

Nest architecture of *Oxaea austera* (Andrenidae, Oxaeinae) and its significance for the interpretation of Uruguayan fossil bee cells

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Abstract

Oxaea austera nests in hard, red lateritic soils with dense grass cover. Some characters of *Oxaea austera* nests conform to the known architecture of the oxaeine nests such as the long, vertical shaft and the radiating, horizontal tunnels connected to vertical cells. The presence of more than one cell per lateral, cells at different depths containing larvae at different stages, and discrete walls in the main and laterals are described for the first time for Oxaeinae. One cell was located at the end of each lateral with others (2–4) near them, in some cases arranged in a row just beneath the lateral. Cells are oriented vertically and consist of a chamber, a spiral closure and an antechamber connected with a lateral. The chamber and antechamber are surrounded by a thick discrete wall. Each nest was occupied by at least two active females indicating communal nesting. They also contained older cells, suggesting the reutilization of the nests by successive generations. Both behaviors may be a response to the difficulties of excavation in hard soils. Communal nesting may be also a defensive behavior against nest cleptoparasites. The shape, size, discrete walls of lateritic soil material, spiral closure, and antechamber of *O. austera* cells closely resemble the fossil bee cells included in the ichnogenus *Palмираichmus* from the early Eocene Asencio Formation of Uruguay. This new evidence reinforces the proposal of extinct representatives of Oxaeinae as its constructor.

Keywords

Oxaea austera, Andrenidae, Oxaeinae, nest architecture, communal nesting, nest reutilization, fossil bee cells

Introduction

The subfamily Oxaeinae is a small group of 22 species of large, robust, hairy bees distributed from southern USA to northern Argentina (Ascher et al. 2006; Michener 2007; Graf and Moure 2012). With eleven species, *Oxaea* is the most speciose of the four genera of Oxaeinae. A distinctive character of some species of *Oxaea*, including *O. austera*, is having the metasoma bright metallic green or blue (Engel 2006). Most species inhabit tropical or subtropical areas of America (Hurd and Linsley 1976). The nesting behavior of the Oxaeinae is poorly known. Bertoni (1911) made some brief observations on *Oxaea austera* in Paraguay, Roberts (1973) described the nest architecture of *Oxaea flavescens* from Colombia, and Linsley and Michener (1962) described a nest of *Mesoxaea nigerrima* from México.

Data on the nest architecture of the Oxaeinae has been reviewed and compared with that of other soil-nesting bees such as the Diphaglossinae (Hurd and Linsley 1976). The nests described to date consist of a single, vertical main shaft and several horizontal laterals, each terminating in a single vertical cell. In particular, the morphology of the cells is distinctive because of the presence of a discrete wall separable from the substrate, their large size, and the presence of an antechamber (Rozen 1992; 1993; Genise and Hazeldine 1998). These two features suggested that the fossil bee cells included in *Palmiraichnus castellanosi* from the Early Eocene Asencio Formation of Uruguay were produced by the Oxaeinae as originally proposed by Genise and Hazeldine (1998).

The objectives of this contribution are: 1. to describe the nest architecture of *Oxaea austera* and some aspects of its nesting behavior; 2. to compare its nest architecture and behavior with other species of Oxaeinae, and: 3. to present new evidence supporting the Oxaeinae as potential constructors of *Palmiraichnus castellanosi* from the Asencio Formation.

Material and methods

Excavations of nests were performed using plastic tubes to trace the shaft while exposing a vertical section of the soil with the nest. The measures taken were: width and height of the tumulus; number, diameter and length of the shaft and laterals; and number of cells per nest. The measures taken from the cells were: the maximum diameter and length of the cell chamber, width of walls and the width and length of the antechamber. The larvae were boiled in water and maintained in 70% alcohol. Collected bees and larvae were deposited in the entomological collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-En), Buenos Aires, Argentina. Cells and parts of tunnels were deposited in the ichnological collection of the same museum (MACN-Icn). Drs. Arturo Roig-Alsina and Luis Compagnucci identified the bees.

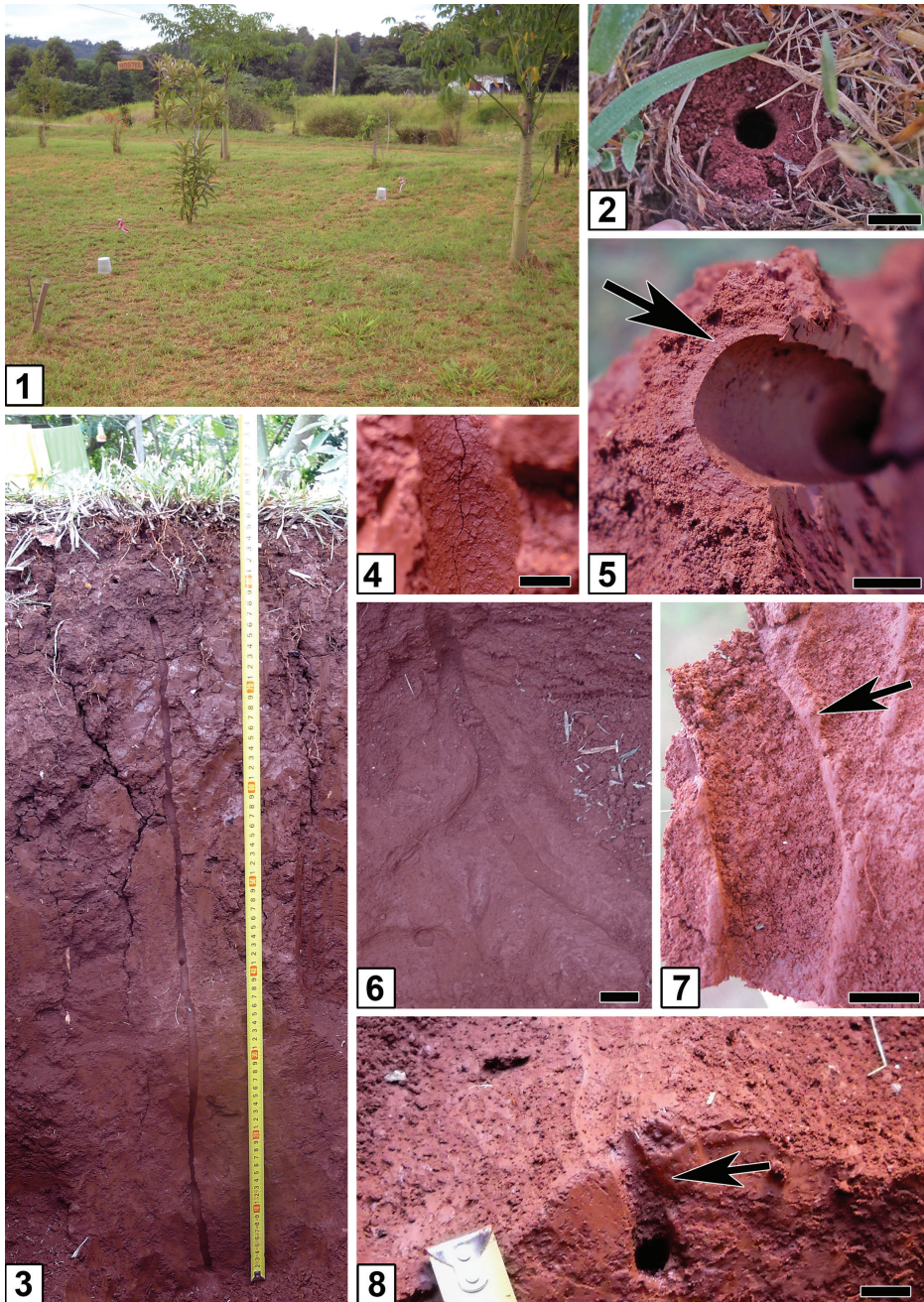
Results

Nesting site and daily activity. The study was carried out from March 10 to 18, 2012 in the Karadya Bioreserve (25°52.233'S, 53°58.167'W), southwards of Andresito, Misiones, Argentina, in the Upper Paraná Atlantic Forest Region (Galindo-Leal and Câmara 2003). The climate is warm, non-seasonal subtropical with a mean annual temperature around 20 °C and a mean annual precipitation around 2000 mm (Servicio Meteorológico Nacional 2012).

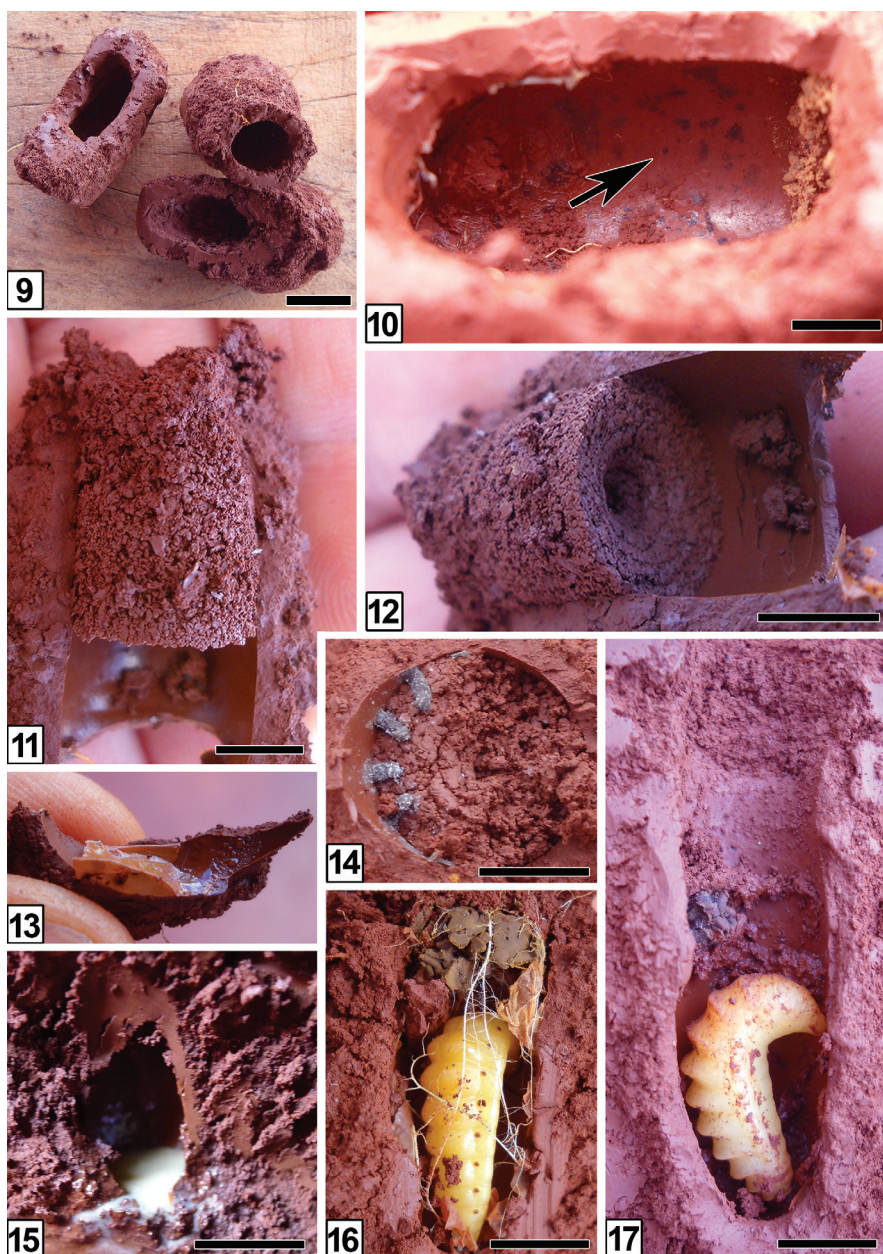
The nests were found in a flat, open, grassy area of 25 m × 20 m near a house (Fig. 1). The soil was red, lateritic, and devoid of rocks or large roots. The upper horizon (30 cm) was extremely hard, probably because of an unusual lack of precipitation during the previous four months. The vegetation consisted of a dense cover of short grasses and a few isolated trees of *Solanum granuloso-leprosum* (Solanaceae).

A total of four active nests were located from 4 m to 18 m away from each other (Fig. 1). One of them was not excavated with the purpose of studying it the next season. However, in a second field trip during December 2012, there was no activity of *Oxaea austera* at the nesting site, nor was this detected during the rest of the season (Julián Baigorria, pers. comm. 2013). Females were observed outside nests from 6:15 am with daylight to 3:00 pm when the entrances were closed from inside. During this period, females completed from 8 to 14 trips, remaining for 2–8 minutes inside the nests between trips. Two females were observed entering the nest that was not excavated. Different conditions were observed in the three excavated nests. In nest 1 (Fig. 18) one active female was collected while leaving the nest and six other females and a single male were collected in the shaft during the excavation of the nest. The six females were found at a depth of about 50 cm, while the male was found deeper at 90 cm. Two active females were collected in nest 2 (Fig. 19) and only one in nest 3 (Fig. 20). Most collected females showed little to no wing wear. Both females of the unexcavated nest and one female in nest 1 and nest 2 showed some wing wear.

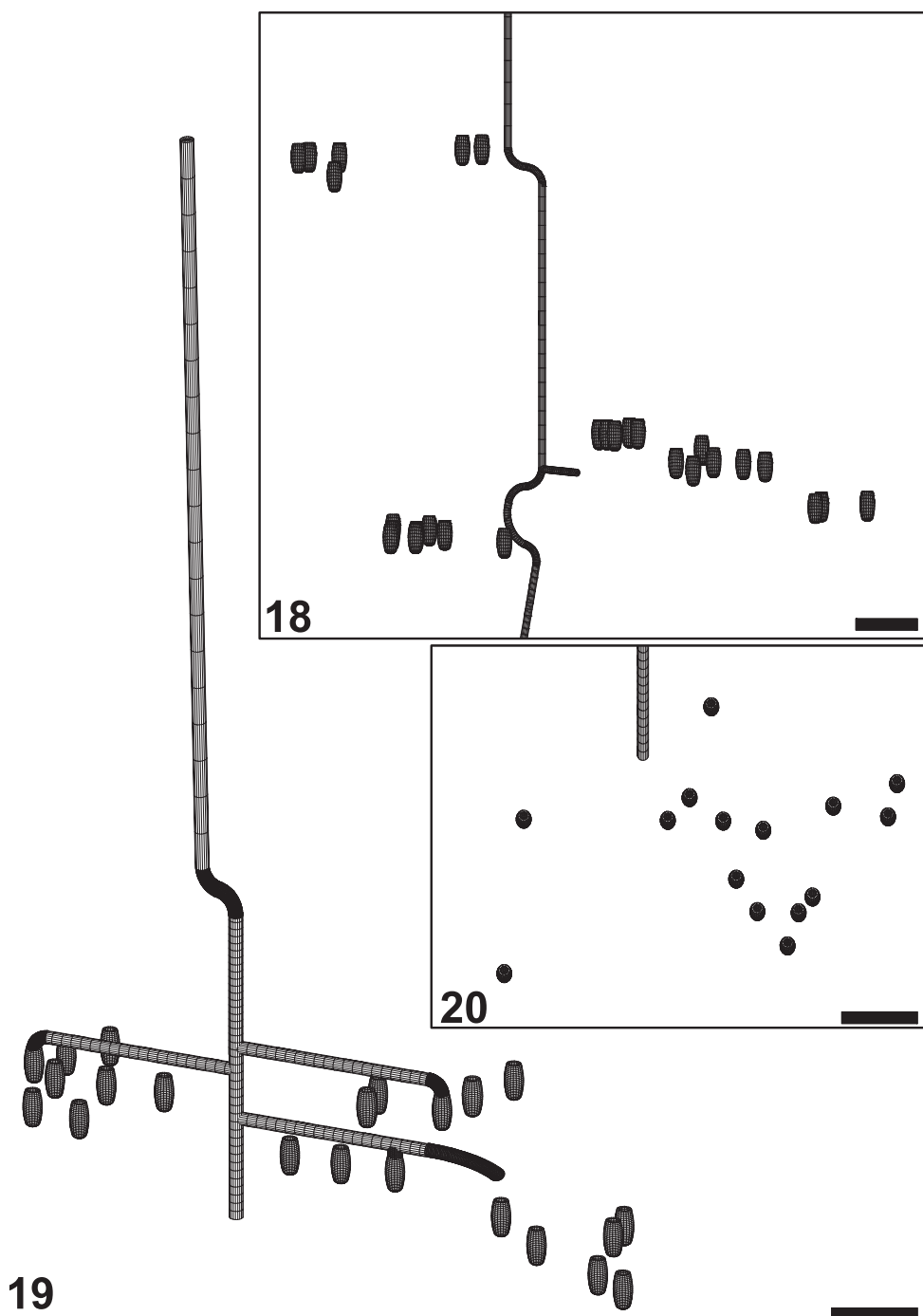
Nest Architecture. Nests entrances were circular with a maximum diameter of 0.9 cm. Each was surrounded by an unconsolidated tumulus, 4.5 cm in maximum diameter and less than 1 cm high (Fig. 2). The nests consisted of one, mostly straight, vertical main shaft, 0.90–1.10 m long and 0.9 cm in diameter, which was circular in cross section (Fig. 3). The main burrow wall consisted of a 2 mm thick layer of packed soil (Fig. 5). The inner surface of the main shaft showed overlapping circular to ovoid concave marks 1.4 mm in maximum diameter (Fig. 4). Horizontal laterals, 10 cm to 37 cm long, radiated from the main shaft at depths ranging from 59 cm to 92 cm (Fig. 6). They had also a discrete 1 mm wall of packed soil (Fig. 7). Laterals were filled with soil after cell closure. Cells appeared at depths from 59 cm to 1.10 m in the different nests. Among the three studied nests, only one (nest 2) (Fig. 19) had lateral tunnels connected to the already filled antechambers of closed cells. Two of them ended in a cell (Fig. 8), whereas a third extended beyond the connected cell (Fig. 19). Other cells (2–4) were present near the tunnels, some arranged in a row just beneath them. The cells, oval and



Figures 1–8. 1 General view of the nesting site of *Oxaea austera* at Karadya Bioreserve 2 Tumulus and open nest entrance, scale: 1 cm 3 Main shaft 4 Surface texture of the first portion of the shaft showing marks, scale: 0.5 cm 5 Cross section of the shaft showing the discrete wall (arrow), scale: 0.5 cm 6 Curved portion of the main tunnel (left) with a lateral one (right) of nest 1 scale: 1 cm 7 A portion of the lateral tunnel showing the discrete wall (arrow), scale: 0.5 cm 8 The antechamber (arrow) connected to the end of the lateral tunnel, scale: 1 cm.



Figures 9–17. **9** Three individual *Oxaea austera* cells removed from soil, scale: 1 cm **10** Black manganese mottles on the inner surface of the chamber (arrow), scale: 0.5 cm **11** Closed cell showing the antechamber filled with unconsolidated soil, scale: 0.5 cm **12** Internal view of a closed cell showing the spiral closure, scale: 0.5 cm **13** Cellophane-like lining **14** Radial arrangement of fecal pellets in contact with the spiral closure, scale: 0.5 cm **15** Longitudinal section of a cell showing the semiliquid provisions, scale: 1 cm **16** Cell with a post-defecating larva, the mass of fecal pellets in the upper part and a mesh of rootlets originally developed between the lining and the soil wall, scale: 0.5 cm. **17** Post-defecating larva inside another cell showing remains of the antechamber, spiral closure and fecal pellets, scale: 0.5 cm.



Figures 18–20. General view of the three excavated *Oxaea austera* nests **18** nest 1 **19** nest 2. **20** nest 3, scales: 5 cm.

elongate, were vertical with the lower end rounded and the upper flat. The chamber was 2.4 cm long and 1.2 cm in maximum diameter ($n = 15$) and the discrete wall 2.3–3.5 mm thick (Fig. 9). The cylindrical antechambers were 1.7 cm long and 1.2 cm in maximum diameter ($n = 15$). The antechamber connected the chamber with the lateral and was filled with unconsolidated, unsorted soil material in closed cells (Fig. 11). The cells (including antechambers) were 4.7 cm long and 2.7 cm in maximum diameter ($n = 15$) and they were easily removable from the soil once dry (Figs 9, 11, 12). The inner surface of the cell chamber was smooth, and except for the closure, it was lined with a shiny semitransparent cellophane-like film (Fig. 13). The spiral cell closure, which separates the chamber from the antechamber, was composed of six whorls of soil material (Fig. 12). Cells contained eggs, pre-defecating and post-defecating larvae. Nest 1 contained 28 cells. The shallowest level with 6 old cells filled with soil was located at a depth of 59 cm. The second level at 90–93 cm had 5 more old cells filled with soil and fecal pellets and 9 new cells containing eggs and young larvae (Fig. 18). At 1.10 m, the lowest level at the opposite side of the shaft, 6 old cells filled with soil and 2 cells containing post-defecating larvae were found. Nest 2 was composed of 22 cells containing eggs or larvae in different stages distributed from 94 cm to 1.10 m (Fig. 19). Nest 3 contained 15 cells at a depth around 76 cm, 13 with mature larvae and two old ones filled with soil (Fig. 20).

Cells with eggs and larvae were less than half filled with whitish yellow semi-liquid provisions (Fig. 15). No bees were observed foraging at flowers. Analysis of pollen from the provisions under SEM showed that it belonged to Fabaceae and Solanaceae. The whitish, elongate eggs were 5 mm long and 1 mm wide and floated horizontally on the provisions. The pre-defecating larvae were curved and white and were mostly submerged in the provisions. The post-defecating larvae, curved and yellowish, were located head up in cells devoid of provisions (Figs 16 and 17). Cells containing post-defecating larvae showed elongate, dark green 1 mm long and 0.5 mm wide fecal pellets with rounded ends. They were disposed radially close to the cell closure and attached to the cell wall (Fig. 14), and in other cases forming a compact green mass on the inner surface of the cell closure (Figs 16 and 17). Some cells with post-defecating larvae show a mesh of rootlets between the soil wall and the lining (Fig. 16). Other cells show black mottles, probably of manganese, on the walls beneath the lining (Fig. 10).

Parasites. Females of *Thalestria spinosa* (Apidae: Nomadinae) were observed flying around and entering the nests of *Oxaea austera*. One cell contained the egg of *O. austera* and a young larva probably of a parasitic bee according with their different morphology. Bertoni (1911) also described the presence of *T. spinosa* (as *T. smaragdina*) near the nests of *O. austera* in Paraguay.

Discussion

The nest architecture of Oxaeinae is scarcely documented in the literature. Most of the knowledge about the biology of Oxaeinae is restricted to descriptions of the immature

stages of certain species (Rozen 1964; Rozen and Rozen 2010) and habits other than nesting such as mating behavior, aggressive territoriality near the nests and flowers, and male aggregations in some *Protoxaea* and *Oxaea* species (Linsley and Michener 1962; Cazier and Linsley 1963; Linsley and Cazier 1972; Hurd and Linsley 1976; Alcock 1990; Oliveira and Castro 2002). Birkmann (1932) (reproduced in Hurd and Linsley 1976 and summarized in Cockerell 1933) mentioned that *Mesoxaea texana* nests in large aggregations. Hurd and Linsley (1976) believed that high concentration of nests observed in *Protoxaea gloriosa* might reflect the scarcity of suitable soil to nest instead of gregarious tendencies. Linsley and Michener (1962) found an isolated nest of *Mesoxaea nigerrima* and Roberts (1973) observed two nests of *Oxaea flavescens* situated ten meters apart. In the studied locality, the nests of *Oxaea austera* were found sparsely distributed over the nesting site. These data suggest that gregariousness in Oxaeinae may depend on the species considered.

Nest entrances of *Oxaea austera* in Paraguay (Bertoni 1911) and of *O. flavescens* in Colombia (Roberts 1973) were concealed by clumps of grass, which was also the case of the *O. austera* nests here studied. *O. flavescens* nested in red-compacted soil (Roberts 1973) and the nest of *Mesoxaea nigerrima* was found in hard soil as well (Linsley and Michener 1962). These records suggest that the Oxaeinae prefer to nest in hard soils with grasses, although observations remain sparse.

Two nests of *Oxaea austera* showed evidence of communal nesting. In both, nest 2 and the unexcavated one, two females were collected while leaving each nest. In the latter case, both females were observed over three days while entering and leaving the nest, and remaining inside together. The evidence provided by nest 1, despite hosting 7 females, is weaker since only one was collected leaving the nest. The remaining 6 females, whose wings showed no evident wear, could have been either females involved in nesting activities or more probably individuals recently emerged from their natal cells, as was probably the case of the male. The presence of cells with eggs indicates that at least one female was actively nesting, and the presence of post-defecating larvae demonstrates that the same or other(s) female(s) had been active for an extended period. Two females entering the same nest was a condition previously mentioned for this species in Paraguay by Bertoni (1911). The occurrence of more than one female of *O. austera* active in the same nest could discourage parasites when one of the females is in the shaft. The cleptoparasitic bee *Thalestria spinosa* was observed entering open entrances of *Oxaea* nests as is typical for Nomadinae (Rozen 1992).

The observations partly confirm those of Roberts (1973) on *Oxaea flavescens*. He studied a single nest with only one active female, and assumed that nests were perennial (i.e. that were used by successive generations of bees for years) based on the long length of the shaft, the estimated large number of cells in a single nest, the slight wing and mandibular wear of the active female, and the presence of mummified larvae, which he attributed to a previous generation. Alternatively, the long shafts and large number of cells can be also explained by communal nesting (i.e. more than one female nesting simultaneously in the same nest) as shown here for *O. austera*, although Roberts (1973) found only a single female in the nest. According to Michener (2007) one

of the conditions that promote communal behavior is very hard soil, because it is much easier to join other bees in a pre-existing nest than to excavate a new nest starting at the surface. At the same time, the presence of old cells containing fecal pellets associated with the main shaft of an active nest in *O. austera* confirms that nests may be used for more than one generation of bees. The upper 1/3 of the main tunnel of *O. austera* was highly packed resulting in discrete walls that were 2 mm thick. These could be the result of intensive trampling by multiple females of the same or successive generations.

Roberts (1973) assumed that nests were deepened by successive generations until females were forced to excavate new ones because of increasing soil moisture or for discouraging cleptoparasites. In nest 1 of *Oxaea austera*, the newest cells were in the intermediate level, neither the shallowest nor the deepest one. In Misiones, under a non-seasonal climate, fluctuations of soil moisture, either by rainfall or changes in water table, might alternatively favor the deepening of nests or the construction of shallower cells. Such fluctuations could be reflected in the different levels containing old as well as new cells in reused nests of *O. austera*.

The nest architecture of *Oxaea austera* is similar to that of many other ground nesting Andrenidae in that it consists of a long, straight, vertical, main shaft and several horizontal laterals ones ending in a single cell (Michener and Lange 1957; Hurd and Linsley 1976). This seems to be a common feature of oxaeine nests as it was observed previously in *Mesoxaea nigerrima* (Linsley & Michener, 1962) and *Oxaea flavescens* Roberts (1973). A major difference between oxaeine nests and nests of other andrenids is that cells are vertically oriented in the former and horizontally oriented in the latter (Rozen 1992).

The number of vertical cells in the nests of *Oxaea austera* ranged from 15 to 28, disposed not only at the end of laterals but also up to 3 in a row beneath them (Fig. 19). This location and the proximity with the tunnel suggest that these cells were formerly connected with the tunnel, which would be extended along with the construction of new cells. This arrangement is different from those previously described for oxaeine nests, where only one cell is located at the end of each lateral (Roberts 1973; Linsley and Michener 1962). The presence of well differentiated levels at different depths showing cells in similar stages (i.e. old and new with eggs, pre and post-defecating larvae) was not described previously in Oxaeinae. In addition, the discrete walls observed in the main and lateral tunnels of *O. austera* are also described for the first time for Oxaeinae. Roberts (1973) described the provisions of *O. flavescens* as "unconsolidated mass of pollen" or "pollen mass". In *O. austera* the provisions are semiliquid as described for *Mesoxaea nigerrima* and *P. gloriosa* (Linsley & Michener, 1962).

The cells of *Oxaea austera* are elongated structures composed of a hard discrete wall and an antechamber, which connects the cell to the lateral tunnel. These cells closely resemble those of *Protoxaea gloriosa* described by Rozen (1993) and illustrated by Genise and Hazeldine (1998). These characters may have been overlooked in described cells of other species of Oxaeinae. Other Andrenidae and the Stenotritidae also construct cells with discrete walls and antechambers (Houston 1984; Rozen 1992, 1993, 1994). The cells of *Protoxaea gloriosa* may show septa in the



Figures 21–22. Fossil bee cells from the early Eocene Asencio Formation of Uruguay **21** external aspect of *Palmiraichnus castellanosi*, scale: 1 cm **22** longitudinal section of *P. castellanosi* showing the chamber and the filled antechamber, scale: 1 cm.

antechamber (Rozen 1993). The females of *Ancylandrena larreae* excavate horizontal lateral tunnels that widen to form an antechamber with discrete walls. The chamber is separated from the antechamber by the spiral closure and the antechamber also contains an external septum and filling (Rozen 1992). The cells of *Ctenocolletes ordensis* (Stenotritidae) are ovoid chambers with discrete walls and a shorter septate antechamber (Houston 1984). Antechambers of these species differ each other in the arrangement and material of their fillings. The cells of *Ancylandrena larreae* and *C. ordensis*, which are filled with solid provisions, are oriented horizontally whereas the cells of *O. austera* and other Oxaeinae, filled with semiliquid provisions are oriented vertically. The discrete wall of *Oxaea austera* cells may be the result of an active building behavior with soil pellets, whereas the wall of tunnels could be more likely the byproduct of packing soil against walls due to repeated trampling or active compression during excavation.

The characters found in cells of *Oxaea austera*, particularly the shape, size, discrete wall, and antechamber, also described for *Protoxaea gloriosa* (Genise & Hazeldine, 1998), supports the proposal that the fossil bee cell *Palmiraichnus castellanosi* (Figs 21 and 22), from the early Eocene Asencio Formation of Uruguay, could be produced by Oxaeinae (Genise and Hazeldine 1998). Reinforcing this hypothesis, *Oxaea austera* and *Oxaea flavescens* (Roberts, 1973) nest in red lateritic, tropical and subtropical soils, the same as the paleosols from the Asencio formation are interpreted to be (González 1999; Bellosi et al. 2004).

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