Chapter 2

The Paleontological Context. Ichnology

Abstract Except for some previous records, the first attempts for the study of the lying tracks on sediments started at the beginning of the nineteenth century, as well as the efforts for creating a suitable terminology. Its installation as a scientific discipline began at the end of the nineteenth century. By middle twentieth century, a modern and organized scheme for the classification of ichnofossils and their location in ichnofacies was proposed. Firstly, the only recognized ichnofacies corresponded to marine environments and were defined by bathymetric levels and particular ichnofossils. Immediately, ichnofacies corresponding to transition environments from those marine to continental were identified. In 1985, the ichnological nomenclature became part of the International Code of Zoological Nomenclature. During the 1970s and 1980s, there were papers describing ichnites of continental origin, events that quickly led to the organization of the formal reconnaissance of environments carrying continental tracks, giving rise to successive ichnofacies. Apart from the paleosurfaces, the ichnological content is rich and quite varied in paleosols and so are the tracks of insect nests, solitary or in groups in these paleosols.

Keywords Ichnology · Continental ichnofacies · Ichnites in paleosols

2.1 Scheme of Continental Ichnofacies

Although inert in themselves, the constructions made by a living organism contain a true flow of information about the needs and intentions of its builder (Lovelock 1979).

Leaving aside some reference to coprolites toward the end of the seventeenth century, the beginnings of ichnology go back to the beginning of the nineteenth century with the description of vertebrate footprints and traces from marine rocks; additional tasks slowly developed and Ichnology attained status of scientific discipline in the last decades of the nineteenth century (Osgood 1975). The term Ichnology was proposed by Buckland in 1836, during the study of invertebrate trace fossils which were interpreted as belonging to algae (“fucoides”) until Nathorst (1881), using the Uniformitarism Principle, proved their zoological origin.

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The attempts for regulating the ichnotaxonomy began very early: In 1853, Jardine proposed naming the tracks with a name finished in ichnus in order to differentiate them from the corporal fossil names, a proposal which was then supported by Seilacher (1953) and Häntzschel (1962).

At the beginning of the twentieth century, Abel and then his disciples continued the ichnological studies introducing main concepts such as bioturbation and biostratification. It was Abel (1935) who also revitalized the vertebrate paleoichnology in Europe, whereas Gilmore and Peabody in North America (from the 1920s to the 1940s) and Rodolfo Casamiquela in South America did so during the 1960s. Richter (1927) began the systematic study which continued until the 1950s when Seilacher (1953) proposed a new methodology in the study and classification of ichnological materials, outlining the model of ichnofacies. He distinguished several marine ichnofacies, developed in specific environments at different bathymetric levels and composed of particular ichnofossils (Seilacher 1964, 1967). The Seilacherian proposal not only assigned the traces to a paleontological nature but also considered the biological activity and sedimentary processes. The initial scheme was improved, being integrated with eight marine ichnofacies and a continental one called Scoyenia, which corresponded to "sandstone and non-marine lutites, commonly red strata" (Seilacher 1953) formed by traces of marine and continental environments of salty environments. The Scoyenia ichnofacies reflects the superposition of sets of fossil traces associated with changes in the substratum consistency, water saturation, generally associated with changes of water levels. Scoyenia shows low ichnodiversity, with the presence of meniscated holes, systems of bilobed holes and arthropod trails. The works by Häntzschel (1962, 1965) accelerated the development of the discipline, marked by a continuous refinement (Osgood 1975). In these works, the information from the stratigraphic record and that from the study of current environments cohabited interactively.

Once the Scoyenia ichnofacies was established, the study of continental ichnology detained (Seilacher 1964). Frey et al. (1984a) questioned the boundaries of such ichnofacies, for being extremely broad and varied, arguing that Scoyenia was only one of the continental ichnofacies which was poorly known and indefinite.

In spite of the early attempts for regulating the norms of ichnologic nomenclature, these did not have official status until the publication of the third edition of the International Code of Zoological Nomenclature in 1985. Until that moment, the continental traces were associated with footprints of vertebrates, coprolites, nests, bones with marks and traces and on plants, whereas those of terrestrial invertebrates were considered doubtful and, incorrectly and scornfully called "snail holes" and "tracks and trails" (Hasiotis and Bown 1992). The 1970s and 1980s showed contributions about continental ichnites, in fluvial and lacustrine environments, interpreted ecologically and ethologically (Bromley and Asgaard 1979). Ratcliffe and Fagerstrom (1980) listed diverse insect groups inhabiting the current plains, comparing their traces with those of the fossil record. Bown (1982) reviewed ichnites and rhizoliths from fluvial deposits of the Oligocene in Egypt, and Laza (1982) described an anthill of the Late Miocene in Argentina. These and other contributions indicated the necessity of assessing different terrestrial environments, organisms that lived in them and the footprints they left. Thus, successive proposals have been added to the continental system of ichnofacies, for instance, the Mermia ichnofacies (Buatois and Mángano 1995a) which corresponds to subaqueous tracks, formed by vertical holes in the shape of Y or U, horizontal holes and others in meniscal shape. The original proposal of the Termitichnus ichnofacies (Smith et al. 1993) was reviewed later by Genise et al. (2000) who suggested to assign such ichnofacies to groups dominated by termite nests in paleosols of closed forest ecosystems under certain humidity and temperature conditions (Melchor et al. 2012). The invertebrate trace fossils are found in numerous continental environments, represented by lithofacies with different degrees of preservation (Hasiotis and Bown 1992), many of them originated in subaqueous environments. However, it is in the paleosols where the fossil traces of vertebrates, invertebrates and especially of insects are more abundant and have greater diversity (Genise 1999). In the modern ichnofacial analysis, all evidence (physical, chemical and biological) must be integrated and used in the interpretation (Frey et al. 1990; Fig. 2.1) The great deal of information resulting from the study of paleosols and their ichnofaunas led to the creation of the Coprinisphaera ichnofacies (Genise et al. 2000), an ichnofacies that gathers all the "Seilacherian" qualifications of recurrence in space and time and at the same time involves great ichnodiversity. This group shows an absolute dominance of chambers as well as systems of holes and chambers. The abundance of coprophagous beetle nests (Coprinisphaera), the most numerous components of this archetypical group, gives the name to this ichnofacies. They inhabited the soils (paleosols) developed in systems of plain deposits or with little relief, in communities (paleocommunities) of dominant Gramineae, but also tree-covered zones. Such ichnofacies consists of a moderate to high diversity of traces that includes various nests of coprophagous beetles, honeycombs of bees—solitary or grouped, wasp nests, anthills, termite mounds, meniscal and smooth tubes (produced by different invertebrates), vertebrate caves, as well as root marks, coprolites, gastrolites and regurgitations. The mentioned list comprises great part of the traces that a group of ichnologists proposed to recognize formally as signs (Genise et al. 2004; Bertling et al. 2006).

Recent studies have brought into debate the need of creating new ichnofacies or ichnosubfacies in the field of continental ichnology, recognizing and limiting specific environments (Melchor et al. 2006; Genise et al. 2008a, b).

More recently, Genise et al. (2010) proposed the creation of Celliforma ichnofacies, identified by the uninterrupted presence of bees and wasps activity in paleosols. Such ichnofacies may indicate biotopes with prevalence of dry climates and poor vegetation cover.

The Skolithos ichnofacies (originally defined in the marine domain) has been tentatively recognized in fluvial deposits of channels and lake deposits of high energy. The ichnofauna is commonly mono-specific, dominated by vertical holes, Y or U shaped (Buatois and Mángano 1998, 2004, 2007; Melchor et al. 2003).

The contemporary continental ichnology can be characterized as one of the most dynamic fields within paleontology and with great potentialities for providing crucial evidence in the reconstruction of life history. The tasks have been focused on two complementary research lines; one of them looks for the characterization of recurrent

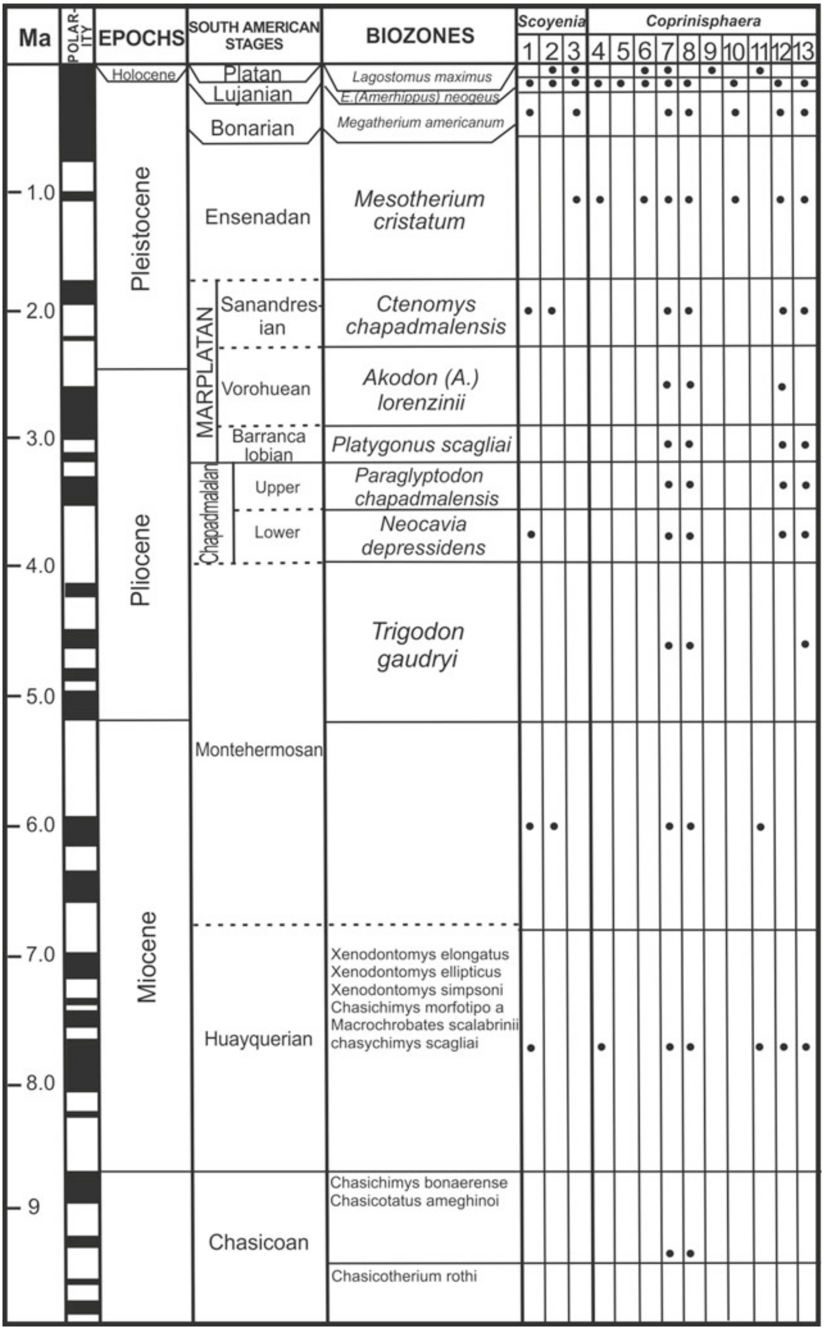

Fig. 2.1 Stratigraphic scheme of the Neogene of the Pampas and the ichnites present in such level (drawing by Marcela Tomeo)

associations with ecological signification and the other one explores evolutionary trends. Thus, the radiation of groups of organisms, the colonization of ecospaces and the appearance of new behaviors are studied (Mángano and Buatois 2001).

In contrast, the proposals of vertebrate ichnofacies, or the incorporation of vertebrate trace fossils for unifying the ichnofacies scheme have been controversial. The principles used for recognizing potential ichnofacies with vertebrate tracks are not the same as those applied for establishing ichnofacies with signs of invertebrate activity. These differences have been recognized and have been suggested for identifying two kinds of ichnofacies: (a) those ichnofacies that reflect interacting behaviors between organisms and substratum (ethoichnofacies) and (b) those that deal with the relationship of tracks and traces with the producer taxonomy (biotaxo-ichnofacies) (Hunt and Lucas 2007). The vertebrate ichnofacies found in fluvial deposits include those of Grallator and Batrachichnus (Hunt and Lucas 2007; Lockley 2007; Lockley et al. 1994).

Although the studies on vertebrate coprolites and the application of ichnotaxonomic names are still in its early stages, coprofacies have been recognized (Hunt et al. 1994), being suggested those of Heteropolacopros and Dicynodontocopros for fluvial sequences (Hunt et al. 1994). The first observations about fossil insect nests in Argentina were carried out by a French researcher, August Bravard (1857a). This author mentioned that in the “toscas (i.e., pedocalcic paleosols) del Río de La Plata” (Pliocene to Early Pleistocene in age), the finding of cells of dipterous chrysalis (which he attributed to the genus Athericea), appearing in a great number surrounding articulated skeletons of fossil mammals, even when the dipterous puparia may have been a fossil body rather than a trace. Ameghino (1880) confirmed such findings in the Luján River basin, Buenos Aires province. His observations were repeated in the coastal outcrops of the cities of Mar del Plata and Miramar, where he mentioned the finding of solitary bee nests such as Ancyloscelis anales Vach in Pliocene–Pleistocene horizons, included in fragments of the “tierras cocidas” (“cooked lands,” Ameghino 1908).

In Uruguay, Serafín Rivas (1900) reviewed hymenopteran nests in old deposits, and in Europe, Schutze (1907) described the first fossil bee cell. In turn, the Russian researchers, pioneers in soil and paleosol studies, when mentioning the finding of small caves of fossorial vertebrates, called them “krotovinas” (mole caves, in Russian) (Subachev 1902), name that was generalized until becoming synonym of excavations made by vertebrates.

During the 1930s, several authors gave impulse to these topics in America. In Argentina, Frenguelli (1930) cited fossil bee nests. Frenguelli (1938a, b; 1939b) published the first descriptions of beetle nests which appear profusely in diverse levels of the Tertiary of Patagonia and the Quaternary of the Pampas, relating these nests to “ancient soils.” Simultaneously, in Uruguay, Roselli (1939) disclosed fossil nests of beetles and bees of the Early Tertiary in this country, using binomial nomenclature for the trace denomination, as it is used nowadays.

In North America, Brown (1934) created the ichnogenus Celliforma for designing fossil bee cells, publishing both papers about the same topic in 1925 and 1941.

Later, such topics were rarely mentioned and, only recently, the insect trace fossils in paleosols began being studied systematically in order to incorporate them to the theoretical body of ichnology (Genise 1999).

The scientific activity on these fields then continued with Estrada (1941), Sauer (1955), Andreis (1972) and a myriad of works during the following years: Laza (1982), Bown and Kraus (1983), Retallack (1984), Laza (1986a, b), Ritchie (1987), Bown and Laza (1990), Retallack (1990), Hasiotis et al. (1993), Genise and Bown (1994a, b), Dubiel and Hasiotis (1994a, b), Trackray (1994), Hasiotis and Dubiel (1995), Laza (1995), Genise and Hazeldine (1995), Genise and Bown (1996), Hasiotis and Demko (1996), Bown et al. (1997), Genise (1997), Laza (1997), Genise et al. (1998), González et al. (1998), Genise (1999), Duringer et al. (2000), Melchor et al. (2002–2006), Laza (2006a, b), Genise et al. (2007), Verde et al. (2006), Duringer et al. (2007), Bedatou et al. (2008), and Cantil et al. (2013), among many others.

The nesting activity of insects on the soils has an extended colonizing capacity; thus, the sediment removal and the incorporation of organic matter make them great soil makers (Retallack 1990).

Great part of the insect trace fossils in paleosols are nests or part of them, that is, structures excavated and/or built by adults for the progeny development. This activity was called Calichnia by Genise and Bown (1994a) in the ethologic classification of ichnites, being added to the previous ones proposed by Ekdale et al. (1984).

Later, Genise et al. (2007) distinguished a new category for the pupation chambers of insects, which they called Pupichnia. The nests have walls, floor coverings and other quite elaborated devices that offer several diagnostic signs for identifying their builders. The need for maintaining special conditions inside the nests leads the adults to use, often, diverse types of organic matter in the construction, providing them with a marked potential of preservation, since the transformation of such materials favors the concentration of salt and oxides increasing the strength of such nests and their subsequent conservation in the soils (Janet 1898). Thus, these hardened constructions, more compact than the soil surrounding them, have greater possibilities of preservation by diagenesis (Genise and Bown 1994a). The morphological variety of such nests reflects the great ichnodiversity that the fossil record keeps, as well as the various reproductive strategies of the different groups. These characters that in some cases were studied through the reconstruction in 3D by computer (Genise and Hazeldine 1998), computerized tomography (Fu et al. 1994a; Laza et al. 1994; Genise and Cladera 1995) and micromorphological analyses (Cosarinski et al. 2004; Zorn et al. 2010). The study of those strategies comprises the dispersion area of the builder, the choice of the environmental conditions of the nest to be built and the food foraging for the offspring, and its characteristics as well, the inherent climatic factors and the coeval vegetation.

The recognition of these relationships has allowed, for instance, paleogeographic and paleoclimatic inferences about fossil nests of ants and termites (Laza 1982, 1995; Bown and Laza 1990, Genise 1997). In turn, the insect trace fossils in paleosols provided the greatest contribution from the paleoichnology to paleoentomology, thanks to the degree of reliability that the possibility of assigning them to define taxons, such as families and genuses, bring about (Genise 1999). The identification of various and numerous insect groups in paleosols of Pampasia allowed extrapolating many of their trophic activities. Therefore, there are cases related to diverse nests of inquilinism of coleoptera Scarabaeinae, the genus Onthophagus and Canthonini, in natural and mammal caves, as well as remains of Squamata in an anthill of Acromyrmex. Activities of granivorism and mirmecoria produced by ants of genus Pogonomyrmex and Pheidole, cannibalism of ants, genus Forelius, and the cases of mutualism of Attini ants with the fungi they cultivate, have also been reported. Coprophagy activities developed by Scarabaeinae, Aphodiinae and Amitermitinae termites, mycetophagy and necrophagy carried out by Scarabaeinae and dermestids, as well as by the ants Solenopsis and Pheidole, have been observed. The revision of the ichnogenus Coprinisphaera (Laza 2006b) through a very important collection allowed discovering a varied amount of cases of inquilinism and predation of insects in nests of such coleoptera and their subsequent occupation as well (Mikulás and Genise 2003; Sánchez and Genise 2009). A new revision of ichnogenus Coprinisphaera (Sánchez 2009) added new and important data to its taxonomy, adopted in the present work.

Nowadays, most part of the insect trace fossils may be assigned to three groups: beetles (Coleoptera), termites (Isoptera) and bees, wasps and ants (Himenoptera). Each one of these big groups presents its own peculiarities and requires specific terminology and ichnotaxobases (Buatois et al. 2002). Meeting these needs, Genise (2000) created the ichnofamily Celliformidae, adding then Pallichnidae, Krausichnidae and Coprinisphaeridae (Genise 2004). Recent studies have brought into question the necessity of creating, in the field of continental ichnology, new ichnofacies or ichno-subfamilies, recognizing and limiting specific environments (Melchor et al. 2006; Genise et al. 2008a, b, 2010) (Fig. 2.2).

2.2 The Ichnological Record in the Cenozoic of Pampasia

2.2.1 Vertebrate Footprints (Fig. 2.3a and b)

Most vertebrate footprints stem from continental environments, marginal to the marine environment such as those of the domain of Scoyenia ichnofacies, or in continental waters of the Mermia ichnofacies. These are environments with a higher content of moisture or which are even partly or fully flooded.

As a historical anecdote, it should be mentioned that the first mention of the finding of fossil vertebrate tracks in South America was in 1839 in Colombia (Buffetaut 2000).

Casamiquela (1983) was the first mentioning findings of vertebrate tracks in the Pampasia area. The first finding was in the Río Negro Formation (Late Miocene of northern Patagonia), close to the mouth of the Río Negro (41° 04´ S–62° 47´ W) and the second one was in Late Pleistocene sedimentary rocks, nearby the locality of

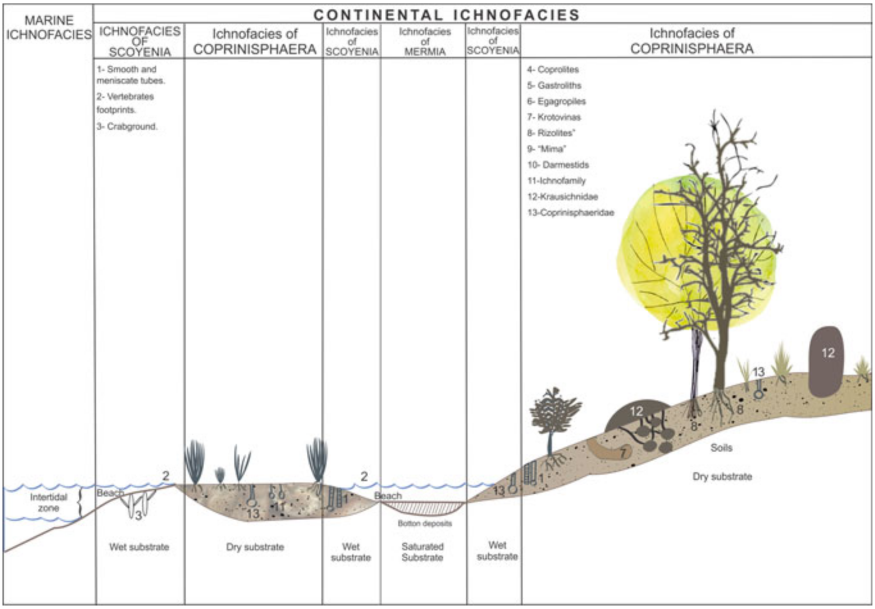

Fig. 2.2 Scheme of continental Ichnofacies in the Neogene of the Pampas (drawing by Marcela Tomeo)

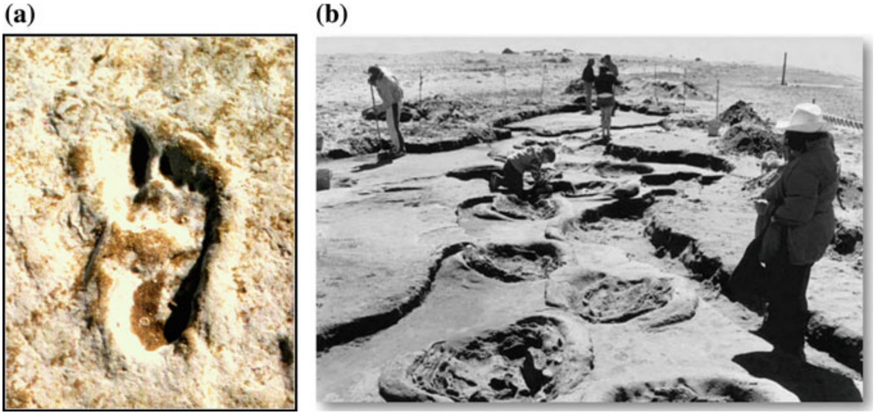

Fig. 2.3 **a** Human footprint at (Monte Hermoso); **b** Mammal tracks (Pehuén-Có locality)

Monte Hermoso (38° 47´ S–61° 53´ W) corresponding to the edentates Megatheriidae and Scelidotheriinae, respectively.

Aramayo and Manera de Bianco (1987a, b, 1 and 2) discovered the ichnite site of vertebrates and invertebrates of Late Pleistocene age to the east of the Pehuén-Có locality (38° 56´ S–61° 53´ W) dated at 12,000 ± 110 ^{14}C years B.P. This finding spread to a new site, with two sectors, 4 km to the west of the mentioned town (the Playa del Barco site) with an age of 16,440 ± 320 ^{14}C years B.P. These sites gave rise to diverse publications where Xenarthra, rodents, carnivores, Liptorerna, Proboscidea, Perissodactyla and Artiodactyla mammals were identified, and among the birds, Phoenicopteriformes, Tinamiformes, Anseriformes and Rheiformes (Aramayo and Manera 1996, 1998, 2000), Aramayo et al. (2003), Manera and Aramayo (2004). Later, Manera et al. (2005) distinguished traces of animal skin in the flange of tracks attributed to Megatherium. In 2005, isolated human tracks were found in the same site, which were dated in 12,000 radiocarbon years B.P. (Aramayo and Manera 2009; Manera et al. 2010).

Quintana et al. (1998) mentioned the presence of mammal ichnites imprinted on sediments of Late Pleistocene age, in the Burucuyá cave, western slope of the Sierra de la Vigilancia (Buenos Aires province). This finding spread then to Gruta del Oro, both sites located in the Sierras de Tandil area.

Aramayo (1999) discovered tracks that were assigned to Promacrauchenia and small rodent crotovinas in the "Rionegrense" sediments of the Atlantic Ocean coast, 30 km westward of the Río Negro mouth. Sometime afterward, Aramayo et al. (2004a, b) found tracks of xenarthrans, ungulates, carnivore marsupials and phororhacoids birds in coetaneous deposits (between the El Cóndor and La Lobería beach resorts; province of Río Negro, 41° 3´ S –62° 53´ W). The sediments corresponding to the Late Miocene-Early Pleistocene epochs were typified as deposits belonging to interdune temporal lagoons, with desiccation crevasses and ripple marks.

Tassara et al. (2005) informed the finding of vertebrate ichnites in the Santa Clara Formation (Late Pleistocene), in the coastal sector of Barrio Parque Camet Norte, in Mar Chiquita county and in the mouth of Arroyo Seco (37° 47´ S–57° 27´ W), both sites in Buenos Aires province.

They recognized four sectors, carriers of the ichnogenuses already mentioned in the Pehuén-Có site.

In sediments of the Early Holocene, 6 km west of the Monte Hermoso locality (southern Buenos Aires province), several hundreds of human footprints, some others of birds and an artiodactyl footpath, were found. The footprints are distributed sporadically around 800 m length at the present coastline (Politis 1993).

Aramayo et al. (2007) pointed out that tracks belonging to tardigrades xenarthrans—adult and young—equids and artiodactyls, which were assigned to the Late Pleistocene, were found in the Monte Hermoso locality (the Camping Americano site, Buenos Aires province).

2.2.2 *Coprolites (Fig. 2.4)*

Coprolites are fossilized feces (of vertebrates and invertebrates) which underwent burial processes and subsequent mineralization for having been deposited in calm flooded zones or in drier zones, where they received fast burial. They can be identified by their morphology, extrusion marks, sutures, gas bubbles and inclusions

Fig. 2.4 Coprolites

such as food waste (either animals and/or plants), being also pollen and phytolith carriers. They can sometimes provide information about the taxonomic identity of the producing organism, due to their shape.

In paleosols of the Cerro Azul Formation (Huayquerian stage, Late Miocene) from the Caleufú locality, province of La Pampa, Argentina (35° 41´ S–64° 40´ W), coprolites of assumed predatory vertebrates were collected that contain microvertebrate remnants. These remains are modified by chewing and digestion and are quite difficult to identify. The materials agglutinated in cemented sand by calcite are of cylindrical shape, 14–16 mm in diameter and 8–21 mm long (Montalvo 2004).

Aceñolaza and Aceñolaza (2004) indicated that numerous vertebrate coprolites had been found in Ituzaingó Formation, in outcrops on the Paraná River banks. Noriega and Areta (2005) pointed out the presence of herbivore coprolites together with remains of insects, plants, ostracods and osseous relics of the huge condor bird Sarcoramphus papa, in the section of Camet Norte locality, level B (Lujanian stage, Buenos Aires province).

Martínez and Ubilla (2004) mentioned the finding of coprolites with tooth and rodent bone inclusions in paleosols of the Sopas Formation (Lujanian stage) in northern Uruguay, venturing that such remains were the result of carnivore activities.

In the Ensenadan stage, sediments from the town of Miramar, Buenos Aires province, a coprolite was found with inclusion of Lagostomus bones, associated with glyptodont remains; this was the reason why the coprolite was attributed to a carnivore mammal.

The presence of feces, attributed to a canine mammal in the Lujanian stage sediments (the Guerrero Member, Late Pleistocene), has been mentioned for the locality of General Guido, Buenos Aires province (Chimento and Rey 2008).

2.2.3 Gastroliths, Enteroliths or Bezoars (Fig. 2.5)

Rounded stones, commonly selected and ingested by reptiles and birds, which help such vertebrates in the inner food milling, are called gastroliths. Their finding was not mentioned in the different levels of the Cenozoic units in Pampasia. The enteroliths of bezoars are formed inside the digestive tract of mammals. These structures can be organic or inorganic; those of organic origin may be formed by fur ingestion (trichobezoars) or plant materials (phytobezoars). Only one finding has been recorded for the region: It corresponds to an accretionary body found by Florentino Ameghino in the Late Pleistocene of the Olivera locality, Luján County, Buenos Aires province. The box where these materials were stored was found many years later in the La Plata Museum; it had also osseous remains of Scelidotherium. It is an ovoid body, partly embedded in “tosca” (Ca carbonate), of 62 × 89 mm in size. Its surface is rough, bright and ocher brown; the analysis of the cuts by diphractograms allowed to identify it as a fossil phosphatic stone (Teruggi et al. 1972).

2.2.4 Egagropiles (Fig. 2.6)

Regurgitations or pellets are waste resulting from the predating activity of several birds, such as Strigidae, Tytonidae, Laridae and Ardeidae, which usually inhabit big trees and places such as caves, caverns or natural cavities. Birds swallow their whole preys—small mammals, fishes, mollusk, birds and insects—whose waste is eliminated in the shape of bolls (pellets). Pellets are characterized for keeping the bones hardly fractured and the cranial bones disarticulated, contributing to the small vertebrate record and thus supplying the fauna sampling in a certain area. The paleontological record mentions them rather frequently calling them “microbonebeds” (Terry 2004). Frenguelli (1928) was the first author to mention them for the coastal cliffs of Buenos Aires Province. Tonni and Fidalgo (1982) mentioned their presence in the outcrops of Punta Hermengo, Miramar County, Buenos Aires province.

Tonni et al. (1993, 1998) informed the finding of two regurgitation accumulations of Strigiforme birds that provided several complete pellets with micromammal and bird remains; the first forming part of the filler of a cave of great edentates located to the SW of the Punta Hermengo locality, General Alvarado County, Buenos Aires province (38° 16´ S–57° 50´ W). The second finding was in the marine cliffs to the N of the city of Mar del Plata (37° 56´ S–57° 32´ W), General Pueyrredón County, Buenos Aires province. Both stratigraphic levels were correlated, and they correspond to the Late Ensenadan stage (Early to Middle Pleistocene).

Fig. 2.5 Gastrolith, enterolith or bezoar

Mazzanti and Quintana (2001) described pellet layers in the filler of the archeological site Cueva Tixi, in Sierra de la Vigilancia, eastern Sierras de Tandil, General Pueyrredón County. Levels D and E have accumulations of pellets, and they were dated in 3255 + - 75 ^{14}C years BP and 10,375 + - 90 ^{14}C years BP, of Holocene and Late Pleistocene age, respectively. Laza (1998, 2001) stated that the pellet accumulations of Cueva Taxi, as well as bird excretions producing them, and probable deposits of bat excrement created a substratum quite favorable for the establishment of beetle populations of the genus Onthophagus, whose nests are associated with such accumulations.

2.2.5 *Krotovinas (Fig. 2.7a, b, and c)*

The first mention about the presence of krotovinas in the Pampasia sediments corresponds to Florentino Ameghino (1880) when pointing out vertebrate caves attributed to vizcacha (a large South American rodent), foxes, mice and tuco-tuco (a smaller rodent) in the Luján River basin, Buenos Aires Province. In 1908, while exploring

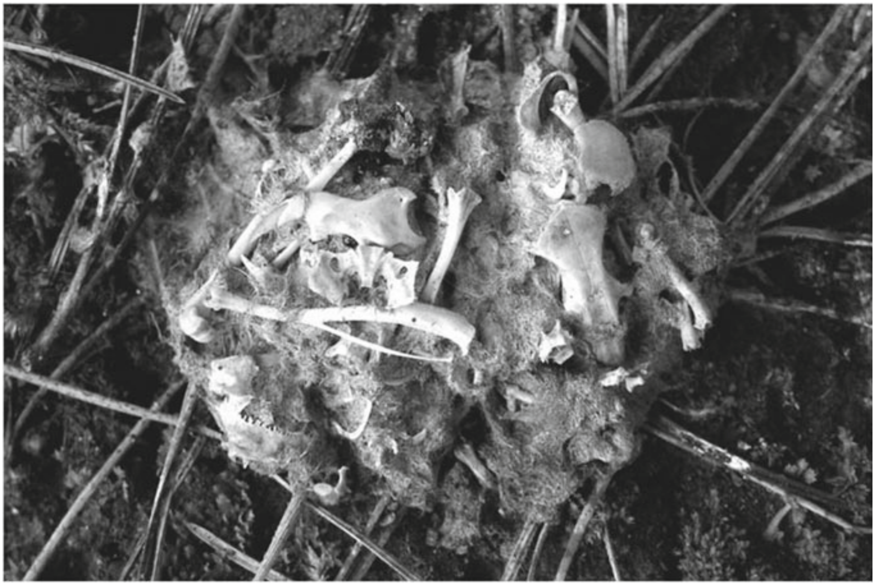

Fig. 2.6 Egagropiles

the Atlantic Ocean coast between the Miramar and Mar del Plata counties, Ameghino observed large and small filled caves at different levels of the Pliocene–Pleistocene sediments, which he assigned to mammals.

Frenguelli pointed out the existence of such caves in his 1921 and 1928 papers arguing that the largest ones prevail in deposits of the "Pre-Belgranense" sediments, belonging to the Marplatan–Ensenadan stages, and attributing them to glyptodonts. This argument was unshared by Kraglievich (1934), who believed that these xenarthrans were unable to dig due to their shell stiffness and the lack of frontal legs suitable for such a task. Frenguelli also mentioned a cave filled with volcanic ashes with remains of Scelidotherium in the locality of Centinela del Mar, Buenos Aires Province (38° 25´ S–58° 09´ W). Rusconi (1937e) attributed these blind caves to the activity of large dasypodidae. In 1967, he wrote that "winding strips of about one meter wide"…"are formed by clayish materials and arranged in small layers up to one mm thick. These materials differ from the adjacent loessoid material" at the surface of the Ensenadan stage sediments of the river banks north of Buenos Aires City (the town of Olivos), in times of lower water level of the Río de La Plata. He also verified that, in some places, these sediments outstand from the surface and, in others, they appear at a lower level due to different diagenetic qualities, illustrating schematically these findings and others in the sediments of the Bonaerian stage in the city of Buenos Aires.

Kraglievich (1952) revealed caves up to 1 m in diameter within the level II of the Vorohué Formation (Marplatan stage). Imbellone and Teruggi (1988) and Imbellone et al. (1990) mentioned that a krotovina was found, formed by sediments of the

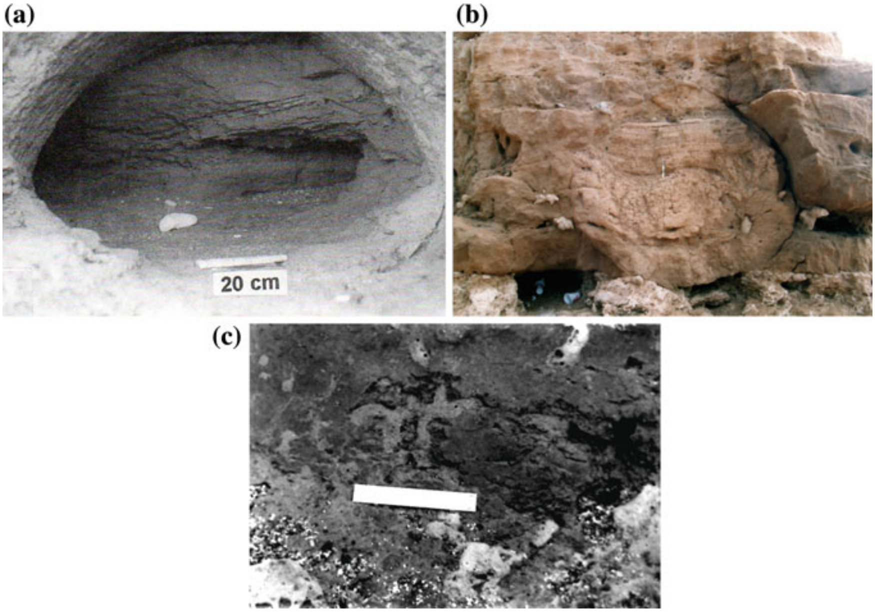

Fig. 2.7 Crotovines (**a**, **b**, and **c**)

Bonaerian stage, in a quarry from Gorina, a locality near the city of La Plata (Buenos Aires province, 34° 54´35” S–58° 00´15” W).

Genise (1989) published the first paleontological observations about caves with Actenomys and associated fauna belonging to the Chapadmalal Formation. He studied 250 caves in Barranca de Los Lobos, Las Palomas beach, Los Lobos, Chapadmalal and Barranca Parodi sites, Buenos Aires Province. The caves mostly had remains of Actenomys and other rodents, notoungulata and small marsupials, in some cases articulated. The caves with Actenomys, of 13 cm in diameter, penetrate in the ground with a slope from 30º to almost vertical and a length up to 5 m. They have lateral ramifications; widening for the displacement in both directions and the possibility of more than one chamber per cave (see associated Scarabaeinae nests). Scognamillo et al. (1998) carried out morphometric studies about the same cave systems with Actenomys in the Barranca de Los Lobos zone, confirming the aforementioned data.

Nabel et al. (1990) carried out geological studies in the San Pedro and Baradero localities.

Their profiles mentioned “one krotovina of 1.50 m in diameter” in the upper part of the basal level (Ensenadan stage) and “krotovinas and bioturbation” in the upper level (Bonaerian stage). Zavala and Navarro (1993) pointed out the presence of krotovinas from 18 cm to 1 m in diameter and up to 4 m long for sediments of the Montehermosan stage, some of them with ramifications, which in the end present significant widening and inclinations of 7°.

Quintana (1992) described a cave found during excavations in the city of Mar del Plata, together with other three findings of similar characteristics. Excavated in sediments of Pleistocene age (the Miramar Formation, Ensenadan stage), the cave consists of two interconnected galleries of 23 and 3 m, with a sealed end, of semicircular section and a plain base of 0.93 m wide and 0.76 m high. Later, Genise and Farina (2012) redescribed such cave together with another one mentioned by Dondas et al. (2009). In such work, the idea, profusely documented, that those caves express foraging activity with their extended and horizontal development is added to the previous observations, since in both examples, the excavations cut lands bearing ant nests, the latter appearing being excavated. The caves show deep unguiform marks performed by the builders, probably a large armadillo (Eutatus, Propraopus, Pampatherium). Their filler contains a big deal of arthropod remains, especially insects, such as ants (Neivamyrmex sp., Acromyrmex sp., Pheidole sp. and Solenopsis sp.), Rhyparochromidae, Tenebrionidae, Staphylinidae, Histeridae, Scarabaeidae, Aphodiidae, Carabidae, Cydnidae, Enicocephalidae and Termitidae. The present author observed caves assignable to rodents with constant diameters of 20 mm presenting vertical and horizontal developments communicated by very pronounced sinuosity in gullies that extend to the south from the site of Punta Hermengo, at levels corresponding to the Ensenadan stage.

Zárate et al. (1998) cited large caves in the Mar del Plata region, Buenos Aires Province, pointing out the presence of footprints of their builders on walls and roofs. The diameter varies from 0.75 to 2 m in the 42 measured caves, some partially filled. Many of the structures go beyond these dimensions, with ramified tunnels excavated up to 5 or 6 m deep, reaching an extension of 20 m. The caves extend throughout all the Cenozoic sequence, and their builders could be Xenarthra, large dasypus and pampaterids as well as Mylodontidae (Scelidotherium and Glossotherium). The studied sites correspond to the localities of Santa Isabel Beach, Baliza Caniú—Serena Beach, Colonia Chapadmalal, Constitución—Camet and Cantera Vialidad.

Vizcaino et al. (2001) added new observations to the mentioned discoveries thanks to anatomic and biomechanical studies of Pleistocene mylodontidae that indicated that their members were well-provided for digging. Iriondo and Krohling (1996), when describing the Carcarañá Formation (Lujanian stage) from Santa Fe province, Argentina, mentioned krotovinas of 0.50 to 0.75 m in diameter in two levels, one of them containing remains of carbonized plants.

De los Reyes et al. (2006) have stated that they found a peculiar taphocenosis associated with a paleocave formed by remains of marsupial Thylophorops together with others of dasypus, ctenomydae and caviidae, and also by coprolites of a possible carnivorous, at levels IX or X of the Chapadmalal Formation, 200 m to the south of the Arroyo Las Brusquitas mouth, General Alvarado County. Such coprolites have ground bony remains assignable to individuals of mentioned fossorial taxa. The authors point out the possible reuse of eutatin caves by marsupials. Dondas et al. (2009) described caves in the area of Mar del Plata, coming from the Miramar Formation, identifying three kinds of galleries: (1) the largest attributed to Glossotherium; (2) somewhat smaller ones assigned to Scelidotherium and (3) assigned to Pampatherium. They recognized the digit marks on the excavation walls for differentiating between mylodontides (two digits) and dasypus (three digits). In one of such caves, they found mounds similar to those attributed to Attini ants by Laza (1982).

Verde and Ubilla (2002) mentioned the presence of krotovinas in the Sopas Formation (Late Pleistocene of Uruguay).

In Brazil, findings of krotovinas were mentioned by Paglarelli Bergqvist and Maciel (1993, 1–2), in the coastal plain of the state of Rio Grande Do Sul (Tapes and Vila Cristal counties). They correspond to large caves in the Lateritas Serra de Tapes Formation and others in the Graxaim Formation, both of Pleistocene age. Three of them have 1 m in diameter, and the other one has an elliptical contour of 0.55 by 0.72 m. They were attributed to cingulates xenarthrans such as Pampatherium, Holmesia and Propraopus. In addition, mammal krotovinas were found in the system Barras Litorales I, also attributed to large dasypus (Buchman et al. 2009). Elorriaga and Visconti (2002) pointed out the presence of krotovinas from the Cerro Azul Formation (Huayquerian Stage, Late Miocene) in road cuts of the National Route 154, southeastern La Pampa Province, Argentina. They are sub-circular from 1.0 to 1.20 m high and 1.0 to 1.60 m wide; the largest one is 3.0 m wide and 0.80 to 2.10 m high (one of them is 9.0 m long). The filler, passive, has plant remains. They were attributed to Scelidotherium or Glossotherium, sensu Vizcaíno et al. (2001). Zárate et al. (2007), while describing the stratigraphy of the Chasicó Formation, mentioned the presence of excavations of 30 cm in diameter without further description.

The present author collected several tiny Scarabaeinae nests (a finding that will be further discussed when dealing with the Coprinisphaeridae Ichnofamily) in the Chapadmalal Formation, in the gully sector called Bajada Martínez de Hoz (Mar del Plata; 38° 08´ S–57° 36´ W), having paleosol levels with numerous caves with Actenomys, one of them forming part of the filler.

2.2.6 Rhizolites (Fig. 2.8)

The root traces are evidence that the rock housing them was exposed to atmospheric phenomena and colonized by plants, thus characterizing a soil. They are called rhizolites and are defined as organic-sedimentary structures; they have been known since the beginning of last century (Todd 1903). The presence of such rhizolites was considered by Andreis (1981) and Retallack (1988) as one of the main attributes of a paleosol. Klappa (1980) has mentioned that the field and petrographic observations indicate that the roots of superior plants produced numerous shapes characteristic of calcretes, which he ordered in five basic types: molds, casts, tubules, root casts s.s. and petrifactions. Kraus and Hasiotis (2006) recommended, in the study framework of the climatic conditions of the past and the environment reconstruction, careful observations and geochemical analyses of rhizolites that help in the interpretation of ancient drainage conditions.

In floodable plains with meandering fluvial systems, developed in arid to subhumid climates such as those developed in Pampasia, intercalations of continental

Fig. 2.8 Rhizolites

limestones carrying rhizolites, sometimes associated to hymenopteran nests (Celliforma), are usually frequent denoting the humidity degree of the plains (Plá et al. 2007).

Frenguelli (1926) related the calcium carbonate casts deposited on roots of living plants with the structures that existed in the Pampean loess. Due to this, he classified them as root casts. Despite the previous records, not much has been studied about the shape and development of such fossil structures and the reference about the presence of rhizolites in the description of numerous paleosols in Pampasia are erratic and infrequent.

2.2.7 Crabs and Their Signs of Activity (Fig. 2.9a, b)

The continental territory periodically flooded by the sea includes a particular habitat where organisms associated with periods of aquatic and sub-aerial life prevail. This habitat was typified as a Scoyenia ichnofacies settlement. One of the most conspicuous groups that inhabited this territory is formed by crabs. Such group shows a wide range of adaptations to the habitat, occupying continental and sea environments of marine and continental waters. The locomotion, excavation and feeding activities of benthic crabs are most appropriate for providing ichnological records, and their caves are abundant in numerous sedimentary environments, from terrigenous sediments to shallow marine environments with abundant carbonate precipitation.

The digging crabs show two behavioral patterns in their task: backward and sideways (Frey et al. 1984b). The burrowed sediments usually form spherical pellets, which once removed from the hole are then deposited outside. Some species use pelletized sediments in the wall construction, extending the duct vertically and horizontally, granting a mamelon texture to the outer surface by the adherence of such pellets.

Fig. 2.9 Signs of activity of crabs (a, b)

The ichnogenuses recognized in the region under study correspond to two forms assignable to constructions of individuals of Callianassa genus, whose characteristics were described by Frey et al. (1984b).

Psilonichnus: These are living spaces formed by predominantly vertical J-, Y- or U-shaped holes, of variable diameter, with lateral branches that are present forming singular or forked cul-de-sac, tending to verticality in a chimney shape. They are related to supralittoral forms; estuary, beach and sand dune dwellers (Nesbit and Campbell 2005).

Ophiomorpha: These are typified as branched tubes with a tridimensional horizontal, slanted or vertical lattice. The external part of the tube is characterized by a bulbous texture due to the gallery reinforcement with pellets. It is interpreted as a feeding and housing construction of a decapod crustacean (Callianasidae). The genus revision carried out by Bromley and Ekdale (1998) referred it to shallow marine environments (barriers from frontal deltas with silt to fine sand sedimentation).

The sea transgressions of the Pleistocene epoch left diverse testimonies of their invasion of the continental margin along the Atlantic Ocean coast of the region under study and linked to these deposits, footprints of the settlement of crab populations are recognized.

As it follows below, there is a record of these deposits:

1. Deposits corresponding to the “Belgranense” marine transgression interposed between the continental sediments of the Ensenadan and Bonaerian stages (Early to Middle Pleistocene) (Cione et al. 2002). They emerge in Santa Clara del Mar, north of the city of Mar del Plata, where ichnites assignable to the ichnogenus Psilonichnus coming from the settlement of crab populations were found.
2. Mouzo et al. (1985) pointed out that a sand layer with tubes cemented by calcium carbonate (Ophiomorpha) from 4 to 10 cm in diameter and between 10 and 50 cm long appeared along 8 km on the beach of Pehuén-Có; they have rough external walls and smooth inner walls, which they attributed to callianassidae. Frenguelli (1928) stated, while describing these outcrops: “The origin of these

pellets is not very clear. They consist of a very sandy and light limestone, and of light grey sandstone forming long irregular cylinders, ramified, of 5 or 6 cm in diameter, solid and excavated tube shaped. The filled cavities probably correspond to burrows belonging to small rodents" … "the petrographic characters of the calcareous sandstone filling them, … often have moulds of small marine bivalves". In the same layer, he found fragmented remains of Paraceros, Equus, Mastodon, Toxodon and Scelidotherium. The same layers were called "Secuencia San José" by Zavala and Quattrocchio (2001), and in its Lower Section (Early Pleistocene), they described Ophiomorpha nodosa bioturbations in life position on thick layers, as well as associated marine fauna. Such environment may correspond to that of a shallow sea in transgression, with non-canalized, high-density irruptions of fluvial currents. Similar deposits were recorded in Uruguay, in the Colonia and Rocha counties. During the Holocene, the marine transgression named as "Querandinense" developed several crab habitats. Rossi et al. (2001) indicated that the stratigraphic sequence in Mar Chiquita (Santa Clara Formation, Late Pleistocene) is intensely bioturbated. Tracks of tubuliform excavations with or without meniscus filled with pellets or sediments prevail. They recognized the ichnogenuses Taenidium, Skolithos and Edaphichnium and also mentioned nests of social insects, systems of arthropod galleries and others not distinguishable, assigning the sequence to the Scoyenia ichnofacies. It is worth pointing out that in these sectors, there were printed ichnites corresponding to two ichnofacies: (a) the soil development during the Lujanian stage, which includes ichnites corresponding to Coprinisphaera ichnofacies; (b) outcrops then covered by the sea during the "Querandiense" marine invasion, when the Scoyenia ichnofacies, carrier, among others, of crab habitat construction tracks, developed. Osterrieth et al. (2004) described a similar situation when presenting the finding of a fossil crab habitat about 8 km to the SW of Mar Chiquita, in Los Cueros Stream, which developed on paleosols dated in 9516 ± 512 ^{14}C years B.P. until around 3950 B.P. The scenery may represent a lagoon estuarial environment. The design and dimension of paleocaves, as well as the found remains point out the presence of Chasmagnatus granulata (Aramayo et al. 2005). The latter authors, while studying the coastal evolution between Monte Hermoso and Pehuén-Có localities, distinguished the succession of three environments for the Holocene:

a. Continental, formed by lenticular silty-sandy bodies.
b. Beaches and coastal lagoons, with lagoon-like deposits and caves with remains of the Chasmagnatus granulata crab that does not live in the area at present.
c. Marine, represented by a platform of sandy-clayey sediments.

2.2.8 Activity of Dermestids

Remains of fossil vertebrates with marks of activity of such coleoptera exist in the La Plata Museum collections. Martin and West (1995) placed these signs of activity in the Cubichnia classification (sensu Seilacher, 1953), whereas Roberts et al. (2007) created the taxon Cubiculum ornatus. Ethological observations showed that insects feed on the vertebrate carcasses exposed to the open air, on dry tissues; they develop their oviposition digging small ovoid cells on the bones where the larvae pupation takes place. Most publications on the subject are based upon the findings related to dinosaur osseous remains affected by the activity of the mentioned coleopteran (Roger 1992; Paik 2000; Britt et al. 2008).

Voglino (1999) mentioned perforations of 2 to 8 mm in diameter that he assigned to dermestids for Paraná gullies in his unit S7 (Bonaerian stage) on Glyptodon, Sclerocalyptus and Morenalaphus bones.

Other insects that predate on osseous remains and dry tissues are the termites (Darry 1911). Recent taphonomic studies in the site Paso Otero, in the Río Quequén Grande, Buenos Aires Province, within Lujanian stage deposits (Late Pleistocene) provided the collections with osseous remains with marks assigned to Isoptera (Pomi and Tonni 2010).

2.2.9 Smooth and Meniscated Tubes (Fig. 2.10a, b)

The anelid activity is recorded very often on soils and sedimentary deposits where they live, and ichnology records these activity signs with the name of Taenidium from which several species are recognized. Taenidium barretti (Bradshaw) was found, associated with levels which recorded numerous and varied vertebrate footprints in the Pehuén-Có locality, Coronel de Marina Rosales County, Buenos Aires Province, in the Guerrero Member of the Luján Formation. The ichnite description corresponds to a cylindrical horizontal winding trace, in part rectilinear, with intersections, without wall and with curved meniscuses, 4 mm thick and 3 mm apart, one from another, lacking fecal components. The trace width ranges between 9 and 12 mm (Aramayo et al. 2005). The possible builders are worms. T. barretti was recorded in alluvial and lacustrine environments, and in flooding plains and fluvial channels (Keighley and Pickerill 1994), a fact verified also by Aramayo and Manera de Bianco (1987a, b). These finding gives these layers the characteristic of being carriers of ichnoforms, corresponding to the Scoyenia ichnofacies in their transit to continental terrigenous environments.

The sites with paleosols of the Cerro Azul Formation (Huayquerian Stage) where Taenidium was found are: (a) Fatraló, Buenos Aires Province, close to the border with the La Pampa province; (b) gullies to the SE of the Utracán shallow lake, in the county of the same name, in La Pampa Province. Zavala and Navarro (1993) pointed out meniscal tubes for the Monte Hermoso Formation (Montehermosan stage) that they assigned to Muensteria (sic) genus. Deschamps et al. (1998) described the biostratigraphy of two sites close to the city of Bahía Blanca, named as "Grumbein" and "Relleno Sanitario Quarry"; in the latter, sediments corresponding to the Chapadmalalan stage, Taenidium associated with roots and vertical tubes were found.

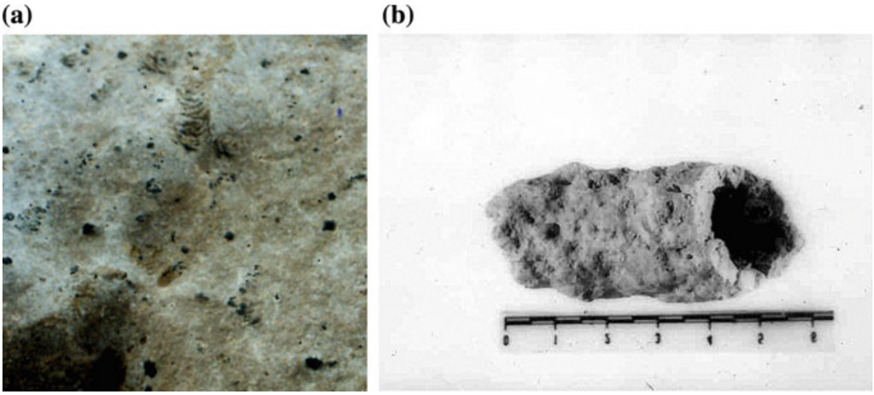

Fig. 2.10 Smoot and meniscated tubes (**a**, **b**)

In sediments of similar age (Chapadmalalan stage), specimens of Taenidium were collected in the marine cliffs of General Pueyrredón County, in the Antenas Militares site (Esteban Soibelzon, personal communication).

Voglino (1999) mentioned, for the Río Paraná gullies, meniscal tubes similar to Taenidium in stratigraphic units corresponding to the Bonaerian stage.

2.2.10 Castrichnus Incolumis Verde et al. (2006) (Fig. 2.11)

In Uruguay, Tacuarembó, Salto and Artigas counties, sediments of the Sopas Formation (Lujanian stages) including paleosols carriers of diverse Ichnofossils emerged. Among these, Castrichnus incolumis and Taenidium serpentinum appeared associated; this fact was interpreted as a compound fossil trace (Verde et al. 2006). C. incolumis was described as chambers of worm stowage, whereas T. serpentinum could correspond to displacement tunnels belonging to those worms. The chambers range from spherical to slightly ovoid, of 30.3 × 28 mm, with walls formed by interwoven pellet layers and covered inside with concentrically smooth pellets. The chamber filler is formed by pellets of 5.4 mm, arranged in cords attached to the wall.

T. serpentinum appear from winding to straight, with diameters between 0.40 and 0.75 mm; the meniscuses are arched and the distance between them is less than the duct diameter. The external molds show the rings corresponding to the meniscuses. They have well-marked borders, without ramifications. The filler is similar to a rock bearer.

The association of C. incolumis with T. serpentinum indicates the worms as potential producers of meniscal holes in paleosols. Similar structures were found by Elisa Beilinson (2010) in the San Andrés Alloformation (Pliocene-Pleistocene) of Buenos Aires Province. They appear associated with calcium protosols. In such geological

Fig. 2.11 Ichnogenus Castrichnus incolumis Verde et al. 2006

sequence, meniscal holes also appeared (Taenidium) with a degree of bioturbation of 4-5 in protosols and Beaconites from 6 to 10 mm in diameter.

2.2.11 *Edaphichnium Bown and Kraus 1983 (Fig. 2.12)*

These structures are cylindrical tubes circularly cut, filled with rounded fecal pellets that give the surface a rough texture. They are horizontal, without ramifications. The finding took place in a quarry in the site of Arturo Seguí, near the city of La Plata, in the Upper Luján Formation, formed by eolian sediments that crown the higher areas in the region. The specimen, arranged horizontally, has a slightly winding extension, and along this extension, it appears to be composed of pellets in some sectors, giving a rough texture. The specimen is 500 mm long and 27 mm in diameter. The description coincides with that of E. lumbricatum of Bown and Kraus (1983), who attributed such structures to oligochaetes. Fragments of Edaphichnium were also found in outcrops of the Buenos Aires Formation, Bonaerian Stage, in the Río Arrecifes, San Antonio de Areco County (34° 22´ S—58° 35´ W), Buenos Aires Province.

2.2.12 *Mima-Type Mounds*

This term corresponds to mounds of two meters high and some ten meters in diameter. Its formation results from—according to several published works—the activity of digger animals, and they were recorded in densities up to 100 mound per hectare.

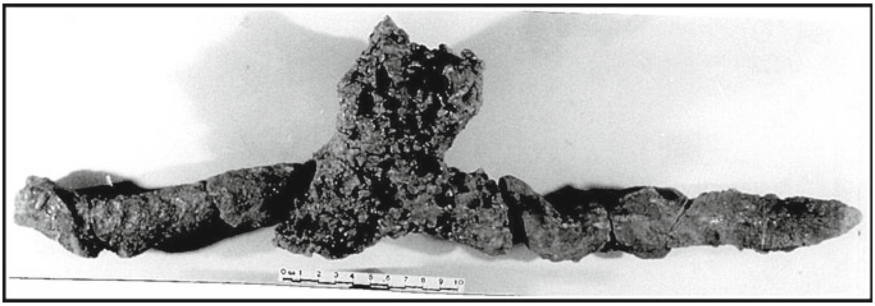

Fig. 2.12 Ichnogenus Edaphichnium Bown and Kraus 1983

Although they only modify the land surface, its relative topographic importance can be kept during long periods and attest environmental changes. Its formation could be due to the sediment displacement—as a result of the excavation—toward the periphery of the activity center, usually placed on higher sites. This phenomenon, observed in several places in North America and Africa, was associated with different families of digger rodents. In Argentina, these burial mounds were detected in the SE of San Luis Province, south of Córdoba Province and north of La Pampa Province (Roig and Cox 1985-86; Cox and Roig 1986). They are up to 3.5 m high and 25 m in diameter. They appear occupied by the digger rodent Ctenomys; the grass Cynodon stabilized the sandy sediments, accelerating the formation of mounds in a process of few years (Roig et al. 1988). In the Buenos Aires Province, Mima-type mounds were observed at 35 km west of the city of Necochea, on route 228 (Cox et al. 1992). They were up to 1.5 m high and 20 m in diameter, without the presence of digger rodents. In an area of 2 ha, 42 mounds were observed, finding caves and other excavations of Chaetopractus and Dasypus (dasypodids xenarthrans) and Solenopsis richteri anthills in 21 of them. Two current species of Ctenomys live nearby, in sand dunes of the Atlantic Ocean coast, dismissing the fact that these rodents lived in those clay soils, difficult to excavate. The mentioned authors (Cox et al. 1992) suggested that the origin of burial mounds resulted from Solenopsis ant activity through numerous generations. The vegetation on the mounds appeared richer than in the surrounding area; this difference may have been caused by myrmecochory. At the same time, the mounds could have served as a mammal habitat settlement.

2.3 Insect Nests in Paleosols

The knowledge about the architecture of insect nests comes from entomology, and some of its terms are also used in ichnology. In this field, even the most complex insect trace fossils can be divided morphologically in two components: tunnels and chambers. Those primary differences in the behavior, as well as many other specific differences, gave rise to the great morphological diversity of insect nidifications and pupation structures in soils and paleosols, thus offering invaluable taxobases for the classification of ichnogenuses and ichnofamilies. Bromley (1990) listed and analyzed the most common characters used as basis for ichnotaxonomy in four ichnotaxobases: (a) general shape, (b) wall structure type, (c) type of ramifications and (d) filler nature. Below, it will be only mentioned and described the current shapes in the territory under study.

2.3.1 Ichnofamily Celliformidae Genise 2000

These are materials composed of a group of morphologically related ichnogenuses, formed by cells constructed by bees for breeding their progeny and whose type ichnogenus is Celliforma Brown 1934. Celliforma, the simplest trace of the group, consists of chambers or its inner molds of different shape (sub-cylindrical, in the shape of drop, bottle, vase, glass and barrel); they have a rounded end and the other truncated or blocked by a welded seal in spiral shape as part of its structure. The ichnofamily includes shapes with antechambers and discrete walls, as well as structures formed by several cells.

Record in paleosols of Pampasia.

Miocene. Cerro Azul Formation, "Huayqueriense" stage. Arroyo El Venado between Guaminí and Carhué counties, Buenos Aires Province.

Miocene. Monte Hermoso Formation, Montehermosan stage. The longest section is located at the coastal cliffs, coronel de Marina Leonardo Rosales County, Buenos Aires Province.

Holocene. "Platense" (Platan stage). Paraná gullies, Baradero County, Buenos Aires Province. Described by Voglino (1999) as: "A cylinder of 20 mm long by 8 mm in diameter, sealed in an end by a concave-convex plug".

2.3.2 Ichnofamily Krausichnidae Genise 2004

This family is formed by structures ranging from complex to very complex that in general are interpreted as assignable to social insects such as ants and termite nests and whose type ichnogenus is Krausichnus (Genise and Bowm 1994b).

A group of ichnogenuses forms part of this ichnofamily. These are formed by chambers associated by tunnel systems of different diameters in many cases. The tunnels appear without scratches and/or intersected by furrows. The chambers lack irradiation tunnels from their top part and are linked by a duct system that interconnect them with other chambers. These chambers can be empty, passively or actively filled and/or can have secondary system of ducts in different diameters and small chambers on or in the wall (Genise 2004a).

2.3.3 Ichnogenus and Ichnospecies Found in Pampasia

2.3.3.1 Anthills

Ichnogenus Attaichnus Kuenzelii Laza 1982 (Fig. 2.13a, b and c)

The identified remains come from the Miocene, Cerro Azul Formation, Huayquerian stage, Salinas Grandes de Hidalgo, Atreuco County, La Pampa Province. The structure, complex and huge, forms a burial mound of 7 m in diameter by 3 m high, consisting of countless globular chambers with shapes and sizes comparable to those of anthills of the current species of Atta genus. The chambers of fungus-growing ants are connected to one another and to outside through two systems of ducts: longer and shorter. The longest ones have access to chambers, generally from their bottom part and form a folded flange within the chamber. The longest intercommunication ducts or galleries have sub-oval diameters between 17 and 20 mm. The shortest ducts interconnect the longest chambers and ducts with diameters ranging between 5 and 10 mm. The dimension of the longest and shortest ducts does not vary. The chambers are globular with somewhat irregular inner and outer surfaces. Both larger diameters range from 140 to 170 mm. The walls, whose thickness is notably irregular (between 15 and 50 mm), define a considerably ample globular cavity. The calcium carbonate may be deposited on the fungus-growing ants inside the chambers. One of the chambers presents in its inner part a tubular cavity or turret with edges somewhat folded in lip-shape. Except for the largest dimension in the fossil specimen—the description coincides totally with those by Gallardo (1916) and Bruch (1917) when describing the Trachymyrmex pruinosus Emery nest belonging to the Attini tribe. It is possible that this character is common to the most evolved tribe members in the nest construction. Possible builders of these structures are the aforementioned characteristics allow the classification of the remains as belonging to ant nests of the genus Atta Fabricius.

After more than forty years, the sediments originally carriers of A. kuenzelii, lost by erosion, recent field and laboratory works cast doubts on the original ascription, attributing anthill of Acromyrmex or Trachymyrmex (Genise et al. 2013) species to Attini. Besides, the idea of sympatry of the mentioned genuses is discarded, not considering that the current populations of the Chaqueña Sub-region, (sensu Morrone 2000–2001) register more abundant nests of Acromyrmex and Trachymyrmex than those of Atta. The work in question does not take into account the paleoecological information supplied by the vertebrate fossils, especially those corresponding to rodents found in different sites of the Cerro Azul Formation in the La Pampa Province.

Record in paleosols of Pampasia: Other specimens were found in the car track placed 7 km to the south of the city of Macachín, La Pampa Province, in a horizon of the same age, carrier of numerous “slag and baked clays.”

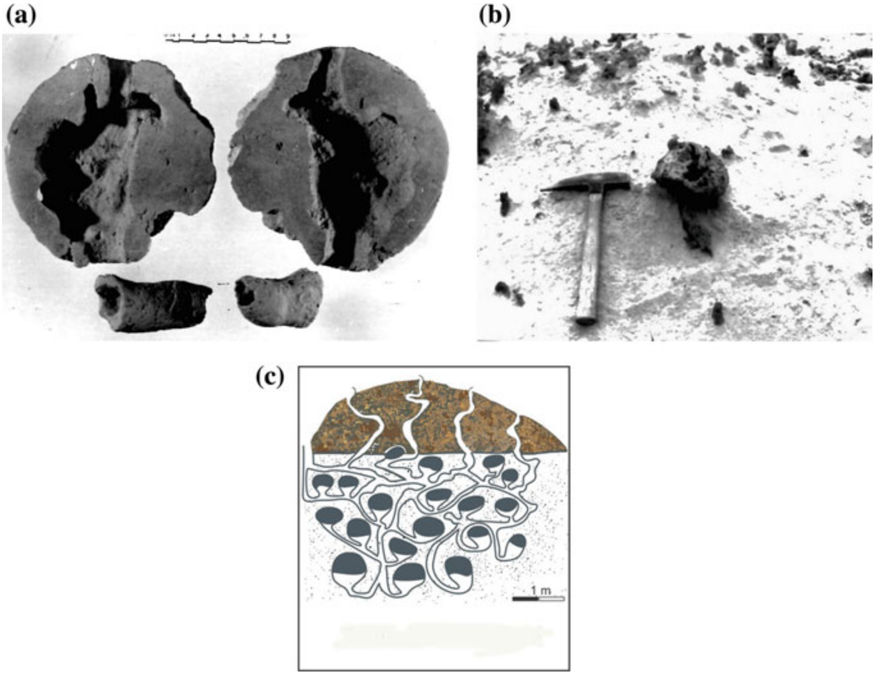

Fig. 2.13 Ichnogenus Attaichnus kuenzelii Laza 1982 (**a**, **b**) **c**, scheme

Ichnogenus Aff. Acromyrmex (Acromyrmex) Close to A. Ambiguus Emery (Fig. 2.14a, b)

The materials come from the site between "Club Náutico" and "Los Tamarindos" beaches, General Alvarado County, Buenos Aires Province. Pliocene, Chapadmalal Formation, Chapalmalalan stage. In that place, it ends in a carbonated horizon (part of a paleosol). The construction has two chambers in an oval shape, totally replaced by "tosca" (i.e., caliche). The upper chamber is larger, 120 mm high and smaller diameter; the lower one is 70 mm high by 60 mm in diameter. Both chambers are 40 mm from each other. The largest chamber shows the inlet and outlet ducting in the shape of inner bubbles (typical of the ichnogenus), upper and lower, while the duct of intermediate connection, replaced by calcium carbonate, is 12 mm in diameter. The hosting rock, when cut, showed sections of ducts filled with dark clay. These ducts, whose sections vary between 5.5 and 9.5 mm, become numerous toward the upper part. Long and short ducts converge at the top of the structure, forming a concentration that may indicate the proximity of the anthill superficial sector.

Possible builders: The observations coincide with the data given by Bonetto (1959), Goncalves (1961) and Weber (1972); for that reason, the nest is recognized as belonging to the species Acromyrmex (Acromyrmex) close to A. ambiguus Emery.

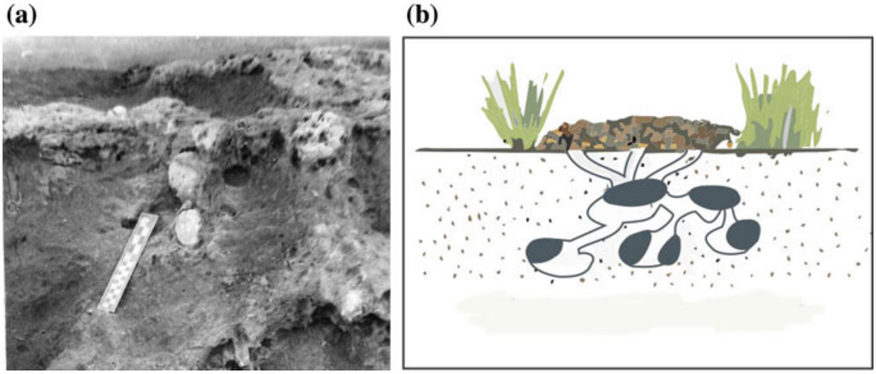

Fig. 2.14 **a** Ichnogenus aff. Acromyrmex (Acromyrmex) close to A. ambiguus Emery; **b** Scheme

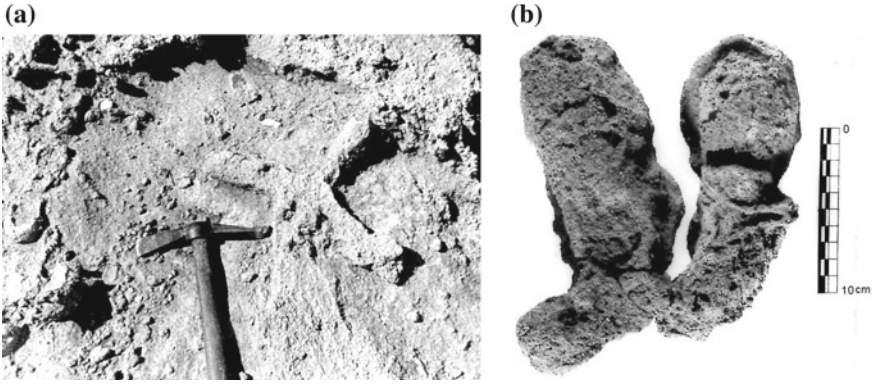

Fig. 2.15 **a** Ichnogenus aff. Acromyrmex (Moellerius) striatus Roger; **b** Scheme

Ichnogenus Aff Acromyrmex (Moellerius) Striatus (Roger) (Fig. 2.15a, b)

The finding comes from the Centinela del Mar locality, General Alvarado County, Buenos Aires Province—Pleistocene, Bonaerian stage—Layer "C" (Tonni et al. 1987, Laza 1997). The preserved structure corresponds to two practically full chamber molds that converge on the filler of a communication duct. Both chambers, of elliptical contour, are about 150 mm long by 60 mm in diameter. Despite the erosion, the inner surface of the polished walls is observed in chambers and communication ducts. The filler is composed of the same rock bearing, cemented by carbonate. A great variety of root molds was found associated with the anthill.

Possible builders: The morphology of the discovered remains coincides with the descriptions made by Bruch (1916), De Santis (1941), Carbonell-Mas (1943), Bonetto (1959) and Goncalves (1961); the material was assigned to a nest of the species Acromyrmex (Moellerius) aff. M. (M.) striatus (Roger).

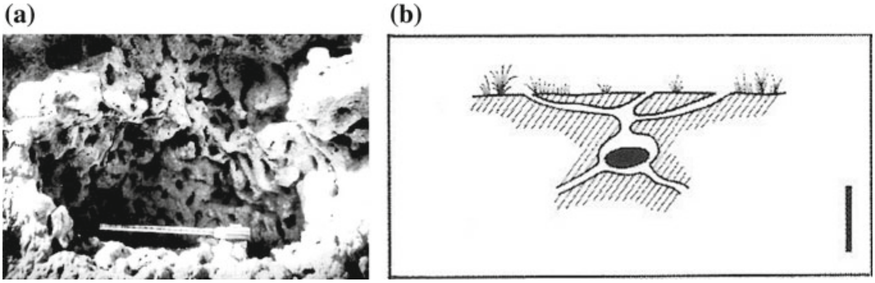

Fig. 2.16 **a** Ichnogenus aff. Acromyrmex (Acromyrmex) lundi Guerin **b** Scheme

Record in paleosols of Pampasia: A second specimen corresponding to the same ichnospecies was found in the longest section of the coastal cliffs from Coronel de Marina Leonardo Rosales County, Buenos Aires Province. Upper levels of the Pliocene Monte Hermoso Formation, Chapalmalalan stage. It was only possible to take photos and measurements of the mentioned specimen.

Ichnogenus Aff. Acromyrmex (Acromyrmex) Lundi Guerin (Fig. 2.16a, b)

This finding took place close to the Río Quequén Grande banks, near the archeological site Zanjón Seco (38° 10′ S–59° 10′ W), Necochea County, Buenos Aires Province. Pleistocene, Guerrero Member of the Luján Formation, Lujanian stage. It was possible only to take photos and measurements of the mentioned specimen (Laza 1997).

The erosion uncovered the central pot and the nearby zone. The general shape of the structure is framed in a trapezoid; the smallest base is 0.60 m and the largest 0.95 m; the height is 0.60 m. The largest part of this figure is irregularly occupied by the chamber. This shows the inner wall with the duct mouths ending into it, many of them tangentially. These features confer a mamelon or pad-like appearance to the chamber inner wall. The diameter of ducts that flow into the chamber is constant, of 10 mm, except for some globular expansions that reach up to 30 mm. The structure is built in silt-clayish sediments with a diagenesis level greater than that of a passive filling—silty-sandy-, which the erosion eliminated.

Possible builders: The general characteristics of the nest coincide with the data given by Gallardo (1916), De Santis (1941), Bonetto (1959) and Weber (1972). The material was assigned to a nest of the species Acromyrmex (Acromyrmex) aff. A. (A.) lundi Guerin.

Ichnogenus Aff. Trachymyrmex Emery (Fig. 2.17)

Frenguelli (1938b) described this fossil; he attributed the spheres to scarabaeinae Phanaeus nests and their gigantism as counterpart to the megafauna of that time

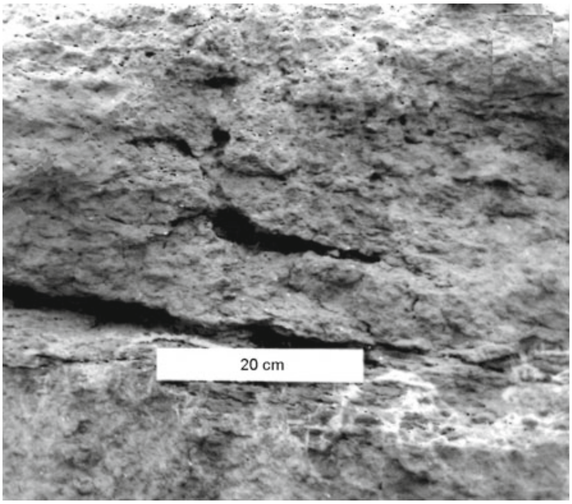

Fig. 2.17 Ichnogenus aff. Trachymyrmex Emery

(Lujanian stage). The examination carried out by the present author dismisses such assignation and attributes the specimens as fillings of both chambers or as fungus-growing ant anthills belonging to the Attini tribe. The description by Frenguelli (1938b) contributes to such assignation: “Its diameter is 82 and 87 mm, respectively, with walls reaching a thickness up to 20 mm and its inlet hole around 16 mm in diameter. The surface and walls formed by greenish grey hardened silt underwent the same diagenetic processes that transformed locally all the sediment in a mass of root pellets irregularly interwoven, in a complex tangle where non concretionary slit portions were trapped in the mesh. These portions, when easily destroyed by erosion and deflation, left rough and cavernous surfaces”. The shape and size of the pieces remind us of the fungus-growing ants of Trachymyrmex Emery, a genus to which they could be doubtfully attributed.

Ichnogenus Aff. Pheidole (Fig. 2.18)

The site where the material was found is placed 8 km SE of the city of Santa Rosa, on the route linking that city with the Cerros Colorados locality, La Pampa Province, Miocene, Cerro Azul Formation, Huayquerian stage.

The fragment measurements, totally impregnated by “tosca”, are the following: 230 × 170 × 135 mm. It has a system of long and short ducts. Many of the short ones of 4 mm end in “cul-de-sac,” while the long ones of 6 mm are scarce. Despite the elaboration of the nest mass, the chambers are relatively scarce; one chamber with a greater tubular form of roughly 65 mm long by 50 mm wide stands out; and the long and short ducts flow into it. The other chambers, also in irregular tubular shape, measuring about 30 × 12 mm, have a limited number of long and short entrances. It was observed that the inner surface of some sectors in the largest chamber and all

Fig. 2.18 Ichnogenus aff. Pheidole actual

the smallest chambers show significant isolation. Inside the largest chamber remains of ants and their cocoons were found, in addition to several dermal plaques of a Squamata, forming part of the filling material.

The 18 cocoons have the morphology assigned to Attini by Wheeler (1910); many of them have sediment incrustations, including a specimen with remains of an ant attached. The extreme of the complete pieces has a sharp end, though most of them have an open end, sign of a possible eclosion. The color of most pieces is light brown, whereas five of the best preserved cocoons are yellowish and the surface shows a silky texture. Their measurements: 5.2–4 mm long; 2.5–3 mm in diameter.

Possible builders: Among the sediments found within the largest chamber, fragmented remains of ants corresponding to the Attini tribe were found. Such fragments correspond to various individuals: sternites and tergites, one coxa and two small pronota, one of them well preserved. The pronotum has diagnostic features, such as the sculptured surface and its thorns; these are identified by their development, orientation and shape. The material presents lateral pronotal thorns more developed, leaning forward; rear mesonotal thorns hardly developed and the lower prenotal ones hardly visible, developed on a bulge. According to observations, illustrations and published diagnosis (Bonetto 1959; Weber 1972; Kusnezov 1978), it is concluded that the found remains correspond to an ant construction related with the genus Pheidole maybe developing shapes adapted to mesophyll environments at that moment.

Associated fauna: next to the ant remains and their cocoons (some of them embedded by "tosca") several dermal scutes, of a Squamata reptile were found. The nests of Attini ants, whose one of the representatives is the ichnofossil under study, usually become sites for oviposition of several reptiles. Vaz Ferreira et al. (1970, 1973) and Ferreira Brandao and Vanzolini (1985) mentioned plentiful examples related to reptile inquilinism in anthills of several species of this tribe.

The 21 scutes are long in shape, irregular, with rounded edges (3 mm long by 2 mm wide). Most of them present a notorious apex with both surfaces granular, light gray; two of them differ in color (dark brown) and in morphology, presenting mamelons in the center of both faces.

Ichnogenus Aff. Pheidole Spininodis Forel (Fig. 2.19)

The material comes from the coastal cliffs to the west of the city of Miramar, General Alvarado County, Buenos Aires Province. Pliocene-Pleistocene, Miramar Formation, Ensenadan stage. It was only possible to photograph and measure this specimen.

The set of chambers and ducts is framed in a vertical surface of 250 mm high by 200 mm wide. The central anthill duct, with a constant diameter of 8 mm, is arranged vertically (with some bends) and the four chambers, horizontally. The first one—upper—is shown with a widening of 30 mm in diameter toward both sides of the central duct; 60 mm underneath there are two chambers at both sides of the central duct of 60 mm long by 20 mm in diameter each one. In the deepest zone, there is a chamber of about 100 mm long by 40 mm wide joining the communication duct, getting narrower until ending in sharp points toward the opposite extreme. The nest was found in a sedimentary package of 450 mm thick, limited in its lower part by a thin and eminent "tosca" layer.

Possible builders: The reviewed structure coincides with Bruch's description and figures assigned to anthilla of Pheidole spininodis Forel (1916).

Ichnogenus Aff. Pogonomyrmex Bruchi Forel (Fig. 2.20)

The original place of the finding is at 400 m to the west of Punta Hermengo, General Alvarado County, Buenos Aires Province. Pliocene-Pleistocene, Miramar Formation, Ensenadan stage. The nest shows two globular chambers of 50 and 70 mm in diameter, and at the same level, other two eroded of the same size. Next to them, there appear overlapped chambers (at different levels) which are vertically long or short ducts of about 60 mm long by 5 mm in diameter. Cuts of several ducts of similar size distributed in the area can be observed. Possible builders: The fossil structure is

Fig. 2.19 Ichnogenus aff. Pheidole spininodis Forel

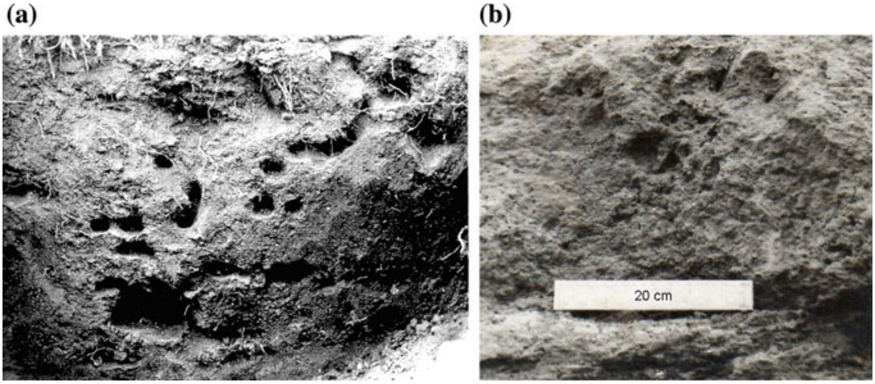

Fig. 2.20 Ichnogenus aff. Pogonomyrmex coarctatus Forel

similar to the nest description of Pogonomyrmex bruchi Forel. The species founding was performed by Bruch (1916) who described the nest.

See also Gallardo (1932) and Kusnezov (1963).

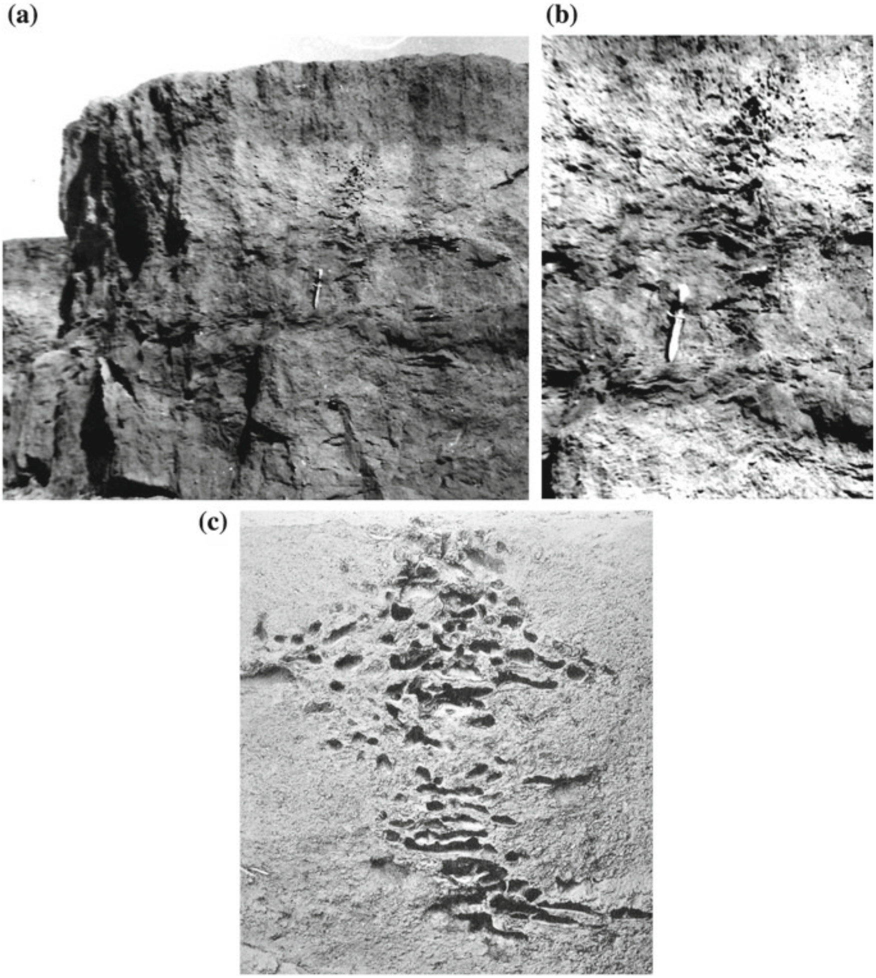

Fig. 2.21 Ichnogenus aff. Forelius chalybaeus Emery (**a**, **b** fossils; **c**, present)

Record in paleosols of Pampasia: Two structures similar in shape and dimension to those previously described were observed in the Monte Hermoso cliffs, at levels corresponding to the Pliocene, Chapalmalalan stage.

Ichnogenus Aff. Forelius Chalybaeus Emery (Fig. 2.21a, b and c)

This ichnofossil was found in Santa Clara del Mar, General Pueyrredón County, Buenos Aires Province. Pleistocene, Guerrero Member of the Luján Formation, Lujanian stage. It was only possible to photograph and measure the specimen.

In a vertical cross section, it may be seen that the nest is developed from a central duct, toward both sides. The chambers follow one another horizontally in depth; elongated (50–80 mm) and narrow (15 mm), linked by a series of secondary ducts almost vertical of 10 mm in diameter that connect the chambers with one another. The nest lateral extension decreases in depth, presenting, in a cross section, a triangular figure whose base is placed at its entrance.

Possible builders: The species Forelius chalybaeus Emery, described and featured by Bruch (1916), is recognized as the builder of the described nest.

Record in paleosols of Pampasia: Two nests similar to the one described were found close to the fishing breakwater in Punta Hermengo, General Alvarado County, in a paleosoil of the same age.

Other Mentions of Anthills in Pampasia

Santa Fe Province, Belgrano County. Pleistocene, Tezanos Pinto Formation. Lujanian stage.

Iriondo and Krohling (1996) indicated "numerous fossil anthills of 2–3 m long and 0.50–2 m high of varied shapes, filled with more consolidated silt, with black "patinas" in the middle portion of the profile. Santa Fe and Buenos Aires Provinces, between Rosario and Campana localities, Río Paraná gullies.

Pleistocene, Bonaerian stage. Voglino (1999) mentions and attributes activity signs to termites or ants, with nests up to 0.50 m long and ducts of 2–3 mm in diameter.

2.3.3.2 Termite Nests

Ichnogenus Tacuruichnus Farinai Genise 1997 (Fig. 2.22a, b)

The impossibility of removing this kind of nest from the paleosol (discussed in Genise and Bown 1994b) limits the holotype designation to the selection of a phototype as representative of the type specimen (Genise 1997), expression applied to other specimens mentioned in this work. The material comes from the coastal cliffs of the Terrazas del Marquesado beach, 1000 m south of Punta Vorohue, General Alvarado County, Buenos Aires Province. Pliocene, Marplatan (Barrancalobian) stage. A section of this trace fossil, cup-shaped, was exposed by natural erosion in the costal cliffs when it was discovered. It is assumed that originally this trace fossil was completed with a sub-aerial mound from which only the basal part, cup-shaped, was preserved in the paleosol, whereas the superficial structure was eroded. The preserved cup was recently exposed laterally by marine erosion, revealing its current shape, its front part lost, and its rear side preserved within the cliff. The diameter of the exposed arch is 80 cm, while the wall is 10 cm wide, and it is perforated by a system of anastomosed tunnels of different diameters between 1 and 7 mm. In the insect traces, as usual, the wall is stronger than the hosting paleosoil and therefore

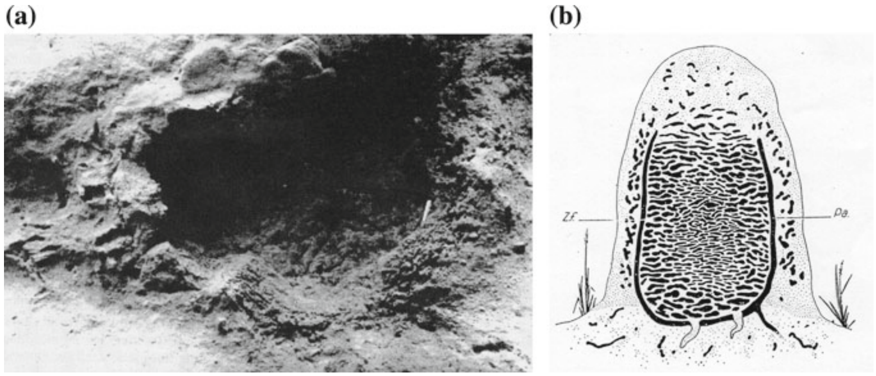

Fig. 2.22 **a** Ichnogenus Tacuruichnus farinai Genise 1997; **b** scheme

it is in relief. The inner part of the cup does not preserve any activity signal and is currently filled with passive sediments. Outside the wall, a system of peripheral galleries can be seen in the cliff at both sides of the cup. The exposed part of this system consists of 2–4 main tunnels in each side, of 10–15 cm long and 1–2 cm wide connected to others of only 1 or 2 mm in diameter. It is possible to observe remains of the tunnels even beyond 30 cm from the wall.

Possible builders: The described architecture is similar to the hypogeous sector of the nest of Cornitermes cumulans Kollar (Nasutitermitinae) (Genise 1997).

See descriptions and figures by Emerson (1952) and Grassé (1984) regarding nests of the aforementioned species.

Record in paleosols of Pampasia:

(a) In paleosols of the lower section of the Atlantic Ocean, coastal outcrops in the city of Mar del Sur, General Alvarado County, Buenos Aires Province, abundant specimens of Tacuruichnus were found. Such levels were attributed to the Middle Pleistocene, Bonaerian stage, Ctenomys kraglievichi Biozone (Eduardo Tonni and Esteban Soibelzon, personal communication).
(b) In 2016, the finding of termite nests in Pleistocene sediments of the Arroyo Toropí, in the province of Corrientes was published by Erra et al. The edited photographs show several Tacuruichnus specimens.

Ichnogenus Barberichnus Bonaerensis Laza 2006a (Fig. 2.23a, b)

The materials corresponding to the holotype were found in excavations carried out in the city of La Plata (51St. Avenue, between the 9th. and 10th. Streets), Buenos Aires Province, in the Pleistocene, lower section of Buenos Aires Formation, Bonaerian stage, Ctenomys kraglievichi Biozone. The two fragments that form part of the holotype belong to the only collected termite nest. The fragments, which correspond to the hypogeous part of the nest, were found very close one another, without totally completing the structure but representing most of it. One piece is 29 × 27 cm, and

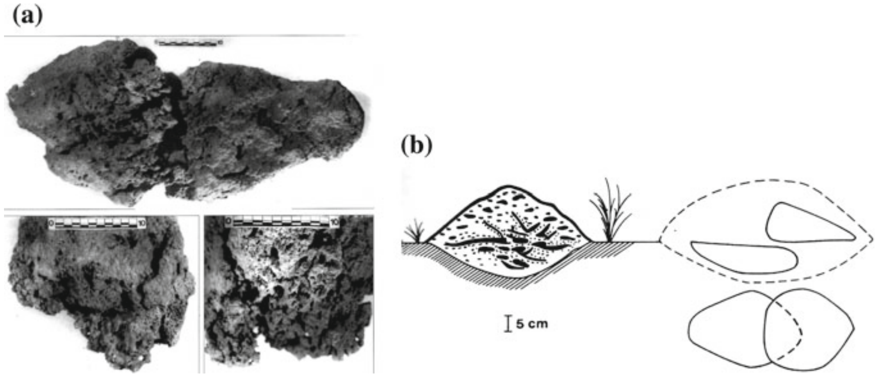

Fig. 2.23 **a** Ichnogenus Barberichnus bonaerensis Laza 2006a; **b** scheme

the other is 37 × 26 cm, and they can be aligned on a horizontal axis suggesting an elongated shape, of around 25 cm high. A system of ducts is observed: (a) longer of oblong section of 13 mm high × 15 mm wide arranged without any apparent order; (b) shorter, of circular section of 1–3 mm. The confluence of several longer ducts causes hollows that are interpreted as chambers—highly irregular- some of 30 × 45 mm. In between the longest ducts, the system of shorter ducts is developed, being highly abundant in some sectors. In the central zone of the termite nest as well as inside some dissected ducts, it can be observed a sharp change of color and texture of the rock. The sediment is light brown with scattered specks of calcium carbonate of 10 mm in diameter, whereas a violet brown halo surrounds the duct and chamber systems. The inner surfaces of the tunnels and chambers appear covered by a patina of waxy appearance. The texture of these surfaces is quite polished, differently from the sediment bearing which is more porous. Possible builders: The general characteristics of these termite nests allow relating them to members of the Termitinae subfamily, with representatives of Amitermes and Termes genuses as possible builders.

Record in paleosols of Pampasia: (a) Sector of coastal cliffs of Punta Negra, Necochea County, Buenos Aires Province. Pliocene, Sanandresian stage. (b) Sector of cliffs of Barranca de Los Lobos, General Pueyrredón County, Buenos Aires Province. Pliocene, Vorohuean stage.

Ichnogenus Aff. Procornitermes Emerson (Fig. 2.24a, b, and c)

The material comes from the gullies placed between Playa Las Palomas and Barranca de Los Lobos, General Pueyrredón County, Buenos Aires Province. Pliocene, Chapalmalal Formation. Chapalmalalan Stage (Banco VIII de Kraglievich 1952) (Laza and Tonni 2004). At levels close to those of the finding, other two specimens were observed, but it was impossible to have access. The piece is sagittally cut oriented to the longest axis (vertical), lacking a small portion in one end. The general

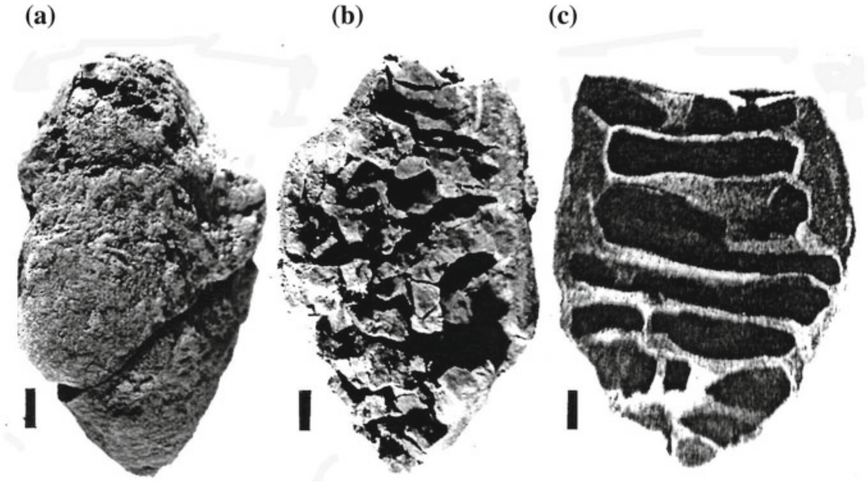

Fig. 2.24 Ichnogenus aff. Procornitermes Emerson (**a**, **b** fossil; **c**, present)

shape corresponds to that of a pine cone with globosity on one side. Within the cut, there are partitions developing and anastomosing which follow directions according to the shortest axis of the piece. The thickness of the walls and inner partitions is constant, between 7 and 10 mm. In between the partitions, there are fine separations that are believed to have been larger at another time, obliterated by “tosca” accretion. In the center of the body, it is observed a partition that separates it medially oriented to the longest axis, whereas an end shows a hollow interpreted as an entry point to the nest. The general dimension is 115 mm high and 70 mm wide.

Possible builders: The dimensions as well as the observations on the present material, descriptions and figures of the known species of the genus allow asserting that the nest belongs to Procornitermes Emerson (Snyder 1949) genus. See also Silvestri (1903), Emerson (1952) and Grassé (1984).

Ichnofamily Coprinisphaeridae Genise 2004

Coprinisphaera is one of the most common trace fossils in paleosols of the Cenozoic of South America and one of the first being recorded (Frenguelli 1938a, Roselli 1939). It has been cited for different localities and ages of the Cenozoic in South America, Europe, Asia, Antarctica and Africa (Genise et al. 2000; Krell, 2000 and references; Laza 2006b; Sánchez 2009). These traces correspond to beetle breeding of the Scarabaeinae subfamily, when isolated to the ichnogenus Coprinisphaera Sauer (1955) and when grouped to the ichnogenus Quirogaichnus (Laza 2006). Each ball has an ovigerous chamber and emergency hole, which gives it a particular additional structure and shape, some of which, identifiable in the fossil specimens constitute ichnotaxobases used for distinguishing different ichnospecies of Coprinisphaera (Laza 2006; Sánchez 2009).

The fossil trace consists of spherical, sub-spherical, piriform and bispherical chambers, formed by a wall with a discreet emergency hole. They can show a small chamber linked to this hole through a corridor and connected outside. The inner cavities have mostly passive filling, being empty in some cases. The chambers are isolated in contact with the matrix or situated in one of its cavities, normally with passive filling.

Such structures were grouped in six ichnospecies (Laza 2006; Sánchez 2009). In this work, only those found in the region under study are mentioned.

Ichnogenus Coprinisphaera Murguiai (Roselli 1939)

It is formed by isolated chambers, spherical and sub-spherical, with a wall quite thick. In one of the poles, the chamber wall is completely perforated by a medium sized hole (around ¼ in equatorial diameter), which has a cylindrical contour in longitudinal section. There are no remains of a secondary chamber or of additional structures around the hole. Inside the chamber there is, as a rule, passive infilling (Sánchez 2009). The type material comes from the Paleocene–Eocene, the Asencio Formation, Uruguay.

The examined specimens show great size variation. Coprinisphaera murguiai reminds the breeding balls built by dung beetles (Scarabaeinae) of Coprini tribe, Dichotomiina sub-tribe (diggers) included in Pattern II of nidification by Halffter and Edmonds (1982) and of Scarabaeini tribe, Canthonina sub-tribe (wheelers) included in Pattern III by the mentioned authors. Assignation based on the isolation condition, spherical shape, wall thickness, possible location of the ovigerous chamber within the provision chamber and current geographic distribution of the Subfamily.

Record in paleosols of Pampasia:

Miocene, Cerro Azul Formation, Huayquerian stage. Arroyo Venado, between Guaminí and Carhué localities, Buenos Aires Province. Provincial Route, 152.2 km from the General Acha locality, from Route 35, La Pampa Province. Gullies to the north of Salinas Grandes de Hidalgo, La Pampa Province. Miocene? Cerro Azul Formation? (Huayquerian stage?). Southern Córdoba Province, in an outcropping paleosoil in interdune valleys.

Miocene, Paso de Las Carretas Formation, Huayquerian-Montehermosan stages. Materials mentioned by Guiñazú (1960) who wrongly attributed the nests to the dynastine Diloboderus. Coronel Pringles Department, San Luis Province. In Paso de Las Carretas Formation, Santa Cruz (1979) mentioned the finding of "vespids and coleoptera nests" in the rivers Quinto and Conlara basins, in San Luis Province.

Miocene, Las Mulitas Formation. Huayquerian-Montehermosan stages. Río Los Chorrillos, tributary of the Río Quinto, San Luis Province. González (1979) mentioned "insect nests".

Pliocene, Irene Formation. Chapalmalalan stage. Río Quequén Salado, Buenos Aires Province.

Pliocene? Monte Hermoso Formation? (Montehermosan stage?), specimens from an excavation at 10–12 m depth in the Hansen farm, between El Zorro and Guisasola railway stations, Coronel Dorrego County, Buenos Aires Province.

Pliocene, Irene Formation, Chapalmalalan stage. Río Quequén Salado near National Route 3, Buenos Aires Province. Several specimens (Aramayo et al. 2004a, b).

Pliocene, Chapalmalal Formation, Chapalmalalan stage. Monte Hermoso cliffs, Coronel de Marina Leonardo Rosales County, Buenos Aires Province.

Pliocene, Chapalmalal Formation, Chapalmalalan stage. Bajada Martínez de Hoz, General Pueyrredón County, Buenos Aires Province. Fifteen small specimens (Tetraechma or next canthonini) found inside caves with Actenomys, close to their passive filling.

Pliocene, San Andrés Formation, Sanandresian stage (Layer "A" of Tonni et al. 1996). Necochea County coastal cliffs, Buenos Aires Province.

Pliocene, Barranca de Los Lobos Formation, Barrancalobian stage. Between Fortín 88 and Las Palomas Beach, General Pueyrredón County, Buenos Aires Province. Bajada Martínez de Hoz, General Pueyrredón County, Buenos Aires Province.

Pliocene, San Andrés Formation, Sanandresian stage. At 100 m to the north of the Chapalmalal Hotels, General Pueyrredón County, Buenos Aires Province. Small nest (Canthonino?) associated to a Conepatus sp. skull.

(b) Punta Negra, 11 km to the west of Necochea (level "A" of Tonni et al. 1996).

Pleistocene, Buenos Aires Formation, Bonaerian stage. Baradero County, Buenos Aires Province. Centinela del Mar Beach, General Alvarado County. Buenos Aires Province.

Pleistocene, Arroyo Seco Formation, Bonaerian stage. Santa Isabel Beach, General Pueyrredón County, Buenos Aires Province.

Pleistocene, Guerrero Member of the Luján Formation, Lujanian stage. Río Salado, Las Flores County, Buenos Aires Province, associated to a Stegomastodon molar.

Pleistocene, Luján Formation, (Guerrero Member), Lujanian stage. Lake Guaminí, Stream El Venado, Buenos Aires Province.

Pleistocene-Holocene, La Postrera Formation, Lujanian stage, Tres Arroyos County, Buenos Aires Province. Level "S" of the archeological site Arroyo Seco I (Fidalgo et al. 1986); several specimens.

Possible remains of Coprinisphaera.

(a) Pleistocene, Tezanos Pinto Formation, Lujanian Stage. Tortugas Locality, Belgrano Department, Santa Fe Province. Iriondo and Krohling (2001) pointed out "nodules that are interpreted as a result of the activity of dung beetles".
(b) Pleistocene, Levels 3 and 4 (Voglino 1999), Río Paraná gullies between the cities of Rosario and Campana.
(c) Late Pleistocene. Coprinisphaera? San Pedro and Baradero cities. Buenos Aires Province (Nabel 1993).
(d) Pleistocene, Toropí and Yupoí Formations, Río Paraná gullies, Empedrado City, Corrientes Province (Lutz and Gallego 2001).

Ichnogenus Coprinisphaera Isp "A" Sánchez 2009 (Fig. 2.25)

Isolated chambers, spherical and sub-spherical, with a quite thick built wall. In one of the poles, the chamber wall includes a cavity or secondary chamber, hemispherical and small, open to the outside. A very narrow passageway on the chamber floor connects it with the main chamber. Within this chamber, there is passive filling as a rule.

The examined specimens show great size variation.

Coprinisphaera isp "A" reminds the breeding balls built by dung beetles (Scarabaeinae) of Coprini tribe, Dichotomiina sub-tribe (diggers) included in Pattern II of nidification by Halffter and Edmonds (1982). Assignation based on the isolation condition, spherical shape, wall thickness, possible location of the ovigerous chamber within the provision chamber and current geographic distribution of the Subfamily.

Record in paleosols of Pampasia:

(a) Pliocene, Irene Formation, Chapalmalalan stage. Río Quequén Salado and National Route 3, Buenos Aires Province. Several specimens (Aramayo et al. 2004a, b).
(b) Luján Formation, Guerrero Member. Stream El Venado, Guaminí County, Buenos Aires Province.

Ichnogenus Coprinisphaera Akatanka Cantil et al. 2013 (Fig. 2.26)

Isolated chambers, bispherical, with a relatively thin built wall. Consisting of a spherical cavity or main chamber connected by a passageway to another secondary one which is smaller and also spherical. Externally, the wall of this structure has a very sharp bottleneck which defines both chambers. Both chambers, as a rule, have passive filling inside. It is the first ichnoshape attributed to a ghoul beetle.

Fig. 2.25 Ichnogenus Coprinisphaera “A” Sánchez 2009

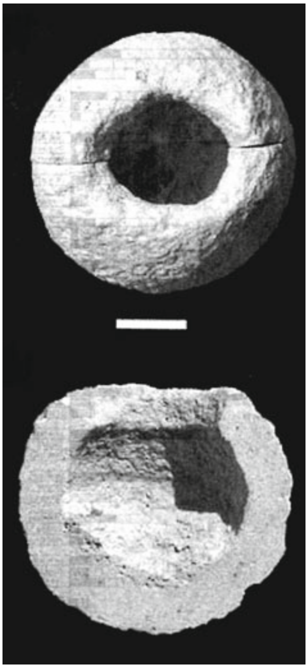

Fig. 2.26 Ichnogenus Coprinisphaera akatanca Cantil et al. 2013

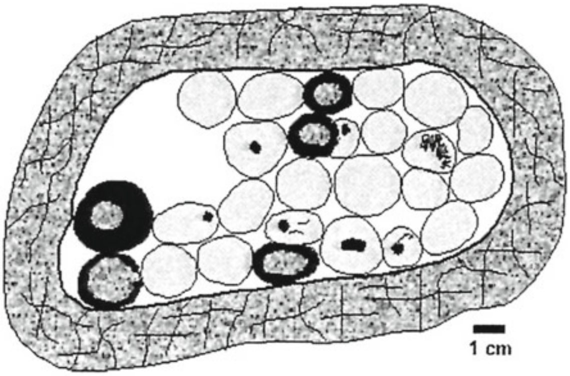

Fig. 2.27 a Ichnogenus Quirogaichnus coniunctus Laza 2006b (a, fossil); b Scheme)

C. akatanka reminds the breeding balls built by beetles (Scarabaeinae) of Coprini tribe, Phanaeina sub-tribe (diggers) of Pattern II of Halffter and Edmonds (1982) and Scarabaeini tribe, Canthonina sub-tribe (wheelers) corresponding to Pattern V of the same authors. Assignation based on the isolation condition, bispherical shape of the ovigerous chamber and current geographic distribution of such beetles.

Record in paleosols of Pampasia: San Andrés Formation, Sanandresian stage (Layer "A" of Tonni et al. 1996). Necochea cliffs, Buenos Aires Province.

Ichnogenus Quirogaichnus Coniunctus Laza 2006b (Fig. 2.27a, b)

The grouping condition of the specimens in a cavity is the main characteristic for separating this ichnogenus from Coprinisphaera Sauer. The specimen grouping is an ichnotaxobase of generic value in other groups of insect trace fossils in paleosols (Genise 2000, 2004). The modern counterpart of this ichnogenus is the type of compound nest of dung beetles defined by Halffter and Edmonds (1982, p. 33) for some Neotropical Canthonina. The materials consist of spherical to sub-spherical chambers grouped in a larger cavity. Such chambers are built by a thin wall and a cylindrical emergency hole. The holotype is formed by 25 spheres from 12 to 22 mm in diameter grouped in a cavity of 125 mm long by 70 mm high; the thickness of the sphere walls is from 2 to 3 mm. Some spheres have holes from 2.7 to 3.4 mm in diameter. Passive filling.

Quirogaichnus coniunctus is similar to compound nests built by beetles of the Scarabaeinae Subfamily, Scarabaeini tribe, Canthonina sub-tribe (wheelers), included in pattern V of nidification of Halffter and Edmonds (1982). The assignation is based on the grouping conditions of the spheres and on the geographic distribution of the subfamily.

Record in paleosols of Pampasia.

Miocene, Cerro Azul Formation, Huayquerian stage. Holotype found in sections of National Route 33 at its intersection with Provincial Route 85, near Guaminí County, Buenos Aires Province.

Miocene, Cerro Azul Formation, Huayquerian stage. Gullies to the south of Provincial Route 152, 2 km. to the east of the town of General Acha, Utracán Department, La Pampa Province. A specimen with its chamber and four nest-balls inside.

Pleistocene, Ensenadan stage. Sitio Los Galpones, Saltos del Guaviyú, Entre Ríos Province. It consists of 10 spherical chambers of 11–27 mm in diameter, without visible holes and thin walls of 4 mm. They were found by J. Frenguelli in 1920 grouped under a glyptodont (Neosclerocalyptus) shell and mentioned then by him in his paper of 1938a.

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