MORPHOLOGICAL VARIATION IN THE ALLANTOPLACENTA WITHIN THE GENUS *MABUYA* (SQUAMATA: SCINCIDAE)

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TITULO: VARIACIÓN MORFOLÓGICA DE LA ALANTOPLACENTA DENTRO DEL GÉNERO *MABUYA* (SQUAMATA: SCINCIDAE).[1]

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PALABRAS CLAVES: Mabuya, placentoma, placas de absorción, placenta, viviparidad.

DESCRIPCIÓN: La alantoplacenta tipo IV ha sido descrita para lagartos escamados del neotrópico del género *Mabuya* de la familia Scincidae. La alantoplacenta tipo IV se caracteriza por tener una gran complejidad morfológica no observada en otros lagartos escamados vivíparos. Aunque un patrón morfológico común ha sido observado en las pocas especies de este linaje que han sido estudias, algunas variaciones morfológicas pueden estar presentes entre especies y poblaciones de este género. Aquí estudiamos las variaciones morfológicas de la alantoplacenta de doce poblaciones del género *Mabuya* distribuidas en diferentes zonas geográficas del norte de Suramérica usando microscopia óptica. En el presente estudio se encontró que todas las especies y poblaciones de *Mabuya* conservan un arreglo general de las estructuras placentales. En el hemisferio embrionario se encuentra un placentoma, paraplacentoma y areolas coriónica; estas estructuras relacionadas a la nutrición histotrófica. Hacia el hemisferio abembriónico son halladas las placas de absorción estructuras especializadas para la transferencia de nutrientes y segmentos respiratorios para el intercambio gaseoso. Sin embargo, en algunas poblaciones algunos rasgos distintivos en el placentoma eran encontrados, como la presencia de células columnares no sincitializadas y células invasivas entre el sincitio uterino y proyecciones apicales de las células coriónicas que irradian e invaginan el sincitio uterino, todas estas características relacionadas a una placenta endoteliocorial localizada. Así mismo encontramos variaciones en la región abembriónica que incluyen una gran complejidad morfológica, como las placas de absorción delimitadas y plegadas y las regiones altamente plegadas (segmentos respiratorios plegados integrados con placas de absorción plegadas). Estas especializaciones presentan una mayor superficie involucradas en el paso de nutrientes e intercambio respiratorio. La replicación y la diferenciación regionalizada de las placas de absorción probablemente son instrumentales en la emergencia de estructuras homologas seriadas especializadas para el transporte de nutrientes, como un placentoma y los diferentes tipos de placas de absorción, así probablemente estos mecanismos subyacen a la evolución de la complejidad placental dentro del género *Mabuya*.

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ABSTRACT

TITLE: MORPHOLOGICAL VARIATION IN THE ALLANTOPLACENTA WITHIN THE GENUS *MABUYA* (SQUAMATA: SCINCIDAE).[1]

AUTHOR: Francisca Milena Leal Carvajalino[2]

KEY WORDS: *Mabuya,* placentome, absorptive plaques, placenta, viviparity.

DESCRIPTION: The type IV allantoplacenta has been described for the New World tropical scincid lizards of the genus *Mabuya*; it possesses the greatest morphological complexity known among viviparous squamates. Although a common morphological pattern has been observed in the few species of this lineage in which the allantoplacental morphology has been studied, some morphological variations may be present among species and populations. Here is studied the morphological variation of the allantoplacenta of twelve populations of the genus *Mabuya* distributed in different geographical areas in North of South America using light microscopy. It is found that all the populations/species conserve a general arrangement of the placental structures. In the embryonic hemisphere there are a placentome, paraplacentome and chorionic areolas; these structures are related to histotrophic nutrition. At the abembryonic hemisphere there are absorptive plaques for histotrophic transfer and respiratory segments for gas exchange. However, in some populations some distinctive features in the placentome were found. The presence in the uterine syncytium of non syncytialized columnar cell groups, and invasive cells and apical projections of the chorionic cells directed toward the uterine syncytium, constituting a localized endotheliochorial placenta. Likewise variations found in the abembryonic region include a greater morphological complexity, such as the folded and delimited absorptive plaques, and highly folded regions at the abembryonic pole (folded respiratory segments integrated with folded absorptive plaques). These specializations allow a larger surface for the passage of nutrients and respiratory exchange. Replication and the regionalized differentiation of the absorptive plaques were probably instrumental in the emergence of specialized structures for nutrient transport such as the placentome and the different types of absorptive plaques, underling the evolution of the placental complexity within the genus *Mabuya* by the morphological variation of serial homologous structures.

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INTRODUCTION

The scincid lizards of genus *Mabuya* are characterized by the greatest placental complexity known in Squamata, which converge with eutherian mammals. Blackburn (1993) established a new placental morphotype for viviparous lizards, the type IV allantoplacenta, following the system proposed by Weekes (1935). This allantoplacental morphotype was described for the Brazilian species *Mabuya heathi* and *Mabuya nigropuctata* (=*Mabuya bistriata*) (Vitt and Blackburn, 1983; Blackburn *et al.,* 1984; Vitt and Blackburn, 1991; Blackburn and Vitt, 1992; Blackburn, 1993; Blackburn and Vitt, 2002; Fleming and Blackburn, 2003). The description was based on the chorioallantoic placental characteristics observed in embryos at advanced stages of gestation and restricted to the embryonic hemisphere of the incubation chamber. The features that define the morphotype refer to the presence of a placentome in the embryonic pole with strong interdigitation between the chorionic epithelium and the uterine syncytium, and the presence of specialized chorionic areolas in the paraplacentomal region. Those placental specializations would be related with the histotrophic nutrition of the embryos, since the ova of these species are microlecithic (Blackburn, 1993; Blackburn and Vitt, 2002).

A more complex placental morphology was described for an Andean population of the genus *Mabuya* (Jerez and Ramírez-Pinilla, 2001). In this population the general characteristics of the chorioallantoic placenta are similar to the type IV allantoplacenta, previously described for the Brazilian species of *Mabuya*. However, Jerez and Ramírez-Pinilla (2001) found a placentome in the embryonic hemisphere, but also a histotrophic active paraplacentome delimited to the rest of the chorioallantoic placenta by small uterine folds and by a chorionic paraplacentomal fold; the chorionic areolas were described in the embryonic hemisphere, but outside the placentome and paraplacentome. In the abembryonic hemisphere, described for the first time, it was observed the presence of an allantoplacenta with absorptive plaques and respiratory segments, thus bearing a mixed function of histotrophic nutrition and gas exchange, respectively. Likewise, studying the morphogenesis of this allantoplacental type, Jerez and Ramírez-Pinilla (2003) found a novel arrangement of extraembryonic membrane morphogenesis for Squamata since the extraembryonic mesoderm does not ingress into the yolk sac and neither an isolated yolk mass nor a yolk cleft are formed. Therefore, the extraembryonic mesoderm surrounds the embryonic chamber completely on its two hemispheres showing in this way a characteristic morphological pattern present in Archosauria and Chelonia but not in other Squamata (Stewart, 1997).

It has been assumed that the type IV allantoplacenta is similar within the whole American lineage of the genus *Mabuya*, however, regarding the allantoplacental morphology only four species have been studied (the Mexican *M. brachypoda*, Villagrán-Santa Cruz et al., 1994; the Brazilian *M. heathi* and *M. nigropunctata* Blackburn *et al.,* 1984; Blackburn and Vitt, 2002; and the Colombian *Mabuya* sp. Jerez and Ramírez-Pinilla, 2001, 2003). Jerez and Ramírez-Pinilla (2001) compared the allantoplacenta of the studied population and museum specimens belonging to other populations and found a similar topology of the allantoplacenta with some small morphological variations among them. Due to the variety of morphological specializations of type IV allantoplacenta and to those morphological variations, they considered that it is possible that those additional areas of nutrient transfer found at the abembryonic hemisphere are probably present in the other species of *Mabuya*. The goal of the present work is to compare the allantoplacental morphology of other populations and other South American species of *Mabuya* in order to establish if the topology and the structure of its placental specializations are similar to those described previously, determining its variability and increasing our knowledge about the placentation in this group of viviparous lizards.

MATERIALS AND METHODS

Early works of the Andean populations of the genus *Mabuya* from the Municipio de Yacopí, Departamento de Cundinamarca, Colombia (North 05°37' West 74°18' altitude 840 m), were temporarily identified as *M. mabouya* (Jerez and Ramírez-Pinilla, 2001, 2003; Ramírez-Pinilla et al., 2002; Gómez and Ramírez-Pinilla, 2004). However, since at present the Andean populations of the genus *Mabuya* lack a clear taxonomic identity (Miralles, 2005), in recent studies these populations from the Colombian Andes on the Western flank of the Cordillera Oriental have been named as *Mabuya* sp. (Ramírez-Pinilla et al., 2006; Ramírez-Pinilla, 2006; Vieira et al., 2007). *Mabuya mabouya* Lacepède (1788) would be restricted to the Lesser Antilles and they are not distributed in the Andean cordillera (Miralles, 2005). In fact Miralles et al., (2005) have described new species of the populations present in the Andes (e.g. *M. meridensis* in the Venezuelan Andes). Regarding the uncertainty about the taxonomic identity of the populations of *Mabuya* from the cordillera of the Colombian Andes, they cannot be assigned to any known species (Miralles et al., 2005); therefore the Andean populations of the genus *Mabuya* will be referred herein as *Mabuya* sp.

For the present study twelve populations of the genus *Mabuya* were analyzed, they were distributed in different geographical areas in North of South America. We used pregnant females in advanced stage of gestation of the populations of *Mabuya* sp., *M. nigropunctata* and *M. guaporicola*. Several populations of *Mabuya* sp. (Curití, Pinchote, Valle de San José, Simacota and Sabana de Torres) were obtained by manual collection, the other populations of *Mabuya* sp. and all the specimens of *M. nigropuctata* and *M. guaporicola* were obtained by loan of museums and herpetological collections (Appendix).

Collected females were euthanized; these females and museum specimens were dissected to extract the oviducts and to obtain the embryonic chambers. All the incubation chambers were observed and photographed through an Olympus stereomicroscope. The obtained incubation chambers of the collected females in the field were fixed in solution of Bouin for 12 hours and subsequently stored in 70% ethanol. The embryonic chambers from museums and herpetological collections were previously fixed in 10% formalin and were stored in 70% ethanol. The embryonic chambers were dissected in two halves to study the abembryonic and embryonic hemispheres, the embryos of each chamber were extracted and their developmental stage was determined following the staging table of Dufaure and Hubert (1961). The studied embryos were between 32-40 developmental stages (Appendix). Placental tissues of the two hemispheres were dehydrated in ethanol series, embedded in paraplast and serially sectioned at 7 µm. Sections were mounted on glass slides coated with albumen and stained with hematoxylin and eosin (Luna, 1969).

Histological sections were analyzed and photographed with an Olympus microscope coupled with digital camera. It was followed the terminology for placental category employed by Stewart and Blackburn (1988) and Blackburn (1993), and also was followed Blackburn (1993), Jerez and Ramírez-Pinilla (2001, 2003) and Ramírez-Pinilla et al., (2006) to describe the morphology and organization of the allantoplacenta, the placental structures, and cellular features.

RESULTS

Placental morphotype and morphological variations

All the populations of *Mabuya* sp., *M. nigropunctata* and *M. guaporicola* exhibit a type IV allantoplacenta, conserving at a general level the histological features and the topological arrangement of the placental structures previously described. Here we show the relative positions of the placental structures and their general morphology.

Placentome

The embryonic chambers containing embryos between 36-40 stages of development of all populations showed a developed placentome located dorsally in the embryonic pole of the incubation chamber, immediately beneath the uterine artery and vein. The placentome is a similar structure in all populations due to its ellipsoidal shape, and the presence of uterine folds that irradiate toward invaginations of the chorioallantois, showing a strong interdigitation between both tissues (Fig. 1). The uterine folds consist of uterine mucosa that forms primary and secondary ramifications with highly vascularized connective tissue and a syncytial epithelium. In the base of the uterine folds, the uterine connective tissue houses active uterine glands whose acines are formed by an epithelium of secretory cuboidal cells. The lumen of uterine glands has secretory material that is liberated by a short duct into the uterine lumen at the interface between the two epithelia. The folds of the chorioallantois are formed by a bilaminar chorionic epithelium with a basal layer of flat cells and an apical layer formed by binucleated giant columnar and thin interstitial cells, the latter frequently with two nuclei.

The two types of cells over the apical layer have long apical microvilli that interlock with those corresponding of the uterine syncytium. The chorionic epithelium lies on a highly vascularized allantois with blood and lymphatic vessels.

The embryonic chambers with embryos in earlier stages of development (between 32 to 35 stages) exhibit the dorsal absorptive plaque that will form the placentome in advanced developmental stages. The dorsal absorptive plaque is characterized by short uterine folds in front of low invaginations of the chorioallantois (Fig 2). The binucleated columnar cells and interstitial cells show microvilli, interlocking with those of the uterine epithelium. In the uterine epithelium the process of syncytialization has begun and areas with low columnar cells together with syncytial regions can be observed.

Although in the placentome of mature placentas (embryos between 36-40 stages of development) of some specimens of *Mabuya* sp. (from Curití, Pinchote and Simacota) the syncytial uterine epithelium seems to be homogeneous, it is possible to distinguish two different groups of cells, which often reach the basal lamina. One of these groups is constituted by columnar cells with apical microvilli that usually have one or two basal nuclei with one or two basophilic nucleoli. These groups of cells are usually located in the basal and lateral region of the uterine folds. They form a single layer of cells arranged in groups of 5 to 10 cells (Fig. 3). The other cellular group observed within the syncytium is constituted by small and irregular cells, with one basophilic nucleus, several nucleoli, and a basophilic cytoplasm that it is hardly differentiated (Fig. 4). Each one of these groups invades the syncytium and barely reaches the basal lamina of the uterine epithelium (Fig. 5). These invasive cells groups exhibit a variable grade of depth in the uterine syncytium (Fig. 6), they are in apposition or in front of the chorionic epithelium, but sometimes can be found in the interface between the two epithelia interrupting the microvillar band between the uterine and chorionic epithelia (Fig. 6). The invasive cells are frequently located in the base, lateral and in the apex of the epithelium of the uterine folds. These groups of invasive cells approach toward blood vessels (Figs. 5, 7) that penetrate into the uterine syncytium in several points; thus they bring the maternal circulation near these invasive irregular shaped cells. The nuclei of these two groups of cells (columnar and invasive cells), are very small compared to the size of the nuclei of the uterine syncytium (Fig. 7).

In the same populations of *Mabuya* sp. with these two cell groups mentioned above, some cells of the chorionic epithelium of the placentome have long apical projections which deeply notch the uterine syncytium (Fig. 8). The chorionic apical projections derive from both giant and interstitial cells and are covered by microvilli (Fig. 9). Several of these apical projections of neighboring chorionic cells frequently converge, forming thin apical projections (Fig. 9). The latter can be observed at several points of the placentome (Fig. 8). In several points of the placentome these convergent apical projections are observed close to or in contact with the invasive cell groups immersed in the uterine syncytium (Figs. 10 - 11). However, the continuity between the invasive cells and chorionic apical projections is not clear due to the artificial separation of the uterine and chorioallantoic components during the histotechnical procedures.

Paraplacentome

The paraplacentome is a peripheral zone to the placentome. Although it is in close proximity to the placentome the paraplacentome does not show an evident interdigitation between the uterine and chorionic epithelia. The paraplacentome is delimited to the rest of the embryonic chamber by the chorioallantoic paraplacentomal fold located in front of the corresponding folds of the uterine mucosa. In all the populations of *Mabuya* sp., and the species *M. nigropunctata* and *M. guaporicola* in the paraplacentomal fold area there is a uterine fold getting into a deep chorionic invagination of the paraplacentomal fold (Fig. 12). The uterine paraplacentomal fold delimits and separates the embryonic pole, corresponding to the placentome and paraplacentome, from the rest of the embryonic chamber. A great part of the paraplacentomal fold is located laterally at the union of the embryonic chamber with the interembryonic space in the mesometrial side of the oviduct. In the paraplacentome the uterine epithelium shows a drastic change, the uterine syncytium characteristic of the placentome changes to an epithelium composed by tall columnar cells in the paraplacentome. The paraplacentomal uterine zone, including the paraplacentomal uterine folds, has a great glandular activity. Numerous uterine glands with abundant secretory granules are observed in their lumen. This secretion is liberated through a glandular duct, opening into the interface between the uterine and chorionic epithelia (Fig. 13). The paraplacentomal chorionic epithelium is similar to the placentomal chorionic epithelium. The chorionic epithelium in the paraplacentomal chorionic fold is polymorphic and stratified. The paraplacentomal chorionic and uterine epithelia show a refracting border due to the interdigitation between the microvillar surfaces of both epithelia, though a brush border similar to that found in the placentome is not observed.

In the embryonic chambers with embryos in earlier developmental stages, the dorsal absorptive plaque is delimited by a short region, the paraplacentomal zone, which in these stages of development shows similar histological characteristics relative to those above described for the fully developed paraplacentome, including those of the paraplacentomal fold.

Chorionic areolas

The chorionic areolas are located outside of the paraplacentomal region, but proximal to the paraplacentomal fold. They are chorionic concavities in apposition to uterine glands that secrete material towards the chorionic cavity. The uterine epithelium consists of low columnar cells; sometimes is observed a small uterine fold that irradiates to the chorionic concavity (Fig. 14). The invagination of the chorionic epithelium is formed by low binucleated columnar cells and low interstitial cells. Despite of having observed embryonic chambers with embryos in late stages of development (stage 40) of the population of *M. guaporicola*, chorionic areolas were not observed.

The populations of *Mabuya* sp. of Curití and Pinchote show chorionic areolas distributed on the embryonic hemisphere, but reaching the abembryonic hemisphere as well. In the embryonic hemisphere they are distributed with more frequency near to the paraplacentomal folds. However, several chorionic areolas reach the abembryonic hemisphere, but reaching a higher concentration in the abembryonic pole region. The abembryonic chorionic areolas are especially related with folded absorptive plaques, and they are numerous below of the yolk sac.

Although the chorionic areolas were described as characteristic structures of the last stages of development (stages 39 and 40) chorionic areolas in formation were observed in embryonic chambers with embryos between 32 to 38 stages of development, located close to the interembryonic regions (Fig. 15). They were found in the population of *Mabuya* sp. from Yacopí, Simacota, Valle de San José, Mutatá and Perijá, and in *M. nigropunctata*. However, in embryonic chambers of the same stages of development of other populations of *Mabuya* sp. (Sabana de Torres, Tierra Alta, Caucasia and Consejo de Ziruma) the chorionic areolas were not observed. Hence, it seems there is an ontogenetic variation in the different populations studied, regarding the time of development of these structures (chorionic areolas) relative to the stage of development of the embryo.

Absorptive plaques

The absorptive plaques are thickening areas of the embryonic chamber; they are small and rounded, and they are distributed especially in the abembryonic hemisphere. The chorionic and uterine epithelia of the absorptive plaques are hypertrophied like in the paraplacentomal region. The chorionic and uterine epithelia are juxtaposed, without interdigitation between them and lacking a recognizable regular microvilli, although a refractant border between the two epithelia is observed. These structures are named simple absorptive plaques (Figs. 16a, 17). In the embryonic chambers of the specimens of *Mabuya* sp. from Curití, simple absorptive plaques can also be observed in proximity to the paraplacentomal fold alternating with chorionic areolas and respiratory segments; thus, simple absorptive plaques are not restricted uniquely to the abembryonic hemisphere.

Simple absorptive plaques are present in all the embryonic chambers studied. However, there are two types of absorptive plaques morphologically more complex than simple absorptive plaques, which are generally restricted to the lateral region and the abembryonic polar region of the embryonic chamber, below and in close proximity to the yolk sac. In the first type, the absorptive plaques are delimited in their periphery by a chorionic invagination in which a uterine fold is inserted (Figs. 16b, 18). The epithelium of the chorionic invagination is formed by squamous cells, whereas the uterine fold epithelium is formed by cuboidal to columnar cells. This type of absorptive plaque is named here as delimited absorptive plaques. They were observed in the abembryonic hemisphere of some populations of *Mabuya* sp. (Curití, Pinchote, Simacota, Valle de San José, Mutatá, Tierra Alta y Caucasia).

The second type of absorptive plaques is structurally even more complex, these absorptive plaques are also delimited, but additionally they have in the central region a small folding and interdigitation between the chorioallantois and uterine mucosa. This type of absorptive plaques is called folded absorptive plaques. The chorioallantoic and uterine tissues show different levels of folding and depths as well; usually they have two, three o more uterine folds in front of the chorioallantoic invaginations (Figs. 16c, 19). The histological features of folded absorptive plaques are similar to those described for simple absorptive plaques. The chorionic epithelium is constituted by columnar binucleated and interstitial cells. The chorionic mucosa exhibits invaginations in which uterine folds interdigitate, the latter epithelium is formed by columnar cells. Folded absorptive plaques are similar to the placentome of a type III allantoplacenta, regarding particular features such as the interdigitation between the chorionic and uterine mucosa (Fig. 16c). Macroscopically folded absorptive plaques show irregular forms, and they are larger than the other two absorptive plaque types (ranging between 3 to 6 mm in diameter). Folded absorptive plaques are restricted to the abembryonic pole, immediately below the yolk sac. Their location becomes evident macroscopically when we remove the yolk sac (Figs. 20, 21). Folded absorptive plaques were observed in embryonic chambers of some populations of *Mabuya* sp. (Curití, Pinchote and Simacota), which also had simple and delimited absorptive plaques.

The three types of absorptive plaques have uterine glands, opening into the interface of the chorionic and uterine epithelia, secreting material through the glandular duct.

The variation represented by the presence of three types of absorptive plaques does not constitute an ontogenetic variation, since some of the embryonic chambers with embryos later than stage 37 only had simple absorptive plaques; in contrast other populations in similar or even earlier stages than 37 already showed all three types or two types of absorptive plaques (simple and delimited) (Table. 1).

In the populations where the coexistence of the three types of absorptive plaques were observed, the regionalization of the embryonic chamber was evident. These embryonic chambers show simple and delimited absorptive plaques on the lateral region, whereas the folded absorptive plaques are located in the abembryonic polar region exclusively. However, in the embryonic chambers that show only one or two types of absorptive plaques (simple, or simple and delimited), the absorptive plaques are dispersed in the whole abembryonic hemisphere including part of the abembryonic polar region.

Respiratory segments

The respiratory segments are found outside of the placentomal and paraplacentomal areas surrounding the absorptive plaques and the chorionic areolas. They are formed by the apposition of thin chorionic and uterine tissues. Both mucosae are lined by squamous epithelia that are closely apposed; thus, the subepithelial capillaries of both mucosae are in close proximity allowing gas exchange between mother and fetus. In these areas endometrial glands are present with cuboidal epithelial cells. In the lumen of these glands were observed eosinophilic granules; however, glandular ducts were not observed (Fig. 22). The respiratory segments are present in all the embryonic chambers.

Folded respiratory segments and highly folded regions

The folded respiratory segments are encountered in the embryonic chambers of *M. guaporicola* and populations of *Mabuya* sp. from Pinchote and Simacota. In *M. guaporicola*, these are characterized by the presence of long uterine folds lined by squamous epithelia, these long uterine folds are interlocking with chorionic invaginations, which are formed by an epithelium of squamous and cuboidal cell patches (Fig. 23). These folded respiratory segments were observed in the whole embryonic chamber, outside the placentomal-paraplacentomal region. They were surrounding simple absorptive plaques.

In the embryonic chambers of the populations of *Mabuya* sp. from Pinchote and Simacota, a structural variation was observed in the folded respiratory segments. The uterine folds are shorter and are formed by an epithelium of cuboidal cells; these uterine folds are in front of chorionic invaginations, which are formed by an epithelium of squamous cells (Fig. 24). Those folded respiratory segments are regionalized in the embryonic chamber, they are localized exclusively on the abembryonic polar region, and they alternate with folded absorptive plaques below and in close proximity to the yolk sac (Fig. 25). Conjunctly, the folded respiratory segments and the folded absorptive plaques form in this way a complex integrate zone, it constitutes an evident highly folded region clearly observed macroscopically below the yolk sac in the abembryonic pole (Figs. 26a, b).

DISCUSSION

The embryonic chambers of all the studied specimens follow the morphological pattern of the allantoplacenta previously described for the population of the Colombian Andes, Municipio de Yacopí, and referred as *Mabuya* sp. (Jerez and Ramírez-Pinilla 2001, 2003, and Ramírez-Pinilla et al. 2006). This topology would represent shared and derived characters of this lineage, although its morphology presents interspecific variations (Fig. 27).

Placentome

The structure of the placentome for the studied populations and species of *Mabuya* is similar to the placentomal structure of the population of *Mabuya* sp. from Yacopí (Jerez and Ramírez-Pinilla, 2001, 2003 and Ramírez-Pinilla et al., 2006) and to *M. heathi* and *M. nigropuctata* (Vitt and Blackburn, 1983; Blackburn et al., 1984; Vitt and Blackburn, 1991;

Blackburn and Vitt, 1992; Blackburn, 1993; Blackburn and Vitt, 2002; Fleming and Blackburn, 2003). However, some interesting features found in the placentome of some populations of *Mabuya* sp. (Curití, Pinchote and Simacota) are the presence of two different groups of cells, placed inside the uterine syncytium, and the presence of apical projections of chorionic cells that irradiate toward the uterine syncytium.

The first group of cells in the uterine syncytium of the placentome is probably constituted by cells that have not culminated their syncytialization process, and could be important in the growth of the uterine syncytium. Blackburn (1993) also found patches of cuboidal to columnar cells together with syncytial areas in the uterine epithelium of the placentome in *M. heathi* and *M. nigropuctata*, suggesting that its presence is a common feature in *Mabuya* placentome.

The second group of cells found inside the uterine syncytium was also observed by Vieira et al., (2007) in ultrathin and semithin section of the placentome of the populations of *Mabuya* sp. from Yacopí, Curití, Pinchote and Valle de San José. They were named invasive cells since they form cellular cords that penetrate deeply in the uterine syncytium (Vieira et al., 2007). These groups of irregular cells are in close proximity to uterine capillaries that impinge the uterine syncytium. Vieira et al., (2007) found that complex double membrane cytoplasmatic projections of these invasive cells surround and contact the capillary from the connective tissue septum that penetrate the uterine syncytium, conferring to the placentome a typical characteristic of a located endotheliochorial placenta. The mechanism involved in the invasion of the chorionic invasive cells towards the uterine syncytium is unknown. Nonetheless, the presence of apical projections of chorionic cells that enter very deep into the uterine syncytium, which seem to be continuous with the invasive cells would partially explain the invasion process. Vieira et al., (2007) have proposed that the invasive cell cords have a chorionic origin, since they show similar ultrastructural features and structural continuity with the chorionic cells. Therefore, it is tentative to question whether the apical projections of the chorionic cells could be involved in the process of invasion toward the uterine epithelium. The convergent apical projections from chorionic cells are anchored into the uterine syncytium in several points of the placentome close to or in continuity with invasive cells cords. It is possible to suggest that a number of invasive cells would leave the chorionic epithelium from those chorionic projections at discrete points of the placentome, forming in this way the invasive cell cords observed deeply inside the uterine syncytium. Hence, the invasive cells and the chorionic apical projections would constitute a continuous structure; however, the histological paraffin preparations produces an artificial separation of the uterine and chorioallantois tissues (Hradecky et al., 1988), thus the relationship of the chorionic apical projections with the invasive cells are not clearly preserved.

We were not able to establish if the non syncytialized columnar cell groups, the invasive cells and the apical projections of the chorionic cells toward the uterine syncytium are present in the placentomes of all sampled populations and species of *Mabuya* studied. They were not observed in embryos at earlier stages of development (32-38), neither in some embryos at advanced stages (39-40) in museum specimens. These histological features probably have not been differentiated in the dorsal absorptive plaque yet. Likewise, in museum specimens with fully developed placentomes these histological characteristics were not observed. It is possible that suboptimal conditions of fixation and/or preservation affect the histological details (Abromavich, 1930).

Paraplacentome

The paraplacentome has similar features in all the studied species and populations and is similar to the description for the Yacopí population of *Mabuya* sp. (Jerez and Ramírez-Pinilla, 2001; Ramírez-Pinilla et al., 2006). Ramírez-Pinilla et al., (2006) found that the paraplacentome is a very important region for maternal-fetal transfer of lipids, in this region there is a great glandular activity from paraplacentomal uterine epithelium of the embryonic chamber and also from the interembryonic spaces (Jerez and Ramírez-Pinilla, 2001). Also, the morphology of this area in all the studied embryonic chambers show numerous active glands, secreting a great quantity of material in the paraplacentome, in a similar way to the population of *Mabuya* sp. from Yacopí.

The paraplacentome is delimited by a uterine paraplacentomal fold that enters into the invagination of the chorionic paraplacentomal fold. This paraplacentomal fold separates the placentome and the paraplacentome from the rest of the embryonic chamber. This paraplacentomal fold was found in all populations and species studied, including *M. nigropunctata* and in the population of *Mabuya* sp. from Yacopí (Jerez and Ramírez-Pinilla, 2001, 2003 and Ramírez-Pinilla et al., 2006). However, it was not described for the embryonic chambers of *M. heathi* and *M. nigropuctata* (Blackburn, 1993; Blackburn and Vitt, 2002). Its detection probably depends on the proper serial section reconstruction of the histological slides and the examination of well preserved material.

In Artiodactyl mammals, of the families Cervidae, Bovidae and Giraffidae, there is a structure called the marginal fold (Mossman, 1987), which presents similar features to the paraplacentomal region and paraplacentomal fold of the embryonic chambers of *Mabuya*, such as its topology and several structural details. In these Artiodactyl families, the marginal fold is characterized by an invagination of the trophoblast which delimits the base of the placentome. In the zone of the marginal fold there is a great amount of histotrophic material from the endometrial glands that open around of the base of the placentome (Mossman, 1987). Due to their histological similarities, the marginal fold and the paraplacentomal fold of the deer and *Mabuya* placentomae can be regarded as convergent structures.

Chorionic areolas

In the studied populations the chorionic areolas were found outside of the embryonic pole. However, these structures were not found in museum specimens of *M. guaporicola*, neither in museum specimens of Colombian *Mabuya* (Jerez and Ramírez-Pinilla, 2001). Jerez and Ramírez-Pinilla (2001) conclude that the absence of chorionic areolas can be a consequence for the inadequate fixation process. As observed by Jerez and Ramírez-Pinilla (2001) for the population of *Mabuya* from

Yacopí, the chorionic areolas are numerous near to the paraplacentomal region but in the embryonic hemisphere. However, the populations of *Mabuya* sp. from Curití and Pinchote exhibit several chorionic areolas in the embryonic hemisphere and in the abembryonic hemisphere as well, indicating that these structures can be regionally expanded to this hemisphere.

Ramírez-Pinilla et al., (2006) found in the population of *Mabuya* sp. from Yacopí that the chorionic areolas are formed starting at stage 39. Nonetheless, some populations have chorionic areolas in formation in embryonic chambers with embryos between the stages 32-37.. The presence or absence of chorionic areolas in the embryonic chambers of these species would represent an ontogenetic variation in the relative time of formation of this structure and it did not constitute an interspecific morphological variation.

Absorptive plaques

Absorptive plaques are present in all populations of *Mabuya* sp., *M. nigropunctata* and *M. guaporicola* and they are evident in the Mexican species *Mabuya brachypoda* as well (Uribe-Aranzábal et al., 2006: Fig. 4D). Therefore, as suggested by Ramírez-Pinilla et al., (2006), they would represent a synapomorphy for *Mabuya* species with type IV allantoplacentation. Besides of the presence of simple absorptive plaques in all the studied species and populations, in this study two additional types of absorptive plaques were described, and they are structurally more complex than simple absorptive plaques. They are termed delimited absorptive plaques (with a marginal fold), and folded absorptive plaques (morphologically similar to the placentome of type III allantoplacentae and with a marginal fold). In the three types active uterine glands are present, which open and secrete materials to the interfaces between the two epithelia. Thus the three types of absorptive plaques would be involved in a significant histotrophic uptake in the transports of nutrient between the maternal and fetal tissues.

The three types of absorptive plaques and the placentome seem to represent an ontogenetic sequence of morphological transformations. For instance, the placentome of *Mabuya* in early stages of development resembles a great dorsal absorptive plaque, morphologically similar to a simple absorptive plaque. Later in development the dorsal absorptive plaque grows and folds itself (Jerez and Ramírez-Pinilla, 2001, 2003), achieving a condition morphologically similar to a delimited and folded absorptive plaque, and finally it forms the placentome in advanced stages of development. Therefore, the placentomal development resembles an ontogenetic sequence that recapitulates the three morphotypes of the absorptive plaques, finally acquiring the great morphological complexity characteristic of the placentome. Likewise, it is possible that the three types of absorptive plaques and the placentome conserve a common ontogeny, as they would be originated from simple absorptive plaques, which later could undergo differentiation reaching a more complex morphology as in the case of the antimesometrially folded absorptive plaques and mesometrially, the most complex, the placentome.

Furthermore, it is probable that the placentome of *Mabuya* and their different types of absorptive plaques are homologous structures, in this case serially homologous structures (Wagner, 1989). It is possible to suggest that the evolution of a structurally complex placenta in *Mabuya* has been facilitated by the replication and differentiation of a modular developmental unit (Oakley, 2003), the absorptive plaques, which are regionalized on the embryonic chamber. Perhaps the latter could be product of regionalized inductive signals affecting absorptive plaques. Consequently replication and differentiation of the absorptive plaques would act as an underling mechanism in the origin of the morphological variation and regionalization observed in these structures.

Therefore in some populations the allantoplacenta shows a higher complexity, presenting a morphologically complex placentome in the embryonic pole and several types of absorptive plaques on the rest of the embryonic chamber. Moreover one of the absorptive plaque types, the folded absorptive plaques, attains a degree of differentiation and regionalization nearly comparable to the dorsal placentome of a type III allantoplacenta. Thus the main morphological features of absorptive plaques and their role in nutrients transport at histotrophic level, suggest that they can be regarded as small placentomes localized in the abembryonic region in the type IV allantoplacenta. In consequence the type IV allantoplacenta could be considered as a polycotyledonary placenta, comparable to the placentae of some Artiodactyl mammals (present within Giraffidae, Antilocapridae and Bovidae). In those mammals the cotyledons show different sizes and different degree of folding (i.e. morphological complexity) (Abromavich, 1930; Mossman, 1987; Hradecky et al., 1988).

Folded respiratory segments and highly folded regions

The folded respiratory segments are called in this way, since their uterine or chorionic components have the histological characteristics of the respiratory segment. These folded respiratory segments were observed in the population of *M. guaporicola* and in the populations of *Mabuya* sp. from Pinchote and Simacota. Similarly, in *M. nigropuctata* Vitt and Blackburn (1991) found that in the non specialized regions of the embryonic chamber there are folded regions, which present the characteristics of respiratory segments, where the uterine and chorionic tissue are interlocked, and the epithelium of both components present squamous cells interexposed in the allantoic and the uterine vasculature. Thus there is a general morphology of folded respiratory segments for gas exchange, but with small histological variations in different populations of the genus *Mabuya*. This folding suggests a larger surface of gas exchange.

In the populations of *Mabuya* sp. from Pinchote and Simacota the folded respiratory segments are also integrated with folded absorptive plaques forming a morphological complex that gives the appearance of an integrated structure, which is regionalized in the abembryonic pole near to and below the yolk sac, and it is termed by us as highly folded regions. Therefore, highly folded regions are structure complexes in the abembryonic pole, which suggests a larger surface for nutrients and gaseous exchange.

The highly folded regions are close to the yolk sac, but it does not present a direct connection with it. The yolk sac of *Mabuya* is characterized by absence of yolk and apparently it does not form any specialized structure for the transfer of nutrients, however, the yolk sac has an ontogenetic critical function in the embryonic development such as the hematopoiesis. On the other hand, the yolk sac is highly vascularized and has hypertrophied endodermal cells (Jerez and Ramírez-Pinilla, 2001, 2003). An additional function for the yolk sac is unknown in *Mabuya*, however, it appears that the presence of the yolk sac probably has an influence in the regionalization of the incubation chamber during embryonic development.

All the populations of *Mabuya* sp., *M. nigropunctata* and *M. guaporicola* conserve a general placental morphotype and a similar pattern of morpho-physiological specializations. However, different features were observed in the topologic arrangement and in the morphology of particular placental structures such as, the absorptive plaques and respiratory segments. These variations in the morphology of the allantoplacental specializations confer a greater morphological complexity to the placenta, such as the folded and delimited absorptive plaques and the highly folded regions in the abembryonic region, those complex structures could bear a larger surface involved in the passage of nutrients and respiratory exchange respectively. Therefore, there is an interesting variability of specialized structures within a common structural plan.

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Table 1. Morphological variations of the absorptive plaques in the embryonic chambers of the populations of *Mabuya* sp., *M. nigropuctata* and *M. guaporicola*.

Species	**Populations**	**Stages of embryonic development**	**Types of absorptive plaques**		
			Simple	***Delimited***	***Folded***
Mabuya sp	Curití	40	Present	Present	Present
	Pinchote	40	Present	Present	Present
	Simacota	35-36	Present	Present	Present
	Valle de San José	32-40	Present	Present	Absent
	†Tierra Alta	37	Present	Present	Absent
	†Mutatá	36	Present	Present	Absent
	†Caucasia	34	Present	Present	**?**
	Sabana de Torres	33	Present	**?**	**?**
	†Consejo de Ziruma	37	Present	Absent	Absent
	†Perijá	37	Present	Absent	Absent
M. nigropuctata	†La Gran Sabana	38	Present	Absent	Absent
M. guaporicola	†Chapada dos Aimaraes	40	Present	Absent	Absent

? = Embryonic chambers with embryos in advanced stages of gestation were not observed. Thus, we cannot determine if the other types of absorptive plaques are presented.
† **=** Museum specimens.

APPENDIX

Acronyms

UIS-R = Colección herpetológica de la Universidad Industrial de Santander, MHUA= Museo Herpetológico de la Universidad de Antioquia, MHNLS = Museo de Historia Natural La Salle, CHUNB = Coleção Herpetológica da Universidade de Brasilia, ED = Stages of embryonic development.

Collected specimens

COLOMBIA, Western flanks of the Cordillera Oriental. *Mabuya* sp. Curití municipality,

Departamento de Santander (N 6°36'16.85" W 73°04'02.74" elevation 1497 m). UIS-R 1382 (ED 40), UIS-R 1430 (ED 40), UIS-R 1475 (ED 40). *Mabuya* sp. Pinchote municipality, Departamento de Santander (N 6°30'30.31" W 73°11'4.30" elevation 1500 m). UIS-R 1396 (ED 40), UIS-R 1476 (ED 40). *Mabuya* sp. Valle de San José municipality, Departamento de Santander (N 6°26'50.16" W 73° 8'39.36" elevation 1248 m). UIS-R 1478 (ED 40), UIS-R 1516 (ED 32), UIS-R 1517 (ED

32). *Mabuya* sp. Simacota municipality, Departamento de Santander (N 6°26'29.47" W 73°20'14.43" elevation 1050 m). UIS-R 1513 (ED 35), UIS-R 1512 (ED 36), UIS-R 1514 (ED 36). *Mabuya* sp. Sabana de Torres municipality, Departamento de Santander (N 7°23'48.32" W 73°29'26.32" elevation 136 m). UIS-R 1532 (ED 33).

Museum specimens

COLOMBIA, Serranía de San Jerónimo. *Mabuya* sp. Mutatá municipality, Departamento de Antioquia (N 7°25'00.00" W 76°25'00.00" elevation 285 m). MHUA 11074 (ED 36).

COLOMBIA, Inter Andean Cauca Valley. *Mabuya* sp. Caucasia municipality, Departamento de Antioquia (N 7°58'59.59" W 75°12'08.97" elevation 52 m). MHUA 10045 (ED 34).

COLOMBIA, Caribbean region. *Mabuya* sp. Tierra Alta municipality, Departamento de Córdoba (N 9°06'00.00" W 75°48'00.00" elevation 5 m). MHUA 11127 (ED 37).

VENEZUELA, North East cost of Lago Maracaibo. *Mabuya* sp. Consejo de Ziruma municipality, Estado de Zulia (N 10°45'26.58" W 71°36'10.66" elevation 1 m). MHNLS 11856 (ED 37).

VENEZUELA, Venezuelan Andes, Sierra de Perijá. *Mabuya* sp. Perijá area, Estado de Zulia (N 10°01'03.14" W 72°57'16.96" elevation 3042 m). MHNLS 11864 (ED 37).

VENEZUELA, Venezuelan Guyana. *Mabuya nigropunctata* La Gran Sabana area, Estado de Bolívar (N 5°34'08.86" W 61°38'24.31" elevation 1210 m). MHNLS 11544 (ED 38).

BRAZIL, *Mabuya guaporicola* Chapada dos Guimaraes, Estado Mato Grosso (S 15°25'0.08" W 55°52'53.99" elevation 559 m). CHUNB 25653 (ED 40), CHUNB 38985 (ED 40).

FIGURES LEGENDS

Figure 1. Placentome of stage 40 embryo of the population of *Mabuya* sp. from Curití. ca, chorioallantois; uf, uterine folds reaching the invaginations of the chorioallantios. Scale bar = 120 µm.

Figure 2. Dorsal absorptive plaque of stage 32 embryo of the population of *Mabuya* sp. from Valle de San José. ca, chorioallantois forming small invaginations; ue, uterine epithelium; eb, embryo. Scale bar = 120 µm.

Figure 3. Columnar cells inside of uterine syncytium in the placentome of the population of *Mabuya* sp. from Curití. cc, columnar cells; us, uterine syncytium; ug, uterine gland; c, chorionic cells. Scale bar= 15 µm.

Figure 4. Invasive cells inside of uterine syncytium in the placentome of the population of *Mabuya* sp. from Curití. ic, invasive cells; us, uterine syncytium; arrow, nuclei with various nucleoli in the invasive cells. Scale bar = 10 µm.

Figure 5. Invasive cells groups barely reach the basal lamina of the uterine syncytium in the placentome of the population of *Mabuya* sp. from Pinchote. ic, invasive cells; bv, blood vessel; us, uterine syncytium; arrow, basal lamina; c, chorionic cells. Scale bar= 15 µm.

Figure 6. Invasive cells groups in the interface between uterine and chorionic epithelia and completely inside of the uterine syncytium in the placentome of the population of *Mabuya* sp. from Curití. ic, invasive cells; bv, blood vessel; us, uterine syncytium; i, interface between uterine and chorionic epithelia; c, chorionic cells. Scale bar = 30 µm.

Figure 7. Nuclei of columnar and irregular cells respect to the nuclei of syncytium uterine in the placentome of the population of *Mabuya* sp. from Pinchote. ic, invasive cells; cc, columnar cells; bv, blood vessel; un, uterine nuclei; arrow, nuclei of irregular cells and columnar cells. Scale bar= 45 µm.

Figure 8. Chorionic apical projections in the placentome of the population of *Mabuya* sp. from Curití.c, chorionic cells; cp, chorionic apical projections; us, uterine syncytium. Scale bar= 25 µm.

Figure 9. Groups of neighboring chorionic apical projections in the placentome of the population of *Mabuya* sp. from Curití. cp, chorionic apical projections; bc, binucleated columnar chorionic cells; in, interstitial chorionic cells Scale bar= 15 µm.

Figure 10. Chorionic apical projections continuous with the irregular cell groups in the placentome of the population of *Mabuya* sp. from Pinchote. cp, chorionic apical projections; c, chorionic cells; ic, invasive cell groups; us, uterine syncytium. Scale bar = 25 µm.

Figure 11. Diagram showing the continuity of chorionic apical projections with the invasive cell groups in several points of the

placentome in the populations of *Mabuya* sp. from Curití, Pinchote and Simacota. cp, chorionic apical projections; bc, binucleated columnar chorionic cells; in, interstitial chorionic cells; ic, invasive cell groups; cc, columnar cells; uc, uterine capillary; us, uterine syncytium; ct, connective tissue. The inset shows a detail of the continuity of chorionic apical projections with the invasive cell groups.

Figure 12. Paraplacentome of the population of *Mabuya* sp. from Curití. pp, paraplacentomal chorionic fold; uf, uterine fold; ca, chorioallantois; ug, uterine gland; arrow, change of chorionic epithelium from columnar to polymorphic and stratified in the paraplacentomal chorionic fold. The inset shows a detailed of paraplacentomal chorionic fold. Scale bar= 125 µm.

Figure 13. Uterine glands in the paraplacentome of the population of *Mabuya* sp. from Curití. ug, uterine gland; ue; uterine epithelium; arrow, abundant secretory granules are liberated in the interface between uterine and chorionic epithelia of the paraplacentomal region; ca, chorioallantois; bv, blood vessel. Scale bar= 60 µm.

Figure 14. Chorionic areolas of the population of *Mabuya* sp. from Curití. ug, uterine gland; arrow, areolar cavity with secretory material;

ue, uterine epithelium; ca, chorioallantois; bv, blood vessels. Scale bar= 50 µm.

Figure 15. Chorionic areolas in formation near to the interembryonic spaces of the population of *Mabuya* sp. from Valle de san José. is, interembryonic spaces; af, chorionic areola in formation. Scale bar= 30 µm.

Figure 16. Diagram showing the three types of absorptive plaques in the populations of *Mabuya*. ue, uterine epithelium; bc, binucleated columnar chorionic cells; in, interstitial chorionic cells; rb, refractant border. a: Simple absorptive plaques. b: Delimited absorptive plaques. uf, uterine fold inserted in chorionic invagination delimiting the absorptive plaques; ci, chorionic invagination c: Folded absorptive plaques. f, folding of uterine mucosa interdigitate with chorionic invaginations in the central region of the absorptive plaques;

Figure 17. Simple absorptive plaques of the population of *Mabuya* sp. from Pinchote. ue, uterine epithelium; ce, chorionic epithelium. Scale bar = 80 µm.

Figure 18. Delimited absorptive plaques of the population of *Mabuya* sp. from Pinchote. ue, uterine epithelium; uf, uterine fold; bv, blood vessels; ce, chorionic epithelium; ci, chorionic invagination. Scale bar = 80 µm.

Figure 19. Folded absorptive plaques of the population of *Mabuya* sp. from Pinchote. ue, uterine epithelium; uf, uterine fold; ce, chorionic epithelium; ci, chorionic invagination; f, folding of uterine mucosa interdigitate with chorionic invaginations. Scale bar = 120 µm.

Figure 20. Folded absorptive plaques near to the yolk sac in the abembryonic region of the population of *Mabuya* sp. from Curití. ys, yolk sac; fp, folded absorptive plaques. Scale bar= 2 mm.

Figure 21. Folded absorptive plaques near to yolk sac in the abembryonic region of the population of *Mabuya* sp. from Curití. arrow, the yolk sac is removed; fp, folded absorptive plaques. Scale bar = 2 mm.

Figure 22. Respiratory segments of the population of *Mabuya* sp. from Curití. ue, uterine epithelium; ug, uterine gland; ce, chorionic epithelium; arrow, subepithelial capillaries of both mucosae are in close proximity to the epithelia. Scale bar = 60 µm.

Figure 23. Folded respiratory segments of the population of *Mabuya guaporicola*. uf, uterine fold; ci, chorionic invagination; arrow, epithelium of cuboidal to squamous cells. Scale bar = 80 µm.

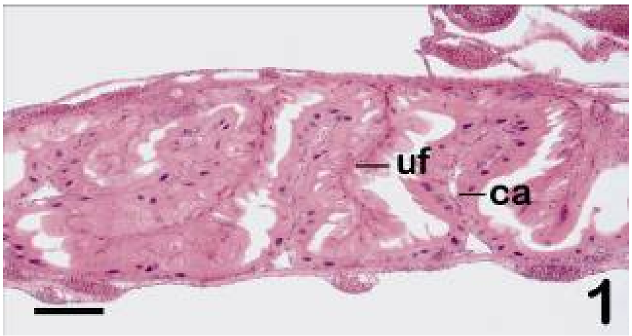
Figure 24. Folded respiratory segments of the population of *Mabuya* sp. From Pinchote. uf, uterine fold; ci, chorionic invaginations; bv, blood vessels. Scale bar = 40 µm.

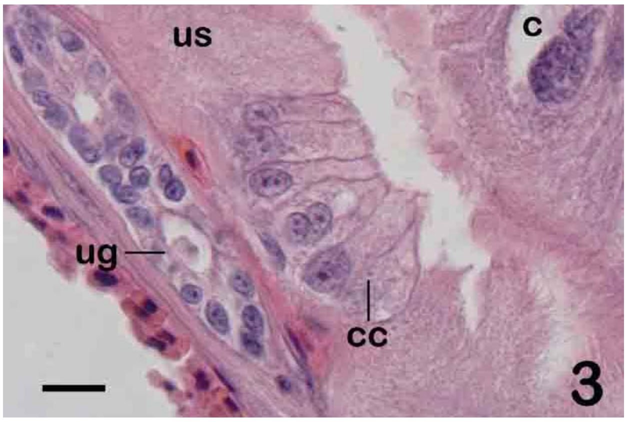
Figure 25. Folded respiratory segments integrated with folded absorptive plaques (Highly folded regions) of the population of *Mabuya* sp. From Simacota. fp, folded absorptive plaques; arrow, folded respiratory segments. Scale bar = 65 µm.

Figure 26. Highly folded regions of the population of *Mabuya* sp. from Simacota. u, uteri; ufp, uterine folds of the folded absorptive plaques; fr, uterine folds of the folded respiratory segments; ca, chorioallantois; ip, chorionic invagination of the folded absorptive plaques; ir, chorionic invaginations of the folded respiratory segments. a,b: Detail of highly folded regions in the uteri and chorioallantois. Scale bar= 2 mm.

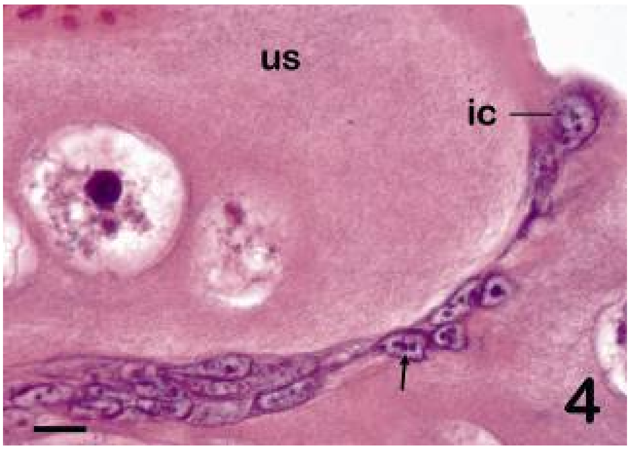
Figure 27. General diagram of the embryonic chamber of all the studied specimens showing the general morphological pattern of the allantoplacenta including the morphological variations encountered. p, placentome; pp, paraplacentome; ca, chorionic areolas; sp, simple absorptive plaques; dp, delimited absorptive plaques; fp, folded absorptive plaques; fr, folded respiratory segments; ys, yolk sac; eb, embryo.

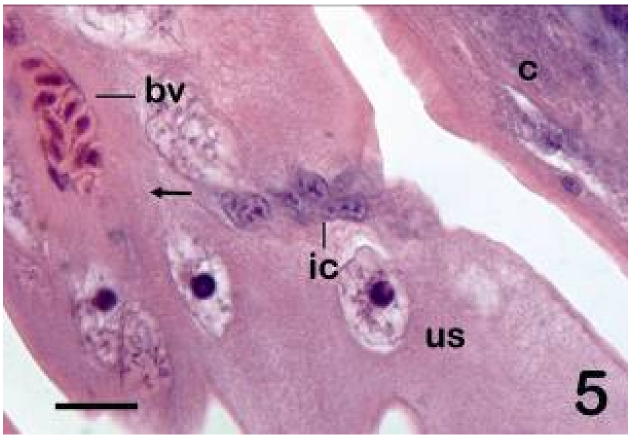
FIGURES 1,2 y 3

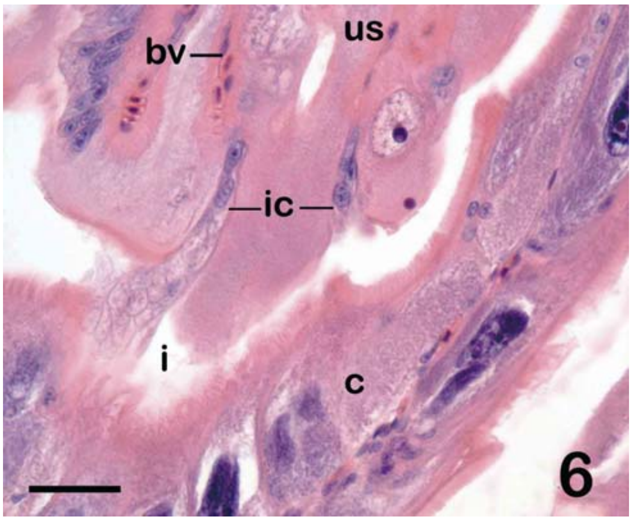




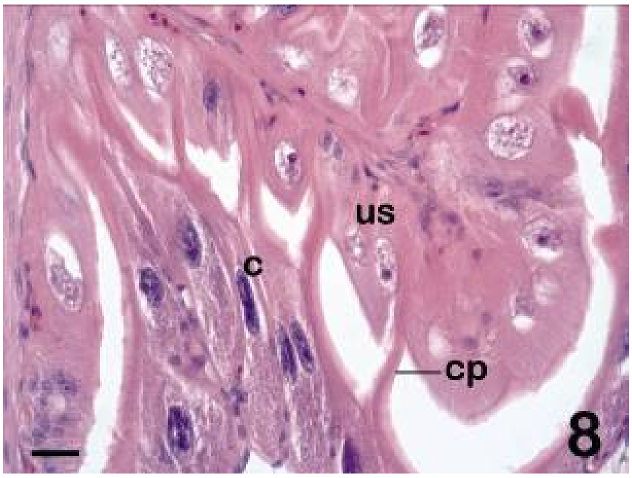
FIGURES 4,5 y 6



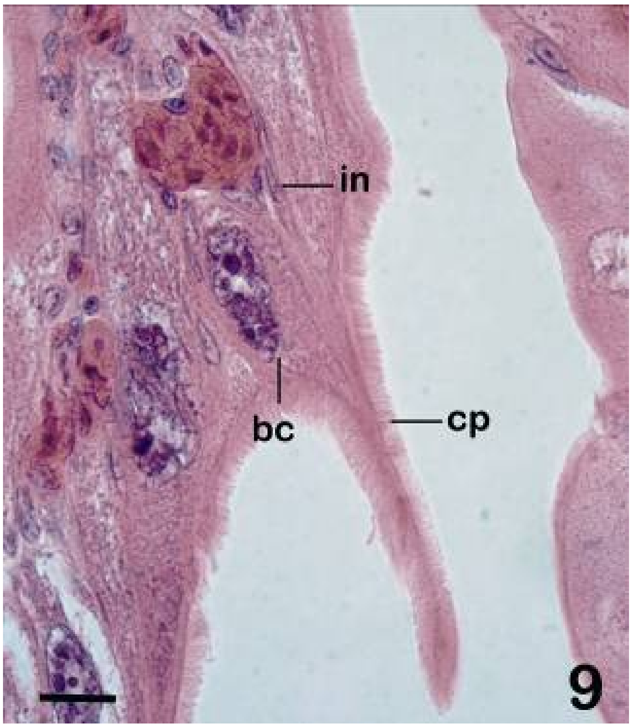


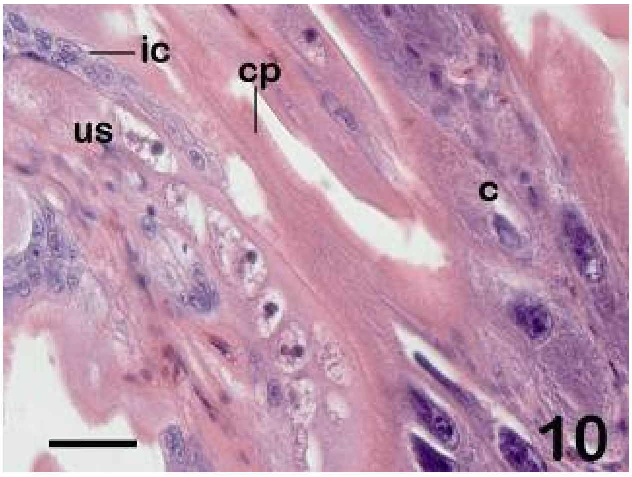


FIGURES 7 y 8

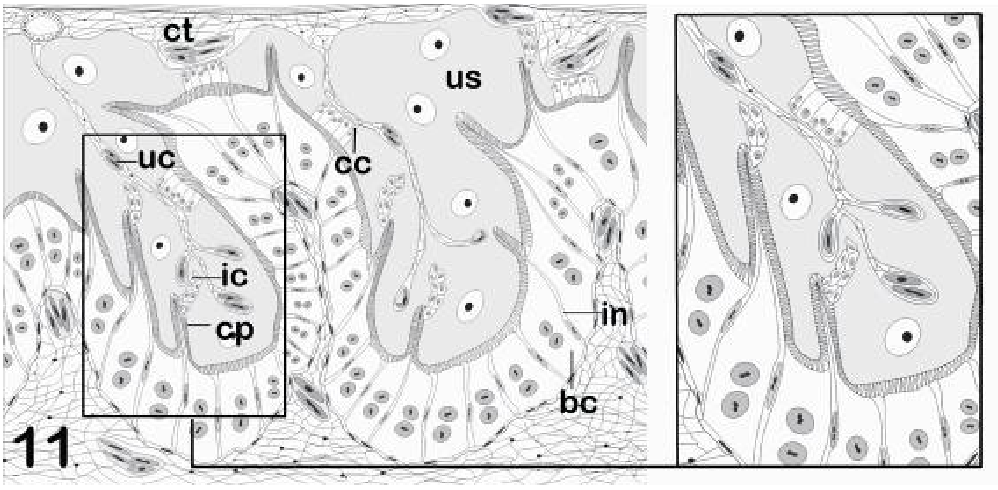


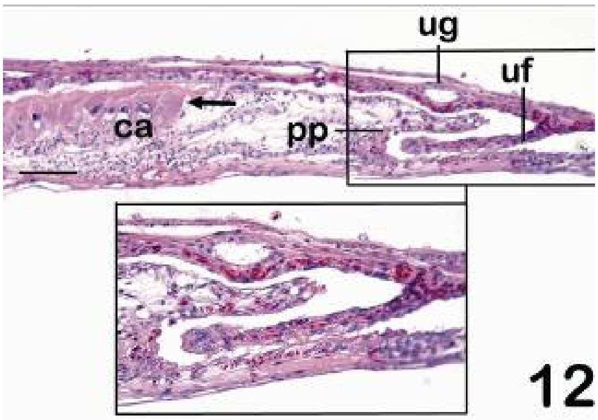
FIGURES 9 y 10

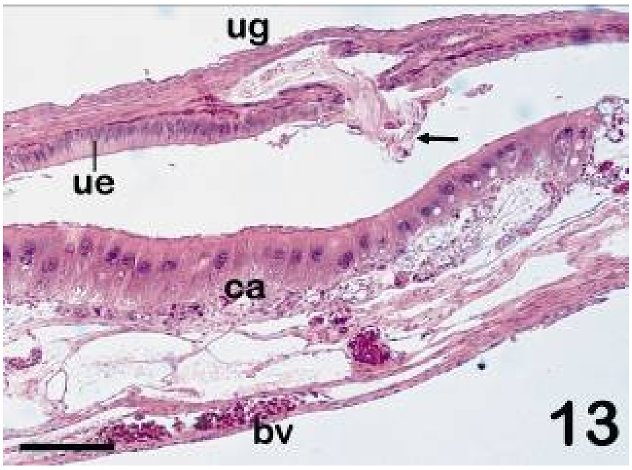




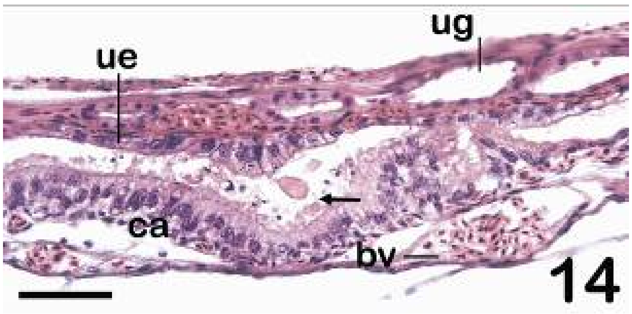
FIGURES 11,12 y 13

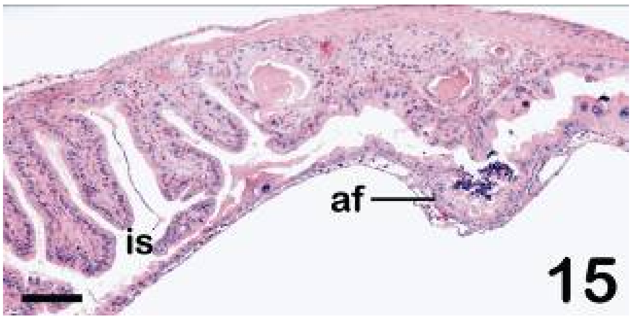


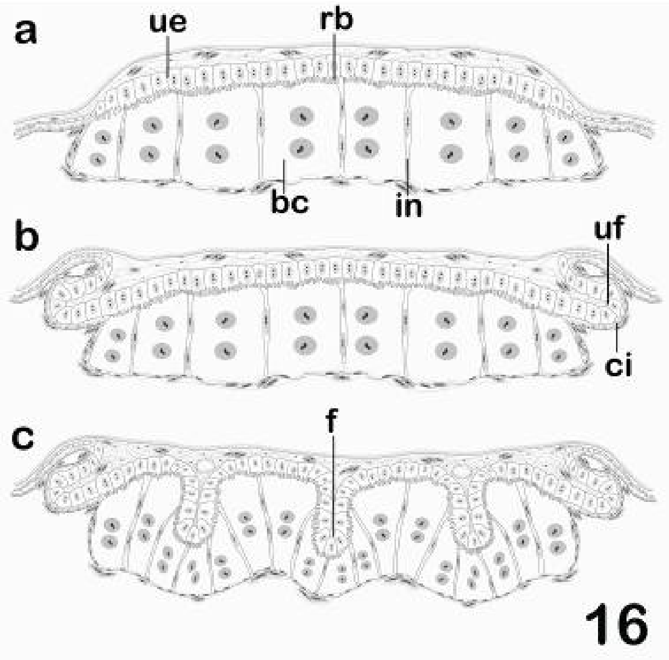




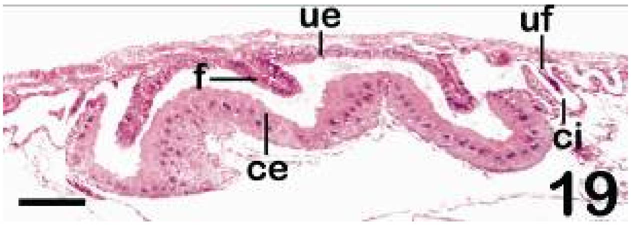
FIGURES 14,15 y 16



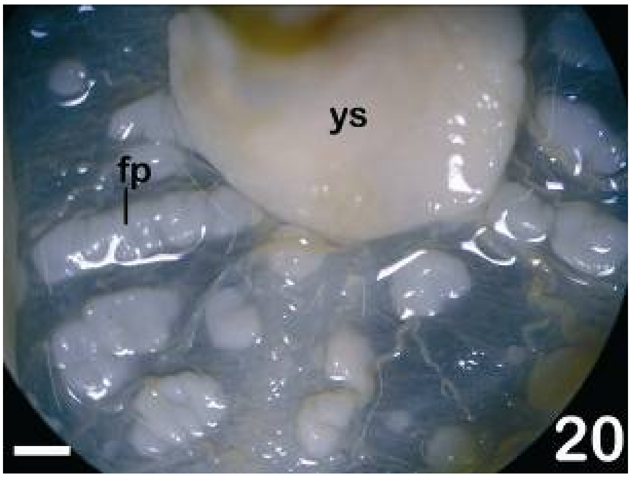


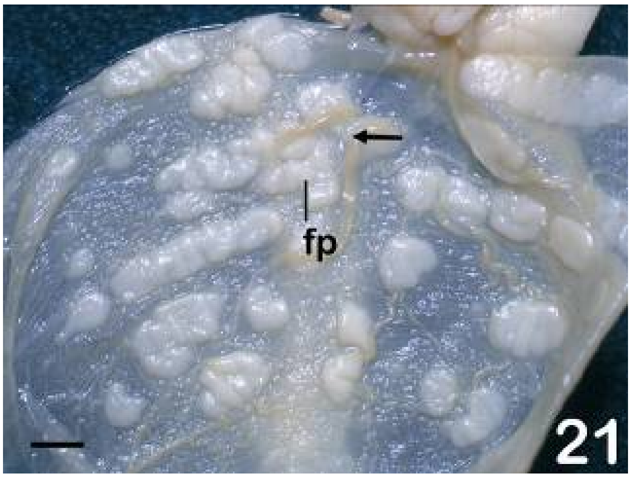


FIGURES 17, 18 y 19

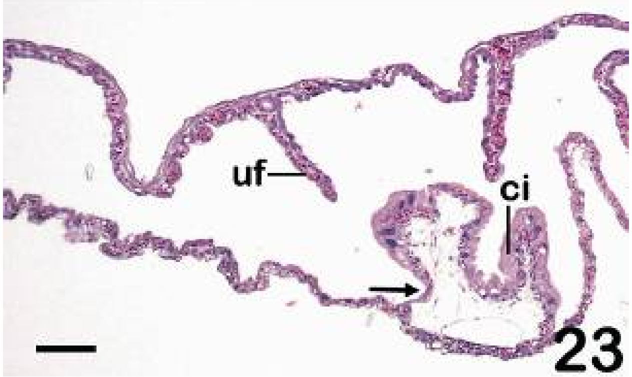


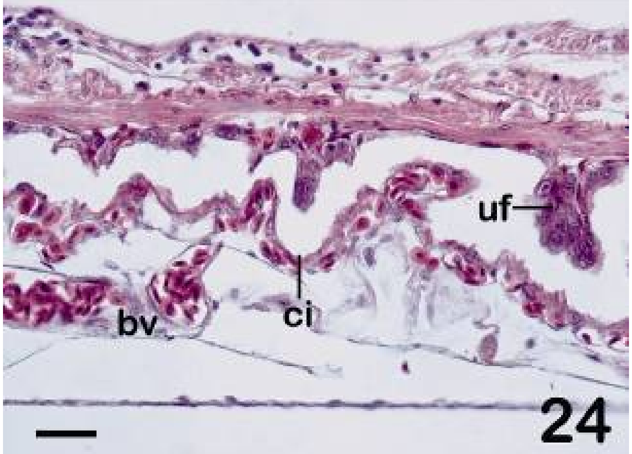
FIGURES 20 y 21



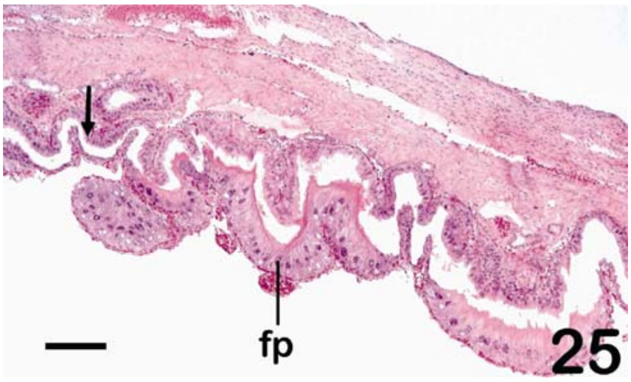


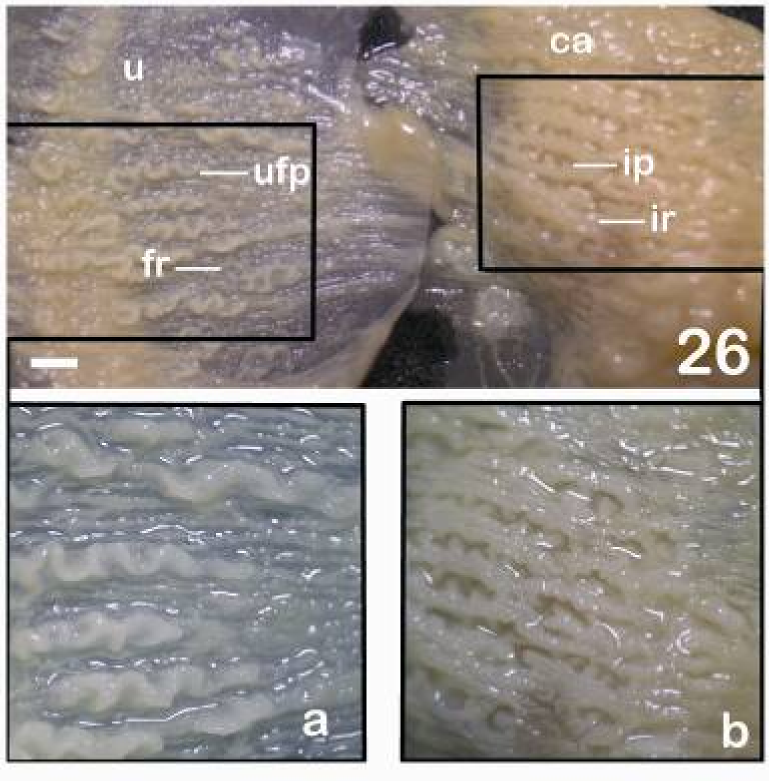
FIGURES 22, 23 y 24





FIGURES 25 y 26





FIGURES 27