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Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems

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Abstract

The range of extant nest architectures for different types of solitary to social insects as well as the key features in their architecture has assisted in the identification of their structures in the geologic record. The recognition and interpretation of complex ichnofossils as the product of insects that indicate varying degrees of sociality represents a major development in the study of continental ichnology. Complex ichnofossils constructed since the Mesozoic by termites (Isoptera), bees (Hymenoptera: Apoidea), wasps (Hymenoptera: Apoidea and Vespoidea), and ants (Hymenoptera: Formicidae) represent unique solutions through degrees of social cooperation to the problems of fossorial life in terrestrial environments. Other such trace-making organisms as various types of beetles and vertebrates also construct a range of simple to complex burrows that indicate solitary, subsocial, and gregarious behaviors. Burrows of vertebrates result from relative degrees of social behavior that are unlike those of social insects. Complex ichnofossils are highly variable in architecture and indicate the type of organism, the number of individuals per nest, the length of time the structure was used, the degree of sociality, and, in some cases, the amount of time the substrate has been exposed to surface processes. A pattern of interconnected structures of varying length, width, height, and number usually distinguishes complex traces. Nests of insect societies have the greatest variability in ichnofossil complexity – being simple to extremely elaborate structures. These traces also preserve major innovations in soil ecosystems that include food hoarding, adaptations to disturbance from flooding and precipitation, enduring unpredictable hypercapnic and hypoxic conditions, and reproductive strategies by employing a subterranean, hemimetabolous or holometabolous life cycle. **Polychresichnia** is proposed for trace fossils that were involved in many simultaneous, multiple behaviors and uses. Aedificichnia and calichnia could likely be subsets of polychresichnia because many of the ichnofossil nests originally included in those categories were protected by the adults during brood rearing, used as living and sleeping quarters for the adults, and used as shelter from adverse weather. Nest architecture is an important source of information on the evolution of behavior of social insects as well as for other social organisms. Many of the organisms mentioned here have trace-fossil records that extend to the earliest Mesozoic and predate their earliest body-fossil records in the Cretaceous. Most of these trace fossils have changed remarkably little in 225 million years, indicating evolutionary stasis of the basic building blocks in nest construction.

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1. Introduction

This paper reviews the range of nest architectures of different types of fossil and extant (living taxa) social insects including termites, ants, bees and wasps, and deals with the key features in their architectures that assist in the identification of their structures in the geologic record. Trace fossils of insect nests are often underutilized because of the misperceptions of their occurrence in the stratigraphic record, their usefulness as fossil evidence, and impact in understanding the evolution of solitary and social insects (e.g., Carpenter and Burnham, 1985; Labandeira and Sepkoski, 1993; Grimaldi, 1996; Thorne et al., 2000). The exceptions to this are the works of Wenzel (1991a) and Michener (2000), which have used some fossil nests of wasps and bees to discuss the biogeographic implications and behavioral evolution of certain groups. These misconceptions stem from marine ichnology which emphasizes that a trace fossil can be made by different types of animals such that the architect can rarely be determined and that continental trace fossils are rarely preserved (Ekdale et al., 1984; Bromley, 1996).

Body fossils have been characteristically used as the literal record of life and the only evidence that is useful to determine the origin and occurrence of insects in deep geologic time. For example, Thorne et al. (2000, p. 79) stated the following concerning pre-Cretaceous ichnofossil evidence of termites:

“Reports of Triassic insect nests (no bodies) were reported as termites (Hasiotis and Dubiel, 1993, Hasiotis and Dubiel, 1995), but can be dismissed with almost complete certainty; these are probably the galleries of cupedoid or some other wood-boring beetles.”

Unfortunately, Thorne et al. (2000) did not examine any of the specimens themselves to determine that the nests were in a paleosol and not in wood and whether the architects were not termites (see Section 5.2 and Fig. 11 for the specimens in question); nor had they consulted life history studies to verify that no known beetles construct fine-grained, three-dimensional epigeal (above-ground) to subterranean structures of elaborate architecture.

The problem is two-fold: (1) basing knowledge of the evolution of insects mainly on body fossils and phylogenetic relationships; and (2) the lack of understanding of insect nests, their distinctive, identifiable characteristics, and preservation potential of organisms and nests in continental settings.

Modern ethological analyses and taxonomy of trace fossils, the fossilized remains of structures produced in association with substrates by various organisms' activities, originated largely in the studies of marine deposits (e.g., Frey, 1975; Ekdale et al., 1984; Bromley, 1996). The pinnacle of ethologic analyses rests in Seilacher's (1953, 1964) behavioral classification of trace fossils, which has been subsequently modified with additional behaviors by recent workers (Frey and Seilacher, 1980; Ekdale et al., 1984; Ekdale and Picard, 1985; Bromley, 1996). Most of the behavioral categories developed for trace fossils in marine environments are also applicable to organisms' behavior in continental environments, which include alluvial (fluvial and overbank), palustrine (marsh, swamp), lacustrine (supralittoral, littoral, profundal), and eolian (erg and coastal dune) settings. These behaviors include dwelling, locomotion, resting, feeding, grazing, trapping and gardening, predation, equilibrium, and escape traces (Seilacher, 1964; Bromley, 1996). Several researchers, however, observed that some continental trace fossils have morphologies that resulted from unique and discrete behaviors not represented by historical ethologic classifications.

Bown and Ratcliffe (1988) proposed the term **aedificichnia** for trace fossils preserved mainly in full relief that were constructed from raw materials extraneous to the substrate in which they occurred. An example of this behavior is *Chubutolithes gaimanensis*, an ichnofossil nest likely to have been constructed by a mud-dauber wasp. Genise and Bown (1994a,b) proposed the term **calichnia** for structures constructed from modified substrate materials and used exclusively for reproduction. Structures likened to bee cells and scarabaeid nests are included in this category, with aedificichnia as a specific subset of calichnia. Genise and Bown (1994a,b) suggested that most continental trace fossils are calichnia. Yet these pro-

posed and established behavioral classifications do not encompass fully the range of behaviors represented by complex ichnofossils constructed by such social insects as termites, bees, wasps, and ants, which have a surprisingly diverse record that extends as far back as the Triassic (e.g., Hasiotis and Dubiel, 1995; Hasiotis and Demko, 1998; Hasiotis, 2000, *in press*). These categories also may not be adequate for complex nests formed as a result of parental, communal, or sub-social behaviors.

2. Insect nests as complex trace fossils

The recognition and interpretation of complex ichnofossils as the product of insects that exhibited a range of degrees of sociality (solitary to eusocial) represents a major development in the study of continental ichnology. Complex ichnofossils constructed since the Mesozoic by termites (Isoptera), bees (Hymenoptera: Apoidea), wasps (Hymenoptera: Apoidea and Vespoidea), and ants (Hymenoptera: Formicidae) are unique solutions to the problems of terrestrial and fossorial life achieved through degrees of social cooperation (Hasiotis, 2000). Today, social insects are diverse, abundant, and ecologically important, constituting 10–40% of the biomass of animals in terrestrial ecosystems (Seger, 1991). A large colony of termites or ants may contain 10^5 – 10^7 individuals and occupy a nest complex more than 10^9 times as massive as the workers that built it (Wilson, 1971; Behnke, 1977; Hölldobler and Wilson, 1990). Social cooperation and eusocial behavior have evolved multiple times in terrestrial insects for performing chores and foraging for food, rearing the young, defending the nest, maintaining nests, and regulating microclimate of the nests (e.g., Wheeler, 1928; Wilson, 1971; Michener, 1974).

Complex ichnofossils are highly variable in architecture and, for the most part, indicate the type of organism, the number of individuals per nest, the length of time the structure was used, the degree of sociality, and in some instances, the amount of time the substrate was exposed to surface processes. A pattern of interconnected shafts,

galleries, and chambers of varying length, width, height, intricacy, and number usually distinguishes complex traces. Nests of insect societies show the greatest range in trace-fossil complexity – simple structures, with a single chamber and one to a few shafts or galleries, to extremely elaborate structures composed of hundreds to thousands of chambers, cells, shafts, and galleries. These ichnofossils also preserve major innovations in soil ecosystems that include (1) food hoarding, (2) adapting to disturbance from flooding and precipitation, (3) enduring unpredictable increased levels of carbon dioxide (hypercapnic) and oxygen deficit (hypoxic) conditions, and (4) reproductive strategies by employing a subterranean, incomplete metamorphosis (hemimetabolous = egg to nymph to adult insect) or complete metamorphosis (holometabolous = egg to larva to pupa to adult) life cycle.

Nest architecture is an important source of information on the evolution of behavior of social insects as well as for other social organisms. Many of the organisms mentioned here have trace-fossil records that extend to the earliest Mesozoic and predate their earliest body fossils, which are preserved in Cretaceous amber and lacustrine deposits. The architecture of most of these trace fossils changed remarkably little in 225 million years, indicating evolutionary stasis in the basic building blocks of nest construction. These trace fossils and some of their modern counterparts are illustrated to demonstrate the striking similarity between ancient and modern complex ichnofossils produced by solitary and social organisms. The activity of some of these organisms has been referred to as *ecosystem engineering* because their physicochemical activities modify the environment and regulate nutrients to biota above and below them in the trophic pyramid (Jones et al., 1994; Lavelle et al., 1997). The intensity and distribution of ant and termite bioturbation suggest that these insects played major roles as ecosystem engineers as far back as the early Mesozoic. Some of the complex burrows and nest architectures of different types of solitary and gregarious invertebrates (e.g., various beetle taxa) and vertebrates (e.g., therapsids and mammals) are distinguished from the burrows of social

organisms. Many of these organisms also have trace-fossil records that extend to the earliest Mesozoic if not older, and many predate their earliest body-fossil records in the Mesozoic and Cenozoic.

3. Degrees of social behavior

Only some insects show truly eusocial behavior where a fixed division of reproductive labor is represented by sterile individuals that work for their parents (Wilson, 1971). Eusociality is found in the Isoptera (termites) and the Hymenoptera (bees, wasps, and ants). All termite and ant taxa are social, while the bees and wasps are solitary to eusocial. Emerson (1938), Noirot (1970), and Grassé (1984) reviewed termite nest architecture, which ranges from simple galleries in wood or soil to the most complex and elaborate structures constructed in the animal kingdom, including those constructed by humans (Noirot, 1970; Wilson, 1971). Even today, however, the nest architecture of many species is still unknown (Noirot, 1970; Grassé, 1984).

Bees and wasps may be solitary, gregarious, communal, semisocial, primitively eusocial, and eusocial (e.g., Stephen et al., 1969; Evans and Eberhard, 1970; Michener, 1974; Ross and Matthews, 1991). This range of behavior is also exhibited in ontogenetic stages of nest formation by the founding female that constructs a simple nest (representing solitary behavior), to the offspring of the mother that expand the nest (representing subsocial behavior), to overlapping broods of offspring that expand and maintain the nest while the founding female serves as its queen and egg-layer (representing social behavior) (Michener, 1974). A similar pattern in nest ontogeny exists for ants and termites (Sudd, 1967; Noirot, 1970), but termite nests are begun by the founding male and female pair and become more elaborate and specialized as the offspring take over the construction (Noirot, 1970).

Nest classifications of bee and wasp social behavior by Sakagami and Michener (1962), Stephen et al. (1969), Evans and Eberhard (1970), and Wenzel (1991a) are too lengthy and complicated to be duplicated here or to be used directly

to classify ichnofossil nests of social insects. Several major problems exist with using modern nest classifications for ichnofossils. There is a pre-existing discontinuity in terminology for the parts of insect nests, which are different for each major group of insect (termites, ants, bees, and wasps). This nomenclatural discontinuity in previous work of each insect group has made it more difficult for researchers to see the similarities among insect nests. Another problem is that only portions of ichnofossil nests may be preserved or observed in outcrop. Also the nest portions that are preserved may be an early part of an ontogenetic series in nest construction. Several nests of increasing complexity observed in outcrop might indicate a range of behaviors similar or different to each other, but were colonies of different ages. Interpretations from these ichnofossils would likely result in different ichnotaxonomic designations for each stage of nest ontogeny if they are not recognized as part of an ontogenetic series. Nest morphology is often plastic to some degree, and structures can vary with respect to local climatic and edaphic (i.e., soil) conditions (e.g., Noirot and Darlington, 2000). Another problem rests in the size of some of the nests, which can range from a simple cavity in the substratum to nest complexes built over 1 km² in area and more than 1 km³ in volume (e.g., Ratcliffe and Greaves, 1940; Noirot and Darlington, 2000). In this instance, only a small portion of the nest might be described ichnotaxonomically from a poorly exposed outcrop, or the different components of the same nest may be interpreted inadvertently as separate behavioral entities unrelated to each other in the same outcrop.

Nevertheless, studies of extant isopteran and hymenopteran nests are useful as clues for recognizing variably complex ichnofossils of possibly social insects similar to those constructed by termites, bees, wasps, and ants. Ichnofossil nests of termites, bees, wasps, and ants also indicate the antiquity of many individuals acting as one **super-organism**, which behaves as a unit of complex and coordinated activities that obtain and assimilate nutrients; produce and raise offspring; and maintain, regulate, and defend the nest (Wheeler, 1928; Wilson, 1971). The entire nest colony ex-

hibits an array of behavioral activities that are analogous to the physiological properties of tissues and organs in a single body (Wilson, 1971). Rare body fossils of nest-constructing social insects provide only a glimpse into the superorganism, but ichnofossil nests of these insects afford the opportunity to explore the manifestations of the array of behaviors they exhibited in deep geologic time.

4. Burrowing signatures: identifying patterns or building blocks of social insect nests

How are masses of thousands of simple burrows constructed by as many beetles or soil bugs to be differentiated from nests composed of an equal number of tunnels constructed by a large colony of ants? How are ant nests distinguished from termite nests or termite nests from bee nests? The key to the most reliable identification rests in the recognition of burrowing signatures and fabrication techniques used by each type of insect. Nests are mosaics of tunnels (shafts and galleries) and chambers that are constructed successively. They are linked together simply or complexly in a diffuse or concentrated manner in one or more patterns through space and time. This results in a vast array of nest architectures that can be preserved in different stages of their ontogenetic development.

Basic styles, techniques, and building blocks are used to construct simple to complex, subterranean, epigeal, and arboreal nests that are unique to termites, bees, wasps, and ants, as based on a plethora of ichnofossil and extant nest evidence. There are, of course, convergence and overlap in construction methods and nest architectures; however, careful scrutiny of nest structures, in most instances, should lead to reliable identification of the builder. Nearly all termite nests (Fig. 1) are composed of galleries and chambers, and are lined with fecal material or are constructed of stercoral – a mixture of masticated plant fibers, feces, and sediment (Noirot, 1970; Noirot and Darlington, 2000). Even in wood, galleries and chambers are lined with compacted fecal material (e.g., Lee and Wood, 1971). Ants, for the most

part, construct nests (Fig. 2) by compacting sediment into place with the head, while a few species use saliva or masticated plant materials to hold sediment in place. Some ants line their galleries and chambers with formic acid produced by the ant, which serves as a fungicide (e.g., Hutchins, 1967; Hölldobler and Wilson, 1990). Several of the ant and termite nest architectures overlap with one another, but details of construction should allow one nest architect to be differentiated from the other.

Solitary to eusocial bees (Figs. 3 and 4) excavate or construct flask-, capsule-, spherical-shaped, to hexagonal-shaped cells and cell clusters or combs (multiple cells that share common walls) in soil and wood (Stephen et al., 1969). These cells are lined smoothly with fine sediment or waxlike bodily secretions or are constructed from other substances extracted from plant materials (Michener, 1974). Many of these cells are enclosed by a spiral cap, but other types of closures are also used (Michener, 1974; J. Rozen, written communication, 1995). Highly organized, hexagonal cells comprise combs constructed mainly of wax that are built in hollows of trees or on branches by honeybees (Michener, 1974). Solitary to eusocial wasps also construct nests similar to those of bees (Figs. 5 and 6), but the cells of solitary wasps are frequently capsule-shaped; they are not lined and smooth-walled; and they are not closed with an upward spiraling cap (e.g., Evans and Eberhard, 1970; Evans, 1985; C.D. Michener, personal communication, 2001). Nests constructed by pollen wasps are quite similar to cells and nests constructed by bees (Gess, 1996), but many of the features described above, particularly the spiral cap and cell lining, can be used to distinguish one from the other (C.D. Michener, personal communication, 2001). Eusocial wasps are commonly known for their subterranean and arboreal paper nests, which are constructed from masticated wood fibers used to produce hexagonal cells in multistoried combs (Ross and Matthews, 1991). Details of termite, ant, bee, and wasp nest architectures are reviewed in later sections of this paper.

Despite the taxonomic and behavioral differences between termites, bees, wasps, and ants, there

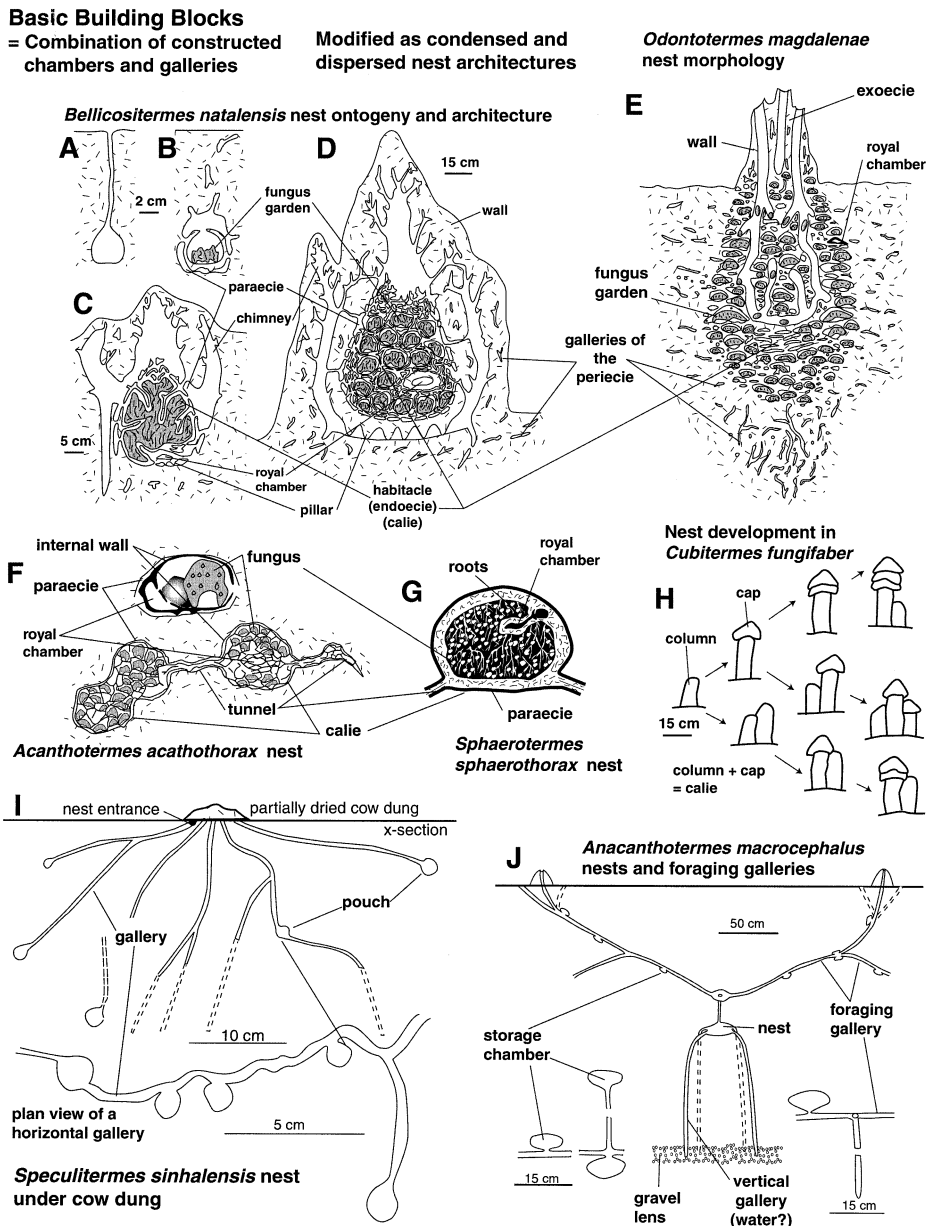


Fig. 1. Examples of extant termite nest morphologies. The basic building blocks of termite nests are constructed chambers and galleries arranged in diffuse or concentrated architectures. (A–D) Nest ontogeny and architecture of *Bellicositermes natalensis*. (E) Nest morphology of *Odontotermes magdalenae*. (F) Polycalic nest of *Acanthotermes acanthothorax*. (G) Calie nest of *Sphaerotermes sphaerothorax*. (H) Nest development in *Cubitermes fungifaber*. (I) Nest morphology of *Speculitermes sinhalensis* constructed beneath dried cow dung. (J) Nest morphology of *Anacanthotermes macrocephalus*. All illustrations redrawn and modified from Noirt (1970) and Roonwal (1970).

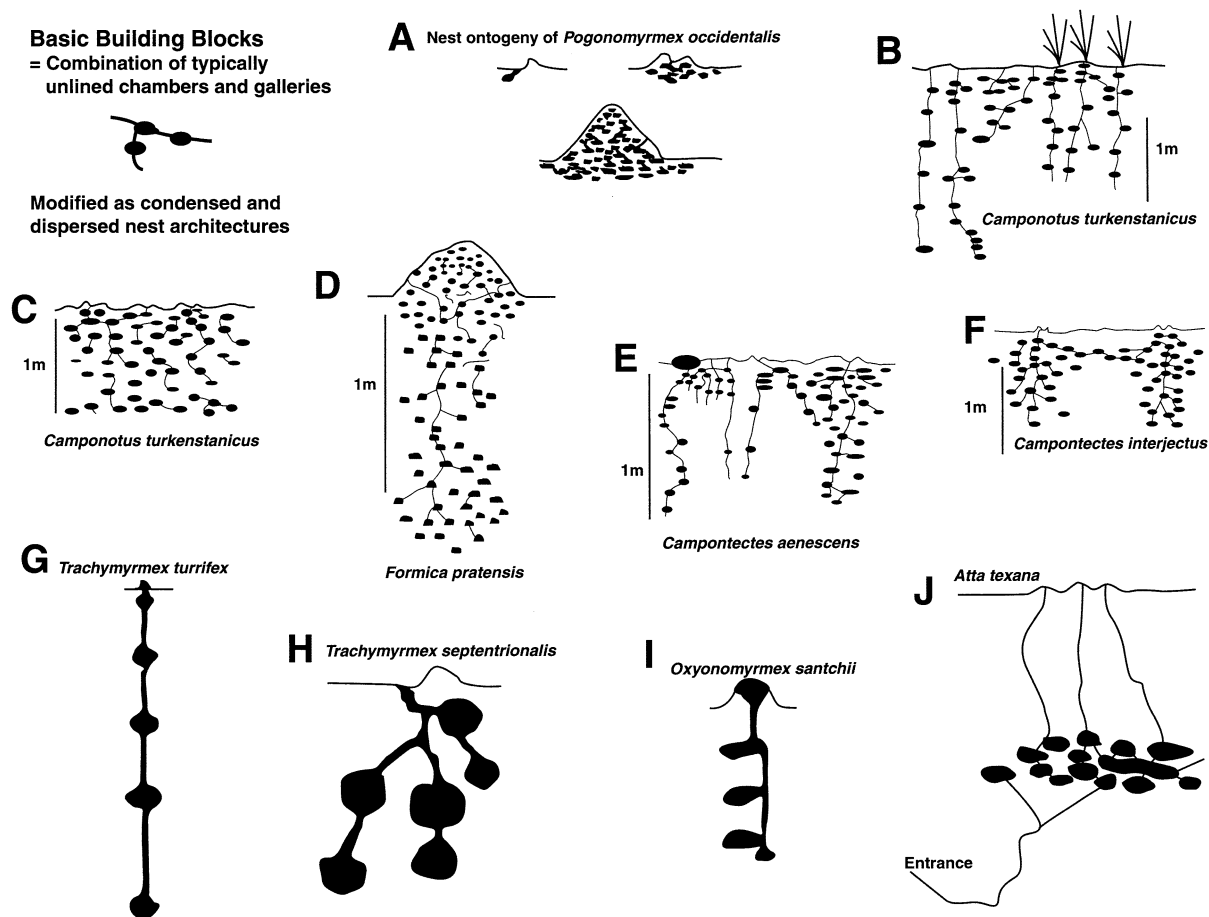


Fig. 2. Examples of extant ant nest morphologies. The basic building blocks of ant nests are unlined chambers and galleries arranged in diffuse or concentrated architectures. (A) Nest morphology and ontogeny of *Pogonomyrmex occidentalis*. Nest morphology of: (B,C) *Camponotus turkenstanicus*; (D) *Formica pratensis*; (E) *Camponotus aenescens*; (F) *Camponotus interjectus*; fungus-gardening ants, (G) *Trachymyrmex turrifex*; (H) *Trachymyrmex septentrionalis*; (I) *Oxyonomyrmex santchii*; (J) *Atta texana*. All illustrations redrawn and modified from Wheeler (1910) and Sudd (1967).

are only so many ways to construct subterranean, epigeal, and arboreal solitary- to social-insect nests. Since nest construction and social behavior have evolved many times among the Isoptera and Hymenoptera, the range of nest architectures exhibited by extant solitary to social insects is likely to have followed similar evolutionary pathways from simple to complex construction. This is also probably true of termites and ants, although they do not have solitary or gregarious taxa (e.g., Wilson, 1971; Seger, 1991). Even the construction of the most elaborate nests begins with the construction of a simple vertical or horizontal burrow

that terminates in a chamber. Ironically, these two types of simple burrows are also excavated or constructed and used by nearly all terrestrial and aquatic burrowing organisms (e.g., Ratcliffe and Fagerstrom, 1980; Hasiotis and Bown, 1992).

5. Architectures of termite nests: simple to complex nests

Ichnofossil and extant termite nests are excavated and constructed edifices, a system of cavities constructed in soil or in wood (e.g., Noirot, 1970;

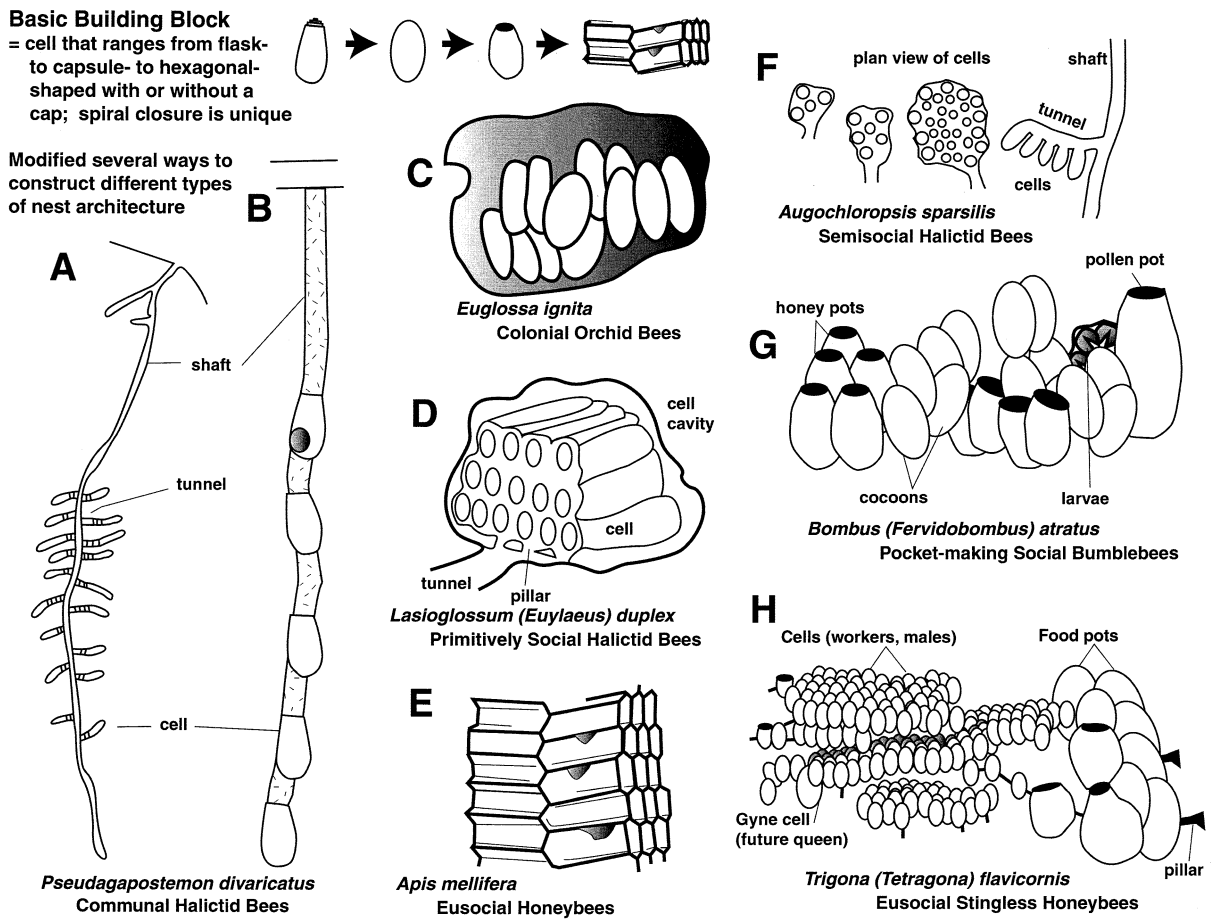


Fig. 3. Examples of extant solitary to eusocial bee nest morphologies. The basic building blocks of bee nests are flask-shaped cells with or without a spiral cap closure, modified several ways to construct different types of nest architectures. (A,B) Nest of the communal halictid bee *Pseudagapostemon divaricatus*. (C) Nest of the colonial orchid bee *Euglossa ignita*. (D) Cell cluster of the primitively social halictid bee *Lasioglossum (Euylaeus) duplex*. (E) Nest of the eusocial honeybee *Apis mellifera*. (F) Nest of the semisocial halictid bee *Augochloropsis sparsilis*. (G) Nest of the pocket-making social bumblebee *Bombus (Fervidobombus) atratus*. (H) Nest of the eusocial stingless honeybee *Trigona (Tetragona) flavicornis*. All figures redrawn and modified from Michener (1974).

Grassé, 1984; Bown, 1982; Hasiotis and Dubiel, 1995; Genise and Bown, 1994b). Nests are constructed in a variety of substrate settings: xylid (wood), subterranean (nests built underground), epigeal (nests that protrude above ground, often with subterranean portions), and arboreal (nests built on the trunk or branch of a tree, but connected to the soil via covered galleries). Each is the product of the collective efforts of many individuals. Termite nests were recognized early as frozen behavior by Konrad Lorenz (cited by Schmidt, 1955 and by Noirot, 1970); in other

words, behavior that is represented by three-dimensional structures. Important for diagnosing termite nests is recognizing that convergence and parallel evolution in neighboring lineages of termites show up in the similarities in nest architecture. The most derived termites (Termitinae) construct subterranean nests that can also be simple and lack distinctive architecture. Thus, there is no correlation between the degree of morphological evolution in the termites and the architectural complexities of their nests (e.g., Noirot, 1970; Noirot and Darlington, 2000). Nests begin as a

Simple to complex nest architectures of soil- and wood-dwelling bees

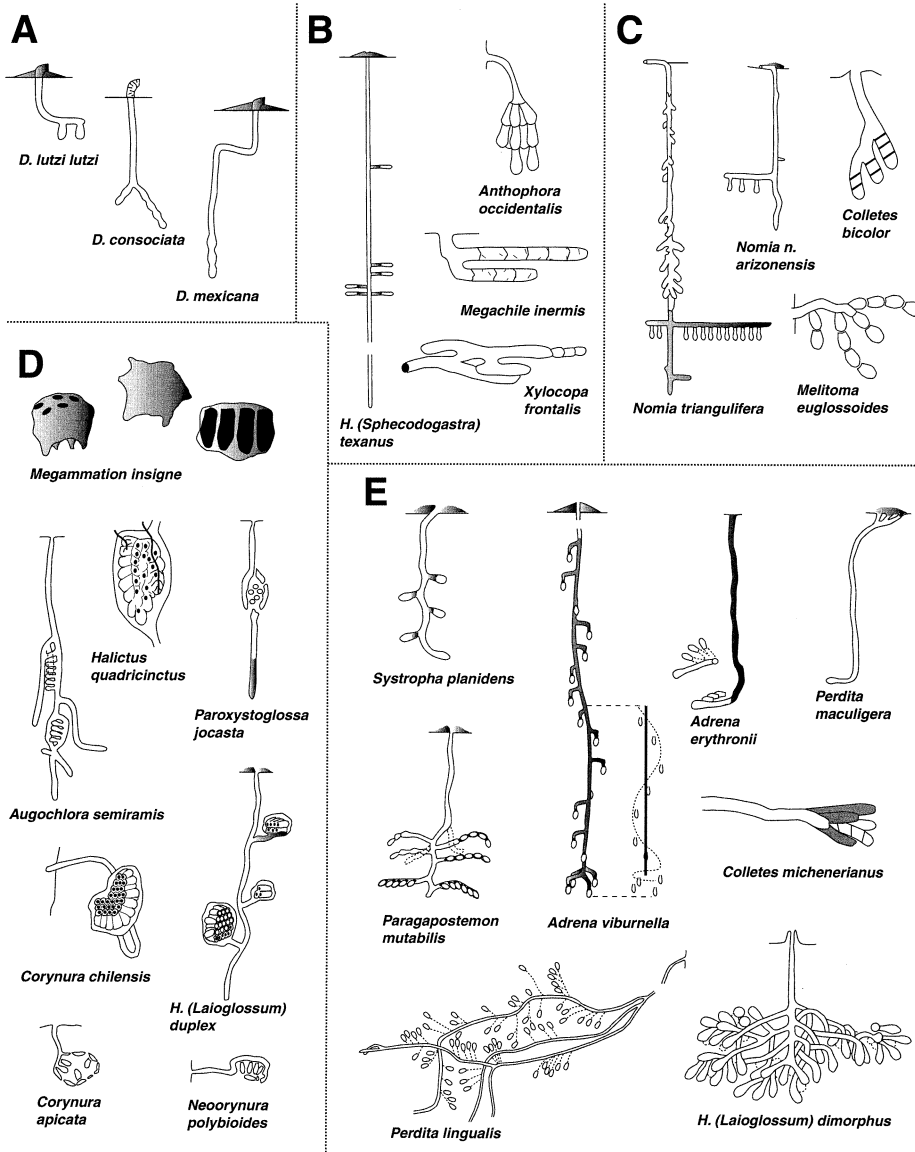


Fig. 4. Examples of extant solitary to eusocial bee nest morphologies. (A) Simple nest architectures in soils constructed by species of *Diadasia*. (B) Simple nests with cells arranged in series and short lateral tunnels constructed by soil (halictid, anthophorid, megachilids) and wood (xylocopid) bees. (C) Simple soil nests with cells arranged in a combination of series and lateral tunnels constructed by colletid, nomad, and melitid bees. (D) Complex cell clusters constructed by halictid, corynurid, neocorynurid, augochlorid, and paroxystoglossid soil bees. (E) Complex architectures of soil nests with cells arranged in a combination of individuals, series, and branches from lateral tunnels constructed by colletid, halictid, perditid, adrenid, and paragapostemid bees. All figures redrawn and modified from [Stephen et al. \(1969\)](#).

Simple to complex nest architecture of solitary to presocial wasps

Basic Building Block

= cell space in which a cocoon is spun by the larva

Modified several ways to construct different types of nest architectures with or without shafts and tunnels

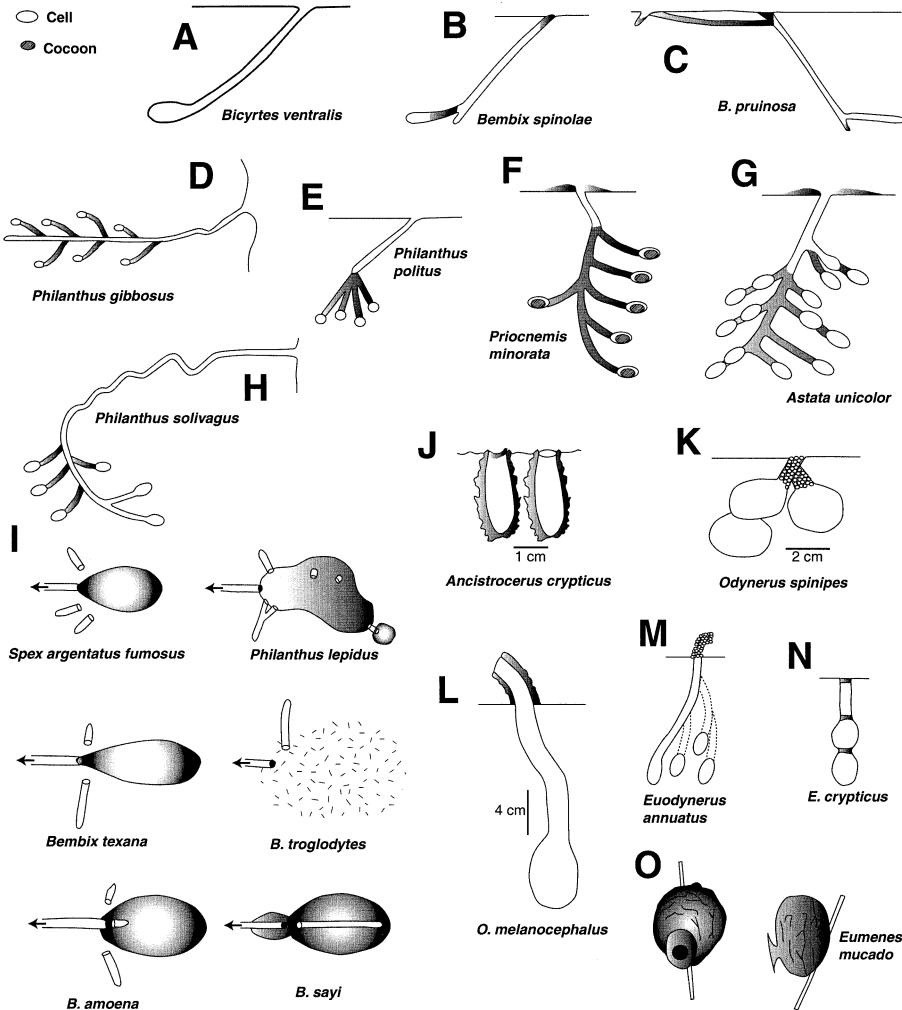
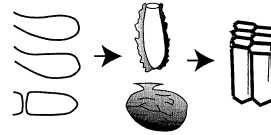


Fig. 5. Examples of extant solitary to presocial wasp nest morphologies. The basic building blocks of wasp nests are unlined, excavated to constructed cells, modified several ways to construct different types of nest architectures. All figures redrawn and modified from [Evans and Eberhard \(1970\)](#), [Spradberry \(1973\)](#), [Evans \(1985\)](#), and [Cowan \(1991\)](#).

simple closed chamber in the substratum. Humus-feeding termites construct nests composed mainly of simple networks of galleries and chambers composed of walls plastered with fecal material since they are constructed, not only dug. The most complex, concentrated nests are constructed

entirely rather than being excavated and are contained within a single cavity surrounded by a nearly continuous wall from which galleries radiate outwards. Many subterranean nests exhibit epigeal construction when the population reaches a critical number. The complexities of the subter-

Nest Architectures of eusocial and highly eusocial wasps (Vespidae)

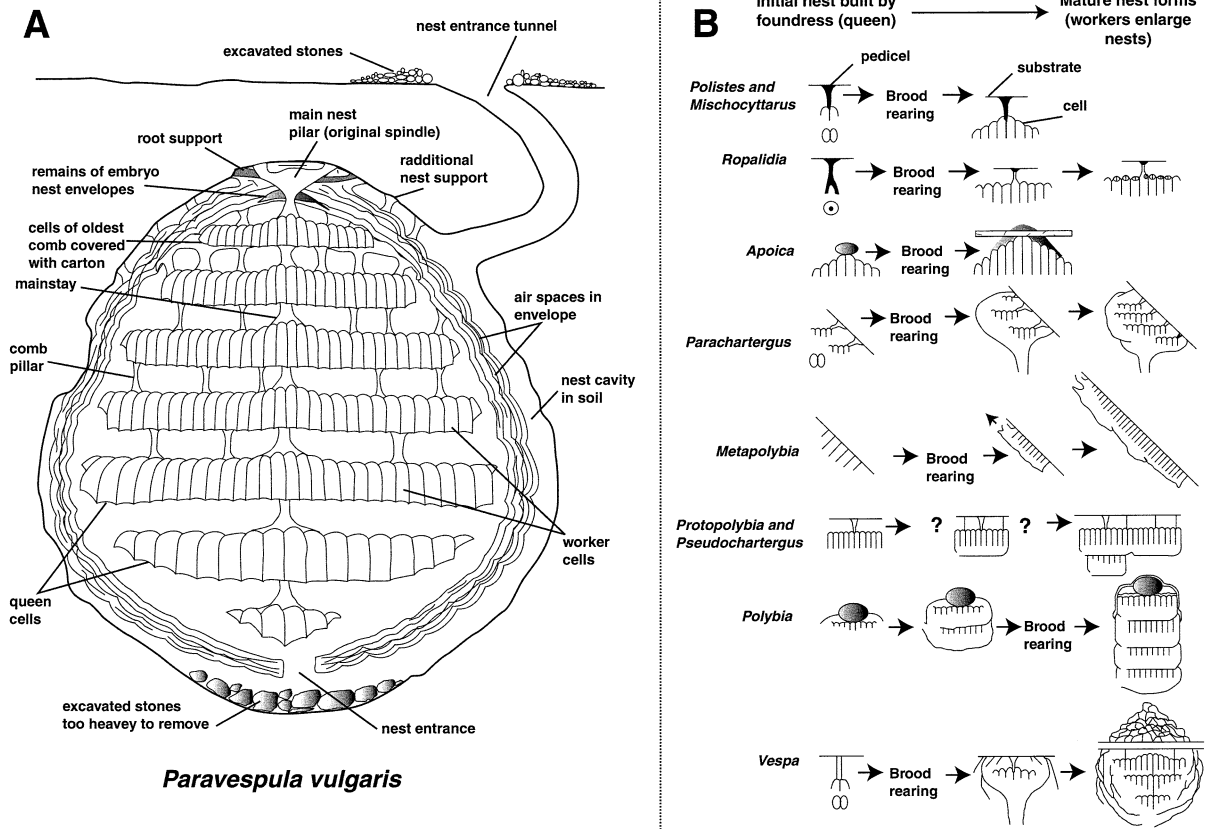


Fig. 6. Examples of extant eusocial wasp nest morphologies. (A) Nest architecture of *Paravespula vulgaris*. (B) Major nest architecture development patterns constructed by eusocial vespid wasps. All figures redrawn and modified from Spradberry (1973), and Wenzel (1991a).

ranean and epigeal portions of the nest are proportional to each other. Some arboreal nests are also believed to have begun with a temporary subterranean component with a later construction of an arboreal nest (Noirot and Darlington, 2000).

5.1. Nests of extant termites

Three types of extant nests (see Fig. 1) are recognized: (1) nests with limited growth (that grow by addition); (2) nests with unlimited growth (including diffuse and some concentrated nests); and (3) nests of potentially limited number of calies (calie = constructed nest unit, each with limited

growth; discussed later) (Grassé, 1984). In general, nests are considered as either concentrated or diffuse with the architecture and construction being quite variable within each type (Noirot and Darlington, 2000). Excavation of galleries in wood is considered to be the most primitive behavior because of the purported phylogenetic relationship of termites to woodroaches (Noirot, 1970; Abe et al., 2000). Nest construction has diverse aspects, but all have two main components: excavation and construction (Noirot, 1970, 1977). The termites use their mandibles to remove particles of the substratum or wood particles. Construction techniques are relatively uniform so that many nests of different termites are

similar to one another. Galleries, walls, ramps, pillars, and floors are built by depositing soil (sand, silt, or clay) or masticated wood with fecal droplets that act as mortar. Predominantly wood-eating species build nests using **carton**, a mixture of masticated wood and fecal droplets. Soil-dwelling termites mix excrement with soil particles to form a material termed **stercoral**. Nests can have both materials used in construction, with earth material used for the external structure, while carton is used for internal construction. Some fungus-growing termites (e.g., Macrotermitinae) ingest clay, mix it with saliva, and regurgitate the mixture as the mortar to hold the structure together (Noirot, 1970).

Excellent reviews and discussions of termite nest morphologies were given by Grassé (1949, 1984), Noirot (1970, 1977), Lee and Wood (1971); however, the main components of diffuse and concentrated nests are summarized here (Fig. 1). Diffuse nests are considered to be the most primitive of subterranean nests. They grow by the addition and extension of galleries. Galleries are enlarged to form chambers in various places of the gallery system (Fig. 1LJ). Concentrated nests are composed of a thick, massive wall that encloses the main portion of the nest in a central cavity (Fig. 1A–D). The nest is clearly discernible from the surrounding substratum. The **habitable** or **endoecie** is the region within the central cavity that contains many rooms or cells, fungus gardens, and the royal chamber, all connected by galleries and ramps (Grassé, 1949; Lee and Wood, 1971). The habitable rests on a flat base and is supported by downward tapering, conical structures called **pillars**. This space between the base of the habitable and pillars is called the **cellar** or **cave**. The massive wall is traversed by a system of galleries that are mainly vertical and differ from nest to nest. Large vertical galleries or channels are referred to as **chimneys**, which are typically large near the base and ramify upwards into smaller, interconnected galleries. The **paraecie** is the area between the habitable and the massive gallery-traversed wall of the nest that is an open air space. The **periecie** is the underground system of galleries that surrounds the nest proper, enclosed by the massive walls. It consists of two

distinct systems. An external gallery system extends for several tens of meters or more around the nest and is associated with a system of large vertical pits. These networks of galleries are used to obtain moisture, food, and clay used in nest construction and to rid the nest of materials and organic matter no longer in use. Some of the largest nests, such as those constructed by *Macrotermes* in the tropics, may have a volume of more than 1000 m³ (Noirot and Darlington, 2000).

Construction and expansion occur by two methods that are likely to represent end members in nest building: reorganization of the substrate to enlarge nests and by addition of new structures to mature, pre-existing structures as the number of individuals in the colony increases (Noirot, 1970). In general, nest size increases with the number of individuals. Growth takes place in many different ways. Accessory nests may form via budding by diffuse nest builders by building structures away from the main nest. Nest excavation by some termites (Kalotermitidae, Termopsidae) via new galleries and enlargement of chambers is associated with feeding. Nest size also increases as older chambers and galleries are abandoned and filled with fecal pellets and with sickened and deceased members of the colony. Among other termites, after the main nest is constructed expansion is through the addition of new structures to increase the size of the nest. *Cubitermes fungifaber* builds two kinds of structures: the cylindrical, vertical column and the mushroom-shaped cap (Fig. 1H). Nests are enlarged by the addition of newly adjoined cylindrical columns or by the addition of caps on top of pre-existing caps. Growth continues by the addition of new columns and caps, never by widening of pre-existing structures. Once constructed, different portions of the nests are not modified for nest enlargement, but walls can be rebuilt if damaged, and interior structures may be modified or repaired to only a limited extent (Noirot, 1970).

The most complex nests are those that are expanded by the addition of new nest centers. These types of nests are mosaics of parts successively constructed and simply linked together. **Polycalic** nests are new structures that are entirely separated from the old structure (Fig. 1F). A **calie**

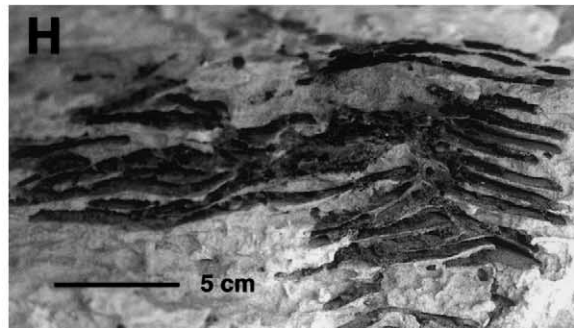
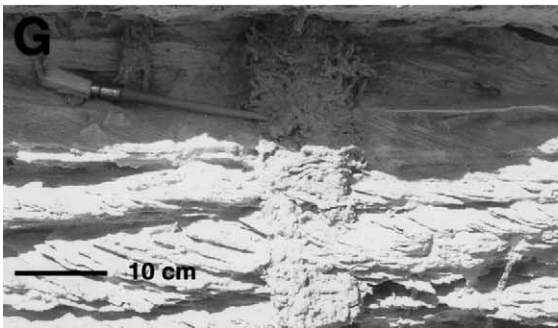
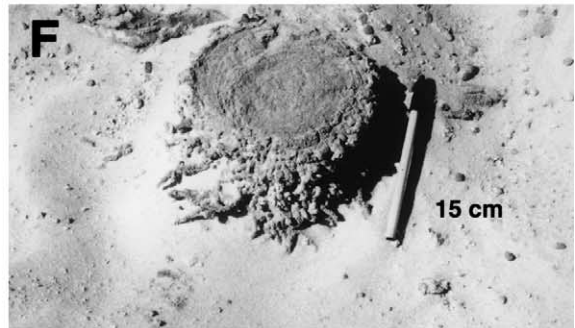
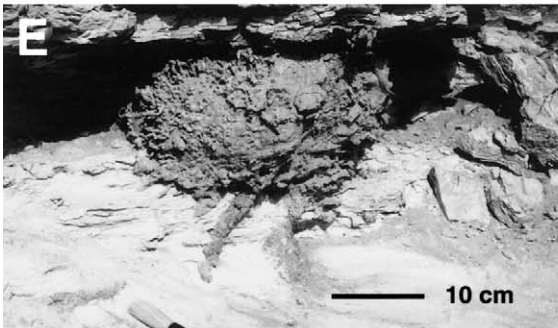
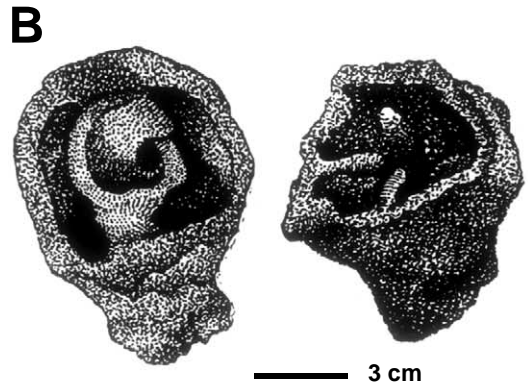
Table 1
Termite nest ichnofossils in the geologic record

Age and formation	Locality	Nest architecture	Ichnotaxonomy	Source
Triassic				
Chinle formation	Petrified Forest National Park, Arizona	Cylindrical calies and associated chambers Elongated shelves	<i>Archeoentomichnus metapolypholeos</i> open nomenclature	Hasiotis and Dubiel, 1995 Hasiotis, in preparation a,b,c
Jurassic				
Morrison Formation	Colorado Plateau and vicinity	Spherical nests Elongated ramp nests Concentrated galleries (horizontal) Concentrated galleries (vertical) Rhizolith specific Rhizolith engulfing	open nomenclature	Hasiotis and Demko, 1996, 1998; Hasiotis, 2002
Cretaceous				
Price River Formation	Price River Canyon, Utah	Spherical nests with galleries	open nomenclature	Hasiotis et al., 1994
Javelina Formation	Brewster County, Texas	Nests in petrified wood; pellets	open nomenclature	Rohr et al., 1986
Paleogene				
Eoc. Willwood Formation	Worland, Wyoming	Concentrated, pelleted fabrics Spherical nests	open nomenclature open nomenclature	Hasiotis and Bown, unpublished data
Eoc. Cayara Formation	Southern Bolivia	Stacked shelves and ramps	cf. <i>Krausichnus trompitus</i>	Hasiotis et al., in preparation a
Eoc.–Olig. Jebel Qatani Formation	Fayum and Qattara Depression, Egypt	Spherical nests, diffuse Spherical nests Spherical nests (diffuse) Stacked hemispheres Stacked shelves and ramps Stacked shelves and ramps	<i>Termitichnus qatranii</i> <i>T. simplicidens</i> <i>Vondrichnus obovatus</i> <i>Fleaglellius pogodas</i> <i>Krausichnus trompitus</i> <i>K. altus</i>	Bown, 1982; Genise and Bown, 1994a,b
Neogene				
Mio. Pinturas Formation	Patagonia, Argentina	Concentrated chambers, galleries Cavity nest	<i>Syntermesichnus fontanae</i> <i>Tacuruichnus farinai</i>	Bown and Laza, 1990 Genise, 1997
Late Plio. Barranca de Los Lobos Formation	Buenos Aires Province, Argentina	Frass in wood cavities	open nomenclature (Kalotermitid)	Rogers, 1938
Late Pliocene deposits	Santa Clara, California	Frass in wood cavities	open nomenclature (Kalotermitid)	Abel, 1935
Late Plio. Laetoli Beds	Laetoli, Tanzania	Concentrated masses Spherical nests, diffuse Spherical nests Stacked shelves and ramps	open nomenclature (nests attributed to species of the Termitidae; cf. <i>Macrotermes</i> , <i>Odotermes</i> , <i>Hodotermes</i>)	Sands, 1987
Quaternary				
Type C1, Table Mountain Series, Cape System	Pretoria, Cape Province, South Africa	Concentrated masses Spherical nests, diffuse Spherical nests	open nomenclature (nests attributed to <i>Microhodotermes</i> or <i>Hodotermes</i>)	Coaton, 1981

(Fig. 1G) or constructed nest unit is repeated in space and time through the life of the colony as long as its increases. A nest can grow by increasing size of existing calies or by the construction of new calies. It is likely that both methods are used in polycalic termite nests. Nest relocation is the extreme of polycalic behavior, where the entire

colony will move into a larger structure at a new location (*Apicotermes desneuxi*). Larger nests are more deeply buried than smaller, shallower ones; however, this tiered style of nest construction is still considered hypothetical (Noirot, 1970).

Important behaviors represented by all nests include (1) avoidance of light, (2) extreme sensi-



tivity to air currents, (3) cellulose-based nutrition, (4) moderate protection from desiccation, and (5) thigmotaxis, which is the response of an organism to a continuous contact with a solid surface. All nests are built in such a way as to regulate the colony's environment with respect to temperature, humidity, internal nest atmosphere, and nest ventilation (Luscher, 1961). Termite nests are enclosed and do not have direct communication with the atmosphere (Noirot, 1970), only tortuous pathways through small openings. Exchange of gases is through a simple to elaborate network of small holes leading to caves or galleries that are connected with the surface.

5.2. Ichnofossil nests

The identification of termite ichnofossils in ancient continental deposits (Table 1) has been based on comparisons to the architectural and surficial elements and the overall structure of extant termite nests (e.g., Bown, 1982; Rohr et al., 1986; Sands, 1987; Genise and Bown, 1994b; Hasiotis and Dubiel, 1995; Hasiotis and Demko, 1996; Genise, 1997; Hasiotis, in press). All the key morphologic features of subterranean termite nests have been found in ancient examples (Figs. 7–11), including the association of ichnofossil nests with rhizoliths and permineralized, damaged roots. Regardless of the age and complexity of the nests, the key criteria in their interpretation as termite nests appear to be the occurrence of lined tunnels and spheroidal structures that are directly associated with each other to form a diffuse or highly concentrated mosaic of structures, indicating the endoecie, paraecie, or periecie of nests (Figs. 7–11). Mesozoic and Cenozoic ichnotaxa are based on the degree of concentration of chambers and galleries, as well as chamber size, shape, and arrangement and the architecture and com-

plexity of galleries. Ichnofossil nests interpreted as having been constructed by termites can be generalized as multiarchitectural, variably conterminous mosaics of chambers and galleries dominated by (1) structure (concentrated or diffuse); (2) size (small to large, shallow to deep); (3) shape (cylindrical, spherical, tabular, globular, and massive); (4) constructional elements (single chamber or many; simple to complex galleries); (5) chamber type (boxlike, ramplike, tabular, or rectilinear); (6) gallery type (simple, compound, or complex); and (7) replication in construction pattern (arrangement of chambers and galleries in space and time). Specific structures or the lack of them may also be used to interpret the ichnofossils of termites. For example, some Jurassic termite nests composed mainly of simple galleries and few chambers are specific to the shape of a rhizolith or engulf the whole shape and surrounding substrate of a rhizolith (Hasiotis and Demko, 1996; Hasiotis, in press). A very large spherical opening in an outcrop of Pliocene strata was interpreted as a termite nest because it was similar to a large central cavity of an extant termite nest but lacked the internal structure of chambers and galleries within the endoecie (Genise, 1997). This same type of termite nest ichnofossil was also described from the Late Jurassic (Hasiotis, in press).

The end result of the analysis of extant termite nests and their use for the interpretation of ichnofossils constructed by termites is the recognition of larger, compound structures composed of interconnected components of variable architecture. If this association is overlooked or not recognized at the outcrop, then the interpretation of the ichnofossil will be incorrect. For example, the galleries of termite nests are similar in appearance to unlined burrows assigned to *Planolites*, vertical shafts likened to *Skolithos*, Y- and T-branched galleries and shafts assigned to *Thalassinoides*,

Fig. 7. Extant and ichnofossil termite nest morphologies. (A) Nest of extant termite *Procornitermes striatus* collected from Argentina (after Hasiotis et al., 1994). (B) Nest of extant termite *Procornitermes cornutus* (modified from Hasiotis and Dubiel, 1995). (C) Nest of extant termite *Macrotermes* sp. in high plateau of Ethiopia; person is approximately 1.9 m tall. (D) Undescribed termite ichnofossil nests as calices from the late Miocene Bakate Formation, Fejej, Ethiopia. (E) Termite ichnofossil nest *Termitichnus qatranii* in the Eocene–Oligocene Jebel Qatrani Formation of the Fayum Depression, Egypt. (F) Natural cross-section through *T. qatranii* from same area as E. (G) Compound gallery system of *T. qatranii* from same area as E (modified from Hasiotis et al., 1994). (H) Termite ichnofossil nest *Krausichnus trompitus* from same area as E (modified from Hasiotis et al., 1994).

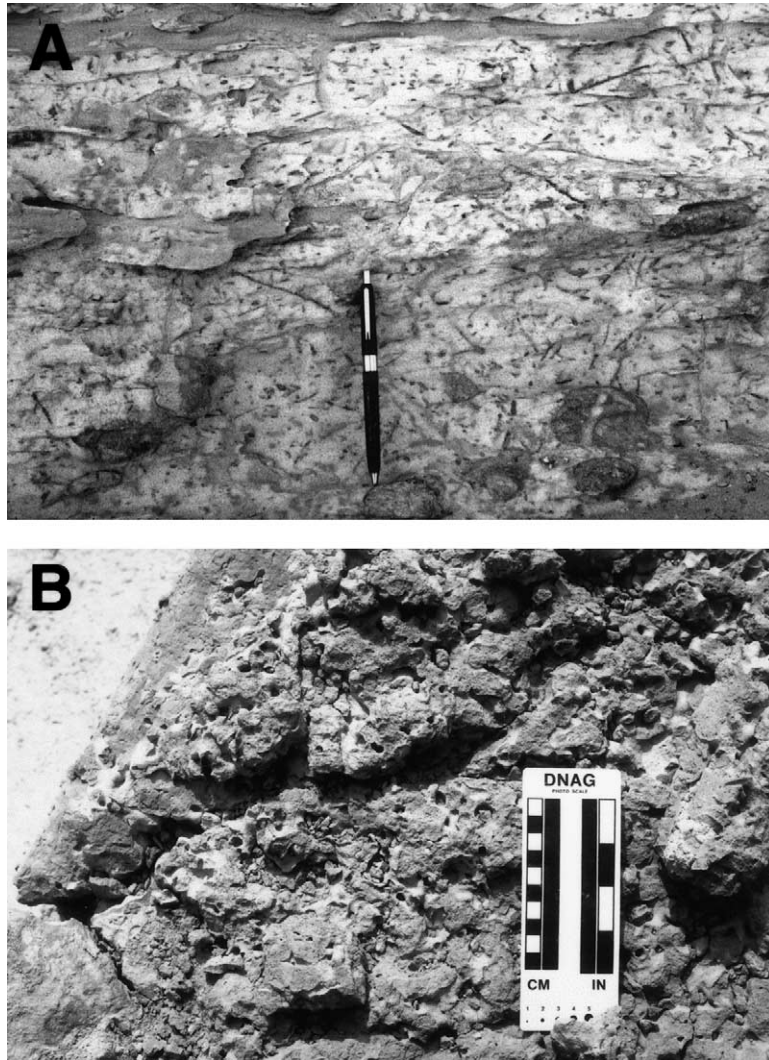


Fig. 8. Ichnofossil termite nest morphologies. (A) Outcrop wall composed of the polycalic ichnofossil nests and simple galleries *Vondrichnus obovatus* from the Eocene–Oligocene Jebel Qatrani Formation of the Fayum Depression, Egypt. (B) Ichnofossil nest *Syntermesichnus fontanae* in the Miocene Pinturas Formation of the Santa Cruz Province, Argentina.

and the lined burrows ascribed to *Palaeophycus*. The chambers grossly resemble massive, globular, or lenticular concretions and may also be misinterpreted as arid-climate weathering features around masses of *Planolites* and *Palaeophycus*.

5.3. Behavioral and paleoecological implications

The ichnofossil nests preserve physical evidence resulting from eusocial behavior by termites. The

intricate nature of the ichnofossil nests, even in the simplest forms, implies that a high degree of cooperation was necessary to maintain the construction of galleries, defend the nest from invaders, regulate and dispose of the nest waste products, and lay eggs and rear young to produce more caste members and future kings and queens (i.e., elates) (Wilson, 1971). This work was most likely carried out by a differentiated caste system of workers, soldiers, and the queen and king. The

size of the nest is likely to have been proportional to the number of individuals in the colony, and large nests, such as those in Upper Jurassic Morrison Formation, may have had as many as a million or more individuals, similar in number to the large nests of *Macrotermes*. Smaller nests, such as those that occur in the Triassic, Jurassic, Eocene, and Oligocene, may have had a thousand to ten thousand individuals, similar in number to the nests of *Microhodotermes* and *Cubitermes* (Noirot, 1970).

The ichnofossil nests illustrate the niche diversification of termites as detritivores. Many of the Mesozoic and early Cenozoic termite nests are composed of an array of nest architectures similar to those of today, implying the use of dead and decaying roots, stems, groundcover, shrubs, and trees as food sources. The similarity of ancient and extant nest morphologies also suggests that ancient termites digested plant material through a symbiotic relationship with cellulose-digesting bacteria in their gut, similar to extant termites (Krishna and Weesner, 1970; Abe et al., 2000). Late Cretaceous wood-boring frass interpreted as termite fecal pellets has distinctive hexagonal or subhexagonal cross-sections (Rogers, 1938; Rohr et al., 1986). These distinguishing features, as observed in modern termite–plant associations (Light et al., 1930), preserve the association between termite, symbiotic gut bacteria, and cellulose. Other nest morphologies, especially those with large open cavities or several chambers occurring in close proximity to one another, suggest fungus gardening. The fungus grown in nests is used as food as well as to regulate the relative humidity of the nest (Noirot, 1970).

6. Architectures of bee nests: solitary to social nests

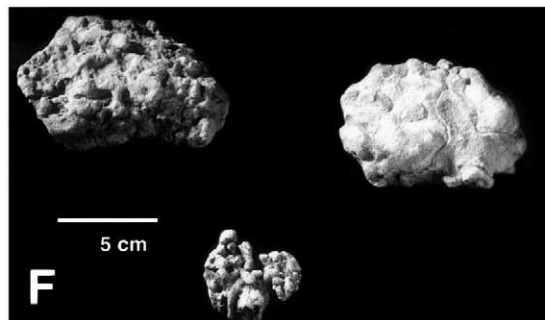
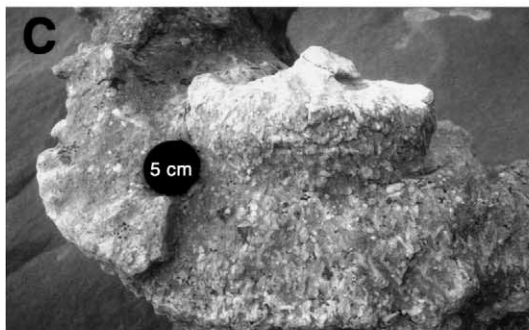
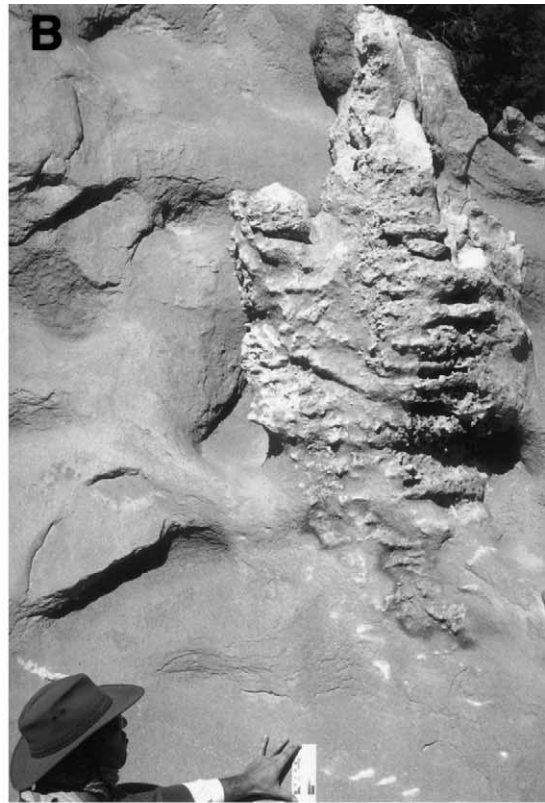
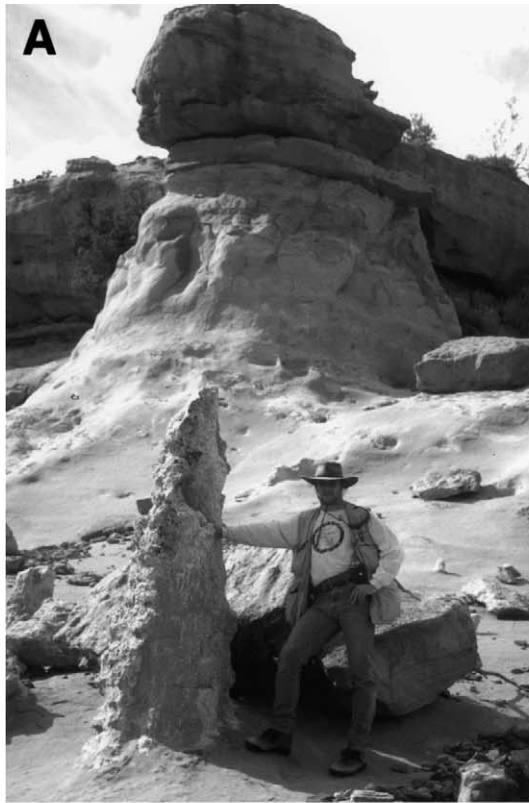
Bees are most diverse in subhumid and arid to semiarid climates, nesting in well-drained soils with abundant vegetation (Sakagami and Michener, 1962; Michener, 1974). They are, however, also found in subtropical and tropical climatic settings. Some nests are excavated and constructed in soil and wood, including hollow stems

and branches, while others are constructed in abandoned rodent burrows and fractures in firm and hard substrates (Stephen et al., 1969). The primary functions of bee nests are protection, brood rearing, and food storage. These functions vary with respect to the degree of sociality. The number of individuals per nest ranges from one female and a few offspring to 60 000 adult honeybees and as many as 180 000 or more individuals in a tropical stingless bee colony (Michener, 1974). For the most recent and thorough review of the bee systematics and associated behavior, consult Michener (2000).

Solitary species construct nests that are similar in basic structure to those of primitively eusocial species in the same family (Michener, 1974). Sakagami and Michener (1962) and Stephen et al. (1969) concluded that within the Halictidae there is no obvious correlation between the degree of sociality and the nest structure, such that some highly social bees construct simpler nests than those constructed by colonial or semisocial bees. Thus, a nest constructed by a lone bee can be similar to one constructed by several bees working together. In some species, nests of solitary, parasocial, and primitively eusocial bees are similar. For this reason, I will discuss the architecture of modern bee nests that are the result of solitary to social behavior and present ancient examples that were constructed most likely by bees with various degrees of social behavior.

6.1. Nests of extant bees

Nests of extant burrowing species (see Figs. 3 and 4) have a wide range of architectures that are excavated and constructed in subterranean and arboreal settings (Stephen et al., 1969). Arboreal nests include those that contain mud or resin cells cemented or constructed in hollow stems, branches, and tree trunks and bored into wood (Michener, 1974) as well as those without mud or resin cells. Nests are used for rearing broods in individual cells or cell clusters or combs and are where females spend most of their time while not foraging. Some nests are excavated exclusively, and cells are not lined or reinforced, whereas other nests are constructed exclusively of ma-



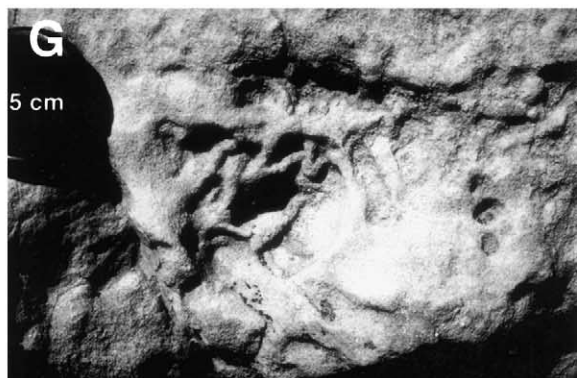
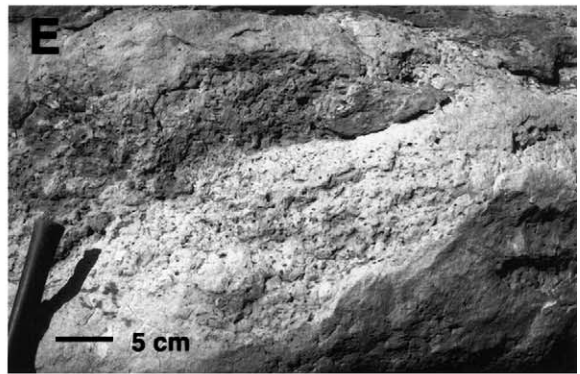
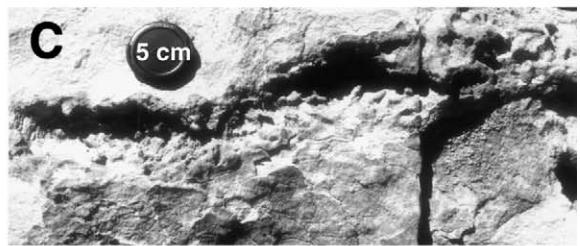
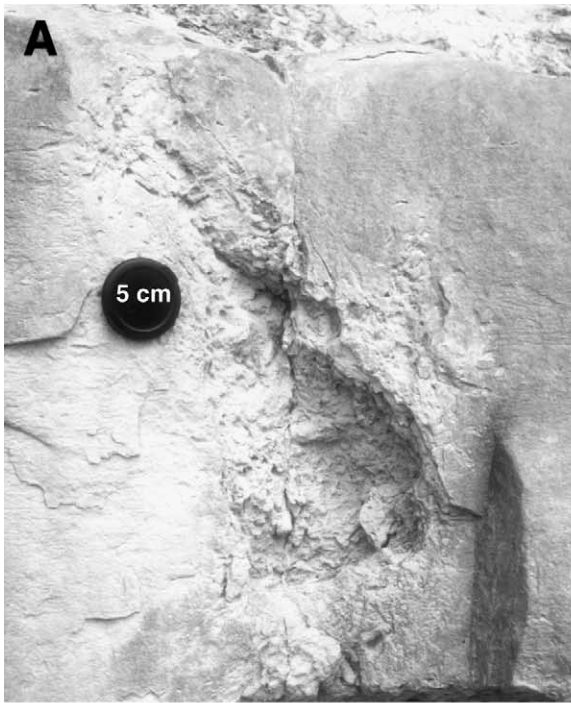
terials brought from outside the nest. Most often nests are constructed in soil that is moist enough for the cell form to be maintained. Non-burrowing bees, such as the honeybees, bumblebees, and some megachilids, construct nests in soil, rock, and wood cavities or in open areas with vegetation (Stephen et al., 1969).

Nests of nearly all solitary to eusocial bees have similar architectural elements of varying use and complexity (Sakagami and Michener, 1962; Stephen et al., 1969; Michener, 1974, 2000; Roubik, 1989). Subterranean nests are excavated and comprise shafts, tunnels, and cells with variable plasticity in nest architecture due to edaphic and seasonal factors. The basic structure of the nest is the brood cell (Stephen et al., 1969). The depth and complexity of the nests vary markedly both within and among species, ranging in depth below ground level from a few centimeters to more than 150 cm. The entrance to the nest may be marked by a **tumulus**, a pile of excavated material deposited outside the entrance, or a **turret** that is composed of excavated material that is smoothed and cemented with saliva. In some ground-dwelling eusocial bees, anastomosing rods are constructed in a funnel-shaped nest entrance and cavity that are used for resting and nest defense (Michener, 1974). The **main burrow** leads from the entrance to the brood cells either directly or through one or more lateral burrows. A main burrow that is more or less vertical is termed a **shaft**; if it is subhorizontal it is termed a **tunnel**. These burrows can contain straight to tortuous shafts and tunnels with the full range occurring in one nest. The burrows may be lined, and some are smoothed; however, burrows leading to cells and cell clusters are reinforced with saliva or se-

cretions from the Dufour's gland. Some nests contain a **blind burrow** that is the extension of the main tunnel below the occurrence of brood cells, which drains water that enters the nest, is a source of excavated material for cell construction, or is used for hibernation or possibly as a refuge from predators (Sakagami and Michener, 1962).

The **brood cell** is constructed by an adult and is a compartment in which a single larva is reared. The dominant shape of cells constructed by bees living in soil, such as the halictids, anthophorids, and adenids, has a weakly to strongly developed flask shape, with the widest part closest to the rounded termination of the cell and the narrowest part at the entrance (Michener, 1974, 2000). Cells constructed by bumblebees, stingless honeybees, and true honeybees are test tube-shaped, spherical, ellipsoidal, capsule-shaped, or hexagonal. The cell symmetry ranges from symmetrical to asymmetrical or curved. Cells in any nest are for the most part of uniform size and shape, but specialized cells or pots are constructed by higher bees that are used for food storage and for development of future queens or drones (Michener, 1974). The cell wall typically has a shiny, smooth appearance because the adult bee polishes the wall with its pygidial plates and smears clay or secretions from the Dufour's gland on the wall, which polymerizes to form a thin to thick waterproof membrane of wax or polyester like that secreted by the Colletidae, or made of wax as in the corbiculate Apidae (Michener, 1974; Batra, 1984). Cells range in number from one to several thousand per nest, with the highest cell numbers occurring in highly social bees (Stephen et al., 1969). Brood cells constructed in burrows are rarely an excavated space but are usually constructed and

Fig. 9. Ichnofossil termite nest morphologies in the eolian deposits in the Recapture Member of the Upper Jurassic Morrison Formation outside Gallup, New Mexico, USA. (A) Portion of subterranean ichnofossil nest that most likely originated at the paleosurface beneath the blocky sandstone deposit that delineates the boundary between the Recapture and Westwater Canyon Members of the Morrison Formation; person is approximately 1.9 m tall. (B) Portion of subterranean ichnofossil nest that shows layered construction of levels with the nest composed of smaller rooms and galleries of the endoecie; note deeper chambers adjacent to 10-cm scale. Also note the lack of primary bedding, which is destroyed from nearly 100% bioturbation by simple galleries. (C,D) Two separate, natural cross-sections through portions of different subterranean ichnofossil nests that show a central open area surrounded by simple and compound galleries with in the endoecie; lens cap 5 cm; scale in cm. (E) Portion of subterranean ichnofossil nest showing large-scale branching morphology of nest; interior composed of interconnected chambers and galleries of a complexly constructed endoecie or periecie. (F) Chambers eroded from larger subterranean nests; punky texture is interpreted to reflect cast of fungus garden within the chamber.

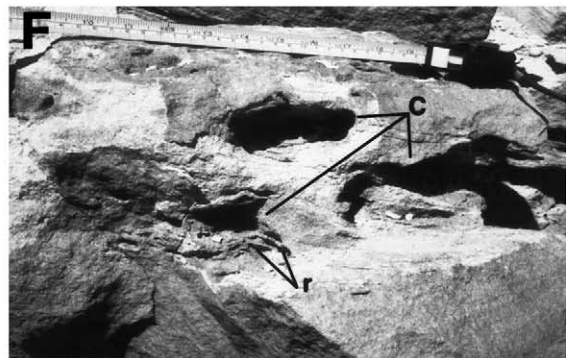
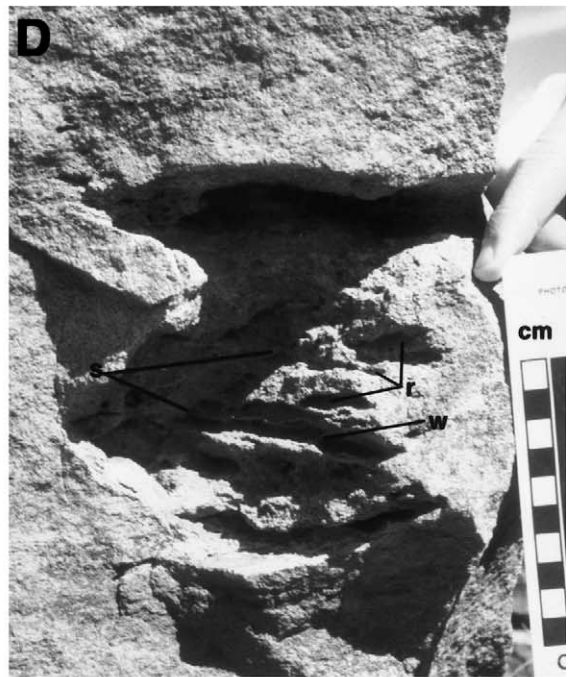
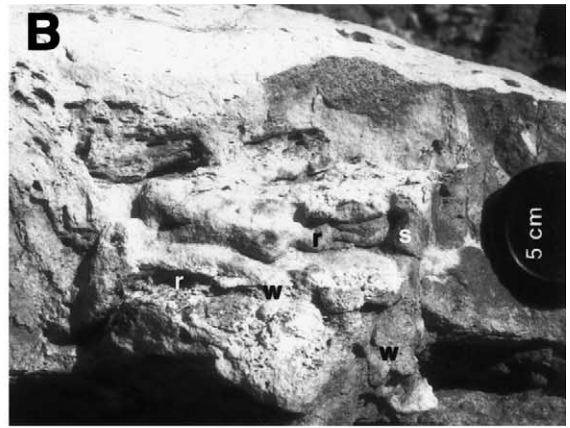
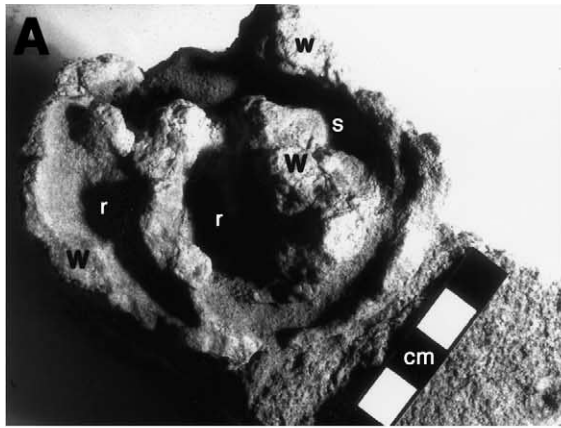


modified cell walls or at least partitions between cells that have been excavated in the substrate or constructed in a cavity. If many cells share walls, they are termed **cell clusters** or **combs**, depending on the number of attached cells. These are surrounded by burrows or air space and are supported by a series of pillars constructed from the substrate. The term **comb** is more commonly used for cells that are separated by thin walls and occur in single or back-to-back constructed layers of hexagonal cells in large numbers (Michener, 1974). Cells are of roughly the same size as the emergent adult. These cells are constructed in a similar fashion in decayed and sound wood. In nests of some bumblebees, a cell is continually enlarged as several larvae grow within one cell. In rare examples, larvae are reared in a common space in a woody, hollow stem or in a boring made by another insect (Michener, 1974). An egg is laid in each cell where a **provision** of pollen, nectar, and other plant materials is placed as a small spherical to elliptical loaf; in some bees, as in the Colletidae, this provision is liquid consisting primarily of nectar and some pollen. This material feeds the larva until it metamorphoses to an adult. In most nests, each cell is sealed with a **cap** from the outside by an adult bee. The cap may be constructed of excavated soil or wood material as a spiral, conical, flattened, or woven plug after oviposition. Within the cell, a cocoon of silk from the salivary glands is spun by the larva prior to pupation. Most larvae spin cocoons before defecation, and the larvae's feces are left inside the cocoon. Many bee larvae inside the cell,

however, do not spin cocoons (Michener, 1974, 2000).

Nests of the highly eusocial Meliponini are surrounded by material composed of a mixture of wax (cerumen), resin, or, sometimes, vegetation, mud, or feces, which forms an envelope around the whole **nest cavity** called **batumen**. The only openings are the entrance and small perforations for ventilation. Layers of this material surrounding the brood chamber are called the **involucrum**. In hollow trees, **batumen plates** are used to seal the nest off from the unused portions of the tree (Michener, 1974, 2000). The structures within the nest cavity are supported by **pillars** and **connectives** made of wax or resin. The pillars support the combs, while connectives support the various sections of the involucrum and comb and pillar support system. These types of nests contain elaborate entrance tubes of various shape and size. In their nests the Meliponini use specially constructed **pots** for the storage of honey and pollen, which are quite different from the brood cells (Fig. 3). The pots are either spherical, capsule-shaped, or elongate cone-shaped containers approaching the appearance of organ pipes. These pots occur in clusters segregated, intermixed, or outside the brood chamber (Michener, 1974). Brood cells are constructed as clusters or combs, or an intermediate between cluster and comb arrangement. The combs are aligned either horizontally, spirally, or, in a few species, vertically and back to back so that the cells open laterally in the opposite direction. This last example is similar to the comb arrangement of the highly eusocial Api-

Fig. 10. Ichnofossil termite nest morphologies in alluvial deposits of the Upper Jurassic Morrison Formation of Colorado and Utah, USA. (A) Subterranean ichnofossil nest with galleries in the wall of the nest between the endoecie and the periecie in the Salt Wash Member of the Henry Mountains, Utah; note the endoecie is connected to the surface and may have had a small exoecie. (B) Natural cross-section through the endoecie of an ichnofossil nest in the Salt Wash Member near Green River, Utah; note the thickened wall that separated the endoecie from the periecie and the preserved remnants of chambers. (C) Natural transverse cross-section through an ichnofossil nest constructed in the secondary rhizolith of a tree in the Salt Wash Member near Ticaboo, Utah (modified from Hasiotis, 2002). (D) Natural vertical cross-section through an ichnofossil nest showing anastomosed galleries and remnants of small chambers in the Salt Wash Member near Naturita, Colorado (modified from Hasiotis, 2002). (E) Natural quasivertical cross-section through an ichnofossil nest that shows concentrated anastomosed galleries in the Brushy Basin Member near Naturita, Colorado. (F) Natural vertical cross-section through an ichnofossil nest showing an internal partition that formed two levels that probably contained smaller rooms in the Salt Wash Member near Aneth, Utah; note several galleries that radiate away from the calie with a large compound gallery to the left of the nest. (G) Natural transverse cross-section through a concentrated ichnofossil nest showing interconnected galleries with two chambers in the center in the Salt Wash Member near Ticaboo, Utah.



ni, or true honeybees (Michener, 1974, 2000). True honeybees construct wax combs of elongate, hexagonal cells in the open or in cavities of hollow trees or in the ground. In these nests, honey is stored within the hexagonal cells. The cells remain open where food for the larvae is provided progressively – that is the larva is fed by the adults as it grows. Cells that contain males are larger than those of the workers, while cells that hold future queens are irregularly shaped ellipsoids and hang as individual cells from the brood combs (Michener, 1974, 2000).

Nests (Fig. 4) can be classified according to the type of cell arrangement (Sakagami and Michener, 1962; modified from Malyshev, 1935). **One-celled nests** contain a single cell at the bottom of the burrow. **Branched nests** are composed of a main burrow from which several lateral burrows diverge and terminate in single cell; the lateral burrows can be reduced so that the cell originates directly from the main burrow. Nests with **linearly arranged cells** have cells that are built end to end in series that may occur in one (allodalous) or more (parodalous) tunnels from the main burrow. **Chambered nests** contain cell clusters that are at least in part surrounded by an excavated cavity (synodalous) or tunnels, including the main shaft.

Characteristics of the nest architecture constructed by bees must be used in combination to identify trace fossils as the products of bee activity (Stephen et al., 1969; Michener, 1974, 2000; Rozen, written communication, 1995; C.D. Michener, personal communication, 2001). Among the most diagnostic features of some bee nests are the cell closures that form a spiral pattern, often referred to as a spiral cap. Not all bee cells, how-

ever, make spiral enclosures, and some wasps' cells have a spiral pattern in cell closures as well (e.g., Gess, 1996). Cell closures are visible only on cells where an adult has not emerged after pupation. Another diagnostic feature of many bee cells is the smooth, internal cell walls lined with very fine-grained clay or a waxlike secretion. Yet, cells that were not completed or that were weathered prior to burial would not have smooth linings. The presence of pollen, spores, or other vegetable-product stores within the cell structure is diagnostic of bee cells. Pollen, spores, and fecal material can also be found along the interior of the cell walls deposited there by the larva as it consumes the provisions. Impressions in the cell wall or remains of a cocoon may be present in the cell, as well as the remains of an immature larva, pupa, or an adult. These features, however, have low preservation potential. The least likely parts of the nest to be preserved are the entrance, shaft, and portions of the tunnels leading to the cells, cell clusters, or combs. Shafts and tunnels leading directly from the cells and from the entrance may be preserved but are most often destroyed by bioturbation by soil biota and by pedogenesis because they are not as durably constructed as the cells themselves (e.g., Michener, 1974). Besides, if they are not in direct connection with variably flask-shaped, lined cells, such shafts and tunnels may have been produced by other soil organisms and could be confused with bee-constructed structures. All these features used together insure more accurate diagnoses of ichnofossil nests constructed by bees, rather than by wasps, beetles, moths, and other cell-forming soil insects (Hasiotis et al., 1996).

Fig. 11. Ichnofossil termite nest morphologies in alluvial deposits in the Petrified Forest Member of the Upper Triassic Chinle of Petrified Forest National Park, Arizona, USA. (A) Natural transverse cross-section through an endoecie of an ichnofossil nest that shows constructed walls (w), rooms (r), and spiral ramp (s) (modified from Hasiotis et al., 1994). (B) Natural quasivertical cross-section through an endoecie of an ichnofossil nest that shows constructed walls (w), rooms (r), and spiral ramp (s). (C) Natural vertical cross-section through a complete endoecie of an ichnofossil nest that shows constructed walls (w), rooms (r), and spiral ramp (s); note that the space of the rooms is preserved with sediment, while the floor (f) of the room has weathered away because of its finer texture from the upper part of the Monitor Butte Member at the Happy Jack Mine. (D) Natural vertical cross-section through an endoecie of an ichnofossil nest that shows constructed walls (w), rooms (r), and spiral ramp (s), galleries, and larger spaces termed caves (modified from Hasiotis et al., 1994). (E) Natural vertical cross-section through an ichnofossil of a diffuse polycalic nest associated with permineralized rhizoliths (pw) that shows excavations around the rhizoliths clusters of rooms (r) or small chambers. (F) Natural vertical cross-section through an ichnofossil of a diffuse polycalic nest associated with the ichnofossils in D and E that shows calices (c) with remnants of internally partitioned rooms (r).

Table 2
Solitary to eusocial bee nest ichnofossils in the geologic record

Age and formation	Locality	Nest architecture	Ichnotaxonomy	Source
Triassic				
Chinle Formation	Petrified Forest National Park, Arizona	Flask-shaped cells in paleosols (isolated, clustered, shared walls) Flask-shaped cells in wood	cf. <i>Celliforma</i> cf. <i>Celliforma</i>	Hasiotis et al., 1995, 1996, in preparation b
Jurassic				
Morrison Formation	Colorado Plateau and vicinity	Flask-shaped cells in paleosols; isolated, clustered, shared walls	cf. <i>Celliforma</i> , cf. <i>Uruguay</i>	Hasiotis and Demko, 1996, 1998; Hasiotis, 2002; Hasiotis et al., in preparation b
Cretaceous				
Lower Dakota Formation	Black Mesa, Arizona	Flask-shaped cells from vertical shafts and horizontal galleries	<i>Celliforma dakotensis</i>	Elliot and Nations, 1998
Paleogene				
L. K–T Ascension Formation	Nueva Palmira, Uruguay	Flask-shaped cell, antechamber Clustered cells arranged in rows Helicoidal cell arrangement	<i>Palmiraichnus castellanosi</i> <i>Uruguay auroranormae</i> , <i>U. rivasi</i> <i>Ellipsoideichnus meyeri</i>	Roselli, 1987; Genise and Bown, 1996; Genise and Hazeldine, 1998a,b
Pal.–Eoc. Claron Formation	Markagunt Plateau, Utah	Flask-shaped cells in paleosols (isolated)	cf. <i>Celliforma</i>	Bown et al., 1997
Pal.–Eoc. Mercedes Formation	Uruguay	Flask-shaped cells	cf. <i>Celliforma</i>	Veroslavsky and Martinez, 1996; Veroslavsky et al., 1997
Eoc. Willwood Formation	Worland, Wyoming	Flask-shaped cells in paleosols (isolated)	cf. <i>Celliforma</i>	Hasiotis and Bown, unpublished data
Eoc. Gran Salitral Formation	La Pampa Province, Argentina	Flask-shaped cells in paleosols; isolated, clustered, shared walls	<i>Celliforma germanica</i> , <i>C. roselli</i> , <i>Rosellichnus</i> isp.	Melchor et al., 2002
Eoc. Bridger Formation	Wyoming	Flask-shaped cells (isolated)	<i>Celliforma spirifer</i> , <i>C. nuda</i> , <i>C. germanica</i>	Brown, 1934, 1935
Oligo. Brule Formation	Badlands National Park, South Dakota	Flask-shaped cells extending horizontally from vertical shaft	<i>Celliforma ficoides</i>	Retallack, 1984
Neogene				
Mio. Pinturas Formation	Patagonia, Argentina	Flask-shaped cells in paleosols (isolated)	<i>Celliforma pinturensis</i> , <i>C. roselli</i>	Genise and Bown, 1994a,b
Mio. Collon-Cura Formation	Rio Negro Province, Argentina	Clustered ovoid cells in rows	<i>Rosellichnus patagonicus</i>	Genise and Bown, 1996
Mio. Hiwegi Formation	Rusinga Island, Kenya	Flask-shaped cells from vertical shafts and horizontal galleries	<i>Celliforma habari</i>	Thackray, 1994
Plio. Baynunah Formation	Abu Dhabi Emirate, UAE	Clustered ovoid cells in rows	<i>Rosellichnus arabicus</i>	Genise and Bown, 1996
Late Plio. Laetoli Beds	Laetoli, Tanzania	Flask-shaped cells in paleosols (isolated and clustered)	cf. <i>Celliforma</i>	Ritchie, 1987
Quaternary				
Pleistocene	South Australia	Cells with antechambers in calcrete (isolated)	<i>Celliforma bedfordi</i> , <i>C. septata</i>	Zeuner and Manning, 1976; Houston, 1987
Pleistocene	Wahiba Sands, Oman	Flask-shaped cells (isolated) Clustered ovoid cells in rows	cf. <i>Celliforma</i> <i>Rosellichnus arabicus</i>	Hasiotis et al., in preparation c
Pleistocene	San Salvador Island	Flask-shaped cells in vertical shafts	cf. <i>Celliforma</i>	White and Curran, 1988; this paper
Pleistocene	Kuala Lumpur, Malaya	Clustered hexagonal cells; combs	open nomenclature	Stauffer, 1979
Upper Pleistocene	Abu Dhabi Emirate, UAE	Clustered ovoid cells in rows	<i>Rosellichnus arabicus</i>	Genise and Bown, 1996

6.2. Ichnofossil nests

The identification of trace fossils interpreted to have been constructed by hymenopterans similar to extant bees (Table 2; Figs. 12–14) is based on comparison to the architectural and surficial elements of nests of extant bees (Figs. 3, 4, 12A) (e.g., Brown, 1935; Zeuner and Manning, 1976; Retallack, 1984; Houston, 1987; Ritchie, 1987; Thackray, 1994; Hasiotis et al., 1995, 1996; Genise and Bown, 1994a, 1996; Hasiotis and Demko, 1996; Bown et al., 1997; Kay et al., 1997; Elliot and Nations, 1998; Genise and Hazeldine,

1998a,b; Hasiotis et al., in preparation b,c). All the key morphologic features of subterranean and arboreal solitary to social bee nests have been found in ancient examples (Figs. 12–14), with the exception of spiral caps on pre-Tertiary cells and the conclusive findings of pollen within black spheres interpreted as provisions in Triassic cells constructed in wood. These interpretations were based on the consistent and unique construction of the brood cell. The Upper Triassic brood cells (Fig. 14) occur in linear and circular series in petrified conifer wood and as isolated, linear, cruciform, and clustered cells attached to vertical and

horizontal burrows in immature to moderately developed paleosols (Hasiotis et al., 1995, 1996, in preparation a,b,c). The Upper Jurassic brood cells (Fig. 13C,D) occur in isolated, linear, grouped, and clustered cells attached to vertical and horizontal burrows in immature to mature paleosols (Hasiotis and Demko, 1996, 1998; Hasiotis, in press). The Upper Cretaceous brood cells (Fig. 13B) occur as individual cells that branch from vertical and horizontal shafts in very immature paleosols (Elliot and Nations, 1998; Hasiotis et al., in preparation a,b,c). These Mesozoic ichnofossils are very similar to ichnofossil nests composed of flask-shaped brood cells in Paleogene, Neogene, and Quaternary deposits (Figs. 3, 4, 12, 13A).

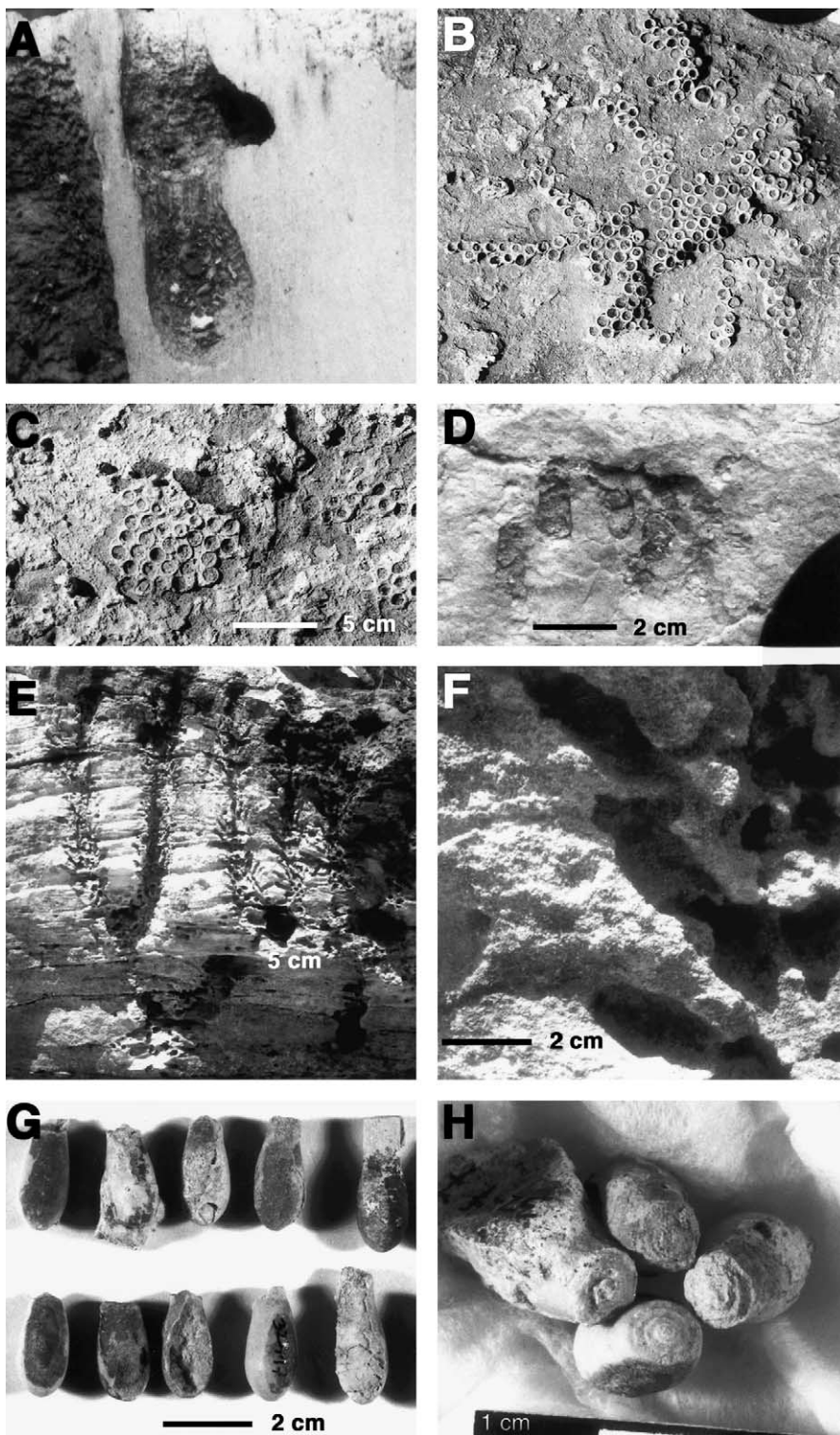
The interpretation of the ichnotaxa described from Mesozoic and Cenozoic continental deposits as bee nests is based on (1) the concentration of brood cells; (2) the size, shape, and arrangement of the brood cells; (3) clustered cells and their arrangement; and (4) the thickness of the external wall and presence of an antechamber (Figs. 12–14). Ichnofossil nests interpreted as having been constructed by bees can be generalized as simple to complex in architecture characterized by diverse brood cell arrangements, the number of cells (few to large numbers of cells), the distribution (vertical to horizontal distribution of cells in one or more rows or columns), and the replication in construction pattern (arrangement of brood cells, cell clusters, and combs in space and time). The range of variation of arrangements of brood cells and number of cells often relates to the degree of sociality exhibited by the constructors (e.g., Thackray, 1994; Genise and Bown, 1996; Elliot and Nations, 1998). Replication in the arrangement and number of brood cells is likely to be useful to delineate between a large accumulation of solitary nests and several ontogenetic phases of nest construction by semisocial to primitively social bees (i.e., Thackray, 1994; Hasiotis and Demko, 1996).

6.3. Behavioral and paleoecological implications

These ichnofossil nests preserve a range of solitary to social behavior of bees from the Triassic

to the present. Regardless of the evidence for the degree of sociality preserved by the bee nest ichnofossils, they indicate different innovations in food hoarding (Vander Wall, 1990), holometabolous brood rearing (Hasiotis, 2000), and nest defense (Wilson, 1971; Michener, 1974). The simplest nests range from a single cell at the terminus of the shaft to nests that were constructed with cells in series off of the shaft or within it. These types of cells indicate relatively short-term food hoarding by the adult on behalf of their offspring through the collection of provisions, which were sealed inside with the egg. This same pattern of cell provisioning is present for more behaviorally advanced bees to the point at which the siblings are fashioning and provisioning cells, while the mother (or queen) tastes the provisions prior to laying an egg and closing the cell (Michener, 1974). In unique cases, cells are reopened or never closed in order to reprovision the cell or feed the larva (Stephen et al., 1969; Michener, 1974); this type of behavior may not be distinguished in the geologic record from other nests where cells are provisioned before they are sealed.

Simple to complex ichnofossil nests that occur in paleosols represent a major innovation in subterranean holometabolous brood rearing because ground-dwelling bees evolved body fluids and construction techniques that (1) provide the egg and provisions some safety from parasites and predators in their subterranean surroundings; (2) enable the cell areas of the nests to drain off excess water or be submerged for short periods of time; and (3) allow the cells to keep out moisture yet maintain internal humidity so as not to spoil the provisions. The most advanced behaviors represented by Pleistocene ichnofossil nests interpreted as honeycombs of true honeybees imply that a high degree of cooperation was necessary to construct brood cells, collect pollen and nectar for provisions, defend the nest from invaders, and regulate the temperature of the nest (Michener, 1974). The size of an ichnofossil nest is likely to be proportional to the number of individuals in the colony. Most of the smaller ichnofossil bee nests probably represent one or several related individuals that constructed 5–24 cells (Stephen



et al., 1969), whereas larger and more complex ichnofossil bee nests were constructed by several related individuals to whole colonies of 100 000 siblings that constructed a single, large nest (Michener, 1974).

7. Architectures of wasp nests: solitary to social nests, cocoons, and combs

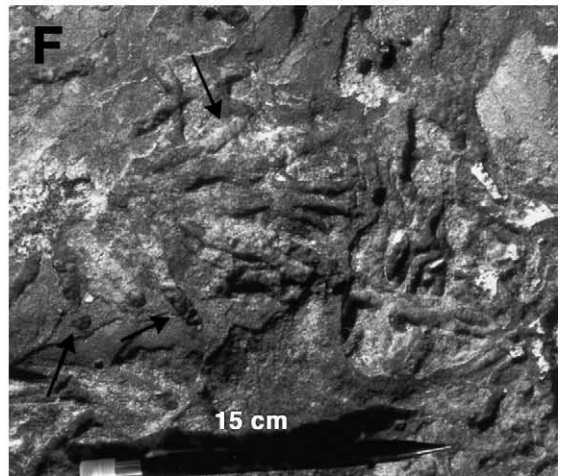
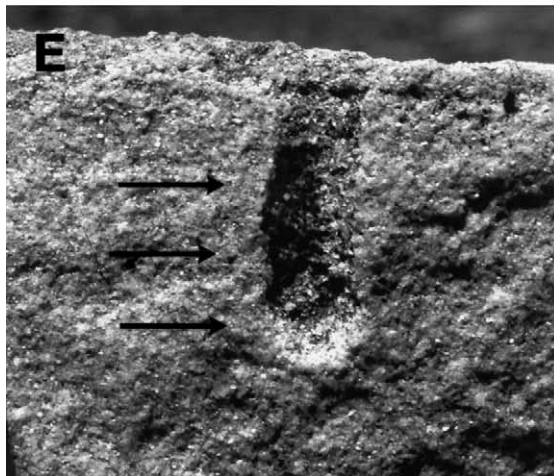
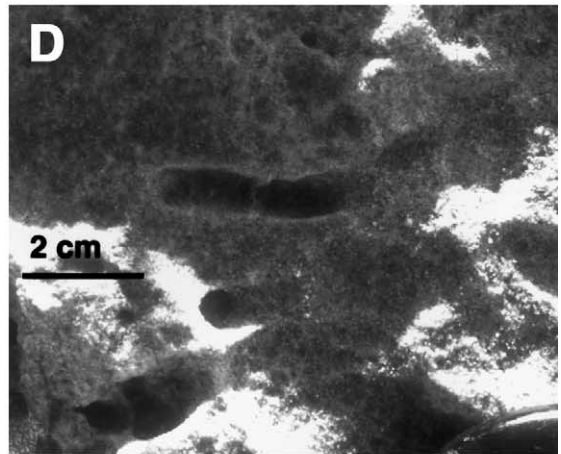
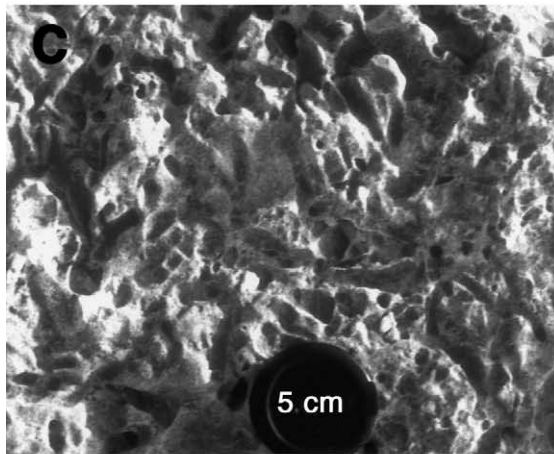
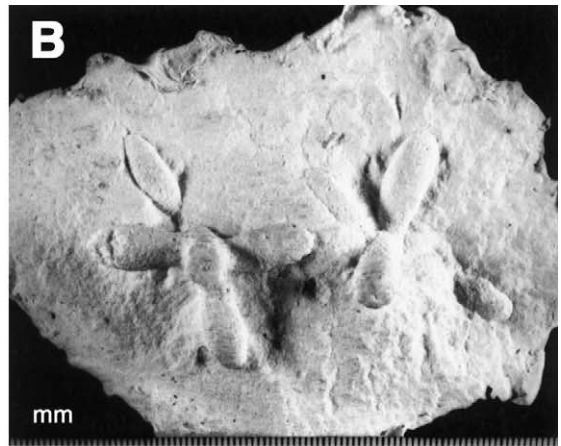
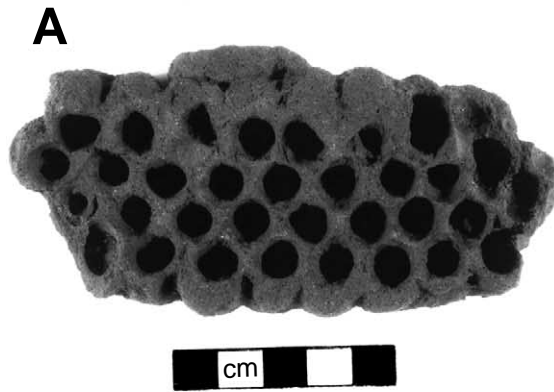
Wasps are a diverse group that includes the sawflies (Symphyta), digger wasps (Sphecidae), spider wasps (Pompilidae), pollen wasps (Masaridae), and the yellow jackets, hornets, and paper wasps (Vespoidea) (Evans and Eberhard, 1970). Of these, the Vespidae and a few members of the Sphecidae are social (Spradberry, 1973; Ross and Matthews, 1991). The most primitive wasps are parasites of plants that do not kill their hosts, whereas other primitive wasps are parasitoids to other insects and eventually kill their hosts (Evans and Eberhard, 1970). Nesting behavior and social organization in wasps range from solitary to eusocial, similar to that seen in bees (Evans and Eberhard, 1970; Ross and Matthews, 1991). The nests of solitary to eusocial wasps have various degrees of complexity that are similar to the nests of bees, but wasp nests are distinct in the details of bauplan, architecture, and materials used. Because of this close resemblance, the modern and ichnofossil, subterranean to arboreal nest morphologies of solitary to eusocial wasps are discussed here. Excellent reviews, detailed monographs, and references on wasp diversity, nesting, and behavior were given by Evans and Eberhard (1970), Iwata (1976), Spradberry (1973), Evans

(1985), Ross and Matthews (1991), and Gess (1996).

In general, wasps have a distribution similar to that of bees (Evans and Eberhard, 1970; Spradberry, 1973; Ross and Matthews, 1991). They appear to be most diverse in subtropical and tropical climates, but they are also common in environments with subhumid and arid to semiarid climates. Wasps nest in an array of subterranean to arboreal settings, where the nests are attached to leaves, branches, cliff faces, and other protected areas. Some nests are excavated and constructed in loose to hard soils and in hollow stems and branches of trees, while others are constructed in abandoned rodent burrows and fractures in both firm and hard substrates (Evans and Eberhard, 1970; Spradberry, 1973). The primary function of wasp nests is to reduce the mortality rate of immature stages (Evans, 1977; Cowan, 1991). The nests of sphecids and vespids provide a site for various degrees of protection, brood rearing, and food storage. These functions vary with respect to the degree of sociality. The number of individuals per nest ranges greatly and is correlated to the size of the nest. Nests of solitary sphecids and presocial vespids are made by a single female. Smaller nests constructed by social wasps (Vespidae) contain a queen and several dozen workers, while other nests may have tens to hundreds of queens with hundreds to tens of thousands of workers. In one extreme, composite nests contain as many as 300 000 workers, with the nest weighing approximately 500 kg (Spradberry, 1973).

There appears to be a correlation between the degree of sociality and the nest structure in

Fig. 12. Extant and ichnofossil nests constructed by bees (Hymenoptera: Apoidea). (A) Cross-section of a flask-shaped brood cell of an extant nest of a carpenter bee (Anthophoridae: Xylocopinae) that was constructed in a pine tree with the main part of the nest constructed to the left of the cell; note the sculpted surficial morphology on the burrow walls. (B) Pleistocene bee nest composed of cell clusters from the Wahiba Sands in Oman (Hasiotis et al., in preparation c); cells are slightly flask-shaped and have internally smooth walls. (C) Pleistocene bee nest composed of cell clusters constructed similar to *Rosellichmus* isp. from the Wahiba Sands in Oman (Hasiotis et al., in preparation c). (D) Natural vertical cross-section of an Oligo–Miocene simple bee nest composed of closely associated flask-shaped cells from the Aragon Province, Spain; note the preservation of the main tunnel and smooth cell walls. (E,F) Natural vertical cross-section (E) and close-up (F) of a Pleistocene bee nest constructed in an eolian carbonate dune from San Salvador Island, Bahamas; note the flask-shaped cells and remnants of smooth cell walls in (F). (G,H) Casts of flask-shaped cells from the Eocene Broken Arrow Formation in Montana; note spiral enclosures (H) constructed by the adult bee and the presence of the caps suggests that egg or larva did not successfully develop. The extension on some of these cells may represent an antechamber (modified from Hasiotis, 2002).



wasps; however, some primitively eusocial and highly eusocial wasps also construct simpler nests similar in architecture to those of solitary wasps (Wenzel, 1991b). Nest architecture of wasps has been used to identify genera, and many details of nest architecture are thought to be species-specific (Ross and Matthews, 1991; Wenzel, 1991b). With few exceptions, the ontogenetic analysis of nest construction by vespids suggests that differences in early phases of nest construction generally distinguish higher, more anciently derived taxa, while differences in later phases distinguish lower, more recently derived taxa (Wenzel, 1991b). It is difficult to distinguish between the simple nests of different families of solitary and presocial wasps, but some forms are distinct enough to determine which were constructed by presocial vespids (e.g., Cowan, 1991). Nests of social sphecid wasps are distinguishable from those of social vespid wasps in that the sphecid nests (1) are much simpler; (2) are composed of silk produced from the females; (3) incorporate pieces of sediment and plants into the construction; (4) were occupied by renters; and (5) do not increase in size through time and are based on the amount of raw materials present at the onset of nest construction (Matthews, 1991). The social sphecids are unique because in all other eusocial insects the nest size is increased through time along with the increase in the number of individuals in the colony. The result of this type of behavior is that social sphecid colonies are limited and very small in number of individuals compared to the social vespids (Matthews, 1991).

7.1. Nests of extant wasps

Nest architecture ranges considerably among

solitary, presocial, primitively eusocial, and eusocial wasps (Figs. 5 and 6) (e.g., Evans and Eberhard, 1970; Iwata, 1976; Spradberry, 1973; Ross and Matthews, 1991; Zahradník, 1991; Wenzel, 1991b; Gess, 1996). Wasp nests are excavated or are constructed from mud or vegetative matter. The cell is also the common building block in wasp nests (Fig. 5), but they are test tube- to capsule-shaped and constructed differently from those of solitary to primitively social bees (Apoidea). Cells in solitary and presocial sphecid and vespid wasp nests can be constructed in parallel series in soils and in hollow stems and are partitioned with mud or vegetable matter (Cowan, 1991). Some nests in hollow stems are so simple that they have no dividers between masses of provisioned eggs (Evans and Eberhard, 1970; Cowan, 1991). Cells can also be constructed in short, individual tunnels (singly or in pairs) originating from the shaft or constructed at the terminus of the shaft. Some simple nests are highly specialized to form small pots or loosely to well-organized masses of cells, such as those constructed by potter wasps and mason wasps (Spradberry, 1973; Cowan, 1991). The most complex nests (Fig. 6) are constructed of tens to hundreds to tens of thousands of juxtaposed cells in a series of combs of variable size, shape, and design, with or without an external envelope to protect the nest (Ross and Matthews, 1991; Zahradník, 1991).

In nearly all soil nests of solitary wasps (also known as nest holes), the nest is excavated by the female by using one or more of the following techniques: raking, pushing, pulling, and carrying (Evans and Eberhard, 1970; modified from Olberg, 1959). The nest contains architectural components similar to those of bees: shaft, tunnel,

Fig. 13. Cenozoic and Mesozoic ichnofossil nests constructed by bees (Hymenoptera: Apoidea). (A) Paleogene ichnofossil nest of a subterranean cell cluster, designated *Uruguay auroranormae*, from Nueva Palmira, Uruguay; cells with internally smooth walls (modified from Hasiotis, 2002). (B) Latex cast of flask-shaped cells arranged in a cruciform pattern constructed from shafts in the Upper Cretaceous Dakota Formation, northeastern Arizona. (C,D) Natural transverse cross-section of hundreds of flask-shaped cells constructed as isolated cells or in series (D) in the Salt Wash Member of the Upper Jurassic Morrison Formation, southeastern Utah; note the remnants of a divider between cells in D. (E) Natural vertical cross-section through an individual flask-shaped cell that is slightly curved in the Salt Wash Member of the Upper Jurassic Morrison Formation, southeastern Utah; note the remnants of a smooth internal wall (arrows) and compacted, aligned sand grains. (F) Natural transverse cross-section of a single nest with flask-shaped cells constructed at the end of short tunnels in the Salt Wash Member of the Upper Jurassic Morrison Formation, southwestern Colorado; note some of the well-preserved cells (arrows).

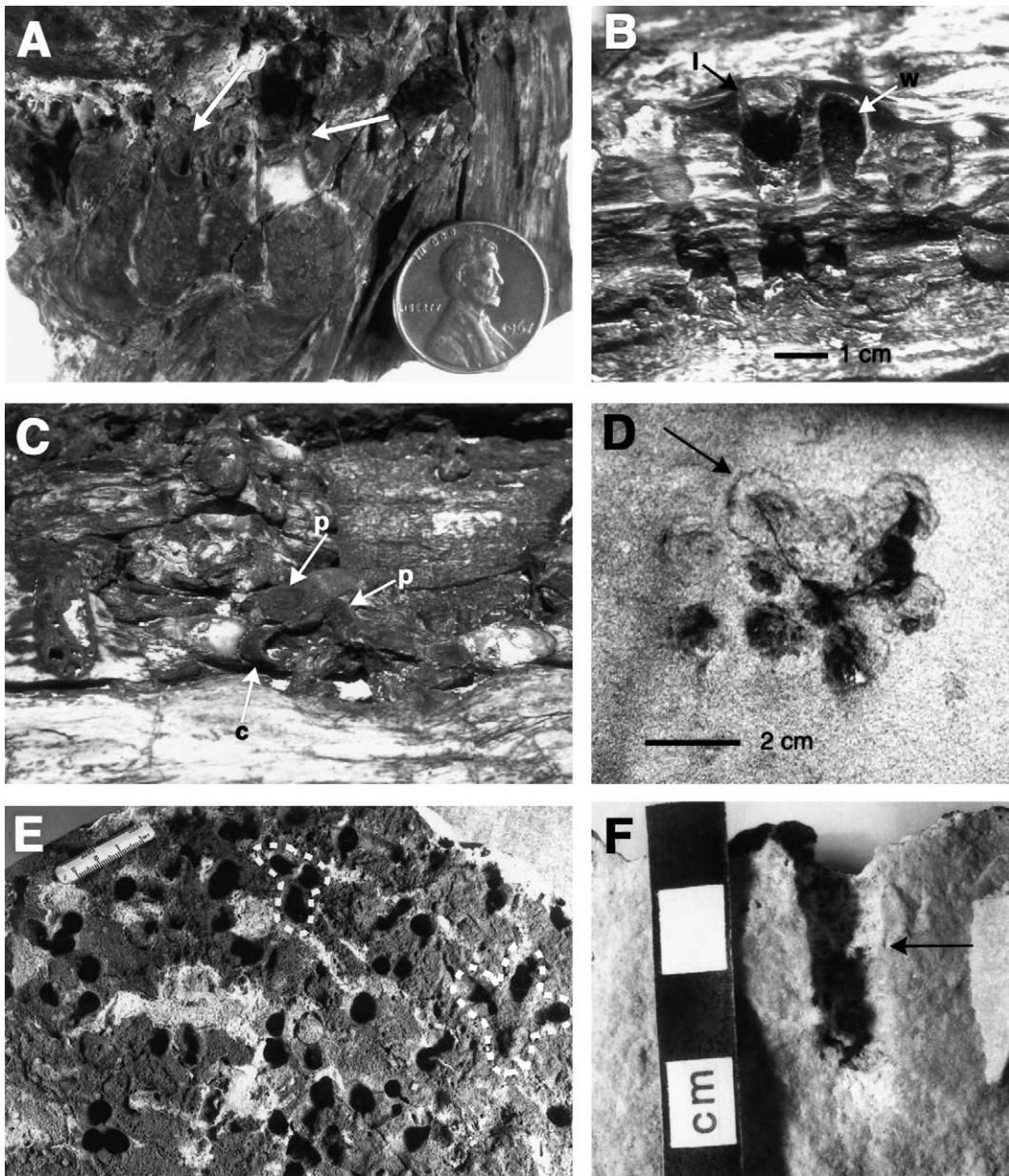


Fig. 14. Ichnofossil nests interpreted to have been constructed by bees (Hymenoptera: Apoidea) from the Monitor Butte and Petrified Forest Members of the Upper Triassic Chinle Formation, Petrified Forest National Park, southeastern Arizona. (A) Flask-shaped cells that were excavated in coniferous wood containing feces along the cell walls, and later permineralized during diagenesis; note cell closures constructed from outside the cell (arrows). (B) Flask-shaped cells excavated in coniferous wood that show cell linings (l) and the probable impression of the weave of a cocoon (w) in another cell. (C) Flask-shaped cells excavated in coniferous wood that show externally constructed caps (c) and what appear to be provisions (p) in the base of some of the cells. (D) Natural transverse cross-section through a cell cluster of 11 cells that share constructed walls (arrow) in an immature paleosol developed in a proximal splay deposit. (E,F) Natural transverse cross-section through an association of flask-shaped cells probably from the same nest that were constructed in isolated to cruciform patterns (dashed line) in an immature paleosol developed in a proximal splay deposit. (F) Close-up of cell with part of the closure (arrow) preserved and the antechamber above.

and cells. The sediment within the cell is pushed into place with the head, tip of the abdomen, or the appendages and has no lining (Evans and Eberhard, 1970; Evans, 1985). The cells are provisioned with adult and larval insects that have been paralyzed or killed by the adult wasp; only the pollen wasp provisions its cells with plant products (Evans and Eberhard, 1970; Gess, 1996). After the cell is provisioned and the egg is laid, the cell is either left open or is blocked by the adult with sediment backfilled from above at the nest entrance or blocked near the cell opening with material from new cell excavations (Evans and Eberhard, 1970). Apparently unique to solitary sphecids is the construction of **accessory burrows** that are quarries for material to close the nest entrance, test burrows, or devices that deter parasitoids. Prior to pupation the larva spins a cocoon, which may take several days to complete (Evans, 1985). The only portion of the original nest and cell constructed by the female that is reinforced is that part where the cocoon is spun by the larva.

Thus the cells of wasp nests are not constructed and encapsulated as are those of bees, which maintain a flask shape to capsule shape because of their construction and lining with bodily secretions or clay (Sakagami and Michener, 1962; Stephen et al., 1969; Michener, 1974). For these reasons, even the simplest nests of bees and wasps can be distinguished from each other in modern and ancient settings. Exceptions to this type of wasp behavior are the nests of pollen wasps and mason wasps, both of the family Vespidae. Pollen wasps provision cells with plant materials, but they construct cells in the same manner as other wasps (Gess, 1996). Mason wasps construct elliptical mud cells within hollow stems, but the cells are also similar to those of other wasps (Spradberry, 1973; Cowan, 1991). In both, the part of the nest most likely to be preserved is that which was reinforced by the pupation cocoon.

Solitary and presocial vespids are classified as (1) burrowers that excavate nests in soils; (2) renters that occupy and modify pre-existing structures; and (3) builders that construct an entire nest from sediment or masticated plant materials (Iwata, 1976; Cowan, 1991). Burrowers construct

nests similar to those of the sphecids (see earlier discussion). Solitary and presocial mud dauber nests are constructed by builders that use moistened pellets of mud which are placed in circular to hemicircular rows to form unique nest forms composed of several to many cells. Renters usurp burrows from other insects or modify abandoned burrows of beetles or other wasps (Cowan, 1991). Solitary vespids amass provisions in the cells in their nests and close them after the egg is laid (Evans and Eberhard, 1970). Presocial vespids practise delayed to progressive provisioning, where the larva is fed until it spins its cocoon. One to several females may take part in provisioning and guarding the nest, which usually has two cells that diverge from a common shaft or tunnel (Cowan, 1991).

Primitively and highly eusocial wasps construct combs of hexagonal cells (Spradberry, 1973; Wenzel, 1991b) that are similar to those found in nests constructed by bees of the genus *Apis* (Michener, 1974, 2000). The wasp nests are made mainly of paper, but in some species mud or a mixture of mud and vegetable matter is used (Turillazzi, 1991; Wenzel, 1991b). The cells remain open where each larva is fed by an adult sibling. The larva scratches the side of its cell to alert the adults to feed it. The cells are closed by the larva as it spins a cocoon for pupation.

Eusocial wasps construct nests almost entirely of vegetable fibers, with the exception of the Central and South American *Polybia*, whose nest envelope is constructed entirely of mud. The primitively eusocial Stenogastrinae build nests of mud or with a mixture of mud and vegetable matter (Evans and Eberhard, 1970). Spradberry (1973) provided a general account of how a eusocial vespid wasp colony constructed its nest through a single season. Raw materials for nest building are vegetable mainly and include wood fibers from solid, fungus-stained, and decayed trees and bark. Gnawing on the bark of living trees also provides nourishment from the sap that flows from the wound. Ringing of the bark can also cause the death of smaller branches of trees. Other living plants used for nest construction include cortical material from non-woody plants. Pulp is stripped off backwards from the wood or plant

grain slowly via biting and scraping with the mandibles. A ball of material is collected and carried in the mandibles back to the nest, where it is thoroughly masticated and mixed with saliva for construction. Sand, silt, and clay particles can also be incorporated in the construction of cells, combs, and the envelope.

The queen initiates the colony by building the **embryo nest** (Fig. 6A). The nest structure is composed of **carton** or wasp paper, which is a form of paper mâché that results from the drying of masticated, moistened wood pulp. This nest is anchored by the **main pillar** to the roof of the cavity as well as to overhanging roots. The nest is composed of a cluster of **cells**, the **comb**, that share walls. The original comb nest is expanded by the workers by adding to the periphery of the original comb and by the addition of new combs that are suspended above and below the original by **pillars**, also known as **pedicels**. The combs eventually resemble sheets of umbrella-shaped structures with the cell openings dorsal of the comb. If the nest is subterranean, the original **cavity** is enlarged to make room for additional combs as the colony increases. A 1–2-cm space exists in the cavity at any one time between the wall and the envelope to allow the workers to excavate soil and build the envelope. Soil is loosened and scraped from the wall by using moisture from water and saliva collected from the larvae. Some soil pellets are carried away to various distances from the nest for disposal, while others are used to close up other burrows and root tubes encountered while enlarging the cavity. The combs are surrounded by an **envelope** constructed predominantly of vegetable fibers, but it can also be constructed of mud and is occasionally connected to the combs by rows of pillars, in a series of shelves. The purpose of the envelope is to form an insulating wall around the combs. Stones that are too heavy to be removed from the nest by the workers accumulate at the base of the cavity. Stones that are removed are found at the nest entrance and grade from coarser to finer away from the entrance.

As the nest size increases, the envelope is torn down from the inside and rebuilt from the outside. Queen cells are larger than worker cells and are added to the periphery of combs containing

the worker cells. Queen cells are eventually added as several combs at the base of the nest. In *Paravespula vulgaris*, for example, worker cells range from 4 to 5 mm in diameter and from 11 to 17 mm in length. Queen cells range from 6 to 7 mm in diameter and from 12 to 16 mm in length. Older combs of the nest that are no longer in use due to the successive accumulation of fecal pellets in the cells are papered over. This process also insulates the active part of the nest and keeps it free from diseases that may stem from decomposing feces. A nest containing about 12 000 cells may be built over a 4-month period with limited communication between nest members as construction progresses. In the example of *P. vulgaris*, there are never more than 50 cells in the embryo nest constructed by the founding queen. A mature nest typically has five to nine combs and may have as many as 14 combs. Perennial nests may have 30 or more combs. Cells range from 1000 to 7000 in immature to intermediate nest stages up to as many as 20 000 or more cells in mature nests.

Construction and maintenance of nests by social wasps requires considerable energy (Spradberry, 1973). Subterranean nest builders must move large amounts of the substratum to hollow out large cavities in which the nest is constructed and continues to grow. Nests are also constructed in hollow tree trunks and branches. The colony can regulate the nest temperature by fanning their wings to increase air flow and cool the nest's interior. Wasps are also known to increase the aperture size of the nest entrance to increase further the ventilation. Moisture is also used to increase the humidity within the nest to cool it down. To raise the temperature of the nest, the adults amass on the combs and increase their activities within the nest as a way of increasing the ambient temperature. Heat conservation is more efficient in large nests due to the lower surface area to volume ratio of a spherical nest. Consistent with this observation is the fact that smaller and immature nests have proportionately thicker envelopes than larger, more mature nests.

7.2. *Ichnofossil nests*

Fewer ichnofossils have been interpreted to

Table 3
Solitary to eusocial wasp nest ichnofossils in the geologic record

Age and formation	Locality	Nest architecture	Ichnotaxonomy	Source
Triassic				
Chinle Formation	Petrified Forest National Park, Arizona	Elliptical ovoids as cocoons; three size classes	open nomenclature	Hasiotis et al., 1995, 1996, in preparation b
Jurassic				
Morrison Formation	Colorado Plateau and vicinity	Elliptical ovoids as cocoons; two size classes	open nomenclature	Hasiotis, 2002; Hasiotis et al., in preparation b
Cretaceous				
Two Medicine Formation	Choteau, Montana	Elliptical ovoids as cocoons; three size classes	open nomenclature	Hasiotis et al., 1996, in preparation b
U. K. Mesa Verde Group?	Gunlock, Utah	Ovoid cell cluster forming a comb	<i>Celliforma favosites</i>	Brown, 1941; Wenzel, 1991a
Paleogene				
Pal.–Eoc. Claron Formation	Markagunt Plateau, Utah	Elliptical ovoids as cocoons; four size classes	open nomenclature	Hasiotis et al., 1996; Bown et al., 1997
Eoc. Sarmiento Formation	Chubut Province, Argentina	Hemicylindrical cell cluster	<i>Chubutolithes gaimanensis</i>	von Iherling, 1922; Bown and Ratcliffe, 1988; Genise and Bown, 1990
Pal.–Eoc. Mercedes Formation	Uruguay	Elliptical ovoids as cocoons	open nomenclature	Veroslavsky and Martinez, 1996; Veroslavsky et al., 1997
Eoc. Willwood Formation	Worland, Wyoming	Elliptical ovoids as cocoons	open nomenclature	Hasiotis and Bown, unpublished data
Eoc. Gran Salitral Formation	La Pampa Province, Argentina	Burrow with cell termination	cf. <i>Maconopsis</i>	
Eoc. Bridger Formation	Wyoming	Elliptical ovoids as cocoons	open nomenclature	Melchor et al., 2002†
Eoc.–Olig. Jebel Qatrani Formation	Fayum Depression, Egypt	Compound vertically tiered cavities	<i>Masrichmus issawii</i>	Evanoff, personal communication in 1996
		Burrow with cell termination	cf. <i>Maconopsis</i>	Bown, 1982
Neogene				
Late Plio. Laetoli Beds	Laetoli, Tanzania	Elliptical ovoids as cocoons	open nomenclature	Ritchie, 1987
Quaternary				
Pleistocene	San Salvador Island	Emergent burrows from central area with ovoids as cells	open nomenclature, ‘cluster burrows’	White and Curran, 1988

have been constructed by wasps than by other solitary to social insects. The identification of ichnofossils interpreted to have been constructed by solitary to eusocial hymenopterans similar to extant wasps (Table 3; Figs. 15 and 16) is based on comparisons to the architectural and surficial elements of extant wasp cocoons and nests (Figs. 5, 6, 15A,B) (e.g., Bown, 1982; Ritchie, 1987; Bown and Ratcliffe, 1988; Genise and Bown, 1990, 1991; Hasiotis et al., 1994, 1995, 1996; Bown et al., 1997; Hasiotis, 2002; Hasiotis et al., in preparation b). All the key morphologic features of subterranean and arboreal wasp nests have been found in several ancient examples (Figs. 15 and 16), with the exception of the actual paper material preserved in a Cretaceous nest from Utah

described by Brown (1941) and reassessed by Wenzel (1991a). Regardless of the age and complexity of these nests, the key criteria in their interpretation as wasp cocoons and nests are (1) the architectural arrangements and high densities of elliptically shaped, faintly to highly weave-textured capsules (Figs. 15C–F and 16A,B,E,F); and (2) the complexity of comb construction and their arrangement (Fig. 16C,D). The variability of arrangements of cocoons and combs often relates to the degree of sociality of the constructors (e.g., Bown, 1982; Ritchie, 1987; Hasiotis et al., 1996, in preparation b; Bown et al., 1997). Large numbers of cocoons that co-occur were likely produced by nests of solitary wasps. Simple combs constructed of mud were likely constructed

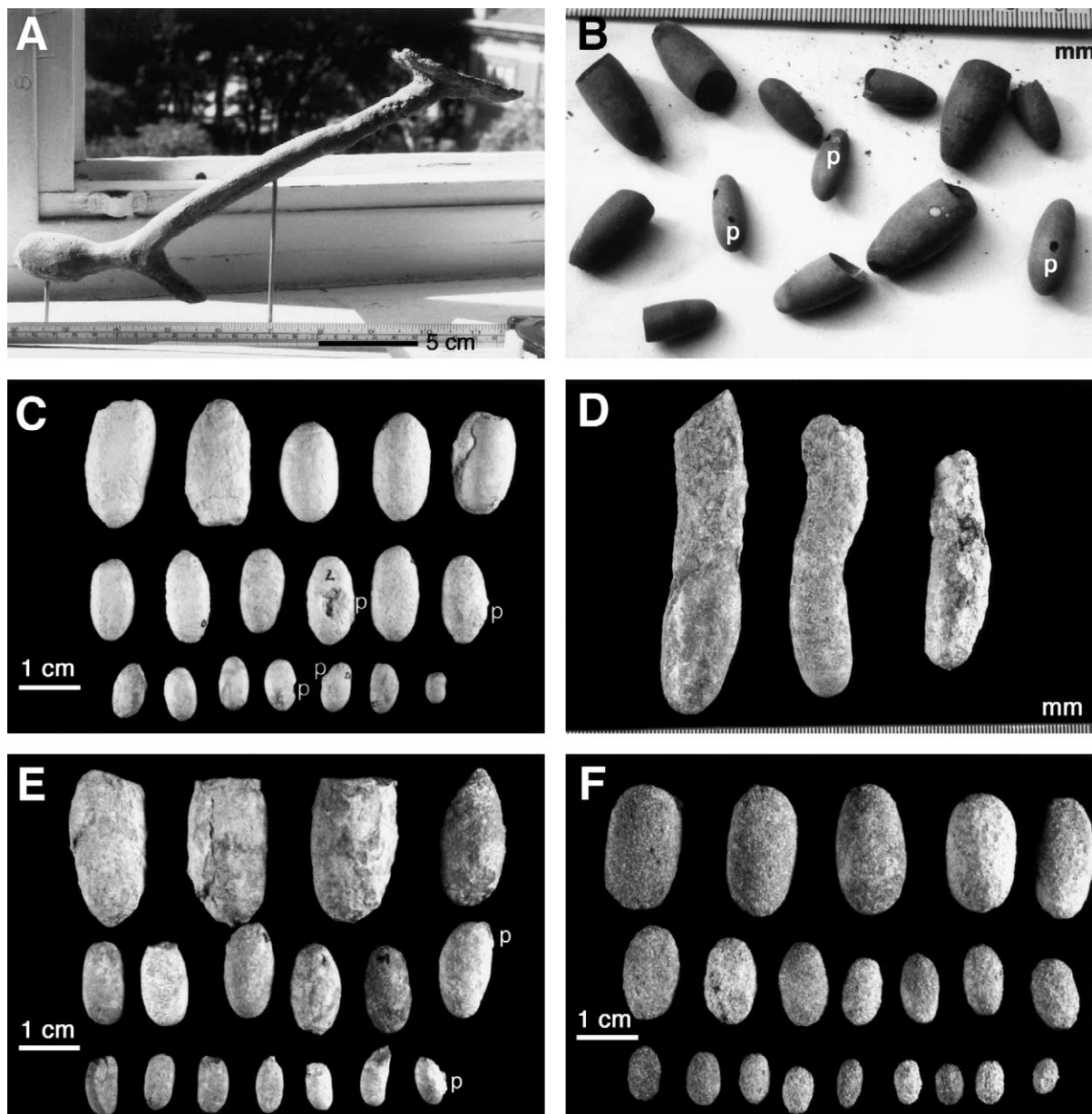


Fig. 15. Extant and ichnofossil nests and cocoons constructed by solitary wasps (Hymenoptera: Sphecidae and Vespidae). (A) Polyester resin cast of a sphecid wasp nest with a single cell at the terminus of the quasihorizontal tunnel. (B) Remains of cocoons from a mud dauber nest which have hatched (opened at the cocoon end) and that were parasitized (p) with the parasitoid wasp leaving a small exit hole; note that all of these cocoons came from the same nest and that size of the cocoon reflects the relative amount of insects used to provision the cell; the larger the cell, the more insects used. (C) Cocoons from the Paleocene–Eocene Claron and Eocene Brianhead Formations of southwestern Utah, some of which were parasitized by a parasitoid wasp and left a small exit hole (p). (D,E) Cocoons from the Upper Cretaceous Two Medicine Formation near Choteau, Montana, some of which were parasitized by a parasitoid wasp and left a small exit hole (p); cocoons in D still have part of the burrow attached to it. (F) Cocoons from the Petrified Forest Member of the Upper Triassic Chinle Formation in Petrified Forest National Park, Arizona. Note cocoons in C–F that share a similar range of morphologies and sizes.

by presocial vespids. Large numbers of combs in an organized nest were probably constructed by eusocial vespids.

Ichnofossils interpreted as cocoons (Figs. 15E,F and 16B,F) have varying degrees of external weave patterns and very similar distribution of capsule size and shapes despite coming from different Mesozoic and Cenozoic continental deposits (Ritchie, 1987; Hasiotis et al., 1995, 1996, in preparation b; Bown et al., 1997). The densities in which these cocoon trace fossils occur are similar to those of extant solitary sphecoid wasps studied by Evans (1966). Ichnofossils interpreted as solitary to presocial nests (Fig. 16C) were constructed by hundreds of aligned, intricately placed pellets of fine-grained material to produce four to five cells connected laterally (Bown and Ratcliffe, 1988). The constructor of these nests is interpreted as a spider-killing wasp (Pompilidae) (Genise and Bown, 1990).

A few of the ichnofossils assigned to cf. *Maconopsis* are interpreted as solitary wasp nests from the Eocene of Wyoming (Bown and Kraus, 1983) and Eocene–Oligocene of Egypt (Bown, 1982). These burrows are simple with a teardrop-shaped cell at the terminus of the inclined shaft. These trace fossils are most similar to sphecoid nests (Bown, 1982; Bown and Kraus, 1983; Hasiotis and Bown, unpublished data).

The lone Upper Cretaceous wasp nest ichnofossil, *Celliforma favosites*, was interpreted to have been constructed by eusocial vespid wasps based on the size, shape, and alignment of cells to produce a comb (Brown, 1941; Wenzel, 1991a). The comb contains about 214 dome-shaped cells arranged in a regular hexagonal pattern that show the walls of the cells that held cocoons of pupating larvae (Wenzel, 1991a).

Eocene to Oligocene ichnofossils (Fig. 16D) interpreted as eusocial vespid wasp nests (T.M. Bown, personal communication, 1998; and herein) have a complicated morphology composed of tiered, flattened lateral chambers, each separated by a space and connected by a vertical projection from top to bottom that nearly bisects each chamber; they are assigned to *Masrichnus issawii* (Bown, 1982). Though not identical to primitively and highly eusocial vespid wasp nests (Ross and

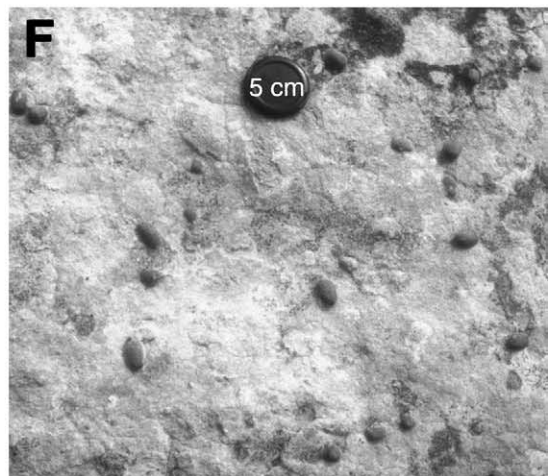
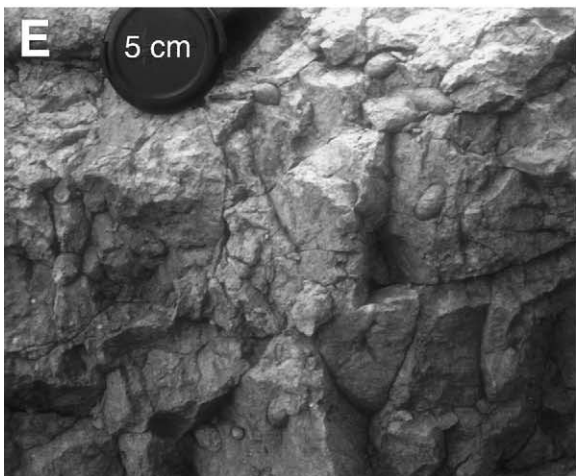
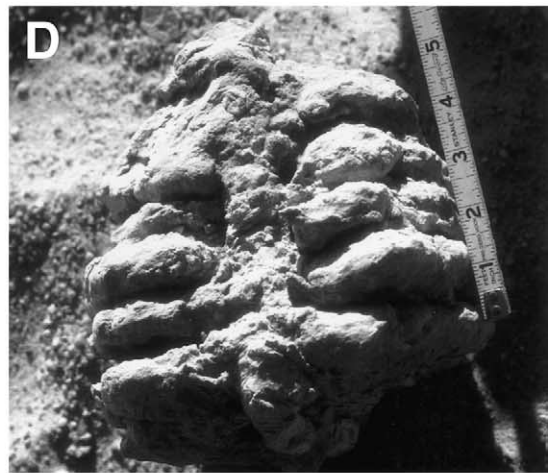
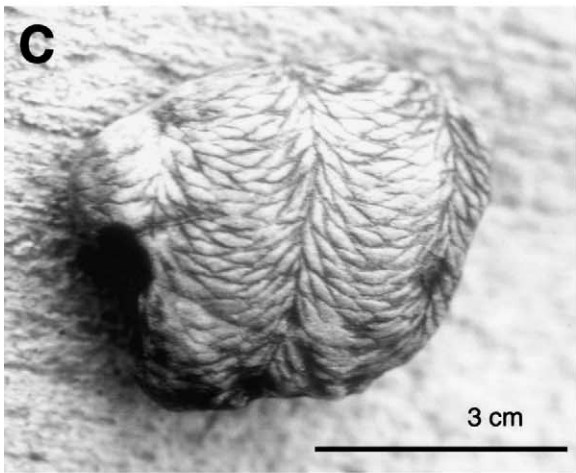
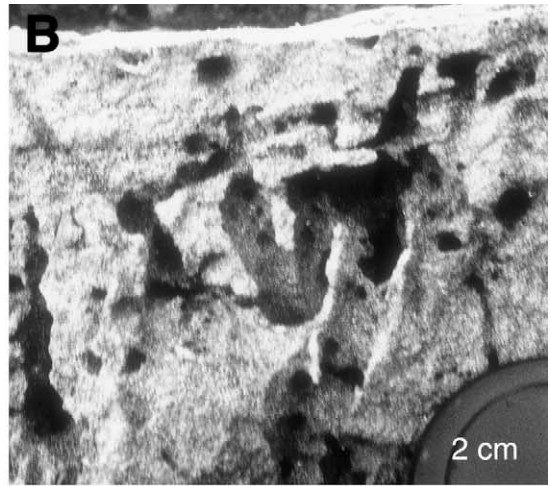
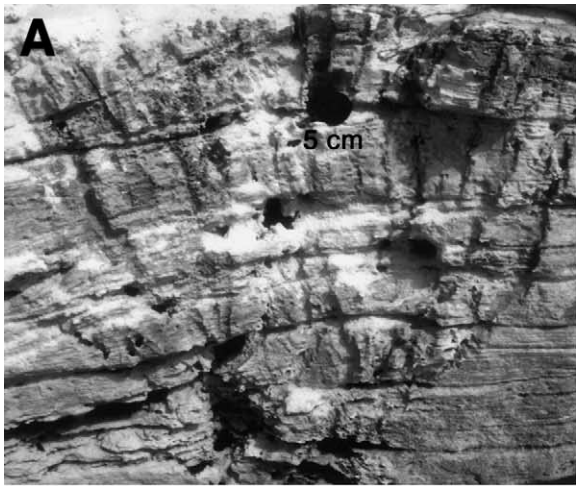
Matthews, 1991), these ichnofossils have characteristics that are unique to the nesting characteristics of higher wasps.

7.3. Behavioral and paleoecological implications

The ichnofossil nests discussed here preserve a range of solitary to social behavior of aculeate wasps from Triassic to present. These nests and cocoons also indicate different innovations in food hoarding (Vander Wall, 1990), holometabolous brood rearing (Hasiotis, 2000), and nest defense (Evans and Eberhard, 1970; Wilson, 1971; Ross and Matthews, 1991). The cocoons and simple nests from Mesozoic and Cenozoic deposits indicate relatively short-term food hoarding of larval and adult insects by the female wasp on behalf of her offspring. In the eusocial vespids, represented by the Cretaceous and Eocene ichnofossils, the pattern of cell provisioning is slightly different: the siblings construct the cells and feed the larvae directly with the best cuts of insect muscles or through regurgitation (Evans and Eberhard, 1970; Spradberry, 1973; Ross and Matthews, 1991). Simple ichnofossil nests and cocoons that occur in paleosols indicate a major innovation in subterranean holometabolous brood rearing because the nests contain no secretions to protect the offspring and provisions. The size of each ichnofossil nest is likely to be proportional to the number of individuals in the colony. Most of the smaller ichnofossil wasp nests with one to more than 14 cells were probably made by one individual (Evans and Eberhard, 1970; Evans, 1985). Small, more complex ichnofossil wasp nests seem likely to represent the work of one or several individuals that constructed one to more than 20 connected cells. Larger complex ichnofossil wasp nests likely represent hundreds to thousands of related individuals that constructed combs of 200 cells or more with colony sizes approaching those of extant eusocial vespid wasps.

8. Architectures of ant nests: simple to complex social nests

Nearly 300 genera and more than 8800 species



of ants (Hymenoptera: Formicidae) have been described, all of which are eusocial. They occur on every continent except Antarctica and in nearly every climate (Wheeler, 1910; Hölldobler and Wilson, 1990). Very little, however, is known about ant nests in soil (Hölldobler and Wilson, 1990), although ant nests have also been recognized as frozen behavior because the nests are manifestations of behavior (Sudd, 1967). Ichnofossil and extant ant nests are excavated and constructed systems of cavities in soil or in wood similar to those of termites (e.g., Wheeler, 1910; Moser, 1963; Hutchins, 1967; Sudd, 1967; Goetsch, 1969; Wilson, 1971; Weber, 1972; Laza, 1982; Hölldobler and Wilson, 1990; Hasiotis and Demko, 1996; Bown et al., 1997). The nests of ants are less complex than those of termites but can be as extensive (Hutchins, 1967; Hölldobler and Wilson, 1990). They are constructed in a variety of substrates: xylic, subterranean, epigeous, and arboreal (nests built on the trunk or branch of a tree; leaves stitched together with silk). Soil nests thought to be most primitive sometimes extend into rotten wood; nests begun in wood may extend into the soil (Sudd, 1967). Each type of nest is the collective product of the efforts of many individuals. Little is known about the convergence and parallel evolution in nest architecture of closely related lineages of ants (Sudd, 1967), but it is most likely that the nest architectures of many different types of ants are similar. In general, the architectural components of most ant nests are relatively simple, but the overall structure can be volumetrically extensive, complex, and different in form from one species to another (Sudd, 1967; Weber, 1972). A characteristic unique to ants is that a single colony may

have several nests, which are built during seasons favorable to the health of the colony. Sudd (1967) described these types of nests as polydomous. Because of this, some ant nests may extend over several tens to hundreds and to possibly thousands of square meters with depths of 2 to more than 6 m, constructed through many generations of ants with different queens (Wheeler, 1910; Moser, 1963; Wilson, 1971). Mature nests of this type may have from 2.5 to 5 million ants at any one time (Weber, 1972). The actual size of the nest and number of inhabitants can never really be known due to the sheer size and complexity of the largest subterranean nests (Wheeler, 1910; Sudd, 1967).

8.1. Nests of extant ants

Two kinds of ants exist today: those that excavate nests and those that are nestless (Sudd, 1967). Those that do not construct nests, such as the driver or army ants, form bivouac swarms with their bodies forming clusters of various sizes in the open and in pre-existing crevices and cavities (Wheeler, 1910; Sudd, 1967; Hölldobler and Wilson, 1990). Ants that construct nests follow a basic plan that begins with a hemispherical to conical mound that is placed in the center of the nest with an entrance to one side (Hutchins, 1967; Sudd, 1967). The architectural elements of nest include **chambers** and **galleries** that can be both concentrated and dispersed in the same nest. Chambers can be oblate, hemispherical or globular in form. Galleries can be of various lengths and diameters, which can form a gridlike to spongy lattice with subhorizontal galleries or subvertically descending shaftlike galleries that inter-

Fig. 16. Extant and ichnofossil nests and cocoons constructed by solitary (Hymenoptera: Sphecidae and Vespidae) and social wasps (Hymenoptera: Vespidae). (A,B) Natural vertical cross-section and close-up (B) of a cluster nest (White and Curran, 1988) in a Pleistocene eolian carbonate dune on San Salvador Island, Bahamas; close-up (B) shows the outline of a cell surrounded by escape burrows from mature wasps. (C) Eocene ichnofossil nest designated *Chubutolithes gaimanensis* from the Chubut Province, Argentina; note the preservation of individual pellets of mud used to construct each cell. (D) Eocene–Oligocene ichnofossil nest designated *Masrichmus issawii* from the Fayum Depression of Egypt; note the complex construction of bilaterally symmetrical tiers nearly bisected by a vertical column (modified from Hasiotis et al., 1994). (E) Natural vertical cross-section of the outcrop with cocoons in a mature paleosol from the Upper Cretaceous Two Medicine Formation near Choteau, Montana; range of sizes for these cocoons in Fig. 13D,E. (F) Natural vertical cross-section of the outcrop with cocoons in a moderately developed paleosol from the Petrified Forest Member of the Upper Triassic Chinle Formation in Petrified Forest National Park, Arizona.

sect at chambers of various sizes. For the most part the chambers and galleries are unlined or, at most, slightly hardened with saliva. Few ants use carton constructed from macerated plant material to construct nests in rotten trees and beneath roots. In general, shallower nests are constructed typically in humid climates or areas with a high water table, whereas deep nests are constructed in dry climates or areas where the water table is deep (Sudd, 1967).

The term *shaft* is not used by ant researchers to describe either the vertical nest entrance or subvertical connections between chambers (e.g., Wheeler, 1910; Hutchins, 1967; Sudd, 1967; Weber, 1972; Hölldobler and Wilson, 1990; Tschinkel, in press); the preferred terms are tunnel or gallery. In this section I will use gallery for the description of extant ant nest features. To describe objectively any ichnofossil nests, however, **shaft** should be used to describe the subvertical connections between (1) the paleosurface and chambers, (2) chambers, or (3) subhorizontal galleries. This is so an interpretation of the nest architecture is not inferred prior to appropriate study of the ichnofossil nest.

Nesting ants (Fig. 2) excavate and construct two basic types of subterranean nests: nests consisting of a shallow maze of horizontal galleries as constructed by such ants as *Lasius alienus* and *Tetramorium caespitum*, and nests dominated by vertical galleries like those constructed by the species of *Formica*, *Prenolepis*, and *Pogonomyrmex* (Sudd, 1967). A variation of the second type of nest is one with vertically tiered chambers without highly organized galleries that are built by *Atta*, *Tetramorium*, *Formica*, and *Pogonomyrmex*, as well as many others (Hutchins, 1967; Sudd, 1967). Horizontally laid out nests range from a relatively shallow maze of short tunnels interconnected with small chambers, as in the nests of *Crematogaster sordidula*, to nests composed of a high density of very short tunnels so that the nest appears spongy, as in those constructed by *Lasius niger*. Still other shallow ant nests are composed of horizontal tunnels that follow roots of surface vegetation and trees where the ants feed on root-feeding aphids and scale insects (Sudd, 1967). Vertically distributed ant nests can be quite large

and deep, such as those constructed by species of *Prenolepis* and *Pogonomyrmex* that collect their food from the surface around the nest. These nests may contain a high density of chambers near the surface that range in size from 2 to 14 cm across and 2 cm in height, which are connected by subhorizontal and subvertical tunnels. Below this cluster of chambers are deeper chambers that are connected through tunnels and continue downward to depths exceeding 2 m. The tiers of chambers are used for storing seeds, waste disposal areas, dwellings, nurseries, and other activities, and form the royal chamber where the queen lays eggs. Mature harvester ant nests in Arizona reach depths of more than 5 m and which contain 436–700 chambers in a 2–3-m diameter (Hutchins, 1967). New chambers and tunnels are constantly dug, and older sites are filled with unwanted nest and excavated material (Wheeler, 1910; Sudd, 1967).

Fungus-gardening ants, such as *Atta texana* and *Trachymyrmex septentrionalis*, construct unique and distinctive subterranean nests that can be small to extremely large (Wheeler, 1910; Moser, 1963; Hutchins, 1967; Weber, 1972). These types of ants construct nests of interconnected galleries and chambers to depths greater than 7 m. Above ground, an area greater than 17 m² contains tens of conical mounds composed of excavated material, with scattered pellets of freshly excavated material between the mounds. Several shallow access galleries that can be up to 33 m long are used by the ants to get to their feeding grounds. The oval to hemispherical chambers range typically from 12 to 33 cm but can reach 67 cm across and nearly 33 cm high. In these structures are found fungus gardens composed of spongy masses that resemble a sphere of latticework (Sudd, 1967) and can reach the size of large watermelons. The floors are often slanted downward to drain water that accumulates from sources external to the nest (Sudd, 1967). A large number of small ants tend to these chambers as gardeners and weeders of the fungus and mushroom gardens. Plant material is brought in and cut into small pieces where it is seeded with bits of fungus. Fungus grows in the chambers, often being suspended by thin rootlets that grow

in the cavity. Foreign fungus brought into the nest is immediately removed. The overall humidity and temperature of the nest are regulated by the ants by opening and closing passages and entrances. Large colonies can contain several million ants. The life span of these colonies extends far beyond the life of the original queen that founded the nest, most likely by adopting newly mated queens into the nest through time. Likewise, the structure and size of the colony continues to grow through time (Hutchins, 1967).

Epigeal nests include mound, thatched, and crevice nests, while arboreal nests include tree, silk, and specialized plant tissue nests, such as the stems, leaves, and thorns of plants (Sudd, 1967). Of these nests, the mound, thatched, tree, and specialized-tissue nests may also be preserved partially in the geologic record. For instance, the subterranean portion of mound or thatched nests has a better chance of preservation than the epigeal portion. The incorporation of plant material in thatched nests may also increase its chances of preservation due to early cementation by soil-chelating complexes that are attracted to the decaying organics (e.g., Hasiotis et al., 1993; Birkeland, 1999). The specialized-plant-tissue and tree nests of ants also have a greater potential for preservation because of the substrates in which they are excavated and constructed.

Ant nests also exhibit an ontogenetic growth pattern from a simple, solitary chamber to large, relatively complex nest architectures (Wheeler, 1910; Sudd, 1967), similar to those of termites, bees, and wasps. New nests are begun by a recently fertilized queen as a simple chamber in the substratum connected to the surface by a single tunnel. She carries a lifetime supply of eggs that number in the hundreds to millions (Wheeler, 1910; Hutchins, 1967; Wilson, 1971). The nest continues to grow with the aid of the first group of workers that hatched in the simple nest. Galleries and chambers of various sizes, shapes, and depths are added, depending on the species of ant. Over the next 1–6 years the nest increases in size until it reaches the appropriate size for the colony (Wheeler, 1910; Weber, 1972; Hölldobler and Wilson, 1990). For many species of ant, however, several queens can be present producing offspring,

while other nests adopt new queens after the previous one has died, and a few are polygynous with large numbers of queens. These types of ants (e.g., species of *Formica*, *Myrmica*, and *Iridomyrmex*) construct nests that result from a unicolony or supercolony that is built by tens of millions of workers and with up to 1 million queens. Through many years, new nests are constructed by the process of budding. Groups of workers and an inseminated queen start a satellite nest, and are spread over very large areas (Hölldobler and Wilson, 1990). Another type of supercolony of ants on the coast of Japan has 45 000 interconnected nests covering an area of 2.7 km² and is composed of over 300 million workers and over 1 million queens. These groups can persist for hundreds of years or more (Higashi and Yamauchi, 1979; Hölldobler and Wilson, 1990). Most recently, a supercolony of imported Argentine ants was discovered to range over 6000 km from Italy to the Spanish Atlantic coast (Giraud et al., 2002). Individuals mix freely between geographically separated nests, whereby workers of the same supercolony are never aggressive toward each other. Thus, these types of geographically separated and genetically differentiated unicolonies form the largest cooperative social unit recorded to date (Giraud et al., 2002). Interestingly, these nests are physically separated from each other, yet they belong to the same unicolony; identification of these types of nests in the geologic record may be impossible.

8.2. *Ichnofossil nests*

Ichnofossils interpreted to have been constructed by ants are the least known of all the ichnofossil nests ascribed to insects that show a range of solitary to social behavior. The ichnofossils interpreted to have been constructed by ants (Fig. 17) are based on comparisons with the architectural and surficial elements of extant ant nests (Fig. 2) (e.g., Bown, 1982; Laza, 1982; Hasiotis et al., 1994; Hasiotis and Demko, 1996; Bown et al., 1997; Hasiotis, 2002; Hasiotis, in press). All the key morphologic features of subterranean ant nests have been found in ancient examples, with the exception of the identification

Table 4
Ant nest ichnofossils in the geologic record

Age and formation	Locality	Nest architecture	Ichnotaxonomy	Source
Triassic				
Chinle Formation	Colorado National Monument, Colorado Mule Ear Diatreme, Utah	Simple interconnected large chambers and galleries Simple interconnected chambers and galleries	open nomenclature cf. <i>Parowanichnus</i>	Hasiotis et al., in preparation b
Jurassic				
Morrison Formation	Colorado Plateau and vicinity	Concentrated, interconnected chambers and galleries	cf. <i>Parowanichnus</i>	Hasiotis and Demko, 1996; Hasiotis, 2002; Hasiotis et al., in preparation b
Cretaceous				
Cedar Mountain Formation	San Rafael Swell, Utah	Simple interconnected chambers and galleries	open nomenclature	Hasiotis and Kirkland, in preparation
Paleogene				
Pal.–Eoc. Claron Formation	Markagunt Plateau, Utah	Concentrated, interconnected chambers and galleries	<i>Parowanichnus formicoides</i>	Bown et al., 1997
Eoc. Willwood Formation	Worland, Wyoming	Simple interconnected chambers and galleries	open nomenclature	Hasiotis and Bown, unpublished data
Oligo–Miocene deposits	Ebro Basin, Spain	Interconnected chambers and galleries	open nomenclature	Hasiotis, 2002
Neogene				
Mio. Santa Cruz Formation	Santa Cruz, Argentina	Interconnected chambers and galleries	open nomenclature	Tauber, 1996
Mio. Epecuen Formation	La Pampa Province, Argentina	Interconnected large, spherical chambers and simple galleries	<i>Attaichnus kuenzeli</i>	Laza, 1982
Plio. Baynunah Formation	Abu Dhabi Emirate, UAE	Interconnected chambers and galleries	open nomenclature	Hasiotis and Bown, unpublished data
Plio. Chapadmalal Formation	Buenos Aires, Argentina	Interconnected chambers and galleries	open nomenclature	Laza, 1995
Plio–Pleist. San Andres Formation	Buenos Aires, Argentina	Interconnected chambers and galleries	open nomenclature	Laza, 1995
Quaternary				
Pleistocene	San Salvador Island	Concentrated, interconnected chambers and galleries	cf. <i>Parowanichnus</i>	Hasiotis and Martin, unpublished data
Pleistocene Tezanos Pintos Formation	Santa Fe, Argentina	Interconnected chambers and galleries	open nomenclature	Iriondo and Krohling, 1996
Pleistocene Lujan Formation	Buenos Aires and Santa Cruz, Argentina	Interconnected chambers and galleries	open nomenclature	Laza, 1997
gPleistocene eolian dunes	Petrified Forest National Park, Arizona	Dispersed, interconnected chambers and galleries	open nomenclature	This paper; Hasiotis, 2002

of formic acid on the walls of galleries and chambers (Fig. 17). The key criteria in their interpretation of ichnofossils as ant nests (Table 4) are (1) the architectural components of chambers and galleries; (2) the repetition of size and shape of chambers and galleries; and (3) the dispersed or concentrated nature of interconnected, unlined chambers and galleries (Fig. 17A–H). The arrangement of the ichnofossil chambers and galleries can be simple (Fig. 17A,B,E) to highly complex and concentrated (Fig. 17D,F–H). The range

in the overall number of chambers and galleries most likely indicates the maturity of the nest (e.g., Sudd, 1967; Hölldobler and Wilson, 1990), but it may also represent different species of ants with smaller nests.

Upper Triassic ichnofossils in Utah and Colorado, tentatively ascribed to a social insect nest, are similar to those constructed by ants (Hasiotis et al., in preparation b). The nests in the Chinle Formation of Utah are surprisingly similar to nest ichnofossils from Paleogene and Neogene deposits

in Europe and elsewhere in North America (Fig. 17B–D). The Utah nests are composed of simple, interconnected quasihorizontal galleries, 0.5 cm in diameter and 2–6 cm long and interspersed with simple elliptical, flattened chambers (~2–3 cm in diameter) pieced together as a network. The Colorado Chinle nests are similar to those in Utah; however, the chambers are large (3–6 cm in diameter), and they are connected by very short galleries (less than 1 cm long). The nest was excavated at a shallow depth and is associated with rhizoliths. Work is still in progress to delineate further the overall architectural and surficial morphologies of these ichnofossils to constrain better their interpretation.

Several distinct forms of Upper Jurassic ichnofossil nests have been described (Hasiotis and Demko, 1996; Hasiotis, in press). The nests are composed of interconnected oblate to hemispherical chambers and galleries spatially distributed as (1) concentrated systems with hundreds to thousands of chambers and galleries (Fig. 17F–H); (2) dispersed systems with 10–25 dispersed polydomal chambers and galleries; and (3) low, concentrated systems with 10–30 closely spaced chambers and galleries (Fig. 17E). The concentrated and dispersed ichnofossil nests are distinctive enough to represent three different types of ants. The Lower Cretaceous Cedar Mountain Formation nest ichnofossil is similar to the dispersed nest type from the Morrison. The similarity between these nest morphologies is not surprising because the Cedar Mountain Formation overlies the Morrison Formation in Utah.

Ichnofossil nests in the Paleocene to Eocene Claron Formation in southwestern Utah are abundant, but only one has been described to date (Bown et al., 1997). *Parowanichnus formicoides* (Fig. 17D) is a relatively diffuse nest composed of a three-dimensional network of chambers (1–5 cm in diameter) and galleries (0.4–1.2 cm in diameter) that radiate away from the center of the nest and gradually decline in number over several meters. Other nests are similar to those of seed-harvesting and fungus-growing ants.

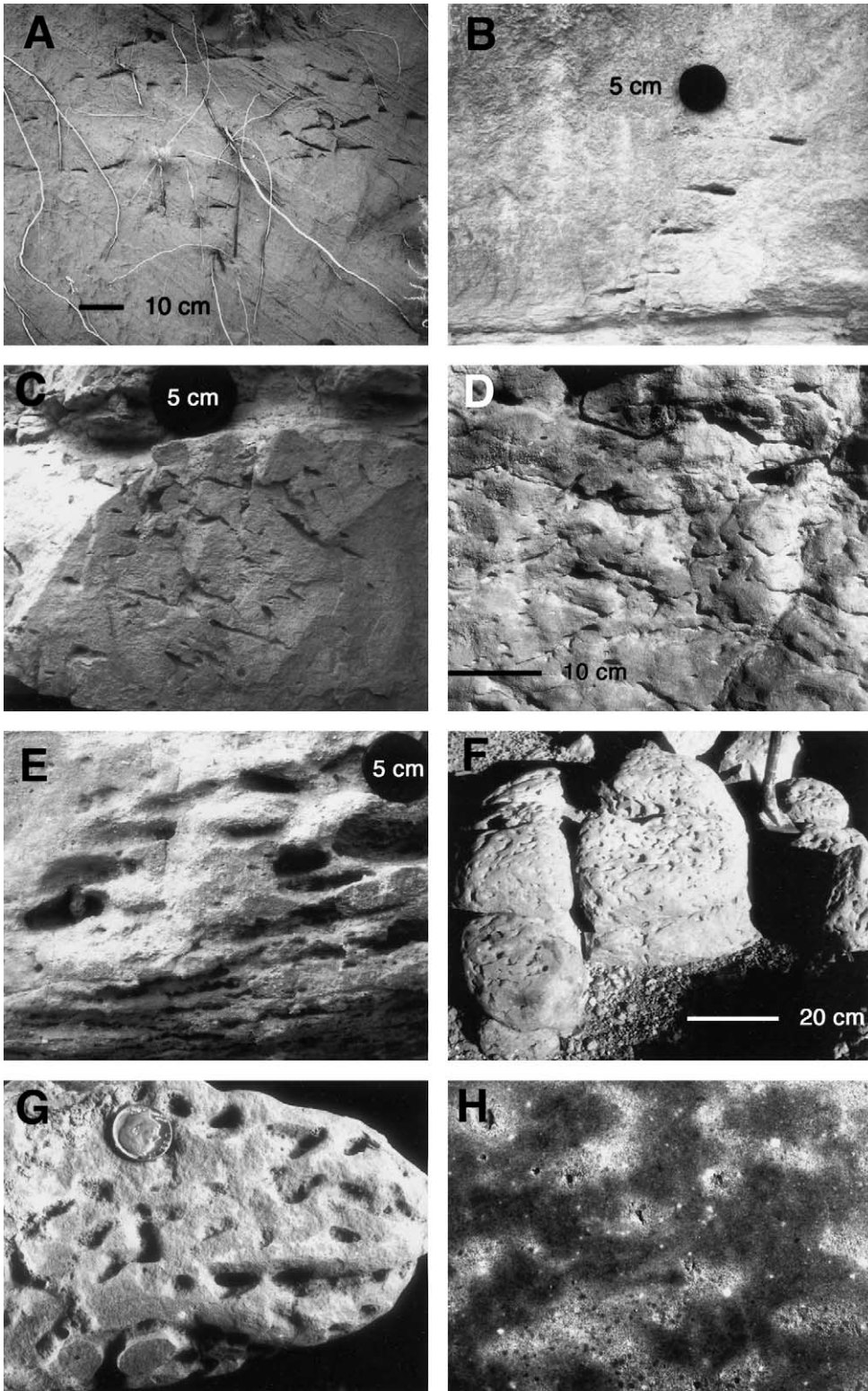
Most Neogene ant nest ichnofossils have been described from South America, but more are being recognized in North America (Table 4)

and western Europe. Ichnofossil nests interpreted to have been constructed by fungus-gardening ants have been described from Quaternary deposits in Argentina (Laza, 1982, 1997). They are characterized by a concentrated network of large, spherical chambers 3–17 cm in diameter that are interconnected by galleries that range from 5 to 9 cm in diameter. The large size and number of chambers of these nests should have a higher preservation potential than smaller nests, but they have not been identified in older deposits until recently (Hasiotis, unpublished data). Several types of ant nest ichnofossils have been identified in Oligocene–Miocene alluvial deposits of the Ebro basin in southeastern Spain (Hasiotis, 2002). One type of ichnofossil nest is characterized as low concentrations of diffuse, stacked, and flattened chambers connected by small shafts (Fig. 17B). The other ichnofossil nest type is dominated by high concentrations of diffuse chambers interconnected by galleries and short shafts (Fig. 17C).

The youngest ichnofossils of ant nests are those preserved in Pleistocene dunes of northeastern Arizona (Fig. 17A). These nests are identical to those constructed by ants that harvest grains from the surface. They can easily be excavated and explored for their three-dimensional morphology because they are not lithified. Since these nests are modern in appearance, they are often overlooked or not reported as ichnofossils.

8.3. Behavioral and paleoecological implications

The composite nature of these complex ichnofossils results from social behavior in ants, indicating cooperation in nest construction and maintenance and probably a division of labor similar to that of modern ants (e.g., Wilson, 1971; Hölldobler and Wilson, 1990). The outcrop occurrences of ichnofossil nests suggest that they were subterranean and constructed in the vadose zone in subaerial conditions. The deeper nests likely indicate that the soil moisture and water table levels were lower in the areas where they occur. Shallower or smaller nests occur in areas that had higher soil moisture and water table levels. The size of each of the ichnofossil nests is likely to be proportional to the number of individuals in



the colony. Most of the smaller nests likely contained smaller numbers of ants (about 100), whereas large complex nests were occupied probably by thousands to millions of related individuals. The main caveat when interpreting the size of ichnofossil nests is that small mature nests must be differentiated from nests at early ontogenetic stages of construction and from large nests that are only partially preserved in the outcrop. This last observation is important since a single nest can cover nearly 3 km² with a great volume of sediment being affected. This size of nest would be difficult to recognize in the outcrop due to limited exposure and the uncertainty that one ichnofossil nest was connected with others nearby.

Ichnofossil ant nests indicate unique innovations in food hoarding (Vander Wall, 1990), holometabolous subterranean brood rearing (Hasiotis, 2000), and sociality (Wilson, 1971; Hölldobler and Wilson, 1990) compared to those of other social insects. The oldest known body fossils show that early ants were pigmented similarly to extant ants, and thus, were not sensitive to sunlight as are termites (Noirot and Darlington, 2000). Ants were less limited in their diet than termites, bees, and wasps and collected a range of food from leaves, seeds, and spores to insects in various stages of development (e.g., Wheeler, 1910). This was likely to have been true of the Mesozoic ants, and their ichnofossil nests served as compartments for the short- and long-term storage of vast quantities of food, although primitive living ants are largely predatory but they also forage for food which is stored in the nest (Hölldobler and Wilson, 1990). In these nests, food was

probably shared with siblings and fed to larvae. The nests themselves were a major innovation in subterranean holometabolous brood rearing because, as with extant nests (Sudd, 1967; Hölldobler and Wilson, 1990), secretions were not used to waterproof the nest interior but, instead, were used as a form of antibiotic against bacteria and fungi, which allowed them to colonize moist subterranean environments filled with microorganisms. For support and strength, the sediment in the walls of chambers and galleries was pounded into place using the ant's head. In times of flooding or water infiltration due to heavy precipitation, the entrances and passageways were temporarily sealed, or the offspring and provisions were relocated by the ants to drier parts of the nest for their protection (Wheeler, 1910; Sudd, 1967).

9. Evolutionary implications of termite, bee, wasp, and ant nest ichnofossils

Based on the age and distribution of body fossils, the termites, bees, wasps, and ants are all thought to have originated in the earliest Cretaceous or in the latest Jurassic. Yet many problems exist in trying to explain the disjointed distribution of most extant taxa of these insects. The interpretation of Cretaceous and older ichnofossils as nests that resulted from the activity of these solitary to social insects, however, has implications for their origin, evolution, biogeography, and social behavior. If the paleogeographic and biogeographic distribution of body fossils, ichnofossils, and extant taxa is integrated with the most

Fig. 17. Ichnofossil nests interpreted to have been constructed by ants (Hymenoptera: Formicidae). (A) Natural vertical cross-section of an ichnofossil ant nest composed of horizontally dominated chambers and galleries in a Pleistocene eolian dune in Petrified Forest National Park, Arizona; note that this nest was recently eroded and no longer exposed. (B) Natural vertical cross-section of Oligo–Miocene ichnofossil ant nest dominated by pancake-shaped, stacked chambers from Aragon Province, Spain. (C) Natural vertical cross-section of Oligocene–Miocene ichnofossil nest composed of horizontally dominated chambers and galleries from Aragon Province, Spain. (D) Natural vertical cross-section of a Paleocene–Eocene Claron Formation ichnofossil ant nest designated *Parowanichnus formicoides* composed of horizontally dominated chambers and galleries, southwestern Utah. (E) Natural vertical cross-section of an ichnofossil nest composed of stacks of tabular chambers connected by simple galleries from the Salt Wash Member of the Upper Jurassic Morrison Formation in southeastern Utah. (F–H) Natural vertical cross-section, close-up (G), and rock section (H) of an ichnofossil nest composed of concentrated chambers and galleries that become diffuse downward into the substrate from the lower part of the Brushy Basin Member of the Upper Jurassic Morrison Formation in southeastern Utah; note the pattern of chambers and galleries also occurs at various scales (G,H) through the nest, which has caused total destruction of the original bedding. (modified from Hasiotis, 2002)

recent plate tectonic configurations for the last 300 million years, then a more accurate time of origin for the Isoptera and higher Hymenoptera can be reconstructed.

9.1. Origins based on fossils

The earliest known termite body fossils are from Lower Cretaceous rocks of Europe, Asia, and North and South America (Jarzembowski, 1981; Krishna, 1990; Martínez-Delclòs and Martinell, 1995; Thorne et al., 2000). Thorne et al. (2000) suggested an origin for termites in the Early Cretaceous or Late Jurassic but not earlier. They used a relatively large database of Cretaceous termite fossils comprising mainly winged elates (i.e., winged termite reproductives that leave the nests in swarms to become future kings and queens of new nests) of the Mastotermitidae, Hodotermitidae, and Termopsidae. The Kalotermitidae have a Paleocene fossil record, and the Rhinotermitidae and Termitidae have an Eocene fossil record. Thorne et al. (2000) based their patterns of diversification on distributions of body fossils prior to the breakup of Gondwana in the Cretaceous and the use of intermittently emergent land bridges for termite radiation and diversification proposed by Emerson (1955) to produce the worldwide distribution of termites today.

This scenario, however, is contradictory. Emerson (1955) discussed the origins of termites occurring as early as the Permian and their dispersal via land bridges and other landmass connections throughout the Triassic, Jurassic, Cretaceous, and Tertiary. Since the development of plate tectonic theories in the late 1960s and early 1970s we have known that land bridges are no longer necessary to distribute faunas and floras from one continent to another. Thorne et al. (2000) focused on the literal interpretation of the termite body-fossil record, which is an artifact of the taphonomic filter, and the hypothesis of a Late Cretaceous dispersal of termites via land bridges as postulated by Emerson (1955).

The earliest known fossil bee is preserved in Upper Cretaceous amber from New Jersey (Michener and Grimaldi, 1988a,b) dated 90–100 Ma. *Trigona prisca* is a stingless honeybee of the Me-

liponinae, a derived family of the neotropical Apidae, which is related to extant, highly eusocial bees and indicates that advanced degrees of social behavior existed by the Late Cretaceous (Michener and Grimaldi, 1988a,b). Most fossil bees come from Paleogene, Neogene, and Quaternary amber and lacustrine deposits of western Europe, eastern China, and western North America (Zeuner and Manning, 1976; Rasnitsyn and Michener, 1991). Michener and Grimaldi (1988b) and Grimaldi (1999) assumed that bees evolved along with angiosperms because today bees are dependent on pollen of flowering plants. Since angiosperms evolved in the Early Cretaceous, it was also assumed that bees and much of their social development also evolved in the Late Cretaceous (Grimaldi, 1999).

The oldest representative of the Aculeata is a fossil of an extinct vespomorph in the family Bethyloymidae from the Upper Jurassic (Rasnitsyn, 1975; Thorne et al., 2000). The earliest known vespoid wasp fossils come from Lower Cretaceous lacustrine deposits (Darling and Sharkey, 1990; Rasnitsyn et al., 1998) dated 110–118 Ma. The origin of the Aculeata was no earlier than the Late Jurassic, but social behavior arose sometime in the Late Cretaceous based on trace fossil evidence (Thorne et al., 2000).

The earliest fossil ants occur in amber from North America (USA and Canada) and are assigned to *Sphecomyrma freyi* (Formicidae: Sphecomyrminae; Wilson et al., 1967; Wilson, 1987). They are thought to be 100 million years old, although some workers believe it to be only 80 million years old (Hölldobler and Wilson, 1990). The deposit from where the amber was recovered, however, has an accepted date of 100 million years, and the upper boundary of the Santonian is now dated at 84 Ma (Geological Society of America Time Scale), from which other fossil ants have been collected (Wilson, 1987). Wilson (1987) concluded that the mid and Late Cretaceous (~100–84 Ma) fossil ants from North America (Alberta and New Jersey), Kazakhstan, and Siberia (Taymyr Peninsula and Magadan) indicate that the Formicidae evolved in the Early Cretaceous. Because ants composed very little of the fauna retrieved from Cretaceous amber com-

pared to the number of ants trapped in Eocene and Oligocene–Miocene (greatest numbers of species) ambers, the adaptive radiation of ants most likely took place no earlier than the Paleogene (Hölldobler and Wilson, 1990). More recently, Agosti et al. (1997), Grimaldi et al. (1997) and Grimaldi (1999) described new and previously collected fossil ants that date back to 110 Ma, and suggested ants arose no earlier than the Early Cretaceous because all pre-Tertiary fossil ants represent primitive taxa. Interestingly, some of the most primitive living ants (*Amblyopone*, genus of primitive ponerines) have a worldwide distribution thought to be derived from the sphecomyrmine–nothomyrmecine clade (Hölldobler and Wilson, 1990).

9.2. Proposed origins

For all of these insects to have the pattern of fossil (body and ichnofossil) and living distributions seen today, they must have originated much earlier than the Early Cretaceous because of the separation of Laurasian and Gondwanan landmasses by water bodies. The termite fossil evidence demonstrates a well-entrenched caste system and social behavior by the Early Cretaceous with nearly worldwide distribution, except that no Mesozoic termites are known from Africa and Australia. Lower Cretaceous fossil wasps mostly from South America and Asia also document the occurrence of the aculeate families Vespidae, Sphecidae, and Bethyridae (Rasnitsyn, 1975; Carpenter and Rasnitsyn, 1990; Grimaldi, 1999 and references therein) and show that the Apocrita were highly diversified by the Early Cretaceous, including most of the major lineages of aculeates and parasitic wasps (Darling and Sharkey, 1990). The occurrence of Cretaceous body fossils demonstrates that ants had a wide distribution across the Laurasian continents of North America and Siberia, which at that time were already separated by the Atlantic Ocean and had been since the Early Jurassic.

The distribution of ichnofossils, body fossils, living solitary to eusocial bee and wasp taxa, and living primitive and derived ants more accurately suggests the origin of isopteran and higher

hymenopteran taxa in the Triassic if not earlier and prior to rifting of Pangea. The life histories and reproductive behavior of these insects indicate that the reproductives (future queens and kings) are poor fliers, poorly adapted for long or harsh travel, and do not disperse far from their original nest. They also avoid crossing water bodies, even those that are relatively narrow, because the reproductives tend to travel over terrain with resources necessary for initiating new nests (e.g., Spradberry, 1973; Michener and Grimaldi, 1988a,b; Eggleton, 2000). Pangea began to break apart in the Late Triassic (~210 Ma), evidenced by rift basins along eastern North America, western Europe, and northwestern Africa (Scotese, 1997). By the Late Jurassic (~152 Ma) the continents that once made up Pangea had already dispersed to form North America, Eurasia, and Gondwana. About 131 Ma or so marks the onset of separation between Africa and South America. By 100 Ma, there was a narrow southern Atlantic Ocean separating Africa from South America, which continues to widen today. India and Madagascar were still joined, but flood basalts were beginning to erupt and ocean water poured into the extensional valleys as they began to separate. Antarctica was still attached to Australia, and both separated from Africa from 150 to 125 Ma, a separation that began around 186 Ma during the Karoo–Ferrar eruption (J. Meert, personal communication, 2002). During the early Late Cretaceous, sea level was at its highest, resulting in the partitioning of continental interiors with the formation of epicontinental seas such as the Western Interior Seaway of North America (Paleogeographic Atlas Project, 1984). By 80 Ma India and Madagascar and Antarctica and Australia were already separated by oceans.

Large water bodies, such as the Late Jurassic to Early to Late Cretaceous Tethys and proto-Atlantic and Pacific oceans, would have stifled the distribution of termites, bees, wasps, and ants we see today because of the limited flight abilities of adults and winged reproductives. For example, most virgin queens of living ants die within hours after leaving the home nest due to overheating, desiccation, predation, and drowning (Hölldobler and Wilson, 1990). Distances traveled range from

a few meters to as far as 10 km, most descending to the ground within a 2-km radius (Hölldobler and Wilson, 1990). Winged termite reproductives are generally poor dispersers across geographical barriers (Eggleton, 2000). Reproductives are poor fliers with bulky bodies and relatively fragile wings, and they share similar patterns and problems of distribution to that of ants (Behnke, 1977; Eggleton, 2000). Living bees and such fossil bees as *Trigona prisca* (oldest fossil bee – Cretaceous) and their ancestors would have been very unlikely to cross even narrow water bodies since colonies were established by gradual progressions of nests. Living *Trigona* has not reached the Antilles, except Trinidad, despite many species in nearby mainland areas (Michener and Grimaldi, 1988b). Wasps also have similar patterns in dispersal and nesting. Nests founded by many species of social wasps tend to have a life span of 6 days to as long as 25 years, depending on the species and the suitability of the nest site with respect to substrate, climate, and other factors (Wilson, 1971; Spradberry, 1973). They do not appear to swarm over large distances, and queens rarely disperse than a mile from their site of origination (Spradberry, 1973).

Based on the diversity and distribution of modern termites, Emerson (1955), Bouillon (1970), and Eggleton (2000) deduced that the termites probably evolved in the Early Triassic or Permian. Bouillon (1970, p. 165), using patterns of vicariance biogeography, suggested that by the beginning of the Jurassic, the Hodotermitidae were present and the Kalotermitidae (and probably the Mastotermitidae based on the phylogeny by Krishna (1970)) and Rhinotermitidae were present by the beginning of the Cretaceous. By the beginning of the Tertiary, the Termitidae (Amitermitinae, Termitinae, and Nausitermitinae) were present, and during the Tertiary the more recent families continued to expand in diversity with the addition of Macrotermitinae and the diversification of the Amitermitinae, Termitinae, and Nausitermitinae. Bouillon (1970) and Eggleton (2000) appropriately recognized the importance of plate movements in shaping the radiation, distribution, and biodiversity of termites. Their shared hypothesis combined with ichnologic

evidence suggests a Permian to Triassic origin (Hasiotis and Dubiel, 1995).

Early Mesozoic ichnofossils similar in morphology to Late Cretaceous and younger nests of soil- and wood-dwelling bees also support a Pangean origin. Michener and Grimaldi (1988b) considered that bees might have had a longer evolutionary history beginning in the Jurassic and may have been associated with the Mesozoic gymnosperm order Bennettitales that had flowerlike bracts around its reproductive structures. The ichnofossils suggest that ancient bees evolved independently of angiosperms until the Cenozoic. The proto-bees likely used gymnosperms as their source of pollen and other plant products (Michener and Grimaldi, 1988b; Hasiotis et al., 1995).

Early Mesozoic ichnofossils similar in morphology to Late Cretaceous and younger solitary (and possibly presocial) wasps, together with the Early Cretaceous diversity of the Aculeata and parasitic wasps (Evans and Eberhard, 1970; Spradberry, 1973), also support an early Mesozoic origin. Because wasps do not rely on flowering plants to provision their nests (with the exception of the pollen wasps, Masarinae), their early evolution was independent of angiosperms and based on the accessibility of such arthropods as spiders, beetles, grasshoppers, crickets, and larval moths (Evans and Eberhard, 1970). The Symphyta were already present by the Early Triassic (Carpenter, 1992) and definitely had an origin that may be as early as the Permian. As stated by Wenzel (1991a), the North American occurrence of *Celliforma favosites* and its interpretation as a nest constructed by *Polistes* compromises the accepted theories that the vespidae evolved on Gondwana and dispersed after South America and Africa separated. The Upper Cretaceous age of *Celliforma favosites* demonstrates that the Polistinae were already present in areas outside Gondwana. A less popular theory (Bequaert, 1932; Carpenter, 1981) is that vespidae wasps have a common northern origin but today are restricted to southeast Asia due to the cooler northern hemispheric climate in the late Neogene and Quaternary. Wenzel (1991a) also suggested that if *Celliforma favosites* were constructed by a form higher in the polistine phylogeny (Carpenter,

1991), then that would not support a Cretaceous origin of the vespids because the fossil is on the wrong continent. Considering the distribution of Cretaceous and pre-Cretaceous ichnofossils interpreted as wasp nests and cocoons, a Permian to Triassic origin of the Aculeata best fits all the paleontologic and tectonic data.

10. Examples of complex nests of solitary to subsocial organisms: precursors to social behavior

Ancient and extant solitary insects and solitary to social vertebrates also construct burrows and nests that are relatively complex in architecture and can be confused easily with ichnofossil nests of social insects (e.g., Walker, 1938; Martin and Bennett, 1977; Ratcliffe and Fagerstrom, 1980; Boucot, 1990; Genise and Bown, 1994a; Bown et al., 1997; Genise and Laza, 1998; Hasiotis et al., 1999; Groenewald et al., 2001). Examples of complex ichnofossil nests of solitary organisms have been documented in continental deposits from mainly the Mesozoic and Cenozoic but they have also been identified in rocks as old as the Late Carboniferous (Boucot, 1990). The complexity is indicated by the number of structural elements used in the overall architecture of the nest: (1) straight or spirally excavated or constructed shafts and tunnels; (2) one or more interconnected shafts or tunnels in various configurations; (3) construction of one or more chambers of varying character within or terminating at the end of a shaft or tunnel; or (4) construction of structural elements within chambers. These elements are constructed by one or more adults, but one or more larvae (i.e., insects) or juveniles (i.e., vertebrates) can also be responsible for the addition or modification of the structural elements in the nest.

10.1. Beetle borings in wood

Various species of beetles attack living, dying, and dead trees (Fig. 18A,B). Trees are attacked mostly for reproductive purposes (e.g., Johnson and Lyon, 1991). After mating, the female scolytid beetle bores into the bark until she reaches the

boundary between the bark and the cambium. Here she bores a curvilinear tunnel of relatively constant diameter that contains notches cut into the tunnel walls. Eggs are laid into each notch where they hatch; from each of these notches the larva bores by eating its way through the surface of the cambium until it is ready to pupate. The galleries bored by the larvae begin with a very narrow diameter, about the size of the recently hatched larvae. The galleries widen in diameter as the larvae continue to grow, backfilling the galleries with frass (masticated wood). The frass of wood-boring beetles is unlike that of wood-eating termites (Light et al., 1930). Each gallery terminates in a slightly expanded cell-like chamber that is grossly similar to cells constructed by bees and wasps where the larvae pupate into adult beetles. Much of the burrow is constructed by the larvae after the female lays her eggs in notches cut into the wall of the main tunnel, from which the egg hatches into a larva and burrows until ready to pupate (Wood, 1982; Johnson and Lyon, 1991). The reproductive cycle of scolytid beetles results in a complex array of galleries radiating from central tunnels that indicate the activity of adults and larvae. Other families of beetles also produce simple to complex tunnels and galleries that are distinct enough to be attributed to those families.

Examples of complex borings in permineralized wood are very similar to those of extant beetles and are attributable to scolytids, buprestids, and cerambycids as early as the Late Carboniferous (Boucot, 1990; Scott, 1992). All of the key morphologic features of wood-boring beetles discussed earlier have been found in trace fossils (Walker, 1938; Blair, 1943; Radwański, 1977; Boucot, 1990; Scott, 1992; Genise, 1995; Genise and Hazeldine, 1995; Hasiotis and Ash, 1998). Examples of complex patterns in wood boring attributable to scolytid and buprestid beetles occur in the Upper Triassic Chinle Formation in northeastern Arizona (e.g., Walker, 1938; Hasiotis and Ash, 1998). Petrified trees from the Jurassic of the western USA and Argentina also contain beetle damage as well as other types of insect damage to the interior of the tree (Genise, 1995; Genise and Hazeldine, 1995; Hasiotis, in press).

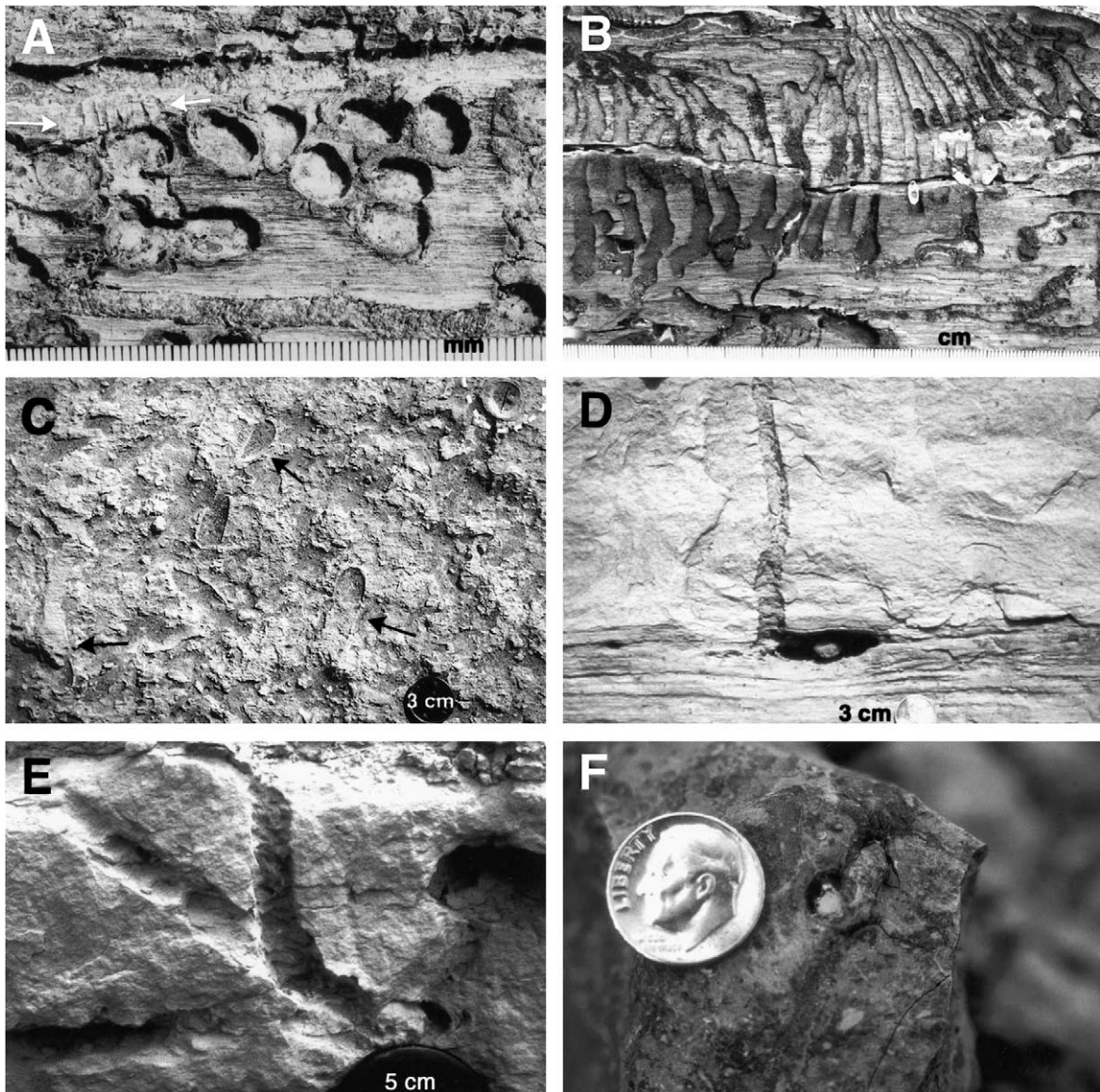


Fig. 18. Complex extant and ichnofossil nests constructed by solitary and presocial insects. (A) Pupation cells of the engraver beetle (Coleoptera: Scolytidae) constructed under the bark and shallow in the wood of a conifer; note the size, shape, and association of the pupation cell and the thick wall of frass, or masticated wood. The cells are connected to the main tunnel (across the top of photo) by very thin tunnels barely visible (directly above cells, left part of photograph) compared to the rest of the structures. (B) Pupation cells of a different species of engraver beetle (Coleoptera: Scolytidae) constructed under the bark and shallow in the wood of a conifer; note how the tunnels increase in diameter toward the pupation cell and its variable morphology from tunnel to tunnel. (C) Weathered bedding-plane exposure of Pleistocene ichnofossil nests interpreted as various dung beetles from the Wahiba Sands in Oman (Hasiotis et al., in preparation c); note the large oblate cells with and without exit burrows (arrows) and a portion of a hemispherical ball in top right of photograph. (D) Natural vertical cross-section of an Oligo-Miocene ichnofossil nest interpreted to be a dung beetle nest in eulittoral lacustrine deposits from Aragon Province, Spain (modified from Hasiotis, 2002); note the preservation of the ball in the chamber. (E) Natural vertical cross-section of an Oligo-Miocene ichnofossil nest interpreted to be a dung beetle nest in an immature paleosol developed on proximal alluvial deposits from Aragon Province, Spain (Hasiotis, in review); note the several tunnels and chambers with the preservation of the ball in one of the chambers (modified from Hasiotis, 2002). (F) Early Eocene ichnofossil designated *Scaphichnium hamatum* interpreted as part of a larger nest of cells stuffed with dung constructed by dung beetles, from Big Horn basin, Wyoming (modified from Hasiotis, 2002).

Complex borings in Cretaceous wood from England have also been attributed to scolytid beetles (Blair, 1943). Excellent examples of complex beetle borings in permineralized wood are also common in Neogene deposits (e.g., Radwański, 1977).

The complex ichnofossils attributable to beetles can be differentiated from the structures produced by wood-dwelling bees and wasps based on key morphologic criteria. The cells at the termination of galleries constructed by beetle larvae, for the most part, are relatively irregular in shape and size (Fig. 18A,B). They are also associated with galleries of irregular dimension that were back-filled with frass (Fig. 18B). The closures on beetle cells were constructed by the larvae from inside the terminal cell or were passively made as a result from the backfilled frass. As discussed in earlier sections, the cells of ichnofossil bee nests (Fig. 14C–F) constructed by the adults are regularly flask-shaped to capsule-shaped, contain smooth walls, and were sealed from the inside out by the adults. Wasps typically construct nests in cavities in wood, but do not bore in wood. Primitive wasps, such as the Symphyta, bore in wood and construct curvilinear tunnels that terminate in a rounded bottom that is not wider than the tunnel (Johnson and Lyon, 1991) and can thus be distinguished from beetles and bees.

The occurrence of borings in petrified wood attests to the presence of beetle activity in the geologic record but also reveals important information about the paleoecologic relationship between the beetles and the trees. For example, the presence of borings all around Triassic and Jurassic tree trunks suggests that the trees were infested while alive (Hasiotis, 2002; Hasiotis, *in press*). If the trees were lying on the ground, only the side facing up would have been attacked. Also, borings similar to those produced by scolytids indicate that the tree was first attacked while living, whereas borings and cavities deeper in the heartwood indicate that the tree was bored after its death while remaining upright. In modern environments, infestations typically occur in localized sections of forests. These activities of Late Jurassic beetles would have killed trees that were too weak to expel the invaders with sap.

10.2. *Dung beetles: nests of chambers and balls*

Adult dung beetles (Coleoptera: Scarabaeidae) construct a range of simple to complex burrow architectures in which they deposit dung in the substrate. Dung is incorporated into the nests as balls rolled above the nest and buried later, dung that is shaped within the nest as balls, and dung that is packed into cells or tunnels (Retallack in Boucot, 1990; Hanski and Cambefort, 1991). These groups have been described as burrow stuffers and above-ground and underground ball makers (Halffter, 1977; Retallack in Boucot, 1990). The dung nests show many variations in construction (e.g., Halffter and Matthews, 1966; Hanski and Cambefort, 1991). The simplest nests are J-shaped and composed of a quasivertical shaft that terminates in a small to large chamber containing one to four or more dung balls. Complex dung beetle nests are similar in architecture to subterranean bee and wasp nests and are composed of a main quasivertical shaft from one or several tunnels that originate and terminate as cells. The cells are merely excavated spherical to elliptical cavities used for backfilled or rolled dung and vegetable material. Complexity in dung beetle nest architecture also includes multiple intervals of small dung balls constructed within side tunnels, appearing like a string of beads, to a single shaft terminating in clusters of juxtaposed tunnels backfilled with dung and other vegetable matter for most of their length. Simple to complex dung beetle nests can reach over 1 m in depth depending on the moisture of the substrate. Still other dung beetles construct balls within dung patties or nearby vegetation (Hanski and Cambefort, 1991). The shape of the balls within subterranean nests ranges from spherical to pear-shaped, and they may be lined with a thin to thick layer of clay (Halffter and Matthews, 1966). The female lays an egg on top of the ball or at the tip of the protrusion. The egg hatches into a larva that proceeds to eat its way into the ball. The larva hollows out the ball by eating all the dung and then transforms into a pupa, and then an adult. In some instances, the parents remain with the brood, protect them from predators, and clean the nest. Beetles that stuff the ends of

tunnels with dung or build small balls in tunnels lay an egg outside the material. The larva hatches from the egg and proceeds to consume the dung. The larva either remains at the end of the tunnel or burrows toward the surface or a location suitable for it to form a pupation chamber, where it completes the reproductive cycle to adulthood (Halffter and Matthews, 1966).

All the key morphologic features of dung beetle nests discussed here have been found in ancient examples recorded as far back as the Late Jurassic (Hasiotis, *in press*). Interestingly, the fossil record of the Scarabaeidae also extends to the Early Jurassic based on body fossils (Crowson, 1981). Most dung beetle ichnofossil nests reported from continental rocks are spherical to pear-shaped balls (Fig. 18C). Many of these ichnofossils have been designated ichnospecies of *Coprinisphaera* and *Pallichmus* (Retallack, 1984; Boucot, 1990; Genise and Bown, 1994a). Other ichnofossil nests are completely preserved and exhibit the positions of the shaft, tunnels, and balls (Fig. 18D,E). These would be classified as composite trace fossils that represent more than one behavior if all the structural elements were preserved, much like termite, bee, wasp, and ant nests but to a lesser extent. There are also examples of ichnofossil nests constructed with cells at the end of tunnels that radiate from a central shaft (Fig. 18F). These types of ichnofossil nests are designated *Scaphichnium hamatum* in the lower Eocene Willwood Formation in Wyoming for the crescentic cell that is preserved (Bown and Kraus, 1983; Hasiotis et al., 1993). Ichnofossil nests assigned to *Monesichnus ameghinoi* have been interpreted as dung beetle nests that are elongate cylinders (Genise and Laza, 1998). Spindle-shaped ichnofossils from the Paleocene–Eocene Claron Formation were also interpreted as having been constructed by dung beetles (Bown et al., 1997). These nests are composed of closely appressed whorls tightly spiraled around an internal, central cavity assigned to several ichnospecies of *Eatonichnus*. The internal cavity contains some evidence of backfilling similar to modern, elongate dung beetle nests. Other examples preserve the backfilled tunnels of larvae that terminate in a pupation chamber. These trace fossils, from Pleistocene

wet interdune deposits, would also represent composite trace fossils if all the structural elements were preserved (Hasiotis et al., *in preparation a,b,c*). Ichnofossil cocoons interpreted as dung beetle pupation cocoons from the Upper Cretaceous of Mongolia have been designated ichnospecies of *Fictovichnus* (Johnston et al., 1996).

The feeding and nesting behavior of coprophagous beetles is excellent evidence for the coevolution of beetles with vegetation, dung-producing, large herbivorous vertebrates, and the detritivore nutrient cycle in soil ecosystems (Halffter and Matthews, 1966; Boucot, 1990). Though they never developed social behavior, the beetles that constructed these nests engaged in some degree of parental care to subsocial behavior as defined by Wilson (1971). The Mesozoic and Cenozoic piles of dung provided a temporary food source and reproductive medium for the dung beetles. The beetles and their larvae also likely adapted elevated tolerances to hypoxia and hypercapnia brought on by decomposing dung within and above the nests (e.g., Holter, 1994). The ichnofossil and body-fossil record suggests that this part of the origin of dung beetles may have been as early as the Permian when the first coleopteran fossil is documented (Crowson, 1981) and when large terrestrial herbivores first became abundant (Hasiotis, 2000).

10.3. Vertebrate burrows

Small to large mammals and reptiles construct burrows of varying architectural complexity and size (e.g., Chamberlain, 1975; Voorhies, 1975; Martin and Bennett, 1977; Bown and Kraus, 1983; Smith, 1987; Groenewald et al., 2001; Hasiotis and Wellner, 1999; Hasiotis, *in press*). Modern vertebrate burrows represent solitary, communal, colonial, and in rare cases eusocial behavior as in the naked mole rats (Walker, 1996). Mammal burrows tend to be the most complex (Voorhies, 1975) and are characterized as subterranean systems that contain one or more openings with shallow vertical shafts that lead to low-angle, diagonal, or spiraling tunnels. The vertically disposed spiraling tubes in vertebrate burrows replace the deep vertical shaft typically used by

such decapod crustaceans as crayfish and crabs (Hasiotis et al., 1999). In the most complex burrow systems multiple entrances, spiral ramps, and adjoining tunnels form underground mazes that can extend over 10 000 m² and contain as many as 20 nest members (Voorhies, 1975).

The ichnofossil record of vertebrate burrows extends as far back as the Early Devonian. These earliest vertebrate ichnofossils are interpreted as lungfish burrows (Allen and Williams, 1981). The oldest evidence of tetrapod burrowing, however, is from the Upper Permian of South Africa (Smith, 1987). These large-diameter burrows were assigned to the ichnogenus *Daimonelix*, and they were interpreted to have been constructed by therapsids (mammal-like reptiles), some of which had fossils of them in the terminal chambers. These burrows were helically spiraled and terminated in a simple chamber, likely containing one family unit (Smith, 1987). Complex burrows from the Lower Triassic of South Africa are much more elaborate than those from the Permian and have multiple branching tunnels and numerous terminal chambers as large as 27 cm long, 11 cm wide, and 7 cm high (Groenewald et al., 2001). These large-diameter burrows (~15 cm wide and 7 cm high) contained 20 individual skeletons and represent multiple cohabitation or extended family units that indicate social behavior. Other Early Triassic vertebrate burrows from Antarctica have simple to complex morphologies that also indicate communal to subsocial behavior (Hasiotis et al., 1999; Miller et al., 2001). Complex ichnofossils from the Upper Jurassic alluvial deposits in southeastern Utah have been interpreted as mammal burrow systems (Hasiotis and Wellner, 1999; Hasiotis, in press). The burrows have a diameter of 5–20 cm and consist of U- or Y-shaped openings. They have shallow to steeply dipping shafts that lead to low-angle, diagonal, or spiraling tunnels. The chambers show various dimensions, and occur in inter-tunnel positions and at the ends of tunnels. The nest morphologies suggest communal or subsocial behavior. The best-known ichnofossil vertebrate nests are those designated *Daimonelix circumaxilis*, which was interpreted convincingly to have been constructed by the Miocene beaver *Paleocaster* (Voorhies, 1975;

Martin and Bennett, 1977). These burrows reach nearly 3 m in depth and terminate in an upwardly inclining large chamber. These burrows are also interpreted to have been constructed and maintained by mammals that exhibited at least communal or subsocial behavior (Martin and Bennett, 1977).

In general, many ancient and extant, subsocial to social vertebrate burrow systems excavated by therapsids and mammals form a pattern of very short vertical shafts, helically spiraled shafts, short to long subhorizontal tunnels of straight to spiral design, and inter-tunnel and terminal chambers (Hasiotis et al., 1999). The shape of the burrow diameter ranges from circular to elliptical but is dominated by a range of elliptical shapes, indicating the shape of the organism that excavated and lived in the burrow. The superficial morphology of these burrows is dominated by a series of linear, longitudinal, and longitudinally crossing scratch marks created by the claws on the manus and pes, and the beak or incisor teeth of the animal during burrow construction and maintenance. The burrow morphologies suggest that they were constructed for long-term use where the organisms maintained a residence, raised young, stored food, disposed of wastes, and coped with episodic inundation by flooding and precipitation (e.g., Voorhies, 1975; Groenewald et al., 2001; Hasiotis, in press).

11. Nest patterns, ichnofabrics, and paleosol development

The ichnofossils discussed herein represent complex, multipurpose structures that were used for dwelling, reproduction, agriculture, food hoarding, deposit feeding, defense, escape, and adaptation to above-ground and below-ground environments. These types of ichnofossil nests and the interpretation of the constructors are often difficult to determine unless the sedimentary fabrics produced by a particular organism's activities with the substrate can be recognized. In the marine realm, the product of this interaction is termed ichnofabric and is defined as all aspects of the texture and structure of sediment resulting

from the bioturbation at all scales (Bromley and Ekdale, 1986). Ichnofabrics are analyzed by such parameters as the types of trace fossils, the activity level within the substrate, and the feeding style represented by the trace fossil (Bromley, 1996). Unique ichnofabrics result from the activity of termites, bees, wasps, and ants that can be recognized by the burrowing signatures and fabrication techniques used by each type of insect (Sections 4–8).

11.1. A new behavioral category for complex trace fossils

Trace fossils that represent the insect nest types described here belong to their own behavioral category where the structures were used to obtain and assimilate nutrients, produce and raise offspring, and maintain, regulate, and defend the nest. These behaviors can be likened to the behavioral categories of dwelling (domichnia), locomotion (repichnia), resting (cubichnia), agriculture and farming (agrichnia), feeding (fodichnia), escaping (fugichnia), and reproduction (calichnia and aedificichnia). *Polychresichnia* (Greek *poly* = many; *chresis* = use; *ichnos* = trace) is proposed for trace fossils that represent many simultaneous multiple behaviors and uses. Aedificichnia and calichnia could likely be subsets of polychresichnia because many of the ichnofossil nests originally included in this category were protected by the adults during brood rearing, used as living and sleeping quarters for the adults, and as shelter from adverse weather. Some nests were likely excavated, constructed, and used exclusively for larval development with the remaining part of the nests (chambers, tunnels, and shaft) used and protected by the adults. Aedificichnia could be used to further characterize nests based on the material that they were constructed above and below ground. For instance, many mud dauber and paper wasp nests would fall into this category since they were constructed with material extraneous to the local substrate. Ultimately all simple and complex nests are meant for mating, reproduction, food storage, and brooding, and include many hominid-built structures such as our apartments, homes, communities, countries, and their infra-

structures. Polychresichnia includes nests of sub-social, parasocial, presocial, primitively social, social, and eusocial behavior displayed by invertebrates and vertebrates. Also included are nests of solitary organisms that exhibit various degrees of parental care and brood rearing, such as some dung beetles and solitary bees and wasps. Examples of trace fossils in this type of behavioral category include *Archeoentomichnus*, *Attaichnus*, *Fleaglellius*, *Krausichnus*, *Masrichnus*, *Parowanichnus*, *Syntermesichnus*, *Termitichnus*, *Tacuruichnus*, and *Vondrichnus*. With further review of the overall nest morphologies of ichnofossil nests interpreted as solitary or communal insects, such ichnotaxa as *Celliforma habari*, *Chubutulithes*, *Rosellichnus*, and *Uruguay* may be considered polychresichnia.

11.2. Ichnofabrics and paleosols

These ichnofossil nests as well as other continental trace fossils indicate the presence of discontinuity surfaces that were formed by varying degrees of pedogenesis (Hasiotis, 2000; Hasiotis and Honey, 2000; Hasiotis, in press). Paleosols are not deposits but the result of postdepositional modifications of alluvial, palustrine, lacustrine, eolian, and transitional-marine deposits that are at least above the water table seasonally. Paleosols also developed on exposed, weathered bedrock (Birkeland, 1999; Retallack, 2001). Pedogenesis occurs at different rates with different results, depending on the rate and frequency of depositional events, distance from sediment source, parent material, the position and fluctuation of groundwater profile, the inherent local topography, the composition of biotic communities, and the climatic setting with regard to temperature and precipitation (e.g., Birkeland, 1999; Bown and Kraus, 1987; Kraus, 1987; Hasiotis, 2000; Retallack, 2001). Soil organisms, including social insects, impact the soil by manipulating sediments and regulating processes that form and destroy soils (Thorpe, 1949; Hole, 1981; Villani et al., 1999; Vittum et al., 1999). Organisms affect soils by mounding, mixing, forming voids, backfilling voids, forming and destroying peds, regulating soil erosion, regulating water and air movement,

regulating plant litter, regulating animal litter, regulating nutrient cycling, regulating biota, and producing special constituents (Hole, 1981). Trace fossils of plants and animals vary in abundance in paleosols from isolated occurrences associated with pedogenic features to thousands of cross-cutting traces that obliterate all bedding and pedogenic structures (e.g., Watson, 1967; Bown, 1982; Bown and Kraus, 1983; Machado, 1983a,b; Hasiotis and Dubiel, 1994; Hasiotis and Honey, 2000).

In the continental realm, the concept of ichnofabrics has been applied analogously to the development of immature to mature paleosols in terrestrial and freshwater-aquatic deposits where the activities of burrowing organisms outpaced pedoturbation (Hasiotis and Honey, 2000). The architectural elements of termite, bee, wasp, and ant ichnofossil nests can also indicate an infrequent, gradual, or rapid accumulation of terrigenous sediment based on the development and intensity of resultant ichnofabrics. Low concentrations of easily recognizable shafts, galleries, cells, and chambers that occur in deposits with abundant primary sedimentary structures indicate immature paleosol development due to a relatively rapid sedimentation rate (Fig. 19A). Relatively moderate concentrations of poorly to well-defined shafts, galleries, cells, and chambers that occur in deposits with little to no primary sedimentary structures with the presence of pedogenic features indicate variably mature paleosol development due to a variably slow to moderate sedimentation rate (Fig. 19B). High concentrations of poorly decipherable shafts, galleries, cells, and chambers that occur in deposits with no primary sedimentary structures and the presence of pedogenic features indicate mature paleosol development due to a relatively slow sedimentation rate or relatively long hiatus in deposition (Fig. 19C). On the other hand, substrates where pedoturbation (i.e., processes of translocation, transformation, additions, and losses of substrate materials) outpaces bioturbation lack appreciable evidence of bioturbation because the traces of plants and animals are destroyed for the most part. Because of these processes and results, ichnofabrics as defined (Bromley and Ekdale, 1986; Droser and Bottjer, 1986;

Bromley, 1996) cannot be directly applied to most patterns of bioturbation in continental deposits.

12. Conclusions

The recognition and interpretation of complex ichnofossils as the product of solitary to eusocial insect activity and solitary to social vertebrate behavior is a major development in continental ichnology. Structural elements, shafts, tunnels, cells, or chambers, used in nest construction form three-dimensional patterns repeated in space and time to construct subterranean, epigeal, and arboreal nests. The recognition of the basic building blocks, constructional techniques, and architectures of these nests is important for the identification of the trace-makers and interpretation of the biologic significance of these complex ichnofossils in the stratigraphic record.

Simple to structurally elaborate ichnofossil nests of termites, ants, bees, and wasps are classified as polychresichnia because many simultaneous behaviors are represented by different interconnected structures. Ichnofossil nests of solitary insects can vary from a diffuse or concentrated occurrence of a shaft or gallery and a chamber, to several shafts and galleries with terminal chambers (or cells). Ichnofossil nests of subsocial to eusocial insects can vary from a diffuse or concentrated occurrence of a shaft with several galleries and chambers (or cells), to hundreds of thousands of shafts and galleries with an equal number of interspersed chambers (or cells). Ichnofossil nests can occur in a volume as small as 10 cm³ to over 10 km³. The size and architectural complexity of these ichnofossil nests is variable depending on the ontogenetic stage of nest development the organisms were in when the colony died. Identification and interpretation of individual or multiple ichnofossil nests in a particular outcrop becomes increasingly difficult as the age of a paleolandscape increases, resulting in pedogenically modified substrates that comprise tens, hundreds, to thousands of generations of nesting individuals or social units, which may or may not be descendants of the original ichnofossil nest constructors.

The biological significance of insect and verte-

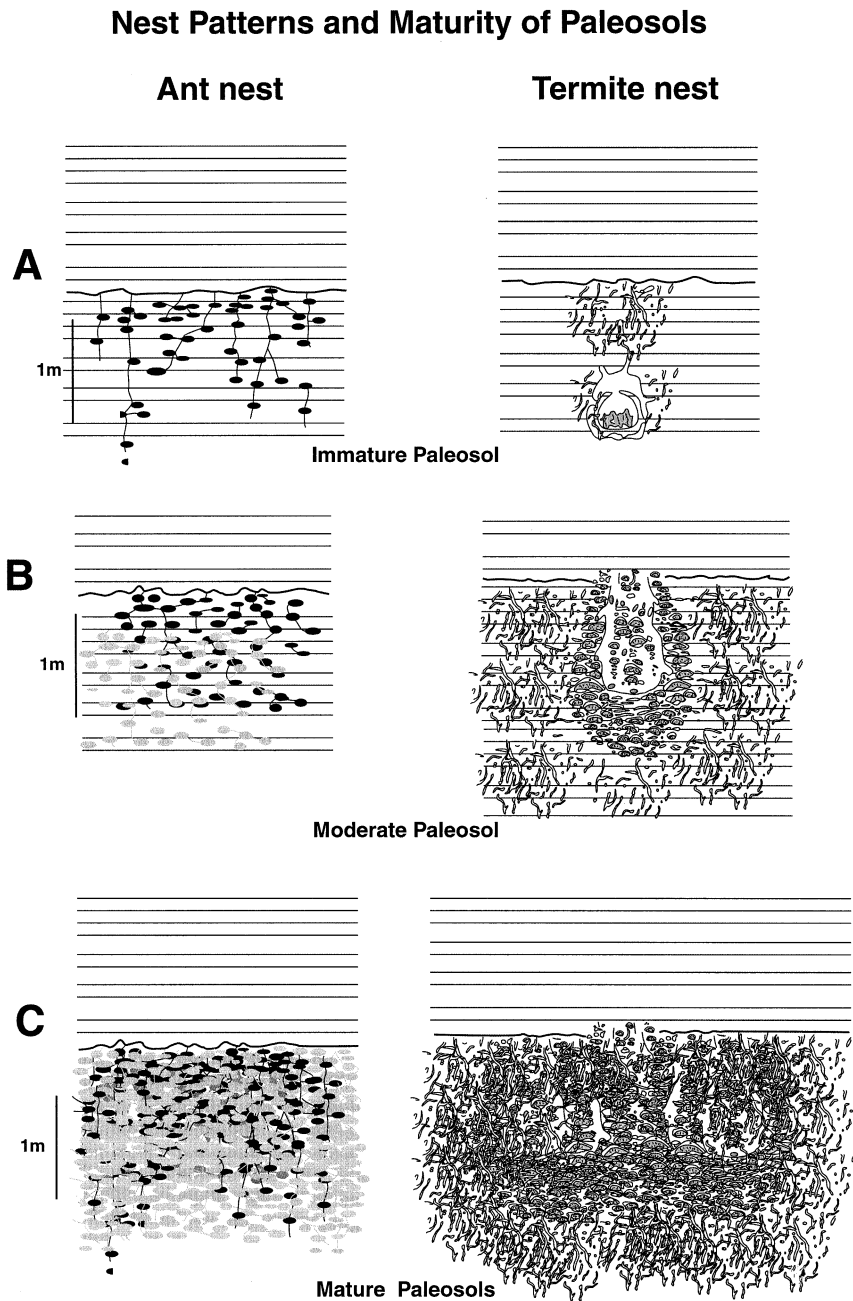


Fig. 19. Relationship between patterns in ichnofossil ant and termite nest architecture and paleosol development. The schematic of nest architectural elements indicates discontinuity surfaces (thicker line) within a succession of alluvial deposits that represent (A) rapid, (B) moderate, or (C) infrequent accumulation of sediment and relative paleosol development from (A) immature, (B) moderate, to (C) mature.

brate complex ichnofossils has been the main emphasis in the study of their variable structural complexity. This approach has been emphasized by Miller (1998, 2001, 2002) for analyzing and understanding structurally elaborate marine burrow systems. The complex and variable behavior represented by these types of ichnofossils has caused ichnotaxonomic problems because several named behaviors (e.g., *Thalassinoides*, *Phycodes*, *Planolites*, etc.) make up dominant or subordinate parts of the burrow system that have been treated traditionally as behaviors that grade from one to another. More notably, the biologic significance of complex marine ichnofossils has been almost completely neglected as they are treated as rarities in the geologic record (Miller, 1998, 2001). The biologic approach used by continental ichnologists is a result of the study of burrow systems of such modern organisms as ants, bees, beetles, crayfish, prairie dogs, termites, and wasps. This approach is both a necessity and a luxury. Burrowing organisms can be studied in their natural settings or under laboratory conditions with relative ease because (1) they inhabit terrestrial settings, (2) their structures are relatively easy to cast and excavate, (3) they can be captured and reared in the laboratory, and (4) an extensive body of literature exists on the life histories and ecologies of many of these organisms. Recognition of behavioral complexity in structurally elaborate continental trace fossils has kept them from being pigeon-holed into pre-existing ichnotaxonomic designations and ethologic classifications, and has led to a profound understanding of the behavior and the organisms that have constructed these trace fossils.

Most of what is known about the evolution and behavior of such social insects as termites, bees, wasps, and ants from the geologic record has been based solely on body fossils. For the most part, however, body fossils are disproportionately under-represented due to taphonomic filters of preservation and diagenesis, compared to the amount of strata recording time. This is evident from the richness of arthropod faunas preserved in amber and in thin beds within shale sequences deposited in long-lived lacustrine basins, both of which occur sporadically in the Late Cretaceous,

Paleogene, and Neogene deposits but are very rare in most Paleozoic and Mesozoic rocks. Ichnofossil nests of these insects, however, are preserved in the geologic record because they were constructed in the near subsurface environment to various depths and were reinforced by physical manipulation or bodily secretions. These ichnofossils were part of the pedogenic modification of continental deposits, and preferentially preserved by soil chelates that were attracted to the organic material in the burrows and burrow walls (Hasiotis and Bown, 1992; Hasiotis et al., 1993). The inherent relationship between nest-building behavior of solitary to social insects and their environment should preserve a larger, disproportionate number of ichnofossils because they are impacted less by the taphonomic filter of preservation and diagenesis compared to body fossils. Information presented here supports the notion that ichnofossils of insect nests may be preserved more often than their body fossils, and thus, may be a more useful tool in understanding the evolution and biogeographic distribution of solitary to social insects through geologic time.

Social cooperation in mammals and the evolution of eusocial behavior in insects are innovations that have been evolved several times. The Isoptera and higher Hymenoptera are among the few insects that construct and maintain nests that are the focal points of their activities (Evans and Eberhard, 1970; Wenzel, 1991b). The nest, no matter how architecturally complex, must have been an important preadaptation for social behavior. Extrinsic pressures forced organisms to adapt to their environment by sharing the responsibility to forage for food, rear the brood and care for the young, defend the nest, and maintain nest structure and construct new sections when necessary (e.g., Wilson, 1971). Continental plate reconstructions strongly suggest that termites, bees, wasps, and ants had their origins in the Triassic prior to the breakup of Pangea. Speculatively, the major environmental and climatic changes during the final amalgamation and movement northward of Pangea (increasing continentality, then increasing seasonality) provided the extrinsic mechanisms that promoted sociality to various degrees within these insects.

The ichnofossil evidence presented herein suggests that social insects have behaved as superorganisms since the early Mesozoic. The structures for shafts, galleries, chambers, and cells used in nests by termites, ants, bees, and wasps have changed remarkably little in 225 million years, indicating evolutionary stasis of the basic building blocks in nest construction. Changes in the complexity of ichnofossil nests and variations in the structural elements that compose these ichnofossils through the Mesozoic and Cenozoic likely indicate the uses of new material collected from a variety of angiosperms. The social behavior seen in the Isoptera and Hymenoptera is believed to have developed through the exchange of food that involved the transmission of social stimuli in a way analogous to translocation of food and hormones throughout the body via the circulatory system of higher animals (Spradberry, 1973). This interaction would have reinforced the behavior of cohabitation and encouraged food hoarding through the construction of diffuse to concentrated nests where foodstuffs would have been stored and grown. The large number of respiring organisms and decaying food caches in close proximity in the nest would have caused major problems in subterranean nests. These potentially adverse conditions were resolved by individuals cooperating to maintain and alter the nest architecture to optimize atmospheric and climatic conditions to the subterranean community.

The intensity and distribution of bioturbation indicated by ichnofossil nests of termites and ants suggest that they played major roles as ecosystem engineers (Jones et al., 1994; Lavelle et al., 1997) since at least the Triassic. The physicochemical activities of these organisms modified the environment and regulated nutrients in the trophic pyramid to biota above and below them. The large numbers of excavated and constructed chambers and galleries in ichnofossil termite and ant nests would have held bits of plant and animal matter gathered from the surface and fed to nest mates. All these passages increased gas exchange with the atmosphere above the surface and allowed infiltration of water from precipitation and flooding. Material that was not used completely was placed along with other nest waste, including infected or

dead nest mates, into abandoned chambers and galleries and backfilled. Other chambers likely contained fungus gardens that were grown to feed the colony and regulate the temperature and humidity inside the nest. The activities represented by the nest architecture of termite and ant ichnofossil nests indicate that these organisms mixed soils, regulated surface and subsurface gas and water exchange, recycled organic material into the subsurface, and affected the trophic behavior of micro-, meso-, macrofauna in the ecosystem.

Thus, variably complex ichnofossils of solitary to social organisms can be thought of as extended organisms (Miller, 2002), structures that function as physiologic projections (Turner, 2000) or extended phenotypes of the trace-makers (Dawkins, 1989). Modern and ancient nests are the manifestation of solitary to social organisms that purposely alter habitats (Jones et al., 1994), modify the effects of disturbance (Lewontin, 2000; Sterelny, 2001), and control food supplies (Vander Wall, 1990). Mesozoic and Cenozoic ichnofossil nests provide fairly reliable evidence that the evolution and diversification of social organisms is the result of the ability of an organism(s) to impose itself on its surroundings and control, to some extent, the future of its offspring and the course of microevolution (e.g., Sterelny, 2001).

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