

Ichnoentomology: a unique approach to insect research

Ichnoentomología: el estudio de los insectos desde una perspectiva única

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Abstract: Ichnoentomology can be defined as the study of insect behavior through the analysis of their traces. These traces are commonly found in soils, wood, leaves, bones, and fruits. If they overcome the taphonomic barrier, insect traces may be preserved in paleosols, petrified wood, fossilized leaf compressions or impressions, as well as in fossilized bones and fruits. Trace fossils provide physical evidence of how and where insects of the past fed, reproduced, and moved, enabling the reconstruction of their evolutionary history and the paleoenvironment they inhabited. This contribution summarizes the study of extant insects carried out by the División Icnología of the Museo Argentino de Ciencias Naturales over the past 30 years. The study of nesting behaviors, nest structures, pupation chambers, and/or cocoons of 135 insect species and other arthropods has enabled the interpretation of numerous trace fossils produced by phylogenetically related fossil species. Among the most notable recent discoveries are *Cellicalichnus krausei*, a 100 Ma bee nest attributed to the tribe Halictini, and *Racemusichnus jacobacciensis*, the largest known solitary insect trace. In commemoration of the 100th anniversary of the Entomological Society of Argentina (SEA), this work aims to highlight a different perspective in the study of insect behavior.

Keywords: Continental ichnology, Insect behavior, Insect traces, Paleosols, Trace fossils.

Resumen: La Ichnoentomología es la disciplina que permite estudiar el comportamiento de los insectos mediante el análisis de sus trazas. Estas son frecuentes en suelos, madera, hojas, huesos y frutos. Sin embargo, sólo algunas trazas logran superar la barrera tafonómica y preservarse en paleosuelos, madera petrificada, impresiones o compresiones en hojas fósiles, huesos o frutos fosilizados. Las trazas fósiles evidencian cómo y dónde los insectos del pasado se alimentaban, reproducían y desplazaban, permitiendo reconstruir su historia evolutiva y los ambientes que habitaron. Aquí se compendia los aportes sobre especies actuales desarrollados durante los últimos 30 años por la División Icnología del Museo Argentino de Ciencias Naturales. Estos incluyen análisis de comportamientos de nidificación, nidos, cámaras pupales y/o capullos de 135 especies de insectos y otros artrópodos, indispensables para poder interpretar las trazas fósiles de productores emparentados con estos representantes actuales. Entre los últimos hallazgos destacados se encuentran *Cellicalichnus krausei*, un nido de abeja de 100 millones de años atribuido a Halictini, y *Racemusichnus jacobacciensis*, la traza fósil de insecto solitario más grande conocida hasta el momento. En el marco del Centenario de la Sociedad Entomológica Argentina (SEA), este trabajo propone una mirada diferente sobre el estudio del comportamiento de los insectos.

Palabras clave: Comportamiento de insectos, Icnología continental, Paleosuelos, Trazas de insectos, Trazas fósiles.

INTRODUCTION

Ichnoentomology focuses on insect traces, which are structures that record the behavior of insects as they modify a substrate, such as soils, wood, leaves, bones, and fruits. These traces include trackways, tunnels, nests, chambers, and cocoons resulting from locomotion, feeding, and nesting behaviors. Insects may excavate or bore the substrate or construct free-standing structures. Such traces are produced by compressing or reworking the substrate, usually by adding liquid secretions or excretions, coarse grains, pasty mammal dung, their feces, malaxated wood, among others. Some of the latter can be incorporated as pellets or as a lining. When the substrate is soil, those traces that are not merely excavated but constructed with pellets or lined with them exhibit greater cementation than the adjacent soil (differential cementation), resulting in higher potential preservation (Genise & Bown, 1994; Genise, 2016). Therefore, although many insects live or complete some stages in the soil, only the traces of some taxa remain preserved in paleosols.

For the last 30 years, entomologists and geologists from the División Icnología of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” have studied the evolution of insect behavior through trace fossils in paleosols, most of which are nests and pupation chambers. These are preserved *in situ* and serve as a diagnostic tool for recognizing paleosols, even in the absence of other pedological features, due to the ability of insects to nest and rework recently deposited sediments (Genise et al., 2004; Genise, 2019). In reliably attributed trace fossils, the ecological preferences of trace producers provide paleoecological and stratigraphical information. Some insect taxa are limited to a geographic range and nest under certain climatic and vegetation conditions, in a specific soil horizon. Larval or pupal stages, as well as the provisions left by their parents, are sensitive to the microenvironment (temperature and humidity) within their chambers (Genise et al., 2000; Genise, 2016). Moreover, some insect trace fossils contain phytoliths, silica particles deposited in intra- and intercellular spaces of plant tissues, providing information about vegetation or other ecological inferences (Sánchez et al., 2010a; Cantil et al., 2020). The characteristics of paleosols containing insect traces also reflect the paleoenvironment in which the producer lived thousands or millions of years ago. Therefore, analyzing insect trace fossils and the associated paleosols is useful for reconstructing the landscape where the producers would have nested. In addition, some trace fossil assemblages are recurrent in similar paleoenvironments worldwide, regardless of age, defining paleosol ichnofacies (Genise et al., 2000 & references therein).

Considering that the insect body fossil record is fragmentary, incomplete, and particularly very scarce in South America, complex

insect traces confidently attributed to particular taxa may represent the only physical evidence of important events in the evolutionary history of some taxa (Genise, 2016). Insect trace fossils are dominant during the Cenozoic of Argentina, but some of them are recorded as late as the Cretaceous (Genise, 2016; Genise et al., 2016). In some cases, insect traces represent the oldest evidence of the existence of a group or the minimum age of appearance of a particular behavior (Genise et al., 2010, 2016, 2020a, b; Sánchez et al., 2010a, b, 2021; Sarzetti et al., 2014a; Cantil et al., 2018, 2020, among others).

Trace fossils are named following the International Code of Zoological Nomenclature based on macro-, meso-, and micromorphological diagnostic characters. Macromorphology refers to the overall shape of the trace, mesomorphology to the surface details of the wall of the trace, and micromorphology to characters that can only be seen under a microscope (Genise, 2016). The more complex the trace, the more specific its attribution can be. Accurate descriptions of the trace fossils are needed to correctly compare them with extant traces and obtain robust attributions, which are essential for making correct inferences about the past. A major problem is that most insect ethological studies omit detailed descriptions of the traces. For example, abundant articles describe the larval stages of dung beetles, but only a few of them (mostly older articles) provide detailed descriptions of the brood balls/masses. Therefore, some attributions of complex trace fossils remain indeterminate, tentative, or taxonomically ambiguous. The incorporation of detailed descriptions of modern insect traces (neoichnology) into entomological articles enhances the scientific value of such contributions by providing a comparative framework to interpret trace fossils and determine modern homologues or behaviorally convergent analogues.

To commemorate the 100th anniversary of the Entomological Society of Argentina, we present here all the neoichnological contributions from those who are or were part of the División Icnología, some of them active or honorary members of the SEA (Table I). These articles were focused on the nesting behavior of insect species (and other arthropods), mostly from Argentina. We also describe which insect traces remain preserved in the fossil record and highlight the latest advances in the evolutionary history of some insect taxa through Ichnoentomology.

STUDIED INSECTS THAT LEAVE PRESERVABLE TRACES

Since 1979, members of the División Icnología have studied extant traces of 128 insect species across 15 provinces of Argentina, one province in Chile, and two departments in Uruguay (Table I). These insects belong to the orders Hymenoptera (bees, wasps, ants, and sawflies), Blattodea (termites), Coleoptera (dung beetles),

Lepidoptera (moths), Hemiptera (cicadas), and Odonata (damselflies).

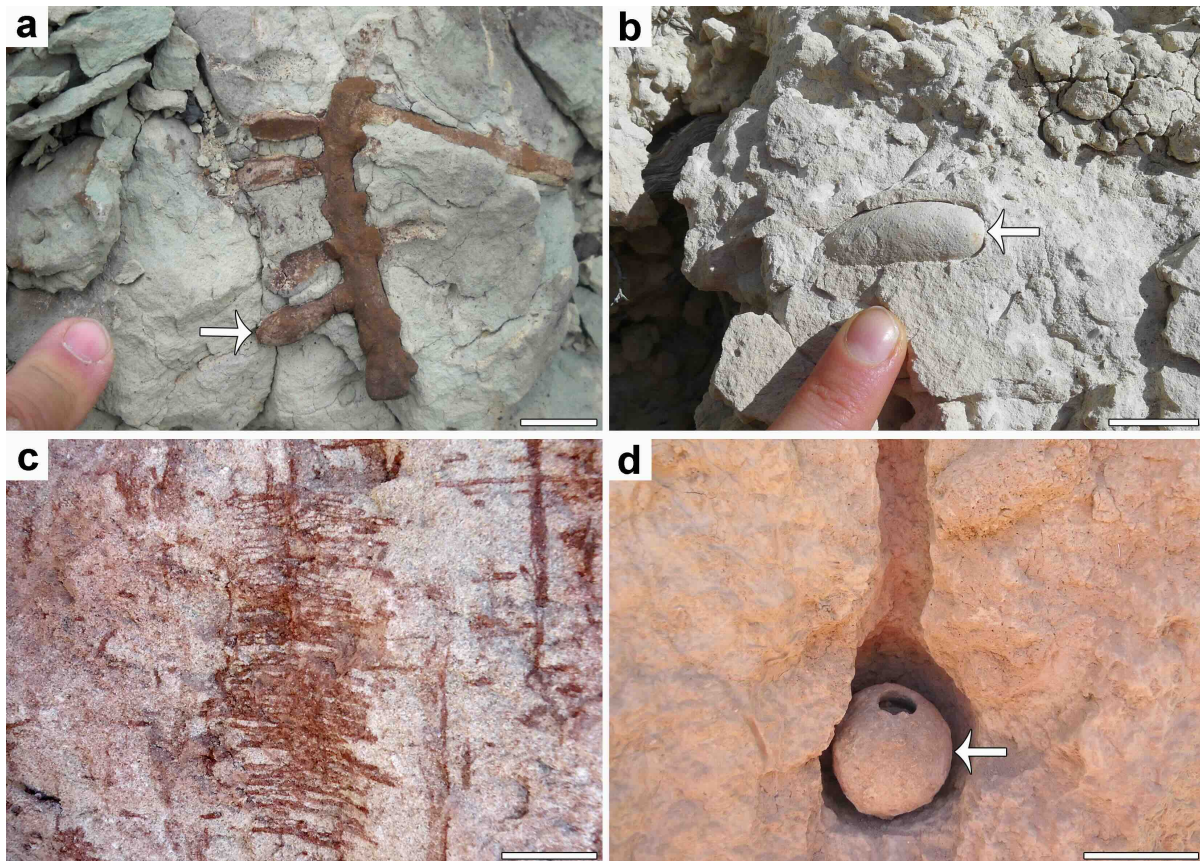


Figure 1

Examples of insect trace fossils from different ichnofamilies in paleosols (*in situ*).

a. Celliformidae, *Celliforma krausei*, a Halictini bee nest from the late Lower Cretaceous Castillo Formation, Chubut province, Argentina. Note the individual cells (arrow) connected to a main tunnel. b. Pallichnidae, *Fictovichnus sciuttoii* (arrow), a wasp cocoon from the same formation and geological age as *C. krausei*. c. Krausichnidae, *Krausichnus sisi*, a polydomous ant nest from the lower Paleogene Maíz Gordo Formation, Salta province, Argentina. d. *Coprinisphaera murguiai* (arrow), a dung beetle brood ball, preserved within its nest from the Pleistocene Tañi del Valle Formation, Tucumán, Argentina. Scale bars= a-b: 2 cm, c: 10 cm, d: 5 cm.

Most bees store pollen or a semi-liquid mixture of pollen and nectar inside cells, which are excavated in the soil and lined with a waterproof secretion that increases their potential for preservation. These cells are connected to a main tunnel, which is usually unlined and rarely preserved, except in cases where nests were reused by successive generations, resulting in substrate compaction (Table I, Bees references). Fossil bee cells are classified within the ichnofamily Celliformidae, which comprises seven ichnogenera based on the morphology of the cells, their clustering, and the presence of a tunnel or shaft (*Celliforma*, *Palmiraichnus*, *Corimbatichnus*, *Rosellichnus*, *Uruguay*, *Elipsodeichnus*, *Cellicalicnhus*; Fig. 1a).

Nests of solitary wasps in soils are generally composed of a tunnel that ends in one or more cells. Unlike bees, wasps provision their cells

with a paralyzed prey and do not need a lining to isolate cells from the soil (Table I, Wasps references). The absence of these linings reduces the potential for preservation of wasp cells and nests, which have not been found as fossils in paleosols.

The spinning of cocoons using silk produced by the labial glands in the final larval stage is a basal trait in Hymenoptera (Rozen et al., 2011). Cocoon characteristics, such as silk composition, shape, size, color, and resistance, differ among bees, wasps, ants, and sawflies. Some wasp cocoons, the hard and coriaceous ones (in Crabronidae or Pompilidae) or the sandy ones (in Crabronidae or Drynidae), show greater preservation potential than silky or membranous cocoons (Table I, Hymenoptera references). Fossil wasp cocoons with distinct shapes and surface morphologies are included in *Fictovichnus* (Pallichnidae; Fig. 1b). However, the attribution of one of the three ichnospecies, *Fictovichnus gobiensis*, remains inconclusive because its simple morphology could also represent the pupation chamber of rhizophagous beetles.

Ants and termites, although phylogenetically unrelated, are eusocial insects that may show nests with similar structures. Most termites construct their nests by adding organic linings made from liquid secretions and/or excretions, often mixed with soil material or coarse particles such as sand, increasing the potential for preservation. In contrast, most ant species excavate their nests, with only a few species applying linings to the walls (Table I, Ants and Termites references). There are no epigeous mounds of ant or termite nests preserved in the geological record. The preservable hypogeous parts of these fossil nests show different architectures and complexity and are grouped in Krausichnidae. It includes the ichnogenera *Archeoentomichnus*, *Attaichnus*, *Barberichnus*, *Coatonichnus*, *Daimoniobarax*, *Fleaglellius*, *Masrichnus*, *Microfavichnus*, *Parowanichnus*, *Socialites*, *Syntermesichnus*, *Tacuruichnus*, *Termitichnus*, *Vondrichnus*,

Laetolichnus, and *Krausichnus* (Fig. 1c). Among these, ichnogenera representing typical or complex nest structures are attributed with greater confidence to either ants or termites.

Table I

Neoichnological contributions on insect species (and other arthropods) by the División Icnología of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”

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Notes: S= soil, H=host (parasites); O= others (wood, leaves). B= nesting behavior; N= nest structure (tunnels, cells, nesting chambers, brood chambers); C= cocoons, pupation chambers. AR= Argentina; CL= Chile; UY= Uruguay

Dung beetle nests exhibit a remarkable architectural diversity. Some subterranean nests consist of a vertical tunnel that ends in a nesting chamber with one or several brood balls. Each brood ball contains a provision (usually dung or carrion) and a single egg, commonly enclosed by a lining of soil material (in some cases mixed with dung fibers) that may vary in thickness. Other nests consist of a vertical tunnel that ends in one or several brood masses, each containing a provision (usually dung) and one or more eggs, occasionally covered by a thin lining of soil material. Both brood balls and brood masses (collectively referred to as brood chambers) may include a pupation chamber, which is constructed by the larva using fecal pellets after consuming the provision. Pupation chambers are also known in dung

beetle species that do not construct brood chambers (Table I, Dung Beetle references). The organic lining in brood chambers and the fecal pellets of pupation chambers favor their preservation potential. The ichnofamily Coprinisphaeridae comprises several fossil morphologies and surface patterns attributed to dung beetles, including isolated brood balls (*Coprinisphaera*), clustered brood balls (*Quirogaichnus*), brood masses (*Racemusichnus*), and pupation chambers (*Eatonichnus*, *Chubutolithes*). Preservation of nesting chambers and tunnels is rare, yet more frequent in younger formations (Fig. 1d).

Moth pupation chambers exhibit a multilayered lining formed by repeated discharges of liquid excretions from the larva and the compaction of the soil by the larva's body (Table I, Moths references). Fossil pupation chambers attributed to moths, which show diverse shapes and internal surface morphologies, are classified under the ichnogenus *Teisseirei* (Coprinisphaeridae).

The feeding chambers of cicada nymphs are associated with plant roots. As the nymph feeds on these roots, they produce liquid excretions that may accumulate at the chamber's base or entirely line its interior (Table I, Cicada references). Fossil cicada feeding chambers, whether partially or fully preserved, often show a groove corresponding to the associated root and are included in *Feoichnus* and *Monesichnus*, respectively (Coprinisphaeridae).

The zygopteran Odonata insert eggs with characteristic shapes into leaves, following a distinctive oviposition pattern (Table I, Damselflies reference). The egg shape and oviposition pattern of damselflies are preserved as traces in fossilized compression/impression leaves and are classified within the ichnogenus *Paleoovoidus* (*Paleoovoididae*).

TRACES OF OTHER ARTHROPODS

In addition to insects, other soil-inhabiting arthropods were examined in order to identify their traces and differentiate them from those left by insects. These include one spider species from the family Nemesiidae and six decapod species belonging to Trichodactylidae and Parastacidae. Some spider nests from Patagonia showing inclined tunnels lined with soil material and silk resemble fossil tunnels with thick lining found in the same region (Table I, Spiders reference). Vertical burrows of freshwater crabs characterized by an oval cross-section and ornamented surface are similar to fossil burrows assigned to the ichnogenus *Capayanichnus* (Table I, Freshwater crabs reference). Lastly, Y-shaped branched structures observed in crayfish burrows are morphologically similar to fossil burrows of the ichnogenus *Loloichnus* (Table I, Crayfishes reference).

NOVEL INSECT BEHAVIORS REVEALED BY NEOICHOLOGY

In the path of interpreting trace fossils, some behavioral studies on extant insect species have yielded remarkable results. For the first time, the pupation chambers of dung beetles were described. Previously, it was assumed that brood balls provided sufficient protection to the larvae, so the construction of pupation chambers was not necessary. However, these structures, showing a helicoidal wall, were found inside the brood balls of *Sulcophanaeus menelas*, *Sulcophanaeus imperator*, *Sulcophanaeus batesi*, *Ontherus sulcator*, *Malagoniella argentina*, and isolated in *Anomiopsoides biloba*, from Buenos Aires and La Rioja, Argentina (Fig. 2a). The helicoidal wall of these pupation chambers was included in a phylogenetic analysis and may represent a synapomorphy for the clade comprising Phanaeini + Eucraniini + Neotropical Canthonini + certain species of Dichotomiini (Sánchez et al., 2010c). Another surprising case was the discovery of bees nesting within horse dung pads. It was reported for *Trichothurgus bolitophilus* from Chubut, Argentina. This discovery was notable not only for the unusual nesting substrate but also for the description of a new *Trichothurgus* species (Sarzetti et al., 2012; Fig. 2b). The presence of an organic lining in ant nests was also documented for the first time. Nests excavated in the sand by *Solenopsis electra* and *Solenopsis* nr. *macdonaghi* from La Pampa and Chubut, Argentina, show organic linings of fecal origin (Genise et al., 2013b; Fig. 2c). These findings are particularly relevant to paleontology because organic linings had previously been associated with termite nests and used as a diagnostic character for attributing fossil nests to termites. Dung beetles (Scarabaeinae) take their name from using dung as provisions. They also use vertebrate and invertebrate remains. We reported the first case of brood chambers in Scarabaeinae provisioned with leaf litter. They were discovered in *Dichotomius carbonarius* from Misiones, Argentina. These brood

chambers, which could not be classified as classical brood balls or brood masses, consisted solely of leaf litter, including larval provisions, and showed a thin outer layer of leaves (Dinghi et al., 2013; Fig. 2d). Finally, to interpret fossil cocoons, a complete comparative morphology of Hymenoptera cocoons was accomplished for the first time. Morphological characters were mapped onto a hymenopteran phylogeny, revealing that the distribution of most of them shows no evident phylogenetic signal (Sarzetti et al., 2019).

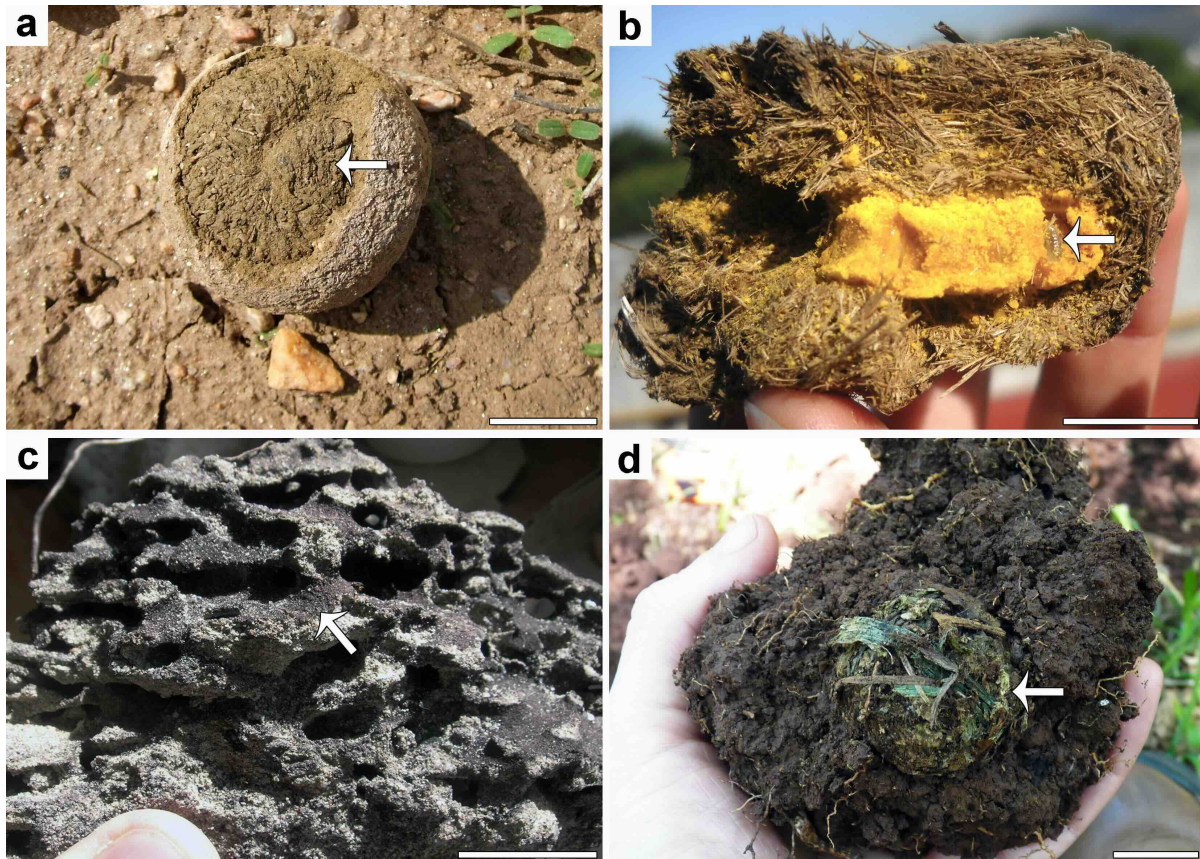


Figure 2

Some remarkable neoichnological discoveries

a. Brood ball of *Malagoniella argentina* containing an helicoidal-walled pupation chamber (arrow). b. Cell of *Trichothurgus bolitophilus* in horse dung. Note the larva (arrow) within the yellow-packed pollen provisions. c. Nest of *Solenopsis* nr. *macdonaghi* with a black organic lining (arrow). d. Brood chamber of *Dichotomius carbonarius* composed entirely of leaf litter (arrow). Scale bars= 2 cm.

INSECT EVOLUTION IN THE LIGHT OF ICHNOENTOMOLOGY

Recent discoveries by members of the División Icnología include several insect trace fossils that have significantly contributed to the knowledge of insect evolution. Among these, *Cellicalichnus krausei* is a fossil bee nest attributed to the tribe Halictini, discovered in the Castillo Formation in Chubut and dated to 100 million years ago. This trace fossil represents the oldest known evidence of crown-group

bees. It has been incorporated into a time-calibrated phylogeny, supporting the hypothesis that bee diversification was earlier than previously thought and occurred in parallel with angiosperm radiation (Genise et al., 2020a; Fig. 1a). *Maichnus wetkaroae* is the first record of odonatan trace fossils in paleosols. Discovered in Lower Cretaceous paleosols from the Piedra Clavada Formation in Santa Cruz, Argentina, it provides the earliest evidence of burrowing behavior in petalurids (Genise et al., 2020b). *Racemusichnus jacobacciensis*, a large-sized fossil structure interpreted as racemose brood masses attributed to Geotrupidae, was found in the Middle Miocene La Pava Formation in Rio Negro, Argentina. These are the largest known trace fossils attributed to solitary insects, and their size may be linked to the elevated global temperatures of the Middle Miocene Climatic Optimum (Sánchez et al., 2021).

Other studies enabled more accurate behavioral or taxonomic attributions. The analysis of *Coprinisphaera* from the Middle Miocene La Pava Formation in Chubut revealed the earliest burst of necrophagous dung beetles in Patagonia (Cantil et al., 2020). This finding was made possible through previous neoichnological studies (Cantil et al., 2014a, b, 2015), which allowed a precise attribution of *Coprinisphaera*, not only regarding its producer group but also to its feeding behavior. Besides, neoichnological studies on the nests of *Onkotermes brevicorniger* in the coastal dunes of Buenos Aires confirmed the attribution of *Laetolichnus kwekai* to termite nests of the ichnofamily Krausichnidae (Genise & Harrison, 2018; Cantil et al., 2021).

Some contributions have provided striking paleoenvironmental reconstructions. Laetoli, in Tanzania, is one of the most famous anthropological localities worldwide; it yielded remains of the early hominin *Australopithecus afarensis* and its putative footprints, as well as *Paranthropus aethiopicus*. The paleoenvironments in which these primitive hominins lived are controversial, and recently, insect trace fossils have contributed to their interpretation. More than 4000 insect trace fossils have been collected and described, including traces of dung beetles, other coleopterans, solitary bees, and termites. Larval mortality, revealed by the absence of emergence from their cells and pupation chambers, indicated instantaneous burial of soils under thick volcanic ash deposits. The scarcity of trace fossils of dung beetles suggested that the ashy soils where these hominins left their footprints had poor grass cover (Genise & Harrison, 2018). The time of appearance of the Patagonian grasslands has been a controversial issue. Ichnological, sedimentological, and paleontological data provide robust evidence that grasslands have existed since the middle Eocene in Patagonia (Bellosi et al., 2021). Finally, a change in the ichnoassemblages from La Pava and Collón Curá formations, from the *Coprinisphaera* to the *Celliforma* ichnofacies, provides evidence of a shift toward more arid conditions in Patagonia during an interval of

global cooling and drying known as the Middle Miocene Climate Transition (Genise et al., 2022).

Further studies are likely to provide new insights into the evolution of the insects, their behaviors, and their interaction with the environment through time. In the Centennial of the SEA, the main aim of this contribution is to encourage entomologists to engage with Ichnoentomology.

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Notes

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