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Morphological diversity in the ichnogenus *Uruguay* Roselli and its behavioral implications

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Abstract. The ichnogenus *Uruguay*, described from the Ascencio Formation of the Republica Oriental del Uruguay (Late Cretaceous-Paleogene), comprises clusters of fossil bee cells. This ichnogenus includes two ichnospecies, *U. auroranormae* Roselli and *U. rivasi* Roselli, characterized by four and three cell rows respectively. The new examined material (74 specimens) is separated in ten groups based on the previously defined ichnotaxobases and additional ones presented herein. These morphological types are analyzed in terms of growth of cluster, trace maker diversity and behavioral plasticity. Morphological diversity in the ichnogenus *Uruguay* suggests the existence of three closely related species of bees, sharing a common nesting site: the constructor of *U. auroranormae*, *U. rivasi* and those of a third unnamed ichnospecies caracterized by the irregular arrangement of cells, which are cylindrical and elongated, in some cases because for their re-use. New ichnotaxobases for the ichnogenus *Uruguay* proposed herein include the outline in plane view, cell bottoms exposed or hidden, presence or absence of antechambers, cylindrical *vs.* more clavate cells, and the elongation of cells.

Key words. Trace fossils. *Uruguay*. Ichnotaxonomy. Morphological diversity. Bee behavior.

Introduction

The purpose of this paper is to review the different morphological types of clusters of fossil bee cells that are included in the ichnogenus *Uruguay* from the Asencio Formation of the República Oriental del Uruguay (Late Cretaceous-Paleogene), described by Roselli (1938) and redescribed by Genise and Bown (1996). These authors recognized two ichnospecies, *U. auroranormae* Roselli and *U. rivasi* Roselli, based on the number of cell rows, four and three respectively. However, new collected material and the exhaustive analysis of the material studied by these authors, reveal the presence of a wide range of morphologies, that does not fit completely into the two described ichnoespecies.

Specimen are housed in the Laboratorio de Icnología, Museo Argentino de Ciencias Naturales (MACN-LI).

The morphological diversity is analyzed in terms of ontogenetic growth of clusters, trace maker diversity and behavior plasticity. Additionaly, it is the aim of this paper to analyze the best ichnotaxonomical arrangement of these traces, which will contribute to a better understanding of the stratigraphy, sedimentology and paleopedology of the Ascencio Formation.

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The ichnogenus *Uruguay* is recorded from the Palacio Member of the Asencio Formation (western Uruguay), which on the basis of its fossils and stratigraphic position has been regarded as late Cretaceous or Paleogene in age by different authors (Genise and Bown, 1996 and references therein).

Results

The examined material is deposited in the Laboratorio de Icnología, Museo Argentino de Ciencias Naturales, and in the Museo Lucas Roselli from Nueva Palmira and part was the same studied by Genise and Bown (1996) and new specimens collected in more recent field trips. This material (74 specimens) is separated in ten groups based on the previously defined ichnotaxobases: number of cell rows, and additional ones presented herein: the outline in plane view, cell bottoms exposed or hidden, presence or absence of antechambers, cylindrical *vs.* more clavate cells, and the elongation of cells. These groups are included in three types based on the similar morphologies found, corresponding, respectively, with *Uruguay auroranormae* Roselli, *U. rivasi* Roselli and a third unnamed ichnospecies characterized by the irregular arrangement of cells (figure 1).

Type A

Cell diameter increasing towards the bottoms of

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the cells, which are clearly distinguished in the back part of the cluster. The front face of the clusters is concave. The cells of the external rows are slightly inclined towards the center of the cluster. *Group I* (8 specimens): clusters having rectangular outline in plane view, four rows of cells, antechambers absent, the number of cells in each row ranges from three to six (figures 1.A, 1.F; Genise and Bown, 1996, fig. 4.A). *Group II* (5 specimens): clusters having rectangular outline in plane view, five rows of cells, antechambers present in some cells, the number of cells in each row ranges from three to six (figure 2.A). Group III (2 specimens): clusters having hexagonal outline in plane view, four rows of cells, antechambers absent, the number of cells in each row ranges from one to three (figure 2.B).

Type B

Clusters having rectangular outline in plane view. Cell diameter increasing towards the bottom of the cell, which in many cases cannot be distinguished at the back part of the cluster. Antechambers present. The front face of the clusters is concave. The cells of the external rows are strongly inclined towards the center of the cluster. *Group IV* (13 specimens): three rows of cells, the number of cells in each row ranges from three to ten, the front face of the clusters does not show a tunnel-like depression longitudinally (figures 1.B, 1.G; Genise and Bown, 1996, fig. 4.C). *Group V* (10 specimens): three to five rows, the front face of the clusters does not show a tunnel-like depression longitudinally, the number of cells in each row ranges from three to eight (figure 2.C). *Group VI* (5 specimens): three to five rows, the front face of the clusters shows a tunnel-like depression longitudinally (figure 2.D) in four specimens and cells completely closed in the third one (Genise and Cladera, 1995, fig. 2.Eb), the number of cells in each row ranges from three to eight.

Type C

Clusters having diverse outlines in plane view (figures 1.C-E). Cells are straight, of uniform diameter and elongated. Individual cell bottoms are distinguished at the back part of the clusters. Antechambers present (figure 1.H). The elongation of cells may correspond either to long chambers or to the presence of two sucessive chambers (figure 2.E). *Group VII* (3 specimens): rectangular and compressed outline, in lateral view cells show a stair-like design (Genise and Cladera, 1995, fig. 2.Ea), cells arranged in three rows, the external ones strongly arched and facing to the center of the cluster, the number of cells in each row ranges from three to five, they are closed and arise from a longitudinal tunnel-like depression (figure 2.F). *Group VIII* (11 specimens): irregular outline, laterally the cell bottoms lay in the same plane, the number of cells in each row ranges from two to five (figure 2.G). *Group IX* (17 specimens): irregular outline, in lateral view cells show a stair-like design (figure 2.H), two to four rows of cells having two to five cells each one, the number of cells in each row ranges from three to five. *Group X* (1 specimen): square outline, laterally the cell bottoms lay in the same plane, the number of cells in each of the five rows ranges from four to five (figure 2.I).

Discussion

Roselli (1987) and Genise and Bown (1996) distinguished two ichnoespecies of *Uruguay*, *U. auroranormae* Roselli and *U. rivasi* Roselli, based mainly on the number of cell rows, four and three respectively, claiming that intermediate morphologies were almost absent or difficult to find in the outcrops. However, the exhaustive analysis of the previously studied material and the newly collected one, reveals the presence of a wide range of morphological types that cannot be included in any of the two ichnoespecies.

The examined material (74 specimens) is separated in ten groups based on the ichnotaxobases proposed by Genise and Bown (1996) and several morphological features that constitute new and useful ichnotaxobases presented herein. The presence of antechambers and the concretioned back part of the clusters where the cell bottoms are undistinguishable in *U. rivasi* Roselli are two features that may be used to separate typical specimens of this ichnoespecies (Group IV) from typical specimens of *U. auroranormae* (Group I), although in the same specimens of this latter ichnospecies, some cells may show antechambers (Group II). The outline of clusters in plane and lateral views are useful to distinguish juvenile specimens (Group III) and also the irregular clusters of group VII to X. The elongation and diameter of cells, which is constant in the specimens of groups VII to X, are other useful ichnotaxobases. The presence of remains of the principal tunnel (Group VI) and the stair-like design of cells (Group VII and IX) are also useful important ichnotaxobases that contribute to the interpretation of the original position of the clusters in the soil and their attachment to the rest of the nest.

Rectangular clusters having three rows of cells always show antechambers and, in addition, cell bottoms are not clearly distinguishable at the back face of the cluster because of the presence of a layer of soil material. These clusters (Group IV) can be considered as the typical specimens of *U. rivasi* described by

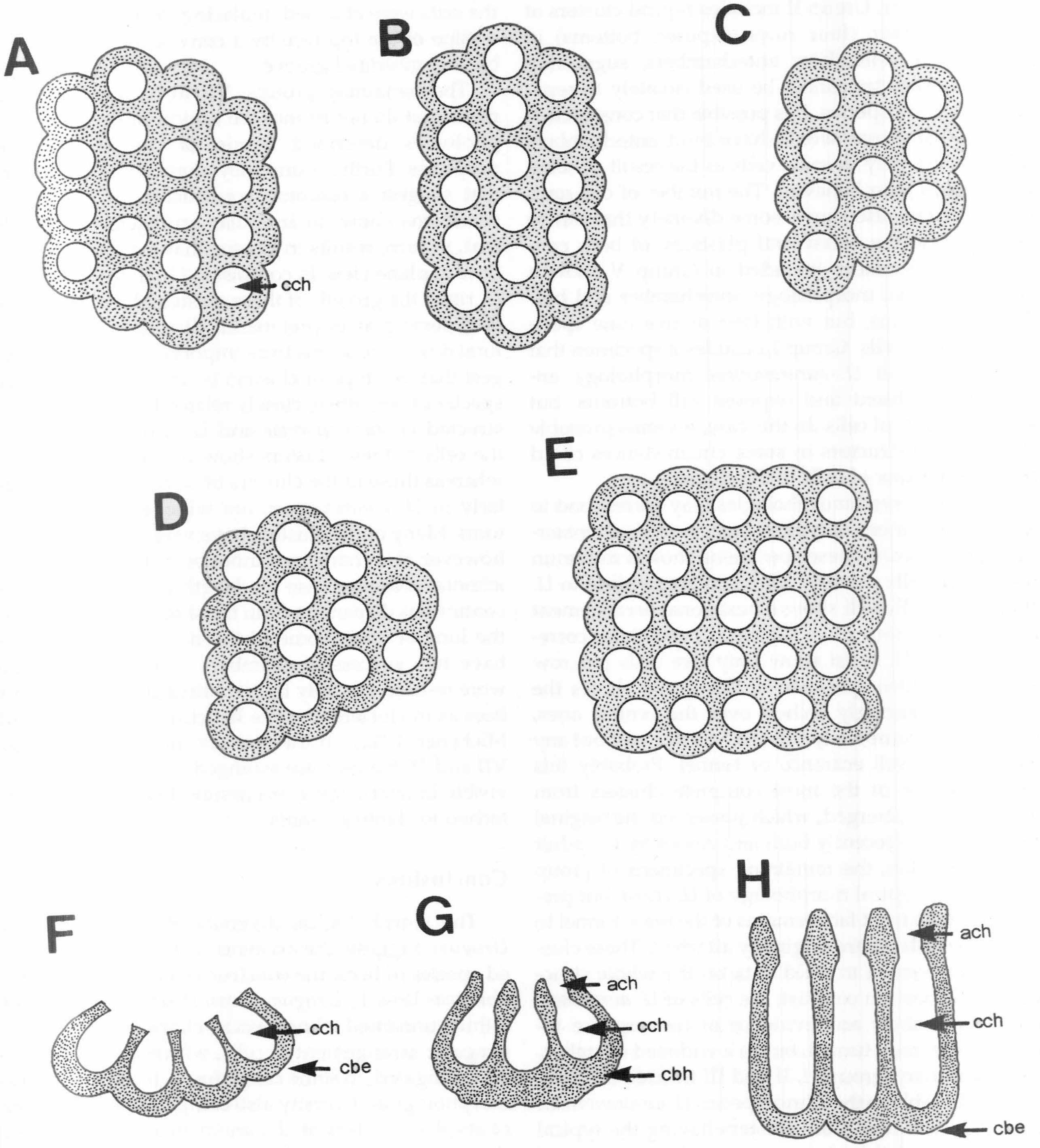

Figure 1. A, Scheme in plane view of typical specimen of ***Uruguay auroranormae*** Roselli showing four rows of cells. **B,** scheme in plane view of typical specimen of ***U. rivasi*** Roselli showing three rows of cells. **C-E,** schemes in plane view of specimens of third unnamed ichnospecies showing diverses arragement of cells. **F,** scheme of section of typical specimen of ***U. auroranormae*** showing absence of antechambers and cells bottoms exposed. **G,** scheme of section of typical specimen of ***U. rivasi*** showing pesence of antechambers and cells bottoms hidden. **H,** scheme of section of specimen of third unnamed ichnospecies showing pesence of antechambers, elongated cells and exposed bottoms. ach, antechamber; cbe, cell bottom exposed; cbh, cell bottom hiden; cch, cell chamber. Scale x 1.

Roselli (1987) and Genise and Bown (1996). In contrast, in rectangular clusters having four rows of cells, these cells lack antechambers and their bottoms are clearly distinguishable at the back part of the clusters (Group I). These specimens are considered the typical *U. auroranormae* described by previous authors. However, Group II includes typical clusters of *U. auroranormae*, (four rows, exposed bottoms) in which some cells show antechambers, suggesting that this character cannot be used isolately to separate both ichnospecies. It is possible that constructors of *U. auroranormae*, would have built antechambers facultatively only in some cells as the result of some plasticity in their behavior. The number of cell rows in the clusters also shows some diversity that can be attributed to the behavioral plasticity of both constructors. Specimens included in Group V show a typical *U. rivasi* morphology, antechamber and hidden cell bottoms, but with four or five (one specimen) rows of cells. Group I includes a specimen that shows a typical *U. auroranormae* morphology, antechambers absent and exposed cell bottoms, but with five rows of cells. In this case, it seems probable that both constructors in some circumstances could add another row of cells to the clusters.

Other observed morphologies may correspond to juvenile specimens of typical clusters of *U. auroranormae* and *U. rivasi*. These specimens show a minimun number of cells per row. Those corresponding to *U. auroranormae* Roselli show a hexagonal arrangement of ten cells in four rows (Group III) and those corresponding to *U. rivasi* show only five cells per row (Group VI). One specimen of this group shows the lateral cells strongly arched over the central ones, producing a completely "closed" cluster without any indication of cell entrance or tunnel. Probably this would be one of the most complete clusters from which no bee emerged, which preserved the original aspect of those recently built and closed by the adult bee. In addition, the remaining specimens of group VI show the typical morphology of *U. rivasi*, but preserving at the front face remains of the main tunnel to which the cells where originally attached. These clusters are important to yield data on the whole structure of the nest. In contrast, the cells of *U. auroranormae* do not show any evidence of convergence towards a common tunnel, but to a widened chamber.

In summary, groups I, II and III include the clusters attributable to the ichnoespecies *U. auroranormae*. Group I assembles those clusters having the typical morphology of the ichnoespecies, whereas those of group II and group III represent morphological variations due to the behavioral plasticity and to different stages in cluster growth respectively. All of them are attributed to the same species of constructor. In turn, groups IV to VI include clusters that can be assigned to the ichnoespecies *U. rivasi*. Group IV includes those clusters with the typical morphology of the ichnoespecies. Those in group V show an additional row of cells attributable to behavioral plasticity, whereas those in group VI represent clusters that have preserved remains of the main tunnel to where the cells were attached, replacing the typical concave outline of the top face by a convex surface sulcated by a longitudinal groove.

The remaining groups, VII to X, involve specimens that do not fit into the typical or atypical morphologies described herein of the known ichnospecies. Furthermore, they share some characters that suggest a common constructor for them. The specimens show an irregular arrangement of cells that, in turn, results in clusters having different outlines in plane view. In contrast to *U. auroranormae* and *U. rivasi* the growth of these clusters does not follow an ordered plan or preferential direction. This behavioral difference seems to be important enough to suggest that this type of clusters is constructed by other species of bee, albeit, closely related to those that constructed *U. auroranormae* and *U. rivasi*. In addition, the cells of these clusters show a constant diameter, whereas those in the clusters of *U. rivasi* and particularly in *U. auroranormae*, are widened at their bottoms. Many of the clusters have very elongated cells; however, this character cannot be used as a clear-cut ichnotaxobase because the length of cells displays a continuous dispersion from the shortest specimens to the longest ones. Some of the most elongated cells have two successive chambers revealing that they were re-used possibly by two distinct generations of bees as in clusters of some halictines (Sakagami and Michener, 1962). In the clusters included in groups VII and IX the cells are arranged in stair-like design, visible in lateral view, suggesting that they were attached to slanting tunnels.

Conclusions

The morphological diversity of the ichnogenus *Uruguay* suggests the existence of three closely related species of bees: the constructors of *Uruguay auroranormae* Roselli, *Uruguay rivasi* Roselli and those of a third unnamed ichnospecies, characterized by the irregular arrangement of cells, which are cylindrical and elongated, in some cases due to their re-use. The morphological diversity also comprises a percentage of atypical clusters of *U. auroranormae* and *U. rivasi*, showing additional cell rows and some antechambers in the case of the former. This diversity is attributed to the behavioral plasticity of their constructors.

Some clusters of both ichnospecies containing a small number of cells could represent the juvenile

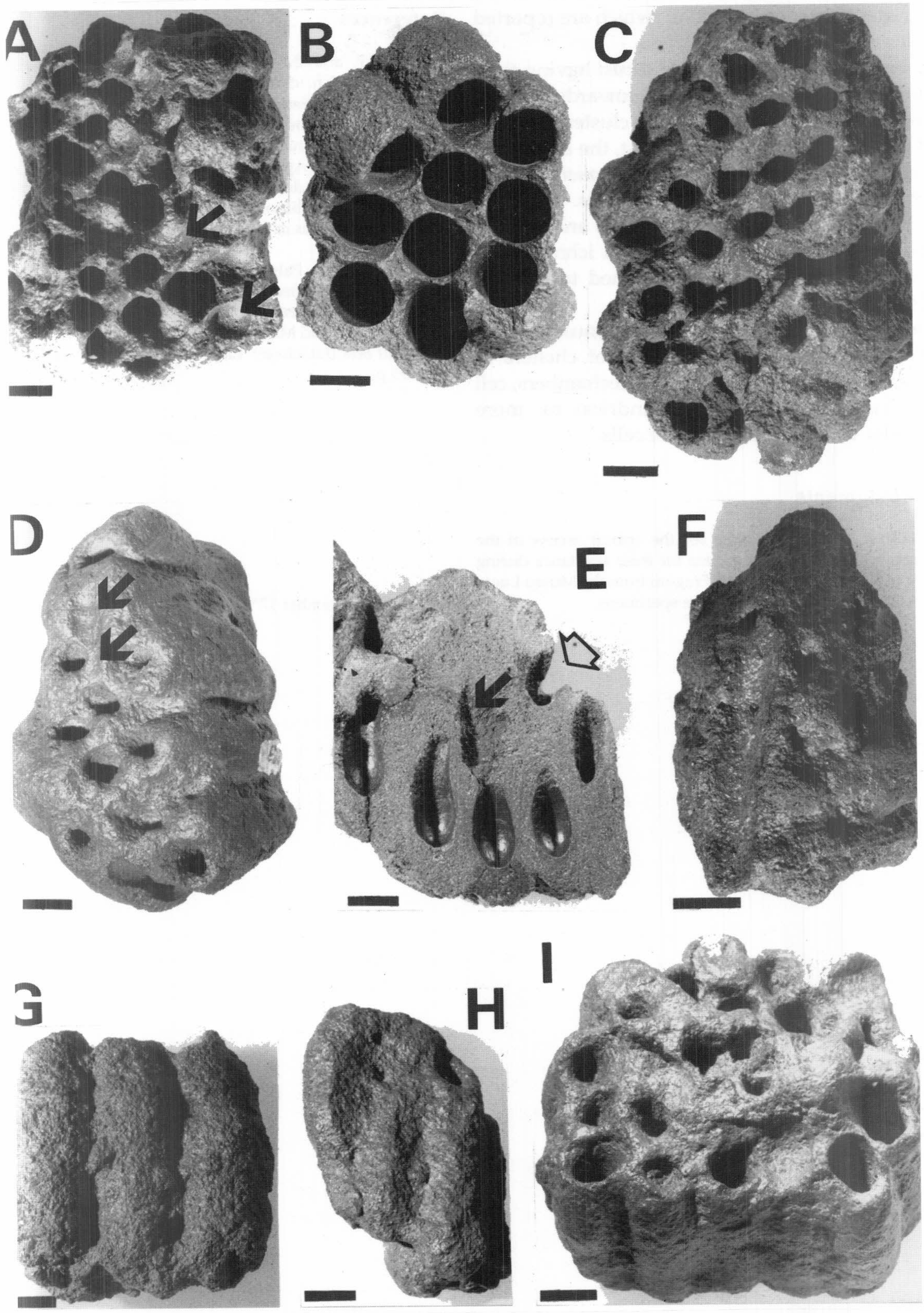

Figure 2. A, specimen of ***Uruguay auroranormae*** Roselli showing additional rows of cells and antechambers (MACN-LI 242). **B,** juvenile specimen of ***U. auroranormae*** (MACN-LI 237). **C,** specimen of ***U. rivasi*** Roselli showing additional rows of cells (MACN-LI 301). **D,** juvenile specimens of ***U. rivasi*** showing remains of a longitudinal tunnel (MACN-LI 237). **E,** elongated cells showing two sucessive chambers (Group IX) (MACN-LI 301). **F,** specimen of Group VII showing closed cells and remains of a longitudinal tunnel (MACN-LI 321). **G,** specimen of Group VIII, showing the cell bottoms laying in the same plane (MACN-LI 345). **H,** specimen of Group IX, showing the stair-like arrangement of cells (MACN-LI 332). **I,** specimen of Group X, showing the square outline in plan view (MACN-LI 306). Scale bars: 1 cm.

stages in the cluster construction, which are reported herein for the first time.

The existence of clusters of *U. rivasi* having their cells closed and/or strongly arched towards of a longitudinal tunnel indicates that these clusters were attached directly to tunnels. In contrast, the absence of antechambers and tunnels in *U. auroranormae* suggests that cells were opened to chambers. The presence of a stair-like arrangement of cells and tunnels in some clusters of the third unnamed ichnospecies could indicate that these were attached to slanting tunnels.

New ichnotaxobases for the ichnogenus *Uruguay* proposed herein include the outline of clusters in plane view, presence or absence of antechambers, cell bottoms exposed or hidden, cylindrical *vs.* more clavate cells, and the elongation of cells.

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