidae larvae and *Daphnia* (*Ctenodaphnia*) sp. fed on these algae and/or organic matter particles (Oliver, 1981; McCauley *et al*., 1990). Zoophagous Chaoboridae larvae preyed on other aquatic larvae and tiny crustaceans (Cook, 1981). The second level of consumers included the family Corixidae, for which a phytophagous and zoophagous diet has been proposed, but these aquatic insects preferentially feed on insect larvae and soft crustaceans (Reynolds, 1975; Murillo & Recasens, 1986). Finally, the salamanders evidenced by coprolites in the San Chils fossil record were the tertiary consumers of the food chain. La Rinconada food chain is similar (Peñalver *et al*., 2016).

Phytophagous insects such as Acrididae (Orthoptera), Thysanoptera, and Pentatomidae (Hemiptera), lived nearby the palaeolake. Orthoptera have chewing feeding habits, whereas Thysanoptera and Hemiptera have piercing-and-sucking habits (see Grimaldi & Engel, 2005). Furthermore, the finding of a *Myrica* sp. leaf with semicircular marks indicates the presence of lepidopteran caterpillars and their adult stages. The piercing/sucking marks on the monocotyledonous leaf cannot be related to a specific insect taxon. Braconidae is represented in San Chils by one specimen; this hymenopteran family has a koinobiont endoparasitic lifestyle based on larval feeding in extant correlates (Wahl & Sharkey, 1993). Adult stages of the dipteran families Bibionidae, Chironomidae and Mycetophilidae require the presence of decomposing organic matter (Schowalter, 2011). The family Bibionidae is especially interesting due to the possible application as a Cenozoic palaeoclimatic indicator, because the genus *Plecia* indicates warm climate while other Bibionidae genera can be related to cooler climates (Collomb *et al*., 2008). Therefore, future findings of Bibionidae specimens in San Chils will enable to improve the palaeoclimatic estimates (Peñalver, 2015).

The San Chils palaeovegetation includes taxa typical of riparian lacustrine environments and it is similar to that recorded in La Rinconada (Barrón & Postigo-Mijarra, 2011; Postigo-Mijarra & Barrón, 2013). Aquatic plants as *Potamogeton* sp. are found in shallow water of extant lakes, plants as Cyperaceae appear in lakesides, and small trees or shrubberies such as *Myrica* sp. correspond to plants growing in flooding areas (Peñalver *et al*., 2016).

8. CONCLUSIONS

The San Chils fossil record has been studied for the first time and several taxa have been identified, resulting in several new additions to the faunistic list for the Miocene of the Ribesalbes-Alcora Basin.

The preservation of the specimens is poor, but the presence of delicate structures and the evidence of the action of microbial mats enable us to consider San Chils as a Konservat-Lagerstätte. The poor preservation of the fossils when compared to the ones from La Rinconada, in the same depositional unit, is due to the weathering of the slabs of rock for more than a century since their extraction from the mine. The San Chils fossil record shows similarities with those from La Rinconada and Rubielos de Mora.

Despite the scarce fossil record found to date in San Chils, it has been possible to infer some general palaeoenvironmental characteristics. The palaeoenvironment corresponds to a typical lacustrine area. Its fossil record includes producers as algae and aquatic plants, and consumers as phytophagous and zoophagous larvae or adult insects, being the presence of salamander coprolites evidence of part of the constituents from a higher trophic level. The fossil record includes terrestrial insects that lived near to the palaeolake and plants typical of lacustrine shores or flooding areas.

One of the main future plans is to carry out a palaeontological excavation in San Chils in order to increase the available samples. It is expected that palynological data obtained from unweathered rock samples extracted under stratigraphic control will improve the palaeoenvironmental reconstruction. That task seems challenging considering that the unit B in San Chils, in the Berita ravine, does not have good rock exposures and that the ancient mines are dangerous or directly inaccessible. Nonetheless, the results obtained in the present research confirm the presence of fossils in San Chils showing palaeobiological similarities to those from La Rinconada. Due to the taphonomic and sedimentological features shared by both localities, San Chils is most likely as rich in fossils of exceptional preservation as La Rinconada.

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