Insect Trace Fossil Associations in Paleosols: The *Coprinisphaera* Ichnofacies

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Analysis of fifty-eight paleosol trace fossil assemblages, ranging from the Triassic to the Recent, allows refinement of continental ichnofacies models and the proposal of a Coprinisphaera *ichnofacies. The* Coprinisphaera *ichnofacies consists of trace fossils of bees, wasps, ants, beetles, termites, and other unassigned insects. Meniscate burrows, mammal caves, and rhizoliths also may be present. This ichnofacies is named after the dung beetle nest* Coprinisphaera, *the most common component of this archetypal assemblage. In mature paleosols, the* Coprinisphaera *ichnofacies has moderate to relatively high trace fossil diversity and high abundance. Ethologically, this assemblage is dominated by nesting traces (calichnia) and exhibits a relatively complex tiering pattern, reflecting variable depths of emplacement of hymenopterous, termite, and dung beetle nests. Common components include the bee cells* Celliforma, Uruguay, Ellipsoideichnus, Palmiraichnus, *and* Rosellichnus; *the wasp nest* Chubutolithes; *the ant traces* Attaichnus *and* Parowanichnus, *and other beetle traces, such as* Monesichnus, Fontanai, *and* Teisseirei. *Termite nests may occur, but are less common components of the* Coprinisphaera *ichnofacies.*

The Coprinisphaera *ichnofacies fulfills all the requirements to qualify as a Seilacherian or archetypal ichnofacies, namely recurrence in time and space, and distinct paleoenvironmental implications. Proposal of the* Coprinisphaera *ichnofacies is based on the analysis of twenty-eight cases, ranging from the? Late Cretaceous to the Recent. The* Coprinisphaera *ichnofacies characterizes paleosols developed in paleoecosystems of herbaceous communities. These herbaceous communities range from dry-and-cold to humid-and-warm climates. More detailed paleoclimatological inferences can be obtained by evaluating the relative abundance of the various traces within the assemblage. A dominance of hymenopterous traces would indicate drier conditions, whereas the presence of termite nests would indicate more humid. The* Coprinisphaera *ichnofacies occurs in paleosols developed in various depositional systems subject to subaerial exposure, such as alluvial plains, desiccated floodplains, crevasse splays, levees, abandoned point bars, and vegetated eolian environments. This and other potential terrestrial ichnofacies are controlled by ecological parameters (e.g., vegetation, climate, and soil) rather than by depositional processes. The association of fossil insect nests indicates the extent of soil development and, consequently, such ichnofossils are one of the best indicators of paleosols.*

The previously proposed Termitichnus *ichnofacies was defined to include all paleosol trace fossil assemblages. However, the available information indicates that terrestrial environments are far more complex. Therefore, it is suggested that the* Termitichnus *ichnofacies as presently defined be abandoned because it does not reflect the diversity of paleosol settings and fails to provide significant paleoecologic information. Formal definition of a* Termitichnus *ichnofacies in a more restricted sense, to include assemblages dominated by termite nests in paleosols of closed forest ecosystems, should await documentation of additional studies to prove recurrence. Other fossil insect-nest associations in paleosols (e.g., halictid nests in calcareous soils) do not have enough recurrence in time and space to be considered Seilacherian ichnofacies, but do represent potential ichnofacies. The model proposed in this paper includes the paleoecologically defined* Coprinisphaera *ichnofacies plus a definite number of associations, each one possessing its own paleoenvironmental implications, which do not show the necessary recurrence to be considered ichnofacies, at present. Climate and vegetation are considered key factors in the shaping of terrestrial ecosystems and should be taken into account for the definition of additional terrestrial ichnofacies.*

INTRODUCTION

Although there are as many continental depositional environments as marine ones, the number of continental ichnofacies is still remarkably lower than the number of marine ichnofacies. While eight marine archetypal assemblages have been formally defined—the *Psilonichnus, Skolithos, Cruziana, Zoophycos, Nereites, Teredolites, Glossi-*

fungites and *Trypanites* ichnofacies (the latter being further subdivided into the *Gnathichnus* and *Entobia* ichnofacies)—only three recurrent continental ichnofacies have been proposed, the *Termitichnus, Scoyenia,* and *Mermia* ichnofacies (Buatois and Mángano, 1995). The fact that our understanding of the ichnology of continental ecosystems still lags behind our knowledge of trace fossils in the marine realm stems, at least in part, from a series of historical preconceptions and misunderstandings. The traditional view is one of a continental record consisting of low-diversity ichnofaunas, simple morphological forms, and scarcity of trace fossils. However, recent research is slowly changing this negative stereotype. Some continental trace fossil assemblages have proved to be quite diverse (e.g., Bown and Kraus, 1983; Buatois and Mángano, 1993; Genise and Bown, 1996), and some of the most complex biogenic sedimentary structures have been recorded in terrestrial environments (e.g., Genise and Bown, 1994a; Genise and Hazeldine, 1998a). Additionally, under favorable taphonomic conditions, continental trace fossils may be fairly abundant (e.g., Zhang et al., 1998). The conventional view also considers that few studies have documented continental ichnofaunas. However, a recent study on continental ichnofaunas performed by Buatois et al. (1998) was based on a dataset of 166 cases, suggesting that the volume of information, though dispersed in the literature, is significant. Much of the data presented herein originates from southern South American localities. This fact reflects, to some extent, the long history of research on insect ichnology in this region (Rivas, 1900; Frenguelli, 1930; Roselli, 1938).

The tripartite ichnofacies model of continental environments proposes the *Termitichnus* ichnofacies in terrestrial environments, the *Scoyenia* ichnofacies in transitional terrestrial to subaqueous settings, and the *Mermia* ichnofacies in permanently subaqueous, lacustrine environments (Buatois and Mángano, 1995, 1998). However, the available data indicate that the terrestrial settings, where insect trace fossils are dominant, is far more complex. Historically, the conceptual framework of ichnology has been based mostly on marine, and, to a lesser extent, lacustrine trace fossil faunas, where insects are not as abundant and diverse as in terrestrial non-aqueous environments.

The objectives of this paper are to review our current knowledge primarily on sediment-associated insect trace fossil assemblages, to present new data about biogenic structures in paleosols, and to propose a model to incorporate this information into the theoretical background of ichnology. Our ultimate aim is to promote further discussion on terrestrial trace fossils and the controls operating on paleosol ichnofacies. In doing so, (1) the broad definition of the *Termitichnus* ichnofacies is re-evaluated, (2) a new archetypal association, the *Coprinisphaera* ichnofacies, is defined formally, and (3) the possibility of additional terrestrial ichnofacies is discussed. A proposal for the *Coprinisphaera* ichnofacies is based on the analysis of twenty-nine examples, ranging from the? Late Cretaceous to the Recent. This paper attempts to emphasize the role of climate and vegetation as key factors on the shaping of paleosol trace fossil assemblages and terrestrial ecosystems.

BASIC CONCEPTS ON INSECT-NESTING BEHAVIOR

The diversity and abundance of insect fossil nests in paleosols and their importance in sedimentologic studies is a consequence of the complex nesting behavior of these invertebrates. Insects are capable of nesting successfully in the most sterile of substrates, such as dune or volcanic ash deposits. This colonizing capacity, together with the reworking of sediments and the incorporation of organic matter as nesting material, make insects one of the most important agents in soil formation. In contrast to many marine traces that can be linked with particular depositional processes, similar insect nests can be found in a wide range of depositional environments that are subjected to similar conditions of subaerial exposure (Fig. 1A-D). Insects are highly sensitive to local ecological constraints, such as soil conditions, microclimate, and vegetation. The term "microclimate" refers to temperature, radiation, humidity, and wind speed near the ground (Unwin and Corbet, 1991). Immediately above the ground, microclimatic conditions depend on local vegetation. Both, microclimate and vegetation ultimately are controlled by climate. A direct consequence of this fact is that fossil insect nests are poor tools to identify primary depositional processes, but are highly accurate at revealing climatic and ecologic controls at the time of nest formation. Continental ichnofacies, based on recurrent insect nest associations, will be controlled by ecological parameters—abiotic and biotic—rather than by sedimentologic processes involved in the generation of the deposit. The association of fossil insect nests is indicative of soil development, even in its primary stages, and consequently these traces are one of the best indicators of paleosols.

Insect nests are structures excavated and/or constructed by the adults for breeding purposes, ethologically included in calichnia (Genise and Bown, 1994a). Larvae, which in many cases are more or less immobile, are confined to cells or chambers that are provisioned by the adults with different kinds of consumable organic matter, such as pollen, nectar, dung, prey items, and plant material. Excessive moisture inside cells produces the decay of provisions, which are attacked by fungi and other saprobic organisms, whereas insufficient moisture produces the dehydration of larvae, which are not protected by a water-resistant cuticle like adults. Some social insects, such as ants, can transport eggs and larvae to alternative sites if their nests are damaged or if the internal conditions become unfavorable. On the other hand, other social insects, including some termites, can reconstruct their nests to recreate the internal microenvironment. Most solitary insects, however, do not revisit their constructions once finished, and are unable to transport larvae to alternative, more favorable sites. Consequently, insect nests should be located at ideal sites where larval physiological requirements match the specific microenvironmental conditions inside cells and chambers. This fact can be exploited to extract paleoecological inferences from fossil insect nests, and it also can be used to determine what type of information can be obtained from analyses of potential continental ichnofacies.

The location of nests can be analyzed from different contexts, based on scale. On a species scale, the location depends on the distributional range of the trace maker,
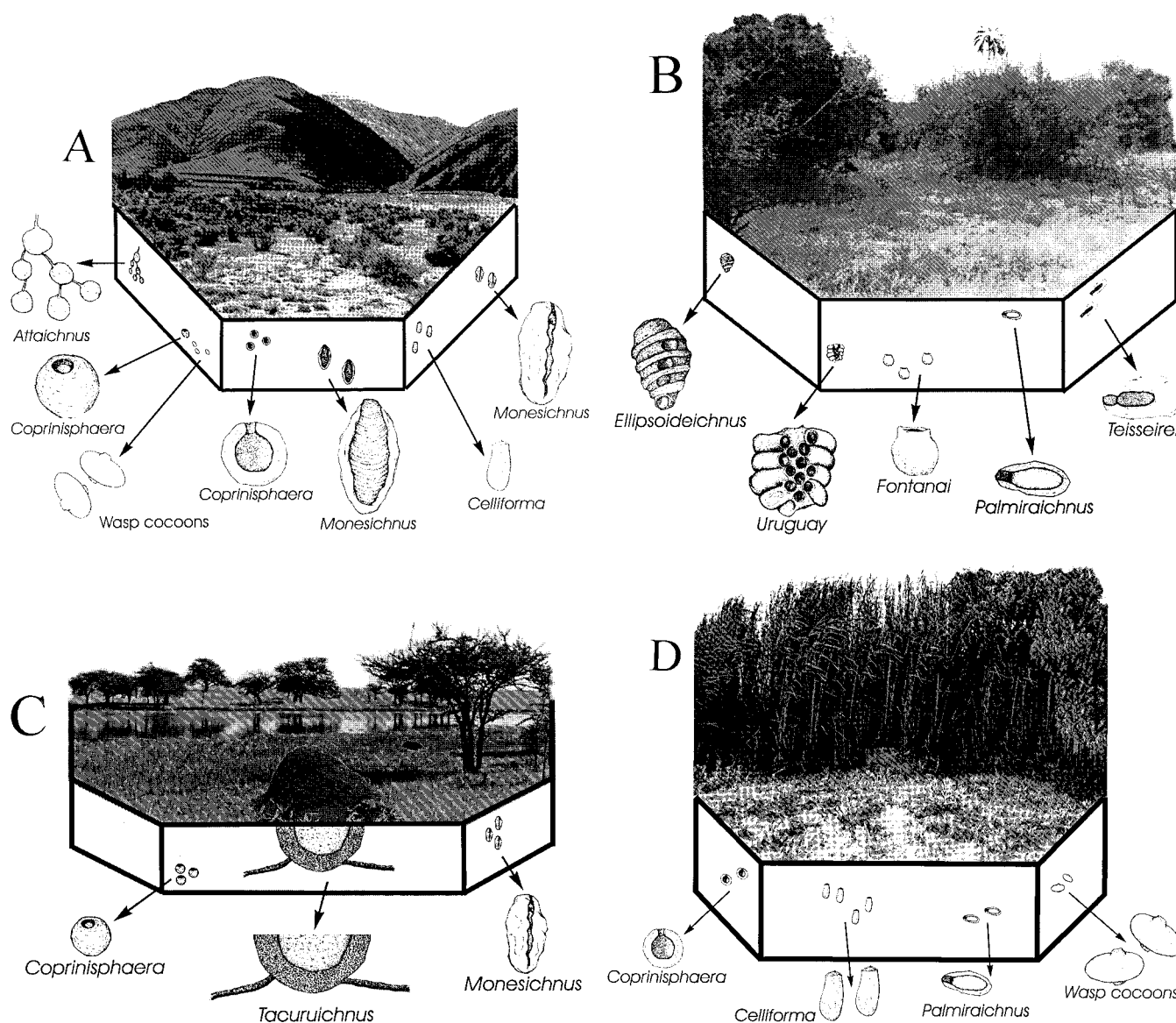
FIGURE 1—Occurrence of the *Coprinisphaera* ichnofacies in paleosols of herbaceous communities developed in different depositional environments. Figure elements show modern environments and associated possible trace assemblages in the fossil record. (A) Proximal alluvial, dominated by dung beetle nests (e.g., *Coprinisphaera* and *Monesichnus*). Ant nests (e.g., *Attaichnus*) and bee traces (e.g., *Celliforma*) may be associated. (B) Vegetated eolian, dominated by hymenopterous nests (e.g., *Celliforma* and *Palmiraichnus*). Dung beetle traces (e.g., *Coprinisphaera*) may be present. (C) Floodplain, dominated by dung beetle (e.g., *Coprinisphaera* and *Monesichnus*) and termite nests (e.g., *Tacuruichnus*). (D) Levee, dominated by bee traces (e.g., *Ellipsoideichnus, Uruguay, Palmiraichnus*) and dung beetle nests (e.g., *Fontanai* and *Teisseirei*).

which in turn is a response to climate and vegetation. This relationship has been exploited successfully to obtain paleoclimatic, paleogeographic, and paleoecologic inferences from fossil termite and ant nests (Laza, 1982, 1995; Bown and Laza, 1990; Genise, 1997). On an individual scale, each adult chooses the nesting site based on different ecological factors, especially soil texture, plant cover, and the local availability of larvae food. The position and depth of the cells and chambers in the soil is determined mostly by moisture requirements of provisions and larvae. This relationship has been used to draw paleopedologic inferences (Hasiotis et al., 1993; González et al., 1998). Additionally, the requirement of oxygen inside cells restricts nests

to well aerated sediments (terrestrial environments), avoiding subaqueous or transitional environments that periodically are submerged. The striking absence of these traces for decades from the ichnologic literature was the direct result of their exclusive presence in the poorly studied terrestrial realm. This preconception also led to their grouping into the single *Termitichnus* ichnofacies, which does not reflect the diversity of terrestrial paleoenvironments.

The study of fossil insect-nest associations provides substantial evidence to extract robust paleoecological inferences that are best attained when tracemakers can be identified. This fact contradicts a methodological rule, ex-

tracted from marine ichnology; that paleoecological and paleoenvironmental interpretations can be based solely on morphology, regardless of the identity of the producer (cf. Bromley, 1996). Constructional features, such as wall, lining, and other structures to isolate provisions and larvae from outside conditions, represent the "fingerprints" used for low-level taxonomic assignments. These sophisticated constructional features later can be recognized in fossil material and can be useful in the assignment of the fabricator to a low-level insect taxon. In many groups, such as termites (Emerson, 1938) and hymenopterans (Genise, 1986), nests can be used as taxonomic characters as useful as body fossil morphological features. For example, most termite genera can be recognized by the morphological features of its species or by the stereotyped architecture of its nests. As Genise (1993, 1995) stated, in the course of following ichnologic principles, if fossil nests are not attributable to extant insect taxa with similar nest construction, then it will be necessary to create a new taxon of extinct tracemakers, unknown from the body-fossil record and behaviorally convergent with extant insect species. Such an assignment would be not only highly improbable, but also would reduce the usefulness of ichnology in paleoenvironmental reconstructions.

The abundance of fossil insect nests in paleosols is not only the result of the highly diversified repertoire of insect-nesting behavior, but also of the high preservational potential of these structures (Genise and Bown, 1994a). Those insect nests more commonly occurring in paleosols, namely bee cells, dung-beetle brood masses, and termite nests, are not merely excavated—rather, they are constructed, at least in part, with secretions, fecal pellets, plant material, and different kinds of organic matter mixed with soil particles. These substances are used to construct walls and linings for isolating larvae and provisions from the outside. The resulting structures are stronger and more resistant than the surrounding soil, and the decay of the organic matter provides a suitable geochemical environment for the concentration of salts and oxyhydrates, which increases their consolidation and preservation in the fossil record (Genise and Bown, 1994a).

CONCEPTUAL BACKGROUND AND METHODS

Seilacherian ichnofacies are defined as trace fossil assemblages that recur through long intervals of geologic time and are more or less characteristic of a given set of environmental conditions (Frey and Pemberton, 1984, 1985). Essential to the ichnofacies concept is their archetypal nature. As noted by Pemberton et al. (1992), the ichnofacies model functions as facies models based upon recurring ichnocoenoses. Facies models are produced through a "distillation" process that concentrates the diagnostic features of a depositional environment and eliminates the local peculiarities or the "noise" of the particular examples (Walker, 1984). Walker (1984) emphasized the role of facies models as a norm for purposes of comparison, framework, and guide for future observations, predictor in new situations, and basis for interpretation.

The validity of the ichnofacies concept has been criticized recently by Goldring (1993, 1995), who considered that present resolution of the ichnofacies model is insufficient for detailed sedimentologic studies. Additionally, he

suggested that the examination of all ecological factors involved is more useful in facies interpretation than archetypal ichnofacies. It has been discussed in the literature, however, that ichnofacies analysis involves the study of all relevant features of trace fossil assemblages, such as preservation, ethology, and trophic type, rather than a mere checklist approach (Howard and Frey, 1975; Frey and Pemberton, 1984; Frey et al., 1990; Pemberton et al., 1992). Thus, ichnofacies analysis includes not only the recognition of discrete ichnofacies, but also their subdivision at a local scale into different assemblages with paleoecological and paleoenvironmental implications (e.g., Frey and Howard, 1985). Also, as stressed by Bromley and Asgaard (1991), an increasing recognition of the taphonomic factors involved in the shaping of particular ichnofacies is strongly desirable.

The archetypal nature of the ichnofacies implies that peculiar local assemblages that do not exhibit recurrence in the stratigraphic record under a similar set of environmental conditions do not qualify as ichnofacies. Any potential ichnofacies should be based on a series of examples carefully selected from the ichnologic record, rather than a mere list of theoretical assemblages or documentation of local examples. As in the case of facies models, the key to an ichnofacies resides in ascertaining the common background shared by different trace fossil assemblages formed under similar environmental controls in rocks of variable age. The methodology advocated in this paper was used by Frey et al. (1984) in their redefinition of the *Scoyenia* ichnofacies, and by Buatois and Mángano (1995) in their proposal of the *Mermia* ichnofacies.

Recently, the relatively new field of continental ichnology gradually has been gaining acceptance and becoming incorporated to the theoretical framework of ichnology (e.g., Hasiotis and Bown, 1992; Genise and Bown, 1994b; Genise, 1995; Buatois and Mángano, 1995; Bromley, 1996; Buatois et al., 1998). Continental ichnologists are compelled to choose between waiting until major controversies are solved in the marine realm or adding their own problems and viewpoints to a fluid scenario. This paper is written under the belief that the second position will prove to be the most fruitful and enriching for ichnology.

Seilacher (1967) recognized five marine ichnofacies and a sixth one, the *Scoyenia* ichnofacies, which subsequently was misused to include all continental trace fossil assemblages (see discussion in Frey et al., 1984). Although ichnologists recognize that continental environments are as diverse as marine settings (Buatois and Mángano, 1995, and references therein), or in an extreme statement, that the number of ichnofacies can be as numerous as the lithofacies within a specific continental environment (Hasiotis and Bown, 1992), relatively little has been done to alter Seilacher's original marine-focused viewpoint. Until recently, few studies addressed the problem of recognizing new continental ichnofacies (e.g., Smith et al., 1993; Buatois and Mángano, 1995; Bromley, 1996).

Smith et al. (1993) defined the *Termitichnus* ichnofacies as a subset of the Seilacherian *Scoyenia* ichnofacies, and included traces from floodplain sediments occurring in paleosols. Buatois and Mángano (1995) noted that considering the *Termitichnus* ichnofacies as a subdivision of the *Scoyenia* ichnofacies implies the misleading notion of equating the latter with continental assemblages. To

TABLE 1—Summary of basic features and environmental significance of the *Coprinisphaera* ichnofacies.

Ichnologic Record	Environmental Implications
Breeding structures (Calichnia) of bees, wasps, ants, beetles, and other undetermined insects dominant; meniscate tubes, mammal caves, and rhizoliths present also; termite nests less common. Moderate to relatively high ichnodiversity and high abundance, particularly in mature paleosols. Relatively complex tiering pattern, reflecting variable depths of emplacement of hymenopterous, termite and dung beetle nests. Typical components include *Coprinisphaera, Celliforma, Uruguay, Ellipsoideichnus, Palmiraichnus, Rosellichnus, Chubutolithes, Attaichnus, Parowanichnus, Monesichnus, Pallichnus, Eatonichnus, Fontanai, Teisseirei, Syntermesichnus,* and *Tacuruichnus.*	Ecosystems of terrestrial herbaceous communities. Within the range of climatic range of the herbaceous communities, abundance of hymenopterous nests suggests more xeric conditions, whereas association with termite nests may indicate a more humid paleoenvironment. Associated sedimentary structures indicative of edaphic processes. Paleosols developed in a wide range of depositional environments, such as alluvial plains, desiccated floodplains, and vegetated eolian deposits.

avoid this problem, Buatois and Mángano (1995) gave the rank of an archetypal ichnofacies to the *Termitichnus* assemblage and expanded its application to all terrestrial environments, such as traces in paleosols. However, this gross-scale definition misses the most interesting ecologic point. By contrast, an extremely restricted definition, like that proposed by Hasiotis and Bown (1992), would result in the proliferation of local, non-recurrent "ichnofacies," probably indistinguishable from ichnocenoses and defined on a scale different from that of marine ichnofacies. The *Coprinisphaera* ichnofacies defined herein fulfills all the requirements to qualify as an archetypal ichnofacies, namely recurrence in time and space and the presence of distinct paleoenvironmental implications. Buatois and Mángano (1995) listed only five paleosol insect trace fossil associations. New information presented herein, including 58 associations, indicates that a model of higher resolution is possible. This model embraces several potential ichnofacies and the *Coprinisphaera* ichnofacies as a fully established Seilacherian ichnofacies.

A fundamental point is to define which paleoenvironmental implications can be obtained from a particular continental ichnofacies; in other words, what ecological or environmental information, such as vegetative cover and depositional processes, can be extracted from an analysis of a continental ichnofacies. Buatois and Mángano (1995) suggested that potentially unrecognized continental ichnofacies would include, for instance, active desert dunes and non-vegetated dry interdunes, linking the ichnofacies concept to depositional conditions and sedimentary environments. Smith et al. (1993) also speculated about recognizing distinct ichnofacies from different terrestrial sedimentary environments (lacustrine, floodplain, terrestrial woodground), but also suggested that floodplains from different climatic regimes could be recognized based on their trace fossil content. Bromley (1996) attempted to find continental equivalents of the well known marine ichnofacies, suggesting the *Rusophycus, Fuersichnus,* and *Mermia* ichnofacies as the continental analogues of the *Cruziana, Zoophycos,* and *Nereites* ichnofacies. The data presented herein reflect that vegetation is the primary factor responsible for deciphering terrestrial ichnofacies. Vegetation depends on the interaction of abiotic factors of ecosystems, especially climate, topography, and soil, and is one of the main controls on the distribution of animals and their traces.

THE *COPRINISPHAERA* ICHNOFACIES

Basic Features

The *Coprinisphaera* ichnofacies consists of trace fossils of bees, wasps, ants, beetles, termites and other undetermined insects (Table 1). Bee traces include *Celliforma, Uruguay, Ellipsoideichnus, Palmiraichnus,* and *Rosellichnus.* Other hymenopterous traces belong to wasps (*Chubutolithes,* wasp cocoons) and ants (e.g., *Attaichnus, Parowanichnus*) and reflect environmental preferences similar to bees. Beetle traces such as *Coprinisphaera, Pallichnus, Eatonichnus, Monesichnus, Fontanai,* and *Teisseirei* are rather common, whereas termite nests, such as *Syntermesichnus* or *Tacuruichnus,* are relatively rare. Additionally, formal documentation of a large number of still unnamed insect traces is still in progress. The *Coprinisphaera* ichnofacies typically displays moderate to relatively high ichnodiversity and high abundance, particularly in mature paleosols. Ethologically, it is dominated by nesting traces (calichnia). Hymenopterous, termite, and dung-beetle nests may be emplaced at different depths, according to the tracemaker involved, yielding important data to recognize stacked paleosols and tiering structure, such as that described by Gonzalez et al. (1998) for the Asencio Formation of Uruguay.

Table 2 summarizes information from fifty eight examples of insect trace fossil assemblages in paleosols. This table shows that the ichnogenus *Coprinisphaera,* associated with other distinct insect trace fossils, is present in 28 of the 58 recorded associations (48%) and in 25 of the 31 South American localities (81%). The ichnogenus *Coprinisphaera* displays a geographic distribution from Antarctica to Ecuador and is also present in a single African locality in Kenya, and probably in a single Asian locality in Pakistan. However, the geographic range of the *Coprinisphaera* ichnofacies is more extended with one example in North America. *Coprinisphaera* is the only recorded insect trace in 11 localities. However, these records most likely reflect occasional collections rather than a systematic ichnological search. *Coprinisphaera* is associated with bee and ant nests in 11 cases; with meniscate burrows in 4 cases and with *Teisseirei* and a termite nest in the remaining two cases.

The presence of the *Coprinisphaera* ichnofacies is well documented from the Paleocene to the Recent, whereas its occurrence during the Late Cretaceous is uncertain. Some

TABLE 2—Paleosol insect trace fossil localities and stratigraphic units. Asterisk shows examples of the *Coprinisphaera* ichnofacies.

Locality	Formation	Age	Insect trace fossils	References
USA, Arizona	Chinle	Late Triassic	*Archeoentomichnus,* bee cells, beetle burrows, meniscate burrows.	Hasiotis and Dubiel (1995)
South Africa	Elliot	Early Jurassic	Termite nests, meniscate burrows.	Smith and Kitching (1997)
USA, Colorado	Morrison	Late Jurasic	Meniscate burrows, beetle burrows, bee nests, termite nests, ant nests.	Hasiotis and Demko (1996)
USA, Arizona	Dakota	Cretaceous	*Celliforma*	Elliott and Nations (1998)
Argentina, Chubut	Laguna Palacios	Late Cretaceous	"insect nests"	Sciutto (1995)
Argentina, Chubut	Bajo Barreal	Late Cretaceous	insect traces	Sciutto and Martínez (1996)
Gobi Desert, Mongolia	Djadokhta	Late Cretaceous	*Fictovichnus*	Johnston et al. (1996)
USA, Utah	Unnamed	Late Cretaceous	*Celliforma favosites*	Brown (1941)
Uruguay, Nueva Palmira	Asencio (Yapeyú Member)	Late Cretaceous	meniscate burrows, termite nests	Genise et al. (1998)
Uruguay, Nueva Palmira (*)	Asencio (Del Palacio Member)	Late Cretaceous— Early Tertiary	*Coprinisphaera, Martinezichnus, Madinaichnus, Teisseirei, Uruguay Rebuffoichnus, Fontanai, Celliforma, Microicoichnus, Monesichnus, Palmiraichnus, Ellipsoideichnus.*	Roselli (1987), Genise and Laza (1998)
Uruguay	Mercedes	Paleocene-Eocene	*Celliforma,* bee nests, wasp cocoons	Veroslavsky and Martínez (1996), Veroslavsky et al. (1997), Genise and Verde (unpubl.)
USA, Utah (*)	Claron	Paleocene Eocene	*Parowanichnus, Celliforma, Eatonichnus,* wasp cocoons.	Bown et al. (1997)
Argentina, Chubut (*)	Río Chico	Paleocene	*Coprinisphaera,* meniscate burrows.	Laza (unpubl.)
USA, Wyoming	Willwood	Early Eocene	*Edaphichnium, Scaphichnium, Macanopsis, Ichnogyrus,* meniscate burrows.	Bown and Kraus (1983), Hasiotis et al. (1993)
Argentina, Chubut and Santa Cruz (*)	Casamayor	Early Eocene	*Coprinisphaera,* meniscate burrows.	Frenguelli (1938), Laza (1986a)
Argentina, Chubut (*)	Musters	Late Eocene	*Coprinisphaera,* meniscate burrows	Laza (1986a)
USA, Wyoming	Bridger	Late Eocene	*Celliforma*	Brown (1934)
Antarctica, Seymour Island (*)	La Meseta	Late Eocene	*Coprinisphaera*	Laza and Reguero (1990)
France	Unnamed	Late Eocene	*Celliforma arvernensis*	Ducreux et al. (1988)
Argentina, Chubut	Sarmiento	Eocene Oligocene	*Chubutolithes gaimanensis*	Bown and Ratcliffe (1988)
Egypt, El Fayum	Jebel Qatrani	Late Eocene—Oligocene	*Termitichnus, Vondrichnus, Fleaglellius, Krausichnus, Masrichnus.*	Bown (1982), Genise and Bown (1994b)
Germany	Unnamed	Oligocene	*Celliforma.*	Schütze (1907)
Argentina, Chubut (*)	Deseado	Oligocene	*Coprinisphaera, Tesseirei.*	Frenguelli (1938), Laza (1986a)
USA, South Dakota	Brule	Oligocene	*Pallichnus, Celliforma.*	Retallack (1984)
Argentina, Mendoza (*)	Rodados lustrosos	Oligocene	*Coprinisphaera.*	Laza (unpubl.)
Argentina (*)	Colhue-Huapi	Late Oligocene.	*Coprinisphaera, Tesseirei?, Celliforma.*	Laza (1986a)
Argentina, Santa Cruz (*)	Pinturas	Early Miocene	*Coprinisphaera, Palmiraichnus, Syntermesichnus.*	Bown and Laza (1990), Genise and Bown (1994a)
Argentina, Santa Cruz (*)	Santa Cruz	Early Miocene	*Coprinisphaera, Celliforma* Ant nests	Genise and Bown (1994a), Tauber (1996)

TABLE 2—Continued.

Locality	Formation	Age	Insect trace fossils	References
USA, Florida	Tampa	Early Miocene	*Celliforma*	Brown (1935)
Ethiopia	Bakate	Early Miocene	Termite nests	Bown and Genise (1993)
Germany	Unnamed	Early Miocene	*Celliforma*	Sauer and Schremmer (1969)
Kenya	Hiwegi	Miocene	*Celliforma,* wasp cocoons.	Thackray (1994)
Honduras, Tegucigalpa	El Periodista (Member)	Miocene	*Palmiraichnus*	Domínguez-Alonso and Coca-Abia (1998)
United Arab Emirates, Abu Dhabi	Baynunah	Late Miocene	*Rosellichnus,* termite nests.	Bown and Genise (1993)
Pakistan (*)	Dhok Pathan	Late Miocene	*Coprinisphaera*-like traces	Retallack (1991)
Argentina, Neuquen, Río Negro, Chubut and Santa Cruz (*)	Collón—Curá	Late Miocene	*Coprinisphaera, Celliforma, Rosellichnus.*	Frenguelli (1939), Genise and Bown (1996), Laza (1986b)
Argentina, San Luis (*)	Paso de las Carretas	Late Miocene	*Coprinisphaera, Celliforma*	Pascual and Bondesio (1981)
Argentina, San Juan (*)	Las Flores	Late Miocene	*Coprinisphaera*	Contreras (1996)
Argentina, Catamarca (*)	Andalhualá	Late Miocene	*Coprinisphaera*	Laza (unpubl.)
Argentina, La Pampa and Buenos Aires (*)	Cerro Azul	Late Miocene	*Attaichnus, Coprinisphaera,* ant nests.	Laza (1982)
United Arab Emirates, Abu Dhabi	Unnamed	Early Pliocene	*Rosellichnus*; ant nests.	Genise and Bown (1996)
Argentina, Buenos Aires (*)	Monte Hermoso	Late Miocene—Early Pliocene	*Coprinisphaera.*	Laza (1986b)
Argentina, Salta and Jujuy (*)	Piquete	Early Pliocene	*Coprinisphaera.*	Alonso et al. (1982)
Kenya (*)	Laetoli	Late Pliocene	*Coprinisphaera, Celliforma,* wasp cocoons, termite nests.	Sands (1987), Ritchie (1987)
Argentina, Buenos Aires (*)	Chapadmalal	Late Pliocene	*Coprinisphaera,* ant nests, termite nests.	Laza (1995)
Argentina, Buenos Aires	Barranca de los Lobos	Late Pliocene	*Tacuruichnus farinai*	Genise (1997)
Argentina, Buenos Aires (*)	San Andrés	Late Pliocene—Early Pleistocene.	*Coprinisphaera,* termite nests, ant nests.	Laza (1995, in press)
India, Punjab	Boulder	Plio-Pleistocene	*Termitichnus,* meniscate burrows.	Tandon and Naug (1984)
Argentina, Entre Ríos and Santa Fé (*)	Ensenada	Early Pleistocene	*Coprinisphaera*	Frenguelli (1938)
Australia	Bridgewater	Pleistocene	*Palmiraichnus bedfordi*	Zeuner and Manning (1976), Houston (1987)
Argentina, Santa Fé (*)	Tezanos Pinto	Late Pleistocene	*Coprinisphaera,* ant nests	Iriondo and Krohling (1996)
Argentina, Buenos Aires (*)	Buenos Aires	Late Pleistocene	*Coprinisphaera,* termite nests.	Laza (1995, unpubl.)
Argentina, Buenos Aires and Santa Fé (*)	Luján	Late Pleistocene	*Coprinisphaera,* ant nests.	Laza (1995, unpubl.)
Uruguay (*)	Sopas	Late Pleistocene	*Coprinisphaera,* meniscate burrows.	Ubilla (1996)
Ecuador (*)	Unnamed	Late Pleistocene	*Coprinisphaera*	Sauer (1955)
Namibia	Homeb Silt	Late Pletistocene	*Termitichnus*?, and nests?, meniscate burrows.	Smith et al. (1993)
Namibia	Sossus Sand (Khommabes Carbonates)	Late Pleistocene	*Termitichnus, Taenidium, Digitichnus*	Smith and Mason (1998)
Argentina, Tucumán (*)	Tafí del Valle	Late Pleistocene	*Coprinisphaera*	Fontaine et al. (1995)

TABLE 3—Paleoenvironmental conditions (e.g., plant formation, climate) of localities in table 2 based on lines of evidence other than trace fossil content. Asterisk shows examples of the *Coprinisphaera* ichnofacies.

Stratigraphic unit	Paleoenvironmental inferences	References
Chinle	Tropical to subtropical. Wet-dry moonsonal climate. Forested areas. Crevasse-splays deposits. Floodplain Gleysols and Alfisols.	Dubiel and Hasiotis (1994 a, b), Hasiotis and Dubiel (1995)
Elliot	Calcic vertisols on seasonally wet floodplains. Warm, subtropical, semi-arid climate.	Smith and Kitching (1997)
Dakota	Subtropical coastal plain setting with meandering streams (bee nests) and adjacent floodplains.	Elliot and Nations (1998)
Rio Chico (*)	Mangrove, swamp woodland, tropical rain forest, mossy forest, *Araucaria* woodland and savanna. Warm and humid conditions. Fluvial deposits with soil development.	Petriella and Archangelsky (1975), Pascual (1984)
Willwood	Lowland intermontane basin. Warm-temperate to subtropical climates. Episodic, moonsonal rainfall. Hydromorphic spodosols. Changing floodplain conditions. Backswamp floras alternating with well-drained soils and arboreal vegetation along ponds margins.	Wing (1980), Bown and Kraus (1983), Hasiotis et al. (1993)
Casamayor (*)	Warm humid climate, forests and savanna. Alluvial plains with soil development.	Andreis et al. (1975), Pascual (1984)
Musters (*)	Seasonal temperate climate. Savannas and open plains. Alluvial plain deposits with soil development.	Andreis (1972), Pascual (1984)
La Meseta (*)	Mixed subtropical and cold temperate plants. Warm and arid conditions. Deltaic deposits.	Romero (1979), Laza and Reguero (1990)
Sarmiento (*)	Herbaceous steppes. Warm temperate climate. Alluvial plain deposits with soil development.	Pascual and Odreman Rivas (1971), Romero (1979)
Jebel Qatrani	Wet tropical forest. Coastal lowland. Moonsonal rainfall. Damp soils. Alluvial bar deposits.	Bown and Kraus (1988), Genise and Bown (1994b)
Deseado (*)	Grasslands. Warm temperate climate. Alluvial plain deposits with soil development.	Gorroño et al. (1979)
Brule	Savanna and open woodland. Broad galleries along streams. Warm temperate. Subhumid. Seasonal climate, dry and cool periods. Calcareous soil. Fluvial deposits.	Retallack (1984)
Rodados Lustrosos (*)	Grasslands. Warm temperate climate. Alluvial plain deposits.	Gorroño et al. (1979)
Colhue-Huapi (*)	Galleries along streams and grasslands. Tropical to subtropical climate. Alluvial plain deposits with soil development.	Pascual and Odreman Rivas (1971)
Pinturas (*)	Successive intervals of ash falls, soil development and erosion. From subhumid, scattered tropical forest to savannas. Pyroclastic eolian deposit.	Bown and Larriestra (1990), Bown and Laza (1990), Genise and Bown (1994a)
Santa Cruz (*)	Warm temperate to subtropical coastal alluvial plain with scattered areas of forest.	Genise and Bown (1994a)
Abu Dhabi (Miocene)	Mesic, low relief savannah. Fluvial deposits.	Genise and Bown (1996)
Collón-Curá (*)	Warm temperate climate. Broad floodplains in a savanna-like environment.	Frenguelli (1939), Genise and Bown (1996)
Paso de las Carretas (*)	Fluvial deposits. Calcareous paleosols. Arid to semiarid conditions.	Di Paola (1994), Di Paola and González (1992)

TABLE 3—Continued.

Stratigraphic unit	Paleoenvironmental inferences	References
Cerro Azul (*)	Savanna and grasslands. Seasonal climate. Subtropical conditions. Fluvial and eolian deposits.	Scillato Yané (1975), Tonni (1977), Laza (1982)
Las Flores (*)	Warm and humid climate. Forests and open areas. Alluvial plain and lacustrine deposits.	Contreras (1996)
Hiwegi	Calcareous paleosols. Fluvially reworked deposits of carbonatitic volcanic ash. Area of shallow lakes. Savanna conditions. Dry forests in lowlands.	Whitworth (1953), Thackray (1994), Retallack and Dugas (1995)
Andalhualá (*)	Warm subtropical climate. Piedmont deposits.	Marshall and Patterson (1981)
Piquete (*)	Warm climate. Intermontane deposits with paleosols.	Alonso et al. (1982)
Chapadmalal (*)	Warm temperate savannas, xeric environments. Alluvial plain and loess-like deposits with secondary water reworking.	Zárate and Fasano (1989)
Barranca de Los Lobos	Warm and wet climate. Savanna. Loess deposits.	Zárate and Fasano (1989)
Laetoli (*)	Semi-arid savanna. Volcanic airfall tuffs.	Ritchie (1987), Sands (1987)
San Andrés (*)	Alluvial plain and eolic deposits with intense pedogenesis. Arid to semiarid open areas. Steppe or prairie environments.	Zárate and Fasano (1989)
Boulder Conglomerate	Deltaic fluviatile deposits. Green paleosols.	Tandon and Naug (1984)
Ensenada (*)	Semiarid to arid climate. Paleosols developed during wetter conditions, with grass cover.	Tonni et al. (unpublished)
Bridgewater	Colluvial soils with calcretes	Houston (1987)
Abu Dhabi (Pleistocene)	Interdune paleosabkha. Sandy soil. Open environment. Low rainfall (200 mm).	Genise and Bown (1996)
Buenos Aires (*)	Semiarid to arid climate. Paleosols developed during wetter conditions, with grass cover.	Tonni et al. (in press)
Tezanos Pinto (*)	Eolian deposits. Semiarid savanna or steppes.	Iriondo and Krohling (1996)
Luján (*)	From dry, cold climate to temperate humid conditions. Floodplain deposits. Steppes and prairies.	Tonni and Laza (1980)
Cangahua (*)	Semiarid savanna or steppes. Grasses.	Sauer (1955)
Homeb Silt	Flood plains. Flash-flood events and deposits. Immature calcic paleosols, semi-arid conditions.	Ollir (1977), Ward (1987), Smith et al. (1993)
Sopas (*)	Flood plains. Ripparian forests. Open areas with patchy forests. Warm and humid conditions.	Ubilla (1996)
Tafi del Valle (*)	Cold temperate climate. Intermontane plains. Fluvial deposits.	Powell and Mulle (1996)

Late Cretaceous formations contain fossil bee cells, coleopteran pupal chambers, wasp nests, and undetermined insect nests (e.g., Brown, 1941; Sciutto, 1995; Johnston et al., 1996; Elliot and Nations, 1998), but assignment to the *Coprinisphaera* ichnofacies is doubtful. Additionally, the oldest record of the ichnogenus *Coprinisphaera* comes from the Del Palacio Member of the Asencio Formation (Uruguay), whose age is still a matter of discussion, variously considered as Late Cretaceous by some and Early Tertiary by others (Genise and Bown, 1996). Since the Paleocene, when this association is unequivocally documented for the first time, it exhibits minimal change to the present. In fact, regional geologists traditionally have

used the *Coprinisphaera* assemblage to recognize Tertiary deposits (H. Leanza, pers. com.).

Although the presence of the ichnogenus *Coprinisphaera* is not necessary to recognize the ichnofacies, *Coprinisphaera* is present in most of the recorded examples. The Claron Formation assemblage is the only example of the *Coprinisphaera* ichnofacies lacking the namesake ichnogenus. This assemblage includes *Celliforma* (bee cells), *Parowanichnus* (ant nest), wasp cocoons, and *Eatonichnus* (a possible dung beetle nest) (Bown et al., 1997) and, hence, has the typical components of the *Coprinisphaera* ichnofacies.

As will be discussed subsequently, other associations

that may be included in the *Coprinisphaera* ichnofacies, such as those occurring in the Mercedes, Brule, and Hiwegi formations, are developed in calcareous soils. Other assemblages, found in the Abu Dhabi, Barranca de Los Lobos, and Bridgewater formations, show only one or two components, commonly bee, ant, or termite trace fossils, and it seems premature to include them in the *Coprinisphaera* ichnofacies.

Paleoecological and Environmental Implications

Further exploration is needed of the specific ecologic requirements of the different tracemakers of the *Coprinisphaera* ichnofacies. Table 3 indicates that there is a strong correlation between the *Coprinisphaera* ichnofacies and herbaceous plant communities. In 24 of the 29 examples of the *Coprinisphaera* ichnofacies, data are available on plant assemblages and occasionally climate. For plant assemblages, we follow the physiognomic classification of UNESCO (Mueller-Dombois and Ellenberg, 1980). In 21 of 24 cases, the ichnogenus *Coprinisphaera* is associated with savannas, grasslands, prairies and/or steppes, all of which are included as subclasses in class V (terrestrial herbaceous communities), which comprises savannas, steppes, meadows, pastures, sedge swamps and herbaceous and half-woody saline swamps, and forb vegetation. In the remaining three cases, data are unavailable.

Tracemakers of *Coprinisphaera*—scarabaeinae dung beetles—provision their nests with excrement of vertebrate herbivores. Consequently, it is reasonable to find a close relationship between their trace fossils and herbaceous paleoenvironments. Most Scarabaeinae inhabit tropical to warm temperate regions, where precipitation exceeds 250 mm per year, average annual temperature is above 15°C (Halffter, 1991), and beetle diversity is related to herbivorous mammal species richness (Hanski and Cambefort, 1991). Until a few years ago (Halffter and Matthews, 1966; Halffter and Edmonds, 1982), it generally was accepted that Scarabaeinae were more abundant in open non-forested areas; however, increasing information suggests that the diversity of species in the tropical forests of South America is by far higher than in the herbaceous formations. Halffter (1991) attempted to explain this distribution from a historical and ecological perspective. He found that in regions where the mammalian megafauna was not extinct, such as Africa, herbaceous formations (i.e., savannas) were still the ecosystems that showed the highest Scarabaeinae diversity. Halffter (1991) postulated that the recent extinction of the mammalian megafauna, the predominance of tropical rain forests, and the adoption of necrophagous and saprophagous habits by scarabaenines (consumption of carrion and rotten fruit instead of dung) were the most important factors that determine the abundance of Scarabaeinae in South American tropical forests. This pattern of distribution seems to be a recent phenomena. The open herbaceous Tertiary and Pleistocene ecosystems must have had a relatively rich dung-beetle fauna compared to forested areas. The nests of most solitary bees are made on bare, dry, light soil exposed to sun where nests of ants and solitary wasps also often occur (Batra, 1984). Michener (1979) stated that fossorial bees (as well as fossorial wasps) are more abundant in warm temperate xeric areas of the world than in the humid trop-

ics, where only non-fossorial bees show considerable diversity. The reason for this distribution is that the larval food is commonly exposed to fungal attack or hygroscopic liquification in humid environments (Roubik, 1989).

Other hymenopteran traces common in the *Coprinisphaera* ichnofacies are produced by wasp and ants. Wasp cocoons are present at Laetoli (Kenya), and *Attaichnus* and other fossil ant nests are present in different Argentine localities of Tertiary and Quaternary age (Table 2). Ants are strongly thermophilic; they are best adapted to temperatures above 20°C. This fact is clearly reflected by their biogeography, with increased diversity and abundance in the hottest habitats on earth (Höldobler and Wilson, 1990). The greatest diversity of ant species is found in tropical rain forests (Kusnezov, 1957). In these habitats, however, waterlogged soils result in mostly arboreous nests, whereas ground nests are more diverse in well-developed soils of arid open areas (Kusnezov, 1963). Other dung-beetle traces (*Fontanai, Monesichnus*) associated with *Coprinisphaera* share similar paleoenvironmental ranges. *Teisseirei* and meniscate burrows, which have unknown affinities, lack any paleoenvironmental attribution.

In summary, most fossorial dung-beetles, ants, bees, and wasps establish their nests in open areas dominated by herbaceous communities. Hymenopterous insects seek bare, dry soil exposed to sun, and dung-beetles find abundant excrement of herbivores. In contrast, termites, the other important group of soil trace makers, display different environmental tolerances. Fossil termite nests are one of the most common traces in paleosols and only occasionally are associated with *Coprinisphaera.* However, to understand the paleoenvironmental significance of this association, it is necessary to analyze the taxonomic affinities of each particular fossil termite nest. Termites as a whole are strongly dependent on atmospheric and soil moisture, and most of them inhabit only tropical rain forests (Hegh, 1922; Kofoid, 1934; Collins, 1969; Krishna, 1970; Grassé, 1986). This preference is opposite to that of dung beetles and hymenopterans.

Termite nests are associated with *Coprinisphaera* in four Tertiary and Quaternary Argentinian localities, and in Laetoli, Kenya. In the latter case, an unnamed fossil termite nest was described and assigned to the Macrotermitinae, which includes wood-, dung- and grass-feeding species whose distribution ranges from tropical rain forest to semiarid steppes (Sands, 1987). The Laetoli ichnocoenosis, composed of *Coprinisphaera, Celliforma,* wasp cocoons, and macrotermes-like termite nests, reflects a paleoenvironment comparable to that of some modern herbaceous plant communities. The Argentinian fossil termite nests associated with *Coprinisphaera* were attributed to the extant genera *Syntermes* (*Syntermesichnus* from Pinturas Formation; Bown and Laza, 1990), *Procornitermes* (Chapadmalal Formation), and *Termes* (San Andrés Formation and Buenos Aires Formation; Laza, 1995, unpubl.). These neotropical genera include species inhabiting both open herbaceous and closed forest formations (Emerson, 1955) and, hence, they are of little use as paleoenvironmental indicators. The case of the Pinturas Formation is analyzed below. In the Chapadmalal, San Andrés, and Buenos Aires formations, other evidence (i.e., fauna, flora) strongly supports open, herbaceous pa-

leoenvironments, indicating that tracemakers were species adapted to these environments.

The different examples assigned to the *Coprinisphaera* ichnofacies correspond to paleosols developed in open, herbaceous settings. Taken independently, the great majority of the components of the *Coprinisphaera* ichnofacies display ecologic constrains to open herbaceous communities (*Coprinisphaera, Celliforma, Palmiraichnus, Rosellichnus, Uruguay, Ellipsoideichnus, Attaichnus, Monesichnus, Fontanai,* wasp cocoons, and ant nests), with the exception of *Teisseirei,* meniscate burrows, and termite nests, which are poorly understood or are not restricted to the open herbaceous plant association. More specifically, analysis of the different examples indicates that within the climatic range of these herbaceous communities, the abundance of hymenopterous nests suggests more xeric conditions, whereas association with termite nests may indicate a more humid paleoenvironment.

One of the most diverse examples of the *Coprinisphaera* ichnofacies is that of the Asencio Formation (Late Cretaceous-Early Tertiary), which is composed of unique bee and dung-beetle trace fossils such as *Ellipsoideichnus, Uruguay,* and *Monesichnus,* among others. The lower ichnodiversity of Neogene formations most likely reflects the lack of systematic ichnological collections rather than environmental changes in South America during the Tertiary (i.e., Pascual and Ortiz Jaureguizar, 1990). The transition of herbaceous communities from wetter subtropical savannas to cold temperate steppes provides the best environmental conditions for the nesting activities of dung-beetles, bees, and some species of termites, as they have become more widespread in southern South America since the middle Miocene when humid forested environments were shifted to northern latitudes (Pascual and Ortiz Jaureguizar, 1990).

In brief, the *Coprinisphaera* ichnofacies is an archetypal association having enough temporal and spatial recurrence to be used reliably as a paleoecological indicator of terrestrial herbaceous communities occurring in paleosols developed in alluvial plains, desiccated floodplains, crevasse splays, levees, abandoned point bars, and vegetated eolian deposits. These herbaceous communities range from dry-and-cold to humid-and-warm climates, and it is possible to obtain additional paleoclimatological precision by considering the relative abundance of the different traces within each particular assemblage.

POTENTIAL PALEOSOL ICHNOFACIES AND THE STATUS OF THE *TERMITICHNUS* ICHNOFACIES

Tables 2 and 3 are compilations of available information about insect trace fossil associations in paleosols and associated depositional environments. These compilations were made in an attempt to recognize possible Seilacherian ichnofacies in continental non-aquatic environments. The recorded associations show different degrees of recurrence in time and space (Table 2) and they can be related with particular paleoenvironments (Table 3). Some insect trace fossil associations shown in Table 2 probably reflect particular paleoenvironments. The Chinle, Morrison, Willwood, Jebel Qatrani, Boulder Conglomerate, and Homeb Silt associations are not recurrent or sufficiently areally extensive to be considered at this point as potential

ichnofacies. The Chinle and Morrison are the only Triassic and Jurassic insect trace fossil associations known, respectively; the Willwood association, as shown in Table 2, reflects a precise paleoenvironment. Table 2 also contains data for a few formations where only one kind of insect trace (other than *Coprinisphaera*) is recorded (the Dakota, Bridger, Sarmiento, and Bridgewater assemblages) to provide as complete a list as possible. In some cases, the absence of other traces is probably related to the lack of detailed studies.

When more than one trace occurs within the same formation, it is still necessary to know if they are present in the same paleosol horizon and, if they belong to the same ichnocoenosis, to be able to relate them to particular paleoenvironmental conditions. Meniscate burrows and possible termite nests are present in the Lower Jurassic Elliot Formation. However, both traces occur in different paleosols under contrasting paleoenvironmental conditions (Smith and Kitching, 1997). The same is true for the Miocene Pinturas and Santa Cruz formations where the lower paleosols are intensively reworked by termites (*Syntermesichnus fontanae*), whereas the upper ones only contain bee and dung-beetle nests (*Celliforma, Palmiraichnus* and *Coprinisphaera*; Genise and Bown, 1994a). In some localities of the Pinturas Formation, termite and dung-beetle traces coexist in the same paleosol. However, it is not clear if the trace makers really were contemporaneous or if dung beetles followed the termites by favoring subsequent drier conditions. In the Willwood Formation, the same paleosol shows a trace fossil succession, reflecting water-table fluctuations and changes in the climatic conditions (Hasiotis et al., 1993). Unfortunately, detailed stratigraphic information is lacking in many cases and, hence, it is not possible to determine whether the insect traces described occur at different paleosols or represent true ichnocoenoses indicative of particular paleoenvironmental conditions. It is expected that further investigation will allow placement of some of these assemblages within a Seilacherian ichnofacies framework.

An association of hackberry endocarps, land snail shells, fossil halictid nests, and other insect traces was recorded in highly calcareous soils in four different Tertiary localities: Sauce Solo and Queguay, Uruguay (Frenguelli, 1930; Veroslavsky and Martínez, 1996; Veroslavsky et al., 1997); South Dakota, USA (Retallack, 1984), and Rusinga Island, Kenya (Thackray, 1994). Some species of modern hackberries (i.e., *Celtis tala, Celtis rusingensis*) grow in calcareous soils (Lahitte and Hurrell, 1994; Retallack and Dugas, 1995) which, in turn, favor the preservation of their woody endocarps as well as land snail shells (Retallack, 1990). Associated with these body fossils are remains of various kinds of bee nests clearly attributable to sweat bees that are preserved in paleosols (Retallack, 1984; Thackray, 1994; Genise and Verde, unpublished data). Halictine bees, as a group, do not show any particular preference for calcareous soils (Sakagami and Michener, 1962). However, data from paleosols compiled herein show that at least some species nested in these soils.

Halictine traces were named *Celliforma ficoides* by Retallack (1984), *Celliforma habari* by Thackray (1994), and *Celliforma* isp. by Veroslavsky and Martínez (1996) and Veroslavsky et al. (1997). However, these traces were described as rows, clusters, or whorls of cells attached to

main tunnels without entrance tunnels, a description that largely exceeds the diagnosis of *Celliforma* (i.e., isolated bee cells). Their morphologies reflect an important behavioral trait, which is a common feature of certain monophyletic groups of sweat bees, two important conditions for considering these insect traces as new ichnotaxa (Genise and Hazeldine, 1998b). The distribution of cells along tunnels is different in each of the four localities, suggesting that more that one ichnotaxon is involved. These new ichnotaxa are associated with isolated bee cells (true *Celliforma*) and wasp cocoons in Uruguay, with *Pallichnus* in South Dakota, and with wasp cocoons in Kenya. These four associations of trace fossils satisfy, in part, the conditions of a Seilacherian ichnofacies. However, in comparison with the *Coprinisphaera* association previously analyzed, the *ficoides-habari* assemblage is still poorly studied and has lower recurrence. Definition of this association as a Seilacherian ichnofacies should await more data and subsequent evaluation of its environmental implications.

The *Coprinisphaera* ichnofacies is defined in terms of a plant community classification, which includes seven constituent classes, a number comparable to the marine ichnofacies recognized at present. However, it would be hazardous at this point to affirm that potential continental ichnofacies will perfectly map onto the plant spectrum. There are additional clues that other ecological parameters may play key roles in explaining the recurrence of certain associations (e.g., calcareous soils). In the highly fluid context of continental ichnology, the emergence of sufficiently important new data is vital to establish what kinds of ecological parameters will play crucial roles in the characterization of additional terrestrial ichnofacies.

The Willwood and Jebel Qatrani associations probably are indicators of plant community classes or subclasses, but at this point they do not display recurrence to be considered as incipient ichnofacies. The paleoenvironment inferred for the Willwood assemblage changes from an aquatic plant community to a wet terrestrial herbaceous community (subclass sedge swamps), whereas the Jebel Qatrani association occurs in closed forests.

There are three different meanings of the term "*Termitichnus* ichnofacies." First, as a possible subset of the *Scoyenia* ichnofacies to characterize terrestrial assemblages, as originally proposed by Smith et al. (1993). Second, as an ichnofacies for all paleosol assemblages at the same hierarchical level of the *Scoyenia* ichnofacies, as emended by Buatois and Mángano (1995). Both are very general and are not useful to characterize the complexity of paleosol insect ichnofaunas. Accordingly, the abandonment of the *Termitichnus* ichnofacies *sensu* Smith et al. (1993) and Buatois and Mángano (1995) is proposed in this paper. A third, more restrictive, potential use is to consider a *Termitichnus* ichnofacies as one dominated by termite nests and characteristic of a certain type of paleosol assemblage; that developed in closed forests. The Jebel Qatrani association, which includes *Termitichnus* and other ichnotaxa attributable to fossil termite nests, would qualify as an example of this *Termitichnus* ichnofacies *sensu strictum*. Unfortunately, additional examples are not known at present and formal proposal of this ichnofacies should await further studies. The example documented by Smith et al. (1993) from the Pleistocene Homeb Silts in Namibia is problematic. Smith et al. (1993) identified their traces as

Termitichnus before the exhaustive redescription of the Jebel Qatrani ichnotaxa by Genise and Bown (1994b). In all probability, the traces illustrated from the Homeb Silts are similar neither to *Termitichnus* nor to any other insect trace fossil; instead they resemble rhizoconcretions. Furthermore, they are not associated with closed forests. Specimens of *Termitichnus* recently described by Smith and Mason (1998) from the Pleistocene Khommabes Carbonates of Namibia are not associated with closed forests but with oases.

In the model suggested herein, several of the associations discussed are not included in any ichnofacies because they do not satisfy the requirement of spatial and temporal recurrence. In contrast to the previous tripartite model, which considered associations at the scale of broadly defined sedimentary environment, our proposal identifies continental ichnofacies that would yield substantial paleoecological data. Depositional conditions are very important abiotic aspects of ecosystems, but only part of the complex structure in which biotic factors play, at least, an equally important role. The great renaissance in studies on sedimentary facies has resulted in a welcome high-resolution classification of sedimentary environments, contributing substantially to our understanding of paleoecosystems. However, integration of abiotic and biotic factors is essential to provide a more accurate picture of paleoenvironments. The environmental implications of the "*Termitichnus* ichnofacies," as well as the others of the tripartite model (Buatois and Mángano, 1995), were based mostly on sedimentological parameters. The modifications proposed herein are based on the addition of the ecological component, such as vegetation, soil, and climate. This integration results in proposing a paleoecologically circumscribed *Coprinisphaera* ichnofacies, plus several other associations, each one having its own distinct paleoenvironmental implications. However, these associations await for verification that they satisfy the necessary temporal recurrence to be considered ichnofacies.

A similar context can be made with the substrate-controlled continental insect trace fossil associations. Information on insect traces in plant remains (wood, fruits, leaves, seeds, etc.) has increased considerably during the last decades but mostly in a non-ichnological context (Genise, 1995). In comparison with the single group attacking wood exposed to the seawater in the *Teredolites* ichnofacies, there is a large number of potential tracemakers involved in the alteration of plant remains. Moreover, an entire petrified forest cannot be transported like an individual log exposed to seawater (Savrda, 1991). Additionally, quantities of wood, leaves, and fruits are not always transported and they typically are preserved in the same soil where they grow (Retallack, 1990; Burnham, 1993), avoiding one of the principal objections to substrate-controlled ichnofacies (Bromley and Asgaard, 1991).

Smith et al. (1993) and Buatois and Mángano (1995) commented on the existence of terrestrial woodground ichnofacies. The problem is more complex because other plant remains aside from wood involved as substrates (e.g., Scott, 1992; Labandeira et al., 1997; Labandeira, in press). Insect trace fossil associations in wood and fruits were recognized from the Triassic of Arizona (Walker, 1938) and Germany (Linck, 1949), the Jurassic of China (Zhou and Zhang, 1989), Utah (Tidwell and Ash, 1990)

and Patagonia (Genise and Hazeldine, 1995), the Cretaceous of Texas (Rohr et al., 1986), England (Jarzembowski, 1990), and Patagonia (Genise, 1995), and the Miocene of Germany (Schenk, 1937; Schmidt et al., 1958). The fragmentary trace fossil record in woodgrounds is in all probability due to the lack of systematic research (Scott, 1992; Labandeira, 1998) rather than to the rapid degradation of the organic substrate as proposed by Bromley and Asgaard (1991). Additionally, it is possible to consider insect traces in fossil bones (Rogers, 1992; Martin and West, 1994), vertebrate coprolites (Chin and Gill, 1996), and lithified substrates (Mikuláš and Cílek, 1998).

CONCLUSIONS

(1) The *Coprinisphaera* ichnofacies proposed herein is characterized by moderate to relatively high ichnodiversity and high abundance of nesting traces (calichnia), including dung-beetle brood masses, bee cells, wasp cocoons, ant nests, and more rarely, termite nests. Meniscate burrows, caves excavated by mammals, and rhizoliths maybe also present.

(2) The *Coprinisphaera* ichnofacies indicates that paleosols developed in ecosystems characterized by herbaceous communities, from warmer and more humid environments (i.e., subtropical savannas) where termite nests may be present, to more temperate and arid environments (i.e., steppes) where hymenopterous nests are dominant.

(3) The *Coprinisphaera* ichnofacies qualifies as an archetypal Seilacherian ichnofacies according to its pronounced recurrence in space and time. Other such fossil-insect nest associations exhibit distinctive paleoecologic implications but do not have sufficient recurrence to be considered ichnofacies at this point. The previously proposed *Termitichnus* ichnofacies (*sensu* Smith et al., 1993; Buatois and Mángano, 1995) is very general, and should be discarded because it does not reflect the diversity of paleosol settings and fails to provide detailed paleoecologic information.

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