UNIVERSIDADE FEDERAL DO ESTADO DO RIO DE JANEIRO

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS - BIODIVERSIDADE NEOTROPICAL (PPGBIO)

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OSTEOLOGIA CRANIANA COMPARADA DE LAGARTOS SCINCÍDEOS BRASILEIROS (GÊNEROS *MABUYA* FITZINGER, 1826 E *TRACHYLEPIS* FITZINGER, 1843)

RIO DE JANEIRO

2019

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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Biodiversidade Neotropical) da Universidade Federal do Estado do Rio de Janeiro como requisito parcial para obtenção do título de Mestre em Ciências Biológicas.

Orientador: Dr. Davor Vrcibradic
Coorientador: Dr. Marcelo de Araújo Soares

Rio De Janeiro

2019

Ficha Catalográfica

Ferreira Junior, Julio Cesar
F383 Osteologia Craniana Comparada de Lagartos Scincídeos Brasileiros (Gêneros Mabuya Fitzinger, 1826 e Trachylepis Fitzinger, 1843) / Julio Cesar Ferreira Junior. -- Rio de Janeiro, 2019.
116 f.

Orientador: Davor Vrcibradic.
Coorientador: Marcelo Araújo Soares.
Dissertação (Mestrado) - Universidade Federal do Estado do Rio de Janeiro, Programa de Pós-Graduação em Ciências Biológicas, 2019.

1. Morfologia craniana. 2. Crânio. 3. Répteis. 4. Mabuyinae. I. Vrcibradic, Davor, orient. II. Araújo Soares, Marcelo, coorient. III. Título.

Julio Cesar Ferreira Junior

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Aprovada em 26 de fevereiro de 2019.

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AGRADECIMENTOS

Agradeço primeiramente a minha família, principalmente ao meu pai Julio César Ferreira, a minha mãe Andréa Rino Ferreira e ao meu irmão Luiz Eduardo Ferreira pelo apoio essencial oferecido por eles, assim como ao meu tio Oswaldo Alex por todo incentivo e pelos importantes conselhos.

Ao meu orientador, Davor Vrcibradic, por toda dedicação, tempo e energia no apoio à minha formação nesses últimos anos, pela confiança e principalmente pelo exemplo como pesquisador. E também por fornecer o material utilizado nesse trabalho, espero que essa parceria continue ainda por muito tempo e gere bons trabalhos.

Ao meu coorientador, Marcelo de Araujo Soares, por ter me apresentado à anatomia animal comparada, por todos esses anos de excelente convívio no Laboratório de Herpetologia da Universidade Castelo Branco, pelos conselhos profissionais e pela orientação e incentivo ao longo de grande parte da minha vida acadêmica.

À doutora Angele dos Reis Martins, ao doutor Leonardo dos Santos Ávilla e à doutora Dimila Mothe Cordeiro dos Santos por aceitarem o convite para compor a banca de defesa e pelo incentivo que me foi dado na defesa de qualificação.

Ao Prof. Dr. Marcelo Britto, chefe de Departamento de Vertebrados do Museu Nacional – UFRJ, pela autorização da utilização do Laboratório de Radiografias do Departamento de Vertebrados do Museu Nacional do Rio de Janeiro.

Gostaria de agradecer aos professores da UNIRIO pelas excelentes aulas ministradas. Ao PPGBIO e à CAPES pela estrutura e pelo financiamento que tornaram possível o desenvolvimento deste trabalho. Agradeço também à minha turma de 2017.1 pelos ótimos momentos que passamos juntos e pelos ensinamentos compartilhados.

Aos meus grandes amigos: Alfredo Maio, Fabiano Paschoal, Leonardo Marinho, Luana Benicio e Taiane Costa, pelos ótimos momentos que passei com cada um.

À Universidade Federal do Rio de Janeiro (UFRJ) que me proporcionou a chance de cursar disciplinas externas e à Universidade Castelo Branco (UCB) e seus coordenadores de biologia: Diego e Fábio, que me permitiram utilizar os laboratório do CEPBIO para desenvolver partes essênciais desse trabalho.

RESUMO

O estudo da evolução do crânio permite compreender como os elementos esqueléticos somáticos e viscerais, que em sua origem nos vertebrados desempenharam papéis muito diferentes, passaram a interagir em diferentes momentos da história evolutiva dos vertebrados, particularmente em Squamata. No entanto, o conhecimento sobre o crânio em membros da subfamília Mabuyinae dos scincideos é muito escasso, especialmente no que diz respeito às variações intragenericamente e interespecificamente. O objetivo deste estudo foi descrever em detalhes o crânio de alguns lagartos neotropicais dos gêneros *Mabuya* e *Trachylepis* (Scincidae; Mabuyinae), com o objetivo de contribuir para estudos de variações morfológicas em crânios scincideos. Utilizamos espécimes da coleção de répteis do Setor de Herpetologia do Museu Nacional - UFRJ. As técnicas utilizadas para o estudo osteológico foram: preparação de material seco (hidratação, desossa e clarificação), diafanização e uso de radiografias digitais. Além disso, alguns crânios secos foram parcialmente desarticulados para o exame de elementos individuais. O crânio de *Mabuya* e *Trachylepis* é relativamente alongado e dorso-ventralmente deprimido. Geralmente, duas fenestras perfuram o crânio na região temporal dos scincideos: supratemporal e infratemporal, localizadas, respectivamente, nas regiões dorsal e lateral do crânio. No entanto, a fenestra supratemporal em *Mabuya* é estreita e menor que a usual em Mabuyinae, e pode até estar ausente, como em *M. agilis*. Este estudo encontrou evidências de que *Mabuya* spp. possuem elementos ósseos que os diferenciam das espécies do gênero *Trachylepis*, bem como de espécies de outros gêneros de Mabuyinae, o que poderia auxiliar no conhecimento das relações taxonômicas e evolutivas entre esses gêneros ou até mesmo caracterizar as sinapomorfias.

Palavras-chave: Morfologia craniana, crânio, répteis, Mabuyinae.

ABSTRACT

The study of the evolution of the skull allows understanding how somatic and visceral skeletal elements, which in vertebrate's origin played very different roles, began to interact at different times of the evolutionary history of vertebrates, particularly Squamatan reptiles. However, knowledge about the skull in members of the scincid subfamily Mabuyinae is very scarce, especially with regard to variations within and between genera and species. The goal of this study was to describe in detail the cranium of some Neotropical lizards of the genera *Mabuya* and *Trachylepis* (Scincidae; Mabuyinae), aiming to contribute to studies of morphological variations in scincid skulls. We used specimens from the collection of reptiles of the Setor de Herpetologia of the Museu Nacional - UFRJ. The techniques used for the osteological study were: the preparation of dry material (hydration, de-boning and clarification), diaphanization and the use of digital radiographs. Also, some dry skulls were partially disarticulated for the examination of individual elements. The skull of *Mabuya* and *Trachylepis* is relatively elongated and dorso-ventrally depressed. Usually two fenestrae pierce the skull in the temporal region of skinks: the supratemporal and the infratemporal fenestrae, located respectively in the dorsal and lateral regions of the skull. However, the supratemporal fenestra in *Mabuya* is narrow and smaller than usual in Mabuyinae, and may even be absent, as in *M. agilis*. This study found evidence that *Mabuya* spp. have bony elements that differentiate them from species of the genus *Trachylepis*, as well as from species in other Mabuyinae genera, which could aid in the knowledge of taxonomic and evolutionary relationships among these genera or even characterize synapomorphies.

Key-words: Cranial morphology, skull, reptile, Mabuyinae.

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CHAPTER 1: CRANIAL OSTEOLOGY OF *TRACHYLEPIS ATLANTICA* (SCHIMIDT, 1945) (LACERTILIA, SCINCIDAE)

INTRODUCTION

The reptilian skull is a highly complex assembly of bone and cartilage, which has a long history of developments and modifications before reaching the reptilian stage (Romer 1956). The results obtained in studies of comparative osteology and intraspecific variability in extant reptiles are of great importance for the taxonomic and evolutionary understanding of the recent species (e.g. Barahona and Barbadillo 1998; Barahona et al. 1998).

The once pan-tropical genus *Mabuya* Fitzinger, 1826, was restricted to the Neotropical region by Mausfeld et al. (2002), with the Old World species currently allocated in seven genera (Karin et al. 2016; Metallinou et al. 2016). These, together with the Asian genera *Dasia* and *Vietnascincus* and the African genus *Eumecia*, currently make up the subfamily Mabuyinae (*sensu* Karin et al. 2016). The largest of the Old World mabuyine genera is *Trachylepis*, with about 100 species distributed mainly in Africa, Madagascar and the Seychelles and Comoros islands in the Indian Ocean (Uetz et al. 2019). The Noronha skink, *T. atlantica* (formerly known as *Mabuya punctata* or *M. maculata*), endemic to the Fernando de Noronha archipelago (located at ca. 350 km from the northeast coast of Brazil; Carleton & Olson 1999), is the only representative of the genus *Trachylepis* in America (Fig. 1.1) and according to molecular studies, is more phylogenetically related to the species of Africa and Madagascar than to the Neotropical ones. (Mausfeld et al. 2002). Thus, the Mabuyine is represented in the Neotropical region by two different lineages. It has been proposed that both *Mabuya* s. str. and *T. atlantica* originated in tropical America by two independent processes of transoceanic colonization from African ancestors in the Miocene (Mausfeld et al. 2002; Carranza & Arnold 2003; Whiting et al. 2006; Miralles and Carranza 2010; Hedges & Conn 2012).

Recently, Hedges & Conn (2012) proposed the division of *Mabuya* (sensu strictu) into 16 different genera and of the family Scincidae into multiple families, but these proposals have been considered controversial and some authors have not adopted them (e.g. Jerez 2012; Pyron et al. 2013; Caicedo-Portilla 2014; Lambert et al. 2015; Pinto-Sánchez et al. 2015; Karin et al. 2016). Thus, we decided to adopt a conservative stance and will consider all Neotropical species as *Mabuya* for the purpose of this study, as well as follow Uetz et al. (2019) in considering the Scincidae as a single family with nine subfamilies (including the Mabuyinae).

Fig. 1.1 - *Trachylepis atlantica* (photo: Davor Vrcibradic)

In the last two decades, there has been a great interest in morphology and anatomy of lizard's skull in an ecological and evolutionary perspective. However, the relationship between variations in many of the major anatomical features remains unknown (Costantini et al. 2010). The results obtained in studies of comparative osteology and intraspecific variability in current faunas are of great importance for the taxonomic determination of the recent species (Barahona and Barbadillo 1998; Barahona et al. 1998). According to Yildrim et al (2015) osteology of lizards is not well known and scincids are one of the least-studied groups of lizards. Information on its ecology, including diet, was published for the population of the continent living in areas of sandbank by Rocha and Vrcibradic (1996; 1999); Vrcibradic and Rocha (1995; 1996; 2002).

Information on the cranial osteology of Mabuyinae is still very scarce, especially with regard to variations within and between genera and species. Only two species of *Mabuya* s. str. (Jerez 2012; Ferreira Jr. and Soares 2015) and a few Old World Mabuyinae currently have available comprehensive data on the structure of the skull of adult individuals (Evans 2008; Jerez 2012; Rastegar-Pouyani et al. 2013; Paluh and Bauer 2017).

This study aimed at the description of the dermocranium and optical-occipital region of the neurocranium of the lizard *Trachylepis atlantica*, to contribute to the understanding of morphological variations in cranial structure in lizards, particularly mabuyine skinks. Previously, a study on the variation of *T. atlantica* (as *Mabuya punctata*) was performed by Travassos (1946), including basic osteological information on its skull and skeleton, but no detailed descriptions of individual cranial bones.

MATERIALS AND METHODS

For this study, specimens housed at the collection of reptiles of the Setor de Herpetologia of the Museu Nacional – Universidade Federal do Rio de Janeiro (MNRJ) were used. Four dry skulls (MNRJ 19062; MNRJ 26877; MNRJ 26878; MNRJ 27113) and two cleared and stained skulls (MNRJ 19044; MNRJ 19051) were prepared according to adaptations of the method proposed by Taylor & Van Dyke (1985), all from adult specimens, according to methods provides on Rocha et al. (2009). Some techniques were used such as a chemical method that consists in hydrating and stripping the dried material and x-ray images (Fig. 1.2), performed using the digital equipment FAXITRON® MX – 20 that provides images in high resolution and is very helpful in this kind of study (Johnson 1955). Also, one skull (19044) was partially disarticulated for the examination of individual bones. One of the dry skulls, MNRJ 26877, was kept in mass base model and graphically represented by the author with the aid of a stereomicroscope (appendix 1). Identifications of anatomical structures were based on Paluh and Bauer (2017) as a general reference.

RESULTS AND DISCUSSION

Overall skull morphology

According to the limits imposed by the scope of this work, the orbital-temporal region of the neurocranium was not described, being basically composed of cartilage. Difficulties in reporting the orbital-temporal region of the neurocranium were also reported for lizards in other families (Jollie 1960).

The skull of *Trachylepis atlantica* is roughly 1.5 times longer than wide, similar to other congeners (Paluh and Bauer 2017). The elements in the maxilla segment may be grouped into regions forming the palate, nasal capsule, orbits, and the temporal region. Six bones compose the region of the palate, of which only the premaxilla and vomer are unpaired. The other bones such as the maxilla, the palatine, the pterygoid and ectopterygoid are paired, with the maxilla and ectopterygoid being located laterally, and the others occupy a medial position. Two fenestrae pierce the skull in the temporal region: the supratemporal and infratemporal fenestrae. However, the supratemporal fenestra in *T. atlantica* is narrow and smaller than the usual in mabuyinae. It is located in the dorsoposterior region of the skull, whereas the infratemporal fenestra is located in the posterolateral region, and the supratemporal arch separates the two openings. The occipital segment may be divided into: orbito-temporal and otic-occipital. The orbito-temporal is the front of the neurocranium. The structures of this region of the skull are of cartilaginous constitution, and are difficult to observe because they tend to break down during dissection and dificcult to observe in cleared and stained skulls. The otic-occipital region is part of the ossified neurocranium.

In *T. atlantica*, the otooccipital present themselves fused and are very difficult to observe individually. They form the lateral margins of the foramen magnum. The otooccipital participates in the articulation of the skull to the vertebral column, and posteriorly it houses part of the membranous labyrinth and promotes the articulation of the occipital segment to the rest of the skull (Evers and Soares 2007). This bone presents the paroccipital processes, which are relatively large, are laterally directed, have a slightly wider distal region, and promote the articulation of the posterior part of the neurocranium with the maxillary segment. Among its osteological notes Travassos (1946) reported that the occipital set is quite developed and well ossified with a large foramen magnum in this species.

The mandible is articulated with the skull through contact with the quadrate bone. It is formed by a pair of anteromedially directed branches united in a symphysis that depart in the lateral direction.

Description of isolated cranial bones

PREMAXILLA (Pmx)

The premaxilla forms the arched anterior margin of the skull. This bone has three processes, one nasal and two laterals. The premaxilla in *T. atlantica* has a posteriorly directed dorsomedial process, the nasal process, which overlaps the anterior mesial portion of the corresponding nasal at an acute angle, shaping a sharp snout in dorsal view. This process inserts between the nasals and partially separates them along the midline.

The horizontal plate is wide and high, forming the most anterior tip of the snout. Ventrally, the plate bears 7 to 10 mostly unicuspid pleurodont teeth aligned along the entire bone edge. Travassos (1946) mentions only four premaxillary teeth for the specimen of *T. atlantica* he examined, but he was most likely referring to the tooth count of just one half of the premaxilla. Posterior to the tooth row, the horizontal plate contacts the maxilla. On the ventral aspect, the premaxilla comes in contact with the vomer by a prominent vertical prevomerine process.

VOMER (Vo)

The vomer can only be seen in ventral view. The central roof of the mouth and the anterior primary palate is formed by the vomer. It contacts the premaxilla and maxilla anteriorly, septomaxilla dorsally, and palatine posteriorly. Its lateral set forms the whole medial area of the nostrils. On the ventral aspect of the skull, it forms the median boundary of the opening of the vomeronasal organ. The anterior end is inserted onto the medial portion of the premaxillary horizontal plate. The lateral margin of the vomer contacts the premaxilla anterolaterally and the maxilla laterally. The two-pointed posterior ends of the vomer run ventrally along the medial palatine border.

MAXILLA (Mx)

This paired bone occupies most of the anterolateral aspects of the skull. Approximately in a triangular shape in lateral view, the maxilla forms the largest part of the snout surface. Each maxilla consists of two wide plates at a right angle: a lateral facial lamina that shapes the lateral extent of the snout, and a ventral palatal lamina that bears the teeth and forms part of the palate anterolaterally. On the lateral surface of each maxilla 5 – 7 labial foramina are present in *T. atlantica*. Dorsally, the facial lamina contacts the nasals anteriorly and the prefrontal posteriorly. The height of the facial lamina is progressively reduced posteriorly, toward the orbital process; at this portion, the facial lamina has extensive contact with the prefrontal. In the most posterior part, the lamina narrows toward the orbital process; the narrowing begins approximately at the point where the maxilla contacts medially the palatine.

PALATINE (Pal)

This is a paired bone that posterior the vomer, prefrontal anterodorsally, pterygoid posteriorly and maxilla laterally. The palatine is flat and represents the middle section of the palate. With the pterygoid form the floor of the orbits and also part of the capsule of the nasal floor. Anteriorly, the palatines contact each other at the sagittal plane, but in the posterior portion they are separated by the piriform recess. The lateral edge of the palatine is concave, laterally, the palatine contacts the maxilla, and recurves ventrally toward the midline. The posterior process becomes flat and pointed, overlapping dorsally the anteromedial process of the pterygoid. Anteriorly, it has a slender vomerine process that contacts the vomer.

PTERYGOID (Ptg)

This is a paired bone whose elements form the posterior half of the palate and diverge laterally in its posterior portion in relation to the median axis of the skull. Each pterygoid has two separated portions that are elongated and irregular. The posterior ramus of this ridge serves as the articulation surface to the pterygoid process of the basisphenoid. Dorsally, slightly behind this point, the pterygoid has a pit where the epipterygoid is inserted. Just posterior to this region the basipterygoid process of the sphenoid articulates with the pterygoid. In *T. atlantica* each pterygoid is Y-shaped. Pterygoid teeth are usually present within a depression on the ventral face of this bone in mabuyines (Greer 1967; Rastegar-Pouyani et al. 2013; Paluh and Bauer 2017), no pterygoid teeth were found in the analyzed specimens of *T. atlantica* in this work, but according to Travassos (1946) there are some small conical teeth in this species, though they fall very easily, leaving no trace.

ECTOPTERYGOID (Ec)

This paired bone serves as contact point between the elements of the palate and the whole cranial roof. Each ectopterygoid is a rectangular bone that contacts the maxilla anteroventrally, the pterygoid posteriorly, and the jugal anterolaterally. The ectopterygoid separates the pterygoid and the maxilla. In *T. atlantica*, the ectopterygoids are tightly sutured to the transverse process of the pterygoid. The lateral end is bent in the anterior portion to match the maxilla orientation; this lateral tip contacts the maxilla anteriorly.

SEPTOMAXILLA (Smx)

The septomaxilla is a paired bone that composes the lateral borders of the nasal capsule and its cartilaginous part covers the vomeronasal apparatus dorsally. This bone is located in the dorsal portion of the vomer, forming part of the nasal septum. Anteriorly each septomaxilla shows a blunt process which is seen in the dorsal view of the skull through the anterior nasal fossa. The main body of the bone forms an elevation over Jacobson's organ with a vertical dorsomedial rim flanking the nasal septum. The septomaxilla is included in the nasal cavity and, in articulated skulls, it can only be seen partially through the nostrils. The ventral border contacts anteriorly the horizontal plate of the premaxilla, laterally with the palatal plate of the maxilla, and posteriorly with the vomer. In *T. atlantica* the septomaxilla is located ventrally the nasals, and is partially covered by them.

NASAL (N)

The anterior edges of this paired bone are slightly separated by the nasal process of the premaxilla. This process sits on a triangular facet at the anterior tips of the nasal and ventrally the middle portion of the bone shows a shallow depression. The nasal contacts the premaxilla medially, posteriorly overlap the frontal and contacts the maxilla and the prefrontal laterally, forming most of the roof of the nasal capsules. These bones overlying a small part of the septomaxilla in *T. atlantica*.

PREFRONTAL (Pr)

The prefrontal is a paired bone that lie on the anterolateral aspects of the skull and form the anterodorsal limit of the orbits. It contacts the maxilla anterolaterally and ventrally, frontal dorsally, palatine medially, nasal anterodorsally, and lacrimal laterally. In some species of this genus the prefrontal can make contact with the jugal through a narrow process (Paluh and Bauer 2017), but in *T. atlantica* the prefrontal has no contact with the jugal. The anterior process forms part of the dorsolateral aspect of the snout, partially separating the nasal and the maxilla. The posterior process is slim and extends along the frontal over the dorsal border of the orbit.

LACRIMAL (L)

This paired bone is located subsequently to the prefrontal and completes the anterior limit of the orbit along with it. It contacts the posterior process of the maxilla ventrally and laterally. Each bone has a small ridge on the external and posterior aspect of the nasolacrimal orifice. The posterior region of the lacrimal could be widely separated or nearly in contact with the anterior process of the jugal in some *Trachylepis* (Paluh and Bauer 2017), but in *T. atlantica* there is a medial contact with it.

FRONTAL (F)

An unpaired bone located on the longitudinal axis of the skull. This is a flattened bone that form most of the dorsal orbital margin and a large part of the cranial roof. It has contact with the nasals anteriorly, the prefrontals anterolaterally, the postfrontals posterolaterally and the parietal posteriorly. In *T. atlantica* the frontal has no contact with the maxilla. This bone is separated from the anterior margin of the orbit by the prefontals and from the posterior margin by the postfrontal. Due to the fusion of the head shield osteoderms some dorsal surface sculpturing may be seen in *T. atlantica*.

JUGAL (J)

Paired bone that forms the lateroposterior margin of the orbit. The jugal is oriented medially and posterodorsally until it approaches the postorbital. The anterior portion of the jugal is dorsally concave, forming the ventral border of the orbit. In *T. atlantica* the jugal has no suture with the postfrontal, due to an interruption of the postorbital bone between them.

POSTFRONTAL (Pf)

This is a paired bone that forms part of the posterodorsal rims of the orbits. The postfrontal in *T. atlantica* has a triangular shape in dorsal view and is in contact with the postorbital laterally, with the frontal anteromedially, and with the parietal posteromedially.

The postfrontal in *Trachylepis* has previously been reported as a Y-shaped bone that may contact the jugal in *T. sulcata* and *T. gonwouoi* (Paluh and Bauer 2017), but in *T. atlantica* the postfrontal has no contact with the jugal.

PARIETAL (P)

This unpaired bone is located posteriorly to the frontal bone, in the medial region of the posterior cranial third. Subsequently the parietal suture to the supratemporal and squamosal in the posterior region. Laterally, the parietal contacts the postfrontal and squamosal, forming the medial border of the supratemporal fenestrae. In *T. atlantica* the parietal has no contact with the postorbital bone. The posterior region of this bone holds two elongate posterior processes and two short posteromedial processes, forming a slight descent in the posterior region. A parietal foramen is present in this genus, and as in all *Trachylepis* previously described, the pineal foramen is in the exact direction of the medial suture of the frontal, nasals and premaxilla, respectively.

POSTORBITAL (Po)

Paired and elongated bone that is best observed in dorsal and lateral views. The postorbitals are positioned posterior to the orbits. It contacts the postfrontal medially, the squamosal posterolaterally and the jugal anterolaterally, but in *T. atlantica* this bone participates in the formation of the orbit and separates the jugal and postfrontal bones from contacting each other.

SQUAMOSAL (Sq)

The squamosal completes with its edge the lateral margin of the supratemporal region and forms the posterolateral rims of the supratemporal fenestra. This paired bone has an anteriorly contact with the postorbital, posteromedially with the supratemporal and posteroventrally with the quadrate. Posteriorly it diverges away from the supratemporal process of the parietal and has a short laterally directed process which sits on the quadrate and extends into the large gap.

SUPRATEMPORAL (St)

Paired bone located in the lateroposterior edge of the skull, between the quadrate and the parietal, and contacts the squamosal anterolaterally. Usually this is a very small bone and hard to observe. In *T. atlantica* the supratemporal appears as a small gently curved structure. The supratemporal is slightly curved ventrally, and it gradually widens from the sharpened anterior end to the posterior end.

QUADRATE (Q)

This paired bone is located in the posterolateral angle of the skull. This is the bone that articulates the skull and the mandible. In *T. atlantica*, the quadrate has a semicircular shape. Its anterior region is convex, while the posterior region is pronouncedly concave, and can be divided into dorsal, ventral, anterior and posterior surfaces.

The dorsal surface is enlarged and flat, and contacts the supratemporal posteriorly and the squamosal dorsally. The contacts between these bones and the quadrate are made through intercalated cartilages rather than rigid sutures. The ventral surface is quite small, and presents a condylar area, which articulates with the mandible. The anterior surface presents a thickening in the dorsal portion, decreasing the thickness of the wall towards the articular condyle. The posterior surface of the quadrate is concave. The dorsal area presents a posteriorly directed cephalic condyle, presenting an articulated surface surrounded by irregular contours, receiving dorsally the squamosal and supratemporal, and dorsomedially the inferior aspect of the paroccipital process of the otooccipital.

EPIPTERYGOID (Eptg)

This paired bone unites the parietal and the pterygoid and can be seen in lateral view. They have the shape of a vertical bar at each side of the parietal, ossifying in the *processus ascendens* of the chondrocranium, and extending obliquely from the anterior tip of the prootic bone to the pterygoid, dorsally to the basipterygoid articulation.

SUPRAOCCIPITAL (So)

It's an unpaired bone that presents itself dorsally in relation to other components of the optical-occipital region. The supraocciopital follows the parietal and forms the back of the head ceiling and the dorsal area of the foramen magnum. This bone is sutured with the posterior portion of the parietal. It contacts the prootic antero-ventrally, the otooccipital laterally, the squamosal anterolaterally and composes the posterior limit of the supratemporal fenestra.

BASISPHENOID (Bas)

This unpaired bone is part of the neurocranium floor situated ventrally and medially in the posterior area of the palatal skull region, suturing posteriorly to the basioccipital and dorsally to the prootic. Presents the anterolaterally processes of the basipterygoid, which are extended distally, anteroventrally directed and fit to the pterygoid, performing the articulation of the neurocranium with the rest of the skull, being a point of mobility between the maxillary and occipital segments.

BASIOCCIPITAL (Ba)

An unpaired bone, such as the basisphenoid. Forms the posterior area of the cranial cavity and the middle region the occipital condyle. It is located ventromedially, accompanying the basisphenoid with no visible suture and forming the floor of the neurocranium. It makes contact anteriorly to the basisphenoid and anterolaterally to the prootic. Posterodorsally presents contact with otooccipital.

PROOTIC (Pro)

Bones that form the lateral cover of the neurocranium and which are presented together with the supraocciopital associated with the inner ear. The prootic is a very irregular bone and hard to observe. The laterodorsal region is slightly concave, and makes contact with the parietal bone through their dorsal surface. It sutures to the supraoccipital in the posterolateral region and ventrolaterally to the basisphenoid and the basioccipital. Subsequently makes contact with the otooccipital.

The prootic features along its middle region a ridge in the anteroposterior direction, called prootic crest, on which the *protractor pterygoid* muscle is inserted (Guerra and Montero, 2009). Along with otooccipital and supraoccipital, the prootic participates in the formation of the tympanic bulla. Ventrally to this, lies an acoustic recess in the bone inner face.

Contributing to the delimitation of the rostral margin of the paroccipital process, the prootic forms the anterolateral wall of the neurocranium in reptiles in general (Stephenson and Stephenson 1956; Torres-Carvajal 2003; Bever et al. 2005; Bell et al. 2009; Khosravani et al. 2011).

Description of isolated mandibular bones

ARTICULAR (Ar)

The articular is the only bone of endochondral origin of the mandible and is formed by ossification of Meckel's cartilage, occupying the posterior end of the mandible (Evers and Soares, 2007). In some groups of lizards presents itself fused to the angular (Paluh and Bauer 2017).

The articular is a laterally flattened bone whose posterior end is wider than the anterior one, it occupies the entire posterior part of the mandible, and articulates with the quadrate bone of the skull. Posterioly, the articular presents the *fovea articularis*, also known as the condylar process. This process is inclined in the posteroventral direction and on its surface are depressions that allow the perfect fit with the quadrate. This joint is made through a concave but irregular articulated surface, which joins the convex surface, also irregular, of the quadrate bone, making a diarthrosis-like joint. In *T. atlantica*, the retro articular process presents as a rounded structure in the posterior direction of the mandible.

ANGULAR (Ag)

Small bone, flat and elongated. It extends ventrally and is situated in the lateroventral region of the mandible, being visible in the lateral and medial views. The anterior end embraces the posteroventral tip of the dentary. The angular presents sutured anteriorly to dentary and splenial, dorsally to the supra-angular and posteriorly and ventrally to articular.

SUPRA-ANGULAR (Sa)

This bone is elongated and together with the articular and angular forms the dorsal and lateral surface of the posterior part of the mandible. Anteriorly, the supra-angular is sutured to the dentary, dorsally to the coronoid, and laterally and ventrally to the articular and angular.

The supra-angular is formed across the posterolateral border and the lateral surface of the mandibular foramen. Its border and side are rounded serving as insertion for the adductor muscle mandibularis externus. On the lateral surface of the supra-angular is also inserted the intermandibularis muscle.

Anteriorly, next to the suture with the coronoid, the supra-angular has a foramen, called the anterior supra-angular foramen. This foramen can be seen in lateral view, in the laterodorsal surface of the mandible near the suture with the coronoid and dentary. Posteriorly, next to the articular, is another foramen, a little smaller, the posterior supra-angular foramen. These foramina serve as passage for the cutaneous branches of the inferior alveolar nerve (Evers and Soares, 2007).

CORONOID (Cor)

This bone is located in the median dorsal portion of the mandible, between the supra-angular and the dentary. Features a triangular recurved aspect, forming a concave surface in the inner face of the mandible.

The coronoid is the highest apical projection of the mandible in relation to other bones. It has three basal processes. These processes give the coronoid a tripod arrangement.

The anterior medial coronoid process is sutured to the dentary anteriorly and to the splenial and supra-angular ventromedially. The anterolateral process promotes the suture of the coronoid to the supra-angular ventrolaterally and anteriorlly penetrates the dentary, presenting completely sutured to it.

SPLENIAL (Spl)

This elongated bone is located in the ventromedial region of the mandible. It's only possible to observe the splenial in the medial view of the mandibles, as well as their dorsal and ventral suture to the dentary. It is sutured to the coronoid dorsoposteriorlly and to the angular posteroventrally.

The mylohyoid foramen, which performs the transmission of anterior mylohyoid nerve, is located in the posterior region of the bone. Another foramen which is positioned in this bone is the anterior alveolar foramen, which gives passage to the lingual branch of the inferior alveolar nerve. In *T. atlantica*, this foramen is in anterior position near the dorsal suture of the splenial with dentary.

DENTARY (D)

This slightly curved bone forms the majority of the anterior half of the mandible. Throughout its dorsal edge of the inner face, the dentary has a gutter-shaped concavity, where the teeth are inserted and also form the replacement teeth. The dentary suture is in contact with the front surfaces of the others mandible bones, but not with the articular. Its anterior extremity is deepened and in a triangular shaped. In *T. atlantica*, the dorsomedial surface of the dentary bears 28-30 pleurodont, hollow teeth with internal replacements. Travassos (1946) mentions 27 dentary teeth for *T. atlantica* based on a single specimen, which is close to the lower counts reported herein.

Remarks

The postorbital bone in *T. atlantica* participates in the formation of the orbit and separates the jugal and the postfrontal bones from each other (Table 1). A similar condition is found in *T. maculilabris* (Jerez 2012). However, this characteristic was not found in other *Trachylepis* (Skinner 1973; Paluh and Bauer 2017), as well as in representatives of other genera of American (Jerez 2012; Ferreira Jr and Soares 2015), Asian (Greer 1986), African (Greer 1967) and Middle-Eastern mabuyine scincids (Rastegar-Pouyani et al. 2013). According to Paluh and Bauer (2017) in *Trachylepis laevis* this bone is either absent or completely fused with the postfrontal, however, in the other African *Trachylepis* species studied in their work (*T. sulcata* e *T. gonwouoi*) and in *Eutropis carinata* (Rao and Ramaswami 1952) and *Heremites vittatus* (Rastegar-Pouyani et al. 2013), the postorbital is present and participates in the formation of the orbit but does not separate the jugal from the postfrontal (Table 1).

The vomer forms the central roof of the mouth, better seen in ventral view. Both in dried and in stained and cleared skulls the suture that separates the two halves of the vomer was partially fused (Table 1). With x-ray images it is possible to see a partial division between these two halves. Some mabuyines, including a few members of the genus *Trachylepis*, apparently have paired vomers (Table 1).

The pterygoid of *T. atlantica* is a Y-shaped bone. Some teeth are usually present within a depression on the ventral face of this bone in mabuyines (Greer 1967; Rastegar-Pouyani et al. 2013; Paluh and Bauer 2017). According to Travassos (1946) there are some small conical teeth in this species, though they fall very easily, leaving no trace. But no pterygoid teeth were found in the analyzed specimens of *T. atlantica* examined in this study. Most mabuyines apparently have pterygoid teeth, but in species of *Trachylepis* these teeth may be present or absent.

Table 1: Some characteristics of the skulls of mabuyine skinks. P = present; A = absent.

Scincid species:	**Postorbital reaching the orbit**	**Paired vomer**	**Pterigoid teeth**	**Reference:**
Trachylepis atlantica	**P***	**A**	**P*****	**<u>This work</u>**
Trachylepis capensis	**P**	**P**	**P**	Skinner (1973)
Trachylepis gonwouoi	**P**	**P**	**P**	Paluh and Bauer (2017)
Trachylepis laevis	**A****	**A**	**A**	Paluh and Bauer (2017)
Trachylepis maculilabris	**P***	**P**	**P**	Jerez (2012)
Trachylepis sulcata	**P**	**A**	**A**	Paluh and Bauer (2017)
Mabuya sp.	**A**	**A**	**A**	Jerez (2012)
Eumecia anchietae	**A****	**-**	**P**	Greer (1967)
Eutropis carinata	**P**	**P**	**P**	Rao e Ramaswami (1952)
Eutropis multifasciata	**A**	**P**	**P**	Greer (1986)
Heremites auratus transcaucasicus	**A**	**A**	**P**	Rastegar-Pouyani et al. (2013)
Heremites vittatus	**P**	**A**	**P**	Rastegar-Pouyani et al. (2013)
Chioninia coctei	**A****	**P**	**A**	Greer (1976)

A – absent; P – present.

* Participates in the formation of the orbit and separates the jugal and the postfrontal bones from reaching each other.

** Postorbital is absent or completely fused with the postfrontal.

*** Pterygoid with small conical teeth difficult to observe (Travassos 1946).

CHAPTER 2: CRANIAL OSTEOLOGY OF FIVE SPECIES OF *MABUYA* FITZINGER, 1826.

INTRODUCTION

The most complicated of all reptilian skeletal structures and the most important in resolutions of classification and problems with phylogeny is the skull. This structure is a highly complex assembly of bone and cartilage, which has a long history of developments and modifications, before reaching the reptilian stage (Romer 1956). Study of skull evolution allows understanding how somatic and visceral skeletal elements, which in its origin played very different roles, began to interact at different times of the evolutionary history of vertebrates (Hofling et al. 1995). The results obtained in studies of comparative osteology and intraspecific variability in current faunas are of great importance for the taxonomic determination of the recent species (Barahona and Barbadillo 1998; Barahona et al. 1998).

Squamate reptiles (lizards, snakes and amphisbaenians) are represented by over 10,000 species, distributed among a wide variety of habitats worldwide. Osteology of lizards is still insufficiently known and scincids are one of the least-studied groups of lizards in this regard (Yildirim et al 2015). The scincid genus *Mabuya* Fitzinger, 1826, once considered pan-tropical, was recently restricted to the Neotropical region (Mausfeld et al. 2002), with the Old World species currently allocated to seven genera (Karin et al. 2016). These genera, together with the Asian genera *Dasia* and *Vietnascincus* and the African limb-reduced genus *Eumecia*, currently make up the subfamily Mabuyinae (sensu Karin et al. 2016). Although relatively uniform in general appearance, *Mabuya* spp. (sensu lato) present variations in terms of body proportions and occupy a range of habitats and micro-habitats.

Recently, Hedges & Conn (2012) proposed the division of *Mabuya* (sensu strictu) into 16 different genera and of the family Scincidae into multiple families, but these proposals are considered controversial and have not been adopted by several authors (e.g. Jerez 2012; Pyron et al. 2013; Caicedo-Portilla 2014; Lambert et al. 2015; Pinto-Sánchez et al. 2015; Karin et al. 2016; Uetz et al. 2019). Herein, we adopt a conservative stance and consider all Neotropical species as *Mabuya* for the purpose of this study. We also follow

Uetz et al. (2019) in considering the Scincidae as a single family and the Mabuyinae as one of its subfamilies rather than a family on its own as proposed by Hedges & Conn (2012).

In South America the Mabuyinae is represented by several species of the genus *Mabuya* s. str. and by *Trachylepis atlantica* (formerly known as *Mabuya punctata* or *M. maculata*), endemic to the Fernando de Noronha archipelago, located at ca. 350 km off the northeast coast of Brazil (Carleton & Olson 1999) which, according to molecular studies, is phylogenetically related to the species of Africa and Madagascar (*Trachylepis* spp.) rather than to the Neotropical ones (Mausfeld et al. 2002). The South American Mabuyinae, therefore, represent two distinct lineages.

Information on cranial morphology of South American Mabuyinae is still very scarce, especially with regard to variations within and between genera and species. So far only two species of *Mabuya* s. str. have available detailed data on the structure of the skull in adults (Jerez 2012; Ferreira Jr. and Soares 2015). In this study the description of the dermocranium and optical-occipital region of the neurocranium of five species of the genus *Mabuya* [*Mabuya agilis* (Fig. 1.1), *Mabuya dorsivittata* (Fig. 1.2), *Mabuya frenata* (Fig. 1.3), *Mabuya macrorhyncha* (Fig. 1.4), and *Mabuya nigropunctata* (Fig. 1.5)] are described, aiming to contribute to studies of cranial osteology in lizards. Due to the limits imposed by the scope of this work, the orbital-temporal region of the neurocranium was not described, as it is basically composed of cartilage. Difficulties in reporting the orbital-temporal region of the neurocranium were also reported for species of the superfamily Gekkota, and of the genera *Heloderma* and *Anniella* (Jolie 1960).

Fig. 2.1 - Mabuya agilis (photo: Davor Vrcibradic)

Fig. 2.2 - *Mabuya dorsivittata* (photo: Leandro Drummond)

Fig. 2.3 - Mabuya frenata (photo: Davor Vrcibradic)

Fig. 2.4 - Mabuya macrorhyncha (photo: Gisele Winck)

Fig. 2.5 - Mabuya nigropunctata (photo: Davor Vrcibradic)

MATERIALS AND METHODS

For this study, specimens from the collection of reptiles of the Setor de Herpetologia of the Museu Nacional, Universidade Federal do Rio de Janeiro – UFRJ were used (Table 1). Skulls of five species were prepared (table 1): *Mabuya agilis* (MNRJ-14259; MNRJ-27107, MNRJ-27108, MNRJ-00000), *Mabuya dorsivittata* (MNRJ-27106; MNRJ-27105, MNRJ-27104), *Mabuya frenata* (MNRJ-6811; MNRJ-6922, MNRJ-6802), *Mabuya macrorhyncha* (MNRJ-17390; MNRJ-17389, MNRJ-24989), *Mabuya nigropunctata* (MNRJ-6024; MNRJ-5912, MNRJ-26876), all from adult specimens, according to methods provides on Vrcibradic and Rocha (2013). Techniques used in the preparation and examination of dry skulls included a chemical method that consists in hydrating and stripping the dried material. Some of the specimens were cleared and stained according to adaptations of the method proposed by Taylor & Van Dyke (1985). Also, x-ray images of some of the skulls were produced using the digital equipment FAXITRON® MX – 20 that provides images in high resolution and is helpful in this kind of study (Johnson 1955). Also, some of the skulls were partially disarticulated for the examination of individual bones. Once prepared, one dried skull of each species was kept in mass base model and graphically represented by the author with the aid of a stereomicroscope (appendix 2).

Especie	Collection sites	Specimen numbers	Preparation techniques
Mabuya agilis	Santa Teresa, ES	MNRJ – 14259	Dry
	São João da Barra - RJ	MNRJ - 27107	Cleared and stained
	São João da Barra - RJ	MNRJ - 27108	Dry
	Santa Teresa, ES	MNRJ - 0000	Dry
Mabuya dorsivittata	Pedra do Sino, Teresópolis – RJ	MNRJ - 27106	Dry
	Pedra do Sino, Teresópolis – RJ	MNRJ - 27105	Cleared and stained
	Joaquina, Florianópolis - SC	MNRJ - 27104	Dry
Mabuya frenata	Valinhos - SP	MNRJ - 6802	Dry
	Valinhos - SP	MNRJ - 6811	Disarticulated
	Valinhos - SP	MNRJ - 6922	Cleared and stained
Mabuya macrorhyncha	Porto do Açu, São João da Barra	MNRJ - 17389	Dry
	Porto do Açu, São João da Barra	MNRJ - 17390	Cleared and stained
	Restinga da Barra de Maricá - RJ	MNRJ - 24989	Dry
Mabuya nigropunctata	Serra da Mesa – GO	MNRJ - 5912	Cleared and stained
	Serra da Mesa – GO	MNRJ - 6024	Disarticulated
	Serra da Mesa – GO	MNRJ - 26876	Dry

Table 1: The *Mabuya* species studied, with the collection sites, voucher numbers of the specimens examined and preparation techiniques:

RESULTS AND DISCUSSION

Overall skull morphology

The skulls of *Mabuya* spp. are wedge-shaped and composed of Dermatocranial bones (premaxilla, vomer, maxilla, palatine, pterygoid, ectopterygoid, septomaxilla, nasal, prefrontal, lacrimal, frontal, jugal, postfrontal, parietal, postorbital, squamosal and supratemporal), Splanchonocranial bones (quadrate and epipterygoid), Neurocranium bones (supraoccipital, basisphenoid, basioccipital and prootic) and Mandibular bones (angular, articular, supra-angular, coronoid, splenial and dentary).

The maximum skull lengths, measured from the most anterior point of the premaxilla to the most posterior point of the retroarticular process, were 14.1 mm for *M. agilis*, 11.3 mm for *M. dorsivittata*, 14.9 mm for *M. frenata*, 14.3 mm for *M. macrorhyncha* and 20.1 mm for *M. nigropunctata*. The maximum skull widths, measured from one lateral extent of the quadrate to the other, were 8.1 mm for *M. agilis*, 6.4 mm for *M. dorsivittata*, 8.5 mm for *M. frenata*, 8.1 mm for *M. macrorhyncha* and 11 mm for *M. nigropunctata*.

Two fenestrae pierce the skull in the temporal region: the supratemporal, located in the dorsal region of the skull, and the infratemporal, located in the lateral region. The supratemporal arch separates the two openings. The supratemporal fenestrae are very reduced in *M. frenata* and *M. dorsivittata* and entirely absent in *M. agilis* due to its enlarged lateral process of the parietal, whereas in *M. macrorhyncha* and *M. nigropunctata* the supratemporal fenestrae are more prominent in relation to the other species.

The skull roof is mostly flat in *Mabuya* spp., with a slight slope near the occipital region. The suborbital fenestra is oval-shaped and is framed by the ectopterygoid and maxilla laterally, by the pterygoid posteriorly, and by the palatine anteromedially.

In *Mabuya* spp. the exoccipital and opisthotic bones present themselves fused and are very difficult to observe, thus they a will be treated in this work as a single structure, the otooccipital. They form the lateral margins of the foramen magnum. The otooccipital complex participates in the articulation of the skull to the vertebral column; posteriorly it houses part of the membranous labyrinth and promotes the articulation of the occipital segment to the rest of the skull. This bone presents the paraoccipital processes, which are relatively large, are laterally directed, have a slightly wider distal region, and perform the articulation of the posterior part of the neurocranium with the maxillary segment.

In *Mabuya* spp. each mandibular ramus consists of the angular, articular, supra-angular, splenial, coronoid and dentary bones. The mandible consists of several bones derived of membrane and an endochondral bone and promotes the articulation with the skull through a contact with the quadrate bone. It is formed by a pair of anteromedially branches united in a symphysis that deviate in the lateral direction and are articulated with the quadrate through the articular bone.

The dentary, the longest bone of the mandible, is slightly curved inward anteriorly. In lateral view, the coronoid bone is visible, although it is reduced in *M. dorsivittata*. The meckelian canal is enclosed by the dentary and splenial, forming a closed tube that continues from the dentary to the mandibular fossa; this is considered a synapomorphy for mabuyine skinks (Paluh and Bauer et al. 2017). The mandibular fossa is bordered by the articular and supra-angular bones. The degree of fusion between these two bones is variable among the five species, with complete fusion in *M. macrorhyncha* and nearly complete separation in the others. According to Paluh and Bauer et al. (2017) these differences in the degree of fusion may reflect interspecific variation or different degrees of ageing.

Table 2: Some counts and measurements of skulls of five species of the genus *Mabuya*.

Character:	***M. agilis***	***M. dorsivittata***	***M. frenata***	***M. macrorhyncha***	***M. nigropunctata***
Number of premaxillary teeth	8-9	12-14	10	9-10	8
Number of maxillary teeth	22-24	21-23	25-26	22-23	27-29
Number of dentary teeth	25-26	23-25	28-30	21-24	32-34
Number of labial foramina	6-8	5	6-7	7	7-8
Area of the pineal foramen*	0.11mm²	0.31mm²	0.13mm²	0.16mm²	0.23mm²
Length of the supratemporal foramen**	Absent	0.66mm	1.1mm	1.8mm	2.6mm
Skull length*	13.8mm	11.1mm	14.5mm	13.9mm	19.6mm
Skull width*	8.0mm	6.2mm	8.4mm	8.1mm	10.8mm

*Mean values of all specimens analyzed.

**Values taken only from specimens that were cleared and stained.

Description of isolated cranial bones

PREMAXILLA (Pmx)

The premaxilla forms the arched anterior margin of the skull and contacts the maxilla posteroventrally, nasals posterodorsally and vomer ventromedially. The nasal process is triangular in dorsal view, directed dorsoposteriorly at an acute angleand inserts between the nasals, partially separating them along the midline. The horizontal plate is wide and high, forming the anteriormost tip of the snout. The base of the nasal process is wide, whereas the distal end tapers to a rounded tip in *M. nigropunctata*, a shortened tip in *M. macrorhyncha* and a prominent tip in *M. agilis*, *M. dorsivittata* and *M. frenata*.

The ventral plate bears mostly unicuspid pleurodont teeth aligned along the entire edge of the bone. The number of teeth vary among the five species (Table 2). Posterior to the tooth row, the horizontal plate contacts the maxilla. There is no contact between the premaxilla and the frontal in *Mabuya* spp., because the nasals lie between them.

Mabuya spp. have a thin, elongated and semicircular palatal process, with the exception of *M. nigropunctata* that presents a more rounded palatal process. Seen in radiographs all five taxa appear to feature paired premaxilla. Both in dried and in stained and cleared skulls the suture that separates the two halves of this bone can only be seen clearly in *M. macrorhyncha* and a faint suture is partially present in *M. dorsivittata*.

VOMER (Vo)

The vomer is a partially fused laminar bone, better seen in ventral view. The central roof of the mouth and the anterior primary palate is formed by the vomer. It contacts the premaxilla and maxilla anteriorly, the septomaxilla dorsally, and the palatine posteriorly. On the ventral aspect of the skull, it forms the median boundary of the opening of Jacobson's organ. The anterior end is inserted into the medial notch of the premaxillary horizontal plate. The lateral margin of the vomer contacts the premaxilla anterolaterally. The pointed posterior end of the vomer runs ventrally along the medial palatine border. *Mabuya nigropunctata* has a proportionately more elongate vomer than the other species.

MAXILLA (Mx)

This paired bone consists of large elements that occupy most of the anterolateral aspects of the skull. With an approximately rectangular shape in lateral view, the maxilla forms most of the snout surface. Each maxilla consists of two wide plates at a right angle: a lateral facial lamina that shapes the lateral extent of the snout, and a ventral palatal lamina that bears the teeth and forms part of the palate anterolaterally. On the lateral surface of each maxilla bears five to eight labial foramina, with variations among species (Table 2).

Dorsally, the facial lamina contacts the nasals anteriorly and the prefrontal posteriorly. The height of the facial lamina is progressively reduced posteriorly, toward the orbital process; at this portion, the facial lamina has extensive contact with the prefrontal, and begins to narrow approximately at the point where the maxilla contacts medially the palatine. Also, the posterior edge forms the anterior border of the lacrimal foramen. In ventral view it is located laterally to the vomer and follows the premaxilla, forming the dental arcade. Each maxilla in *Mabuya* spp. bears between 21 and 29 teeth, depending on the species (Table 2).

The anterior tip of the maxilla is more ventrally inclined in *M. agilis*, *M. dorsivittata* and especially in *M. frenata*, whereas in *M. nigropunctata* it is perpendicular to its posterior portion, and in *M. macrorhyncha* the anterior border is dorsally inclined. The total height of the dorsal process is greater in *M. nigropunctata* compared to its congeners. The posterior process does not contact the ectopterygoid medially in *M. dorsivittata* and is overlapped greatly by the jugal in all five taxa. The maxillary teeth of *M. agilis* appear to be more robust and blunter compared to those of its congeners, while in *M. nigropunctata* they appear to be smaller and more fragile.

PALATINE (Pal)

This is a paired bone that follows the vomer, contacts the prefrontal anterodorsally, pterygoid posteriorly and maxilla laterally. The palatines are flat and represent the middle section of the palate. Together with the pterygoid they form the floor of the orbits and also part of the capsule of the nasal floor. Medially, the palatines contact each other in *M. dorsivittata* and *M. frenata* and are separated in the other species, and in the posterior portion they are separated by the piriform recess in all five taxa. While in the other species the palatines are completely separated, in *M. macrorhyncha* the gap between them is the widest of all. The lateral edge of the palatine is concave, contacts the maxilla, and curves ventrally toward the midline. According to Paluh and Bauer (2017) the vomerine facet of the palatine curves inwards and covers a portion of the choanal duct. The posterior process becomes flat and pointed, overlapping dorsally the anteromedial process of the pterygoid. Anteriorly, it has a slender vomerine process that contacts the vomer (Paluh and Bauer 2017).

PTERYGOID (Ptg)

This is a paired bone whose elements form the posterior half of the palate and lateralize in the posterior direction in its posterior portion in relation to the median axis of the skull. This bone contacts the palatine and ectopterygoid anteriorly, epipterygoid dorsally, sphenoid medially, and quadrate posterolaterally. Each pterygoid has two separated portions that are elongated and irregular. The posterior ramus of this ridge serves as the articulation surface to the pterygoid process of the basisphenoid. Dorsally, slightly behind this point, the pterygoid has a pit where the epipterygoid is inserted. Just posterior to this region the basipterygoid process of the basisphenoid articulates with the pterygoid.

No pterygoid teeth were found in the analyzed specimens of any species of *Mabuya* examined in this study. The quadrate process originates behind the fossa that accommodates the base of the epipterygoid bone. The process extends posteriorly in a curved line in *M. frenata* and *M macrorhyncha*, and in a straight line in *M. agilis, M. dorsivittata* and *M. nigropunctata,* to contact the posteromedial edge of the quadrate. The knob-like basipterygoid process of the pterygoid contacts the basipterygoid and increases the tendency of the pterygoids to spread apart (Paluh and Bauer 2017).

ECTOPTERYGOID (Ec)

This paired bone serves as contact point between the elements of the palate and the whole cranial roof. Each ectopterygoid is crescent-shaped bone that contacts the maxilla anteroventrally, the pterygoid posteriorly, and the jugal anterolaterally. The ectopterygoid forms a bridge of contact and articulation between the pterygoid and the maxilla. The lateral end is bent in the anterior portion to match the maxilla orientation. In *Mabuya* spp. the ectopterygoid is slightly curved downward in lateral view and is a Y-shaped bone with a longitudinal groove where the ectopterygoid process of the pterygoid fits. The posterior process of the ectopterygoid is shorter in *M. macrorhyncha* than in its congeners.

SEPTOMAXILLA (Smx)

The septomaxilla is a paired bone that composes the lateral borders of the nasal capsule and its cartilaginous part covers the vomeronasal apparatus dorsally. This bone is located in the dorsal portion of the vomer, forming part of the nasal septum. Anteriorly each septomaxilla shows a blunt process which is seen in the dorsal view of the skull through the anterior nasal fossa. The septomaxilla is included in the nasal cavity and, in articulated skulls, it can only be seen partially through the nostrils. The ventral border contacts anteriorly the horizontal plate of the premaxilla, laterally the palatal plate of the maxilla, and posteriorly the vomer. In *Mabuya* spp. the septomaxilla is located under the nasals, and is partially covered by them.

NASAL (N)

The anterior edges of this paired bone are slightly separated by the nasal process of the premaxilla. This process sits on a triangular facet at the anterior tips of the nasal. Ventrally the middle portion of this bone shows a shallow depression. The nasal contacts the premaxilla medially, the frontal posteriorly and the maxilla and the prefrontal laterally, forming most of the roof of the nasal capsules.

In all five taxa the nasals have contact with the prefrontal. The posterior process is crescent-shaped in *M. agilis*, *M. dorsivittata* and *M. nigropunctata*, but is slightly rectangular in *M. frenata* and *M. macrorhyncha*. Dorsally, the anterior process of the prefrontal overlaps the lateral portion of the dorsoposterior surface of the nasal in *M. frenata* and *M. nigropunctata* and slightly overlaps it in *M. agilis* and *M. macrorhyncha*. The nasals are in contact with each other, only being partially separated by the medial process of the frontal posteriorly and by the nasal process of the premaxilla.

PREFRONTAL (Pr)

The prefrontal is a crescent-shaped paired bone that lies on the anterolateral portion of the skull and forms the anterodorsal rims of the orbits. It contacts the maxilla anterolaterally and ventrally, the frontal dorsally, the palatine medially, the nasal anterodorsally, and the lacrimal laterally. In some species of mabuyines in other genera the prefrontal can contact the jugal through a narrow process (Paluh and Bauer 2017). The anterior process forms part of the dorsolateral aspect of the snout, partially separating the nasal and the maxilla. The posterior process is slim and extends along the frontal over the dorsal border of the orbit. This bone is shorter in *M. nigropunctata* and slightly thicker in *M. frenata* compared to the other three taxa.

LACRIMAL (L)

This paired bone is located subsequently to the prefrontal. It contacts the posterior process of the maxilla ventrally and laterally. Each bone has a small ridge on the external and posterior aspect of the nasolacrimal orifice. According to Kluge (1967) the lacrimal in lizards is variable in shape and ranges from a long club-shaped element which may project beyond the anterior edge of the jugal and articulate with the maxilla to a small round ossification as it is in *Mabuya* spp.

The posterior region of the lacrimal is in medial contact with the anterior process of the jugal in *M. agilis*, *M. frenata*, *M. macrorhyncha* and *M. nigropunctata*. However, it nearly contacts the jugal in *M. dorsivittata*. It also contacts the posterior process of the maxilla ventrally and completes the anterior orbit along with it. The medial edge of the lacrimal forms the posterolateral margin of the lacrimal foramen (Paluh and Bauer 2017). The lacrimal foramen lies between the prefrontal and maxilla in the anteroventral rim of the orbital fossa.

FRONTAL (F)

An unpaired bone located on the longitudinal axis of the skull. This is a flattened bone that forms most of the dorsal orbital margin and a substantial portion of the cranial roof. It contacts the nasals anteriorly, the prefrontals anterolaterally, the postfrontals posterolaterally and the parietal posteriorly. On the ventral surface, the edges of the frontal become thick and round forming the supraorbital ridges forming a tunnel that occupies the middle third of the frontal and houses the olfactory stalks (Kluge 1967).

In *Mabuya* spp. the frontal has no contact with the maxilla. Due to the fusion of the head shield osteoderms some dorsal surface sculpturing may be seen in *Mabuya* spp., corresponding to the frontal, frontoparietal, and interparietal scales. The anterior medial process and the lateral process are variable in shape, *Mabuya nigropunctata* has more pointed processes, whereas in *M. agilis* and *M. dorsivittata* they have a rounded tip and in *M. frenata* and *M. macrorhyncha* they have a very reduced tip. The dorsal surface of the frontal is slightly concave in *M. agilis* and *M. frenata*, but it resembles a straight structure in their other three congeners.

JUGAL (J)

This is a paired bone that forms the lateral margin of the orbit. The jugal is transversally oriented and medially directed until it approaches the postorbital. The anterior portion of the jugal is dorsally concave, forming the ventral border of the orbit. Each jugal articulates anteriorly with the maxillae, posteriorly with the postorbital, posterodorsally with the postfrontal and they also contact the ectopterygoids anteroventrally. The anterior process is much narrower, flaring out dorsally into the posterior process.

This bone is thinner in *M. frenata* and slightly thicker in *M. nigropunctata* compared to the other three taxa. The posterior process is rounded, while the anterior process is pointed. The anterior process of the jugal is shorter in *M. dorsivittata*, barely extending beyond the length of the ectopterygoid, whereas the anterior process in the other taxa extend beyond the ectopterygoid, overlap the posterior process of the maxilla and narrowly contact the lacrimal laterally. The jugal does not participate in the lacrimal foramen in these five species, but medially it borders a shallow groove that is a continuation of this foramen. The jugal is less recumbent in *M. agilis* and *M. frenata* than in the other taxa.

POSTFRONTAL (Pf)

This is a paired bone that forms part of the posterodorsal rims of the orbits. The postfrontal in *Mabuya* spp. is in contact with the postorbital laterally, with the frontal anteromedially, with the jugal anterolaterally and with the parietal posteromedially. The postfrontal is more concave medially in *T. frenata* than in the other taxa, due to the convex projection produced by the anterolateral portion of the parietal and posterolateral region of the frontal.

The anterior process is wide at the base and tapers to a pointed tip where it contacts the frontal. The lateral process is shorter than the anterior process, curves ventrolaterally, and contacts the jugal laterally in all five taxa. The posterior process is much broader than the anterior and lateral processes, especially in *M. agilis* and *M. dorsivittata*, resulting in the absence and reduction of the supratemporal fenestra, respectively. The postfrontal keeps constant contact with the postorbital laterally in all five taxa.

PARIETAL (P)

The parietal is a quadrangular unpaired bone located posteriorly to the frontal bone, in the medial region of the posterior third of the cranium. Posterolaterally the parietal is sutured to the supratemporal and squamosal. Laterally, the parietal contacts the postfrontal and squamosal, forming the medial border of the supratemporal fenestrae, when present. The parietal also contacts the prootic laterodorsally and the supraoccipital posteriorly. The posterior region of this bone has two elongate posterior processes, forming a slight descent in the posterior region. The parietal bears the pineal foramen in all five taxa. The size of this foramen varies according to the species (Table 2).

The parietal is concave in *M. agilis, M. dorsivittata*, *M. frenata* and *M. nigropunctata* yielding a slanted frontal that forms a relatively domed skull table. In *M. macrorhyncha,* however, the parietal forms a relatively flat skull table with the frontal, sloping only in the most posterior portion of the skull. The parietal of *M. nigropunctata* has pointed anterolateral projections that correspond to the elongated posterolateral projections of the frontal, whereas in the other taxa these projections are rounded. A bridge-like process between the parietal and the supraoccipital is present on the posterior edge of the parietal in *M. agilis*, *M. dorsivittata*, *M. frenata* and *M. nigropunctata*, but in *M. macrorhyncha* this process was not visible. Dorsal surface sculpturing, corresponding to the interparietal and parietal scales, is present in all five taxa. According to Paluh and Bauer (2017) this sculpturing is due to the fusion of the head shield osteoderms to the underlying bone.

POSTORBITAL (Po)

Paired and elongated bone that is best observed in dorsal and lateral views. Each postorbital contacts the postfrontal medially, the squamosal posterolaterally and the jugal anterolaterally. The size and surface contact between the squamosal and postorbital are smaller in *M. agilis* and *M. nigropunctata* in comparison with the other three taxa.

SQUAMOSAL (Sq)

The squamosal completes with its edge the lateral margin of the supratemporal region and forms the posterolateral rims of the supratemporal fenestra. This paired bone is anteriorly in contact with the postorbital, posteromedially with the supratemporal and posteriorly with the quadrate. Posteriorly it diverges away from the supratemporal process of the parietal and has a short laterally directed process that interacts with the squamosal notch of the quadrate. The squamosal of *M. dorsivittata* has a medial extension before reaching the supratemporal bone, and the same extension is seen in *M. agilis* but to a lesser degree. The squamosal of *M. macrorhyncha* is relatively longer than those of its congeners.

SUPRATEMPORAL (St)

Paired bone located in the posterolateral edge of the skull, between the quadrate and the parietal, contacting the squamosal anterolaterally. Usually this is a very small bone and hard to observe. The supratemporal is slightly curved ventrally, and it gradually widens from the sharpened anterior end to the posterior end. In *Mabuya* spp. this bone appears as a small gently curved structure.

The supratemporal of *M. agilis* and *M. macrorhyncha* are proportionally the shortest among the five taxa examined and has the most limited contact with the posterior process of the parietal, while the supratemporal of *M. dorsivittata* is the longest and that of *M. frenata* the widest. Only in *M. dorsivittata* and *M. nigropunctata* this bone participates in the formation of the supratemporal fenestra.

Description of isolated splanchonocranial bones

QUADRATE (Q)

This paired bone is located in the posterolateral angle of the skull. It is posteromedially directed contacting the braincase dorsomedially and function as the basis for articulation between the cranium and the mandible. It is composed by a posteriorly curved column structure and by a posteriorly pronounced concave conch. Its anterior region is convex, while the posterior region is pronouncedly concave, and can be divided into dorsal, ventral, anterior and posterior surfaces. The dorsal surface is enlarged, flat and makes contact with the supratemporal posteriorly, and with the squamosal and prootic dorsally.

Ventrally, the quadrate articulates with the pterygoid and the cartilaginous pad of the articular of the mandible. The contacts between the supratemporal and squamosal are made through intercalated cartilages rather than rigid sutures. The ventral surface is quite small, and presents a condylar area, which articulates with the mandible. The anterior surface presents a thickening in the dorsal portion, decreasing the thickness of the wall towards the articular condyle. The posterior surface of the quadrate is concave. A squamosal notch lies anterolaterally enclosed to the cephalic condyle in *Mabuya* spp. In lateral view, the quadrate of *M. dorsivittata* is wider in relation to height compared to the other species.

EPIPTERYGOID (Eptg)

This paired bone unites the parietal and the pterygoid and can be seen in the lateral view. Each pterygoid has the shape of a vertical bar at each side of the parietal, ossifying in the *processus ascendens* of the chondrocranium, and extending obliquely from the anterior tip of the prootic bone to the pterygoid, dorsally to the basipterygoid articulation. The epipterygoid of *M. macrorhyncha* is straight, while this element is slightly curved in its congeners. This bone is notably thinner in *M. macrorhyncha* and slightly thicker in *M. frenata* compared to the other three taxa.

Description of isolated neurocranium bones

SUPRAOCCIPITAL (So)

It's an unpaired bone that presents itself dorsally in relation to other components of the optical-occipital region. The supraocciopital follows the parietal and forms the back of the head ceiling and the dorsal area of the foramen magnum. This bone is sutured with the posterior portion of the parietal, and contacts the prootic anteroventrally and the otooccipital laterally. Dorsally it is slightly convex, medially constricted and possesses two enlarged ridges laterally, which are better seen in *M. dorsivittata*, *M. macrorhyncha* and *M. nigropunctata*. The posterolateral walls of the supraoccipitial house the dorsal portion of the optic capsules (Paluh and Bauer 2017).

BASISPHENOID (Bas)

This unpaired bone is also mentioned as parabasisphenoid because it results from a fusion between the basisphenoid and the dermatocranial parasphenoid. It forms part of the neurocranium floor situated ventrally and medially in the posterior area of the palatal skull region, contacting the basioccipital posteriorly, with no visible suture, and the prootic dorsally. Presents the anterolateral processes of the basipterygoid, which are extended distally, anteroventrally directed and fit to the pterygoid, performing the articulation of the neurocranium with the rest of the skull, being a point of mobility between the maxillary and occipital segments.

Anteriorly, the basisphenoid bears paired trabeculae, from which a cartilaginous rod or parasphenoid process originates. The parasphenoid process extends to the posterior extent of the palatine in all five taxa. The basipterygoid processes are oriented anterolaterally, with expanded distal facets that articulate with the basipterygoid process of the pterygoid. In ventral view the basipterygoid process gently overlap the pterygoid in most species, but in *M. dorsivittata* this process is elongated and it almost surpasses the pterygoid.

BASIOCCIPITAL (Ba)

An unpaired bone, such as the basisphenoid. Forms the posterior area of the cranial cavity and the middle region the occipital condyle. It is located ventromedially, accompanying the basisphenoid with no visible suture and forming the floor of the neurocranium. It contacts the basisphenoid anteriorly and the prootic anterolaterally. Posterodorsally it has contact with the otoccipital. The basioccipital also forms the middle part of the ventral edge of the foramen magnum, and presents two moderately developed lateral processes. In *Mabuya* spp. the basioccipital contacts the basishpenoid with no visible suture.

PROOTIC (Pro)

Bones that form the lateral cover of the neurocranium and which are presented together with the supraocciopital and harbor the anterior section of the membranous labyrinth of the inner ear (Kluge, 1962). The prootic is a very irregular bone and hard to observe. The laterodorsal region is slightly concave, and makes contact with the parietal bone through their dorsal surface. It sutures to the supraoccipital in the posterolateral region and ventrolaterally to the basisphenoid and the basioccipital. Its articulation with the basioccipital is firm and somewhat indistinguishable. Subsequently, it makes contact with the otooccipital. The prootic features along its middle region a ridge in the anteroposterior direction, called the prootic crest, which serves as the point of insertion of the muscle *protractor pterygoidei*. The most prominent feature of the prootic is the anterodorsally extended *crista alaris*, which bears the enlarged tracks of the anterior and horizontal semicircular canals (Paluh and Bauer 2017).

Along with otooccipital and supraoccipital, the prootic participates in the formation of the tympanic bulla. Ventrally to this, lies an acoustic recess in the bone's inner face. Contributing to the delimitation of the rostral margin of the paroccipital process, the prootic forms the anterolateral wall of the neurocranium in reptiles in general (Stephenson and Stephenson 1956; Torres-Carvajal 2003; Bever et al. 2005; Bell et al. 2009; Khosravani et al. 2011).

Description of isolated mandibular bones

ARTICULAR (Ar)

This bone is also referred to as prearticular by some authors, due to a co-ossification process with this structure. It is the only bone in the mandible that is of endochondral origin and is formed by ossification of Meckel's cartilage, occupying the posterior end of the mandible. In some groups of lizards, it is fused with the angular (Paluh and Bauer 2017). The articular is a laterally flattened bone whose ventral end is wider than the dorsal one, it occupies the entire posterior part of the mandible, and articulates with the quadrate bone of the skull. Posterioly, the articular presents the *fovea articularis*, also known as the condylar process. This process is inclined in the posteroventral direction and has depressions on its surface that allows it to fit with the quadrate. This joint is made through a concave but irregular articulated surface, which joins the convex surface, also irregular, of the quadrate bone, making a diarthrosis-like joint.

In *Mabuya* spp., the retroarticular process is a flattened and posteromedially elongated structure in the posterior direction of the mandible. The retroarticular process in *M. agilis* and *M. dorsivittata* are smaller than in the other taxa.

ANGULAR (Ag)

Small bone, flat and elongated. It extends ventrally and is situated in the lateroventral region of the mandible, being visible in the lateral and medial views. The anterior end embraces the posteroventral tip of the dentary. The angular is sutured anteriorly to the dentary and splenial, dorsally to the supra-angular and posteriorly and ventrally to the articular. The angular in *M. macrorhyncha* is reduced compared to the other taxa, while in *M. nigropunctata* and *M. frenata* the angular has an elongated and dorsally directed posterior process.

SUPRA-ANGULAR (Sa)

This bone is elongated and together with the articular and angular forms the dorsal and lateral surface of the posterior part of the mandible. Anteriorly, the supra-angular is sutured to the dentary, dorsally to the coronoid, and laterally and ventrally to the articular and angular. The supra-angular is formed across the posterolateral border and the lateral surface of the mandibular foramen. Its border and side are rounded serving as insertion for the *adductor mandibularis externus* muscle. On the lateral surface of the supra-angular the *intermandibularis* muscle is also inserted.

The articular and supra-angular are fused in *M. macrorhyncha*, while these two bones are almost completely separated in the other taxa. Anteriorly, next to the suture with the coronoid, the supra-angular has a foramen, called the anterior supra-angular foramen, visible in *M. frenata*, *M. macrorhyncha* and *M. nigropunctata*. This foramen can be seen in lateral view, in the laterodorsal surface of the mandible near the suture with the coronoid and dentary. Posteriorly, next to the articular, is another foramen, a little smaller, the posterior supra-angular foramen, which is present in all five taxa. Through these foramina occurs the passage of the cutaneous branches of the inferior alveolar nerve.

CORONOID (Cor)

This bone is located in the median dorsal portion of the mandible, between the supra-angular and the dentary. It has a triangular recurved aspect, forming a concave surface in the inner face of the mandible. The coronoid is the highest apical projection of the mandible in relation to other bones. It has three basal processes. These processes give the coronoid a tripod arrangement. The anterior medial coronoid process is sutured to the dentary anteriorly and to the splenial and supra-angular ventromedially. The anterolateral process promotes the suture of the coronoid to the supra-angular ventrolaterally and anteriorlly penetrates the dentary, presenting itself completely sutured to it. The apical, lateral and posterior regions of the coronoid receive the insertion of the *adductor mandibularis externus*, *medius*, and *profundus* muscles.

The coronoid eminence is laterally compressed and relatively reduced in *M. dorsivittata* compared to the other four taxa. The anterolateral process of the coronoid contacts the dentary and splenial, and in *M. dorsivittata* it is more anteriorly extended than in the other taxa, almost reaching the anterior inferior alveolar foramen.

SPLENIAL (Spl)

This elongated bone is located in the ventromedial region of the mandible. It is only visible in the lingual view of the mandibles, as well as their dorsal and ventral suture to the dentary. It is sutured to the coronoid dorsally and to the angular posteroventrally.

A large, anterior inferior alveolar foramen is present in all five taxa, which gives passage to the lingual branch of the inferior alveolar nerve. In *Mabuya* spp. this foramen is in anterior position near the dorsal suture of the splenial with dentary. Another foramen positioned in this bone is the anterior mylohyoid foramen, which performs the transmission of anterior mylohyoid nerve, located posteroventraly to the anterior inferior alveolar foramen, but is only present in *M. agilis*, *M. frenata* and *M. nigropunctata*.

DENTARY (D)

This slightly dorsally curved bone forms the major part of the anterior half of the mandible. Throughout its dorsal edge of the inner face, the dentary has a gutter-shaped concavity, where the teeth are inserted and also form the replacement teeth. The dentary suture is in contact with the front surfaces of the other bones in the mandible, except the articular. Its anterior extremity is deepened and has a triangular shape.

The dorsomedial surface of the dentary may have 25-26 teeth in *M. agilis*, 23-25 in *M. dorsivittata*, 28-30 in *M. frenata*, 21-24 in *M. macrorhyncha* and 32-34 in *M. nigropunctata* (Table 2). These teeth are cylindrical, hollow, with internal replacements and pleurodont with pointed crowns in all five taxa. The lateral side of the dentary is slightly rounded and has 3-4 mental foramina in *M. nigropunctata*, 4-5 in *M. dosivittata* and *M. agilis*, 6 in *M. frenata* and 6-7 in *M. macrorhyncha*. The angular process is nearly the same length of the cornoid process in *M. nigropunctata*, but in the other taxa the angular process is longer than the coronoid process. The dentary of *M. dorsivittata* and *M. macrorhyncha* is shorter compared to those of its congeners.

Cranial comparison with *Trachylepis atlantica*

The supratemporal fenestrae in *Mabuya* spp. are narrow and smaller than in *T. atlantica* and entirely absent in *M. agilis* due to its enlarged postfrontals. In *Mabuya* spp. each jugal articulates posterodorsally with the postfrontal, but in *T. atlantica* the postorbital bone participates in the formation of the orbit and separates the jugal and the postfrontal bones from each other. In all other *Trachylepis* whose crania have been described the postorbital bone participates in the formation of the orbit (though not always separating the jugal from the postfrontal), except in *T. laevis*, which lacks the postorbital (see Chapter 1). In contrast, in *Mabuya* spp. the postorbital does not reach the orbit (Jerez 2012; present study). This may represent an additional diagnostic character to distinguish between the genera *Trachylepis* and *Mabuya*.

The number of premaxilary teeth varies from 8-14 in *Mabuya* spp. and from 7-10 in *T. atlantica*. There is no contact between the premaxilla and the frontal in both genera, because the nasals lie between them. Both in dried and in stained and cleared skulls the suture that separates the two halves of the premaxilla can only be seen clearly in *M. macrorhyncha* and a faint partial suture is visible in *M. dorsivittata*. Although with x-ray images it is possible to see a clear division between these two halves in *Mabuya* spp., in *T. atlantica* this division its not very clear in none of the mentioned techniques.

The palatines contact each other in *M. dorsivittata* and *M. frenata*, while in the other *Mabuya* species they are completely separated, most markedly in *M. macrorhyncha*. In *T. atlantica* the palatines are slightly separated. Also, *T. atlantica* has a proportionately more elongate and thinner vomer than *Mabuya* spp.

No pterygoid teeth were found in any of the analyzed specimens of all five species examined in this study, and they were also reported as absent in an undescribed species of *Mabuya* studied by Jerez (2012). Thus, *Mabuya* appears to consistently lack pterygoid teeth. On the other hand, species of *Trachylepis* may present or lack these teeth (see Chapter 1). According to Travassos (1946) there are some small conical teeth in the pterygoid in *T. atlantica*, although they fall off very easily, leaving no trace.

The dentary, the longest bone in the mandible, is slightly curved inward anteriorly in *Mabuya* spp. and more so in *T. atlantica*. Its dorsomedial surface may have 21-34 teeth in *Mabuya* spp. and 28-30 in *T. atlantica*. The lateral side of the dentary is slightly rounded and may have 3-7 mental foramina in *Mabuya* spp., but *T. atlantica* has only four in all analized especimens. In lateral view, the coronoid process is visible, although it is more prominent in *T. atlantica*.

Those traits reinforce the differentiation of *Trachylepis* species from Neotropical *Mabuya* and may represent taxonomically useful data.

GENERAL CONCLUSIONS

Diagnostic features of the Mabuyinae are (in most species) nine teeth on the premaxillary, a Meckelian furrow completely closed by overlapping and an opening in the middle surface of the mandible from which Meckel's cartilage originates (Hedges 2014). *Trachylepis atlantica* possesses 8-10 premaxillary teeth, whereas *Mabuya* spp. have 8-14 premaxillary teeth. Both *T. atlantica* and *Mabuya* spp. possess an obliterated Meckelian canal. They also feature a parietal bone delimited along its posterior margins by the supratemporal bones and a transverse enlarged nuchal, also postulated morphological diagnosis of Mabuyinae according to Hedges (2014).

One of the purposes of this study was to try to identify cranial structures with potential taxonomic utility. This study adds to the knowledge of cranial osteology of the genera *Mabuya and Trachylepis* and provides some new insights on the cranial variations in those scincids. It reveals a new diagnostic character to differentiate between these two genera: the condition of the postorbital bone relative to the orbit (reaching vs. not reaching orbit). Also, it corroborates that *Mabuya* s. str. always lack pterygoid teeth and tends to have a higher number of premaxillary teeth compared to other mabuyine genera.

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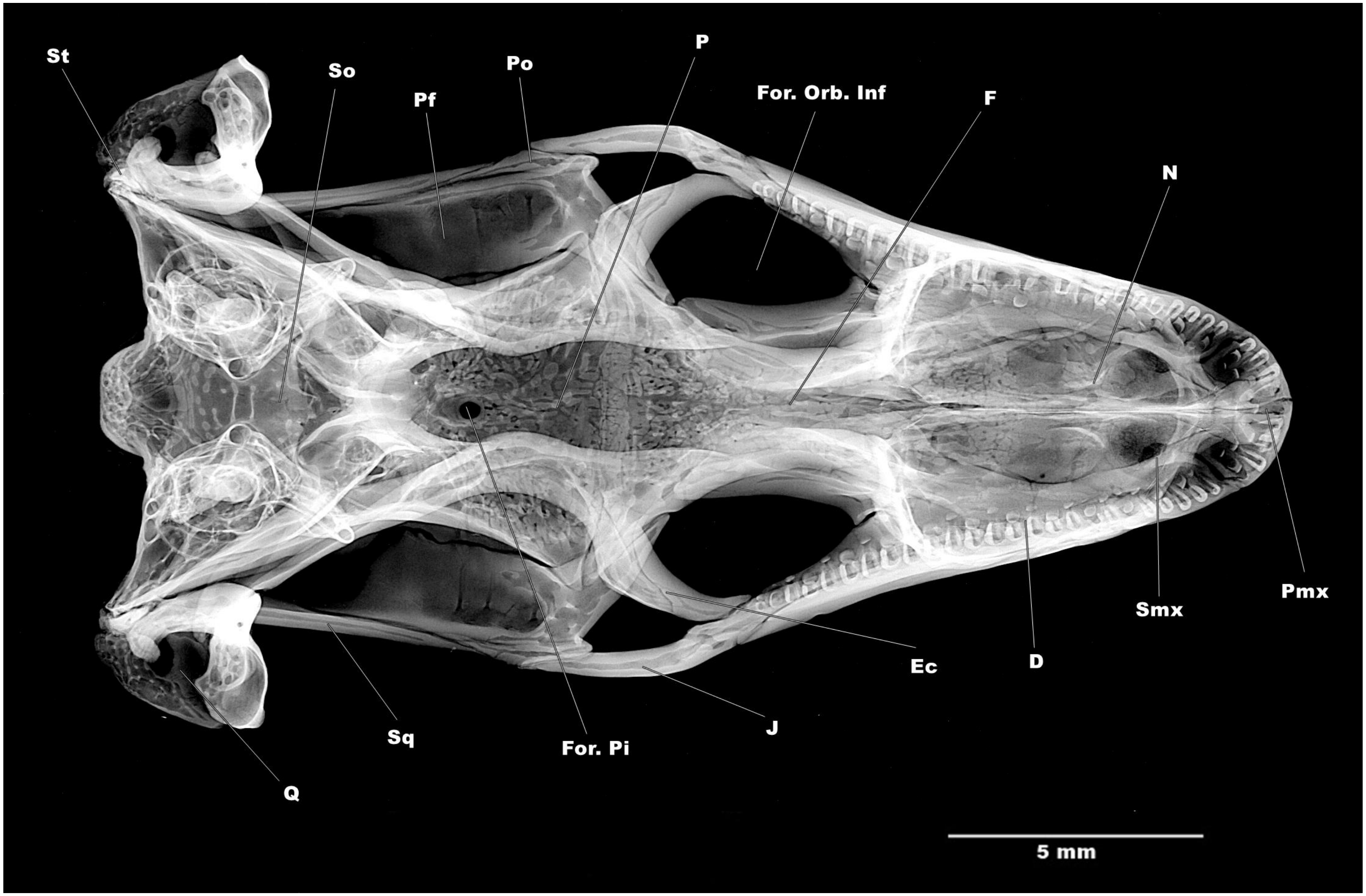

FIG. A1.1 – Radiography of the skull of *Trachylepis atlantica* MNRJ 26877 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

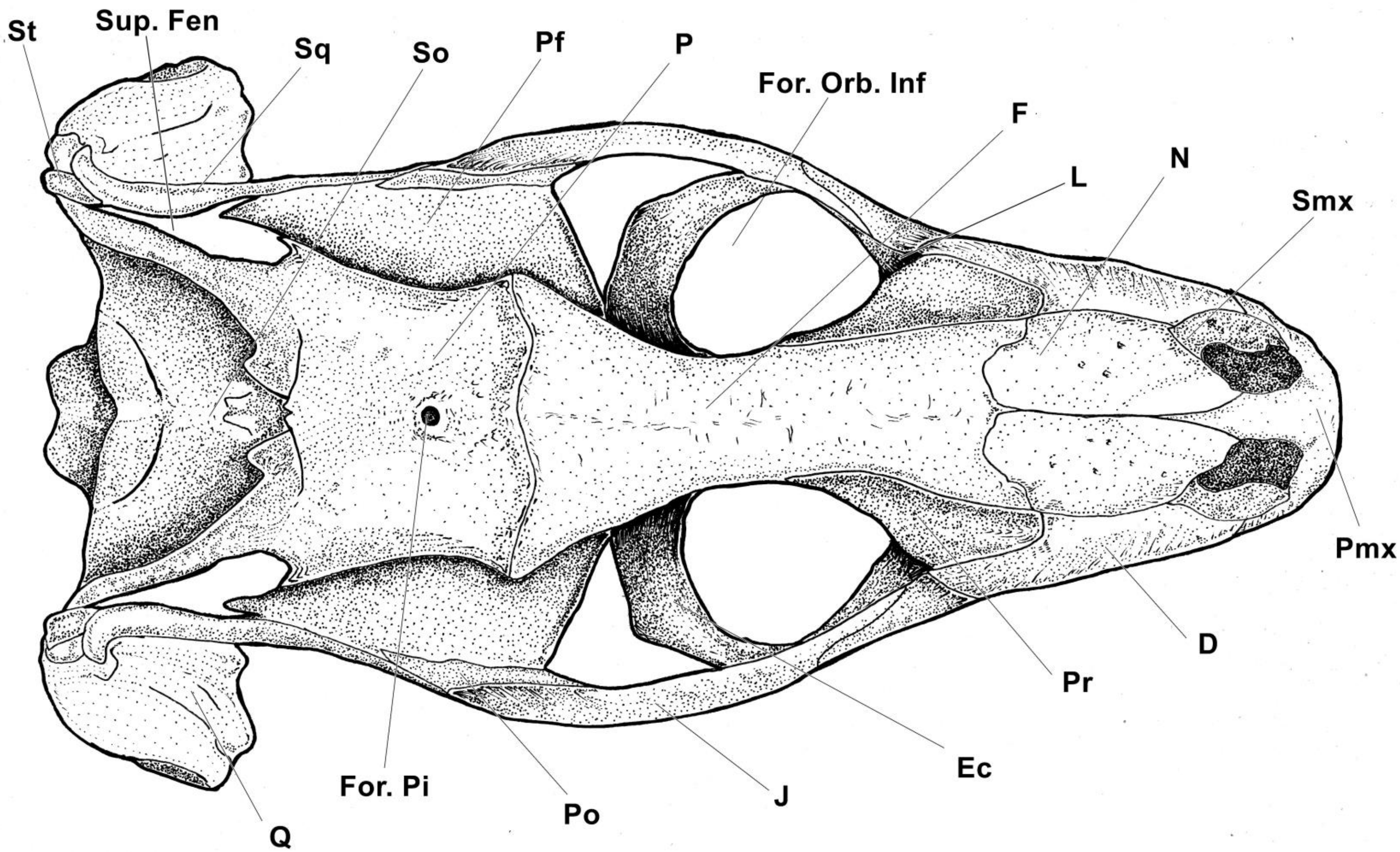

FIG. A1.2 – Illustration of the skull of *Trachylepis atlantica* MNRJ 26877 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Pr – prefrontal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal; Sup. Fen – supratemporal fenestra.

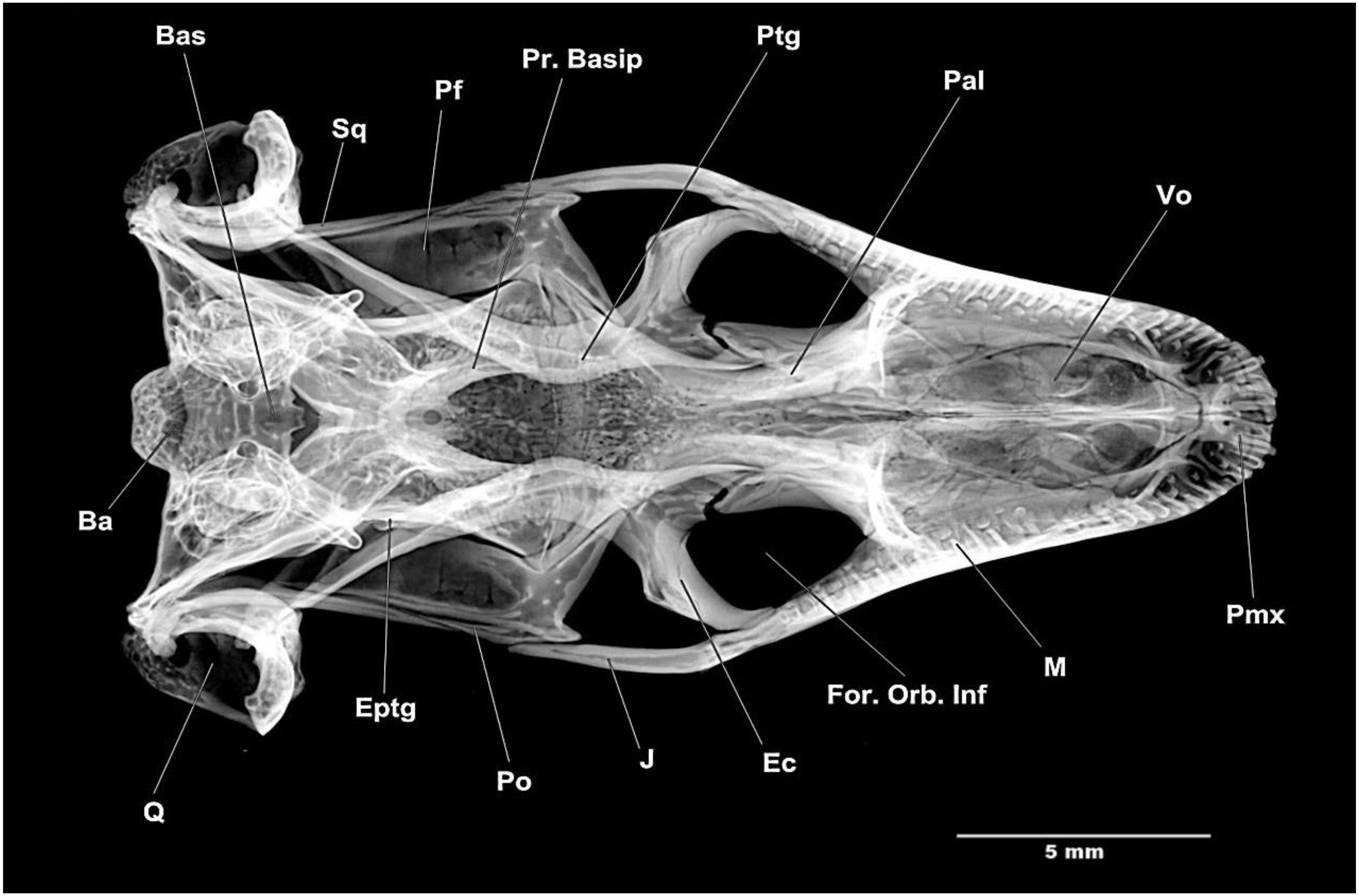

FIG. A1.3 – Radiography of the skull of *Trachylepis atlantica* MNRJ 26877 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; Eptg – epipterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

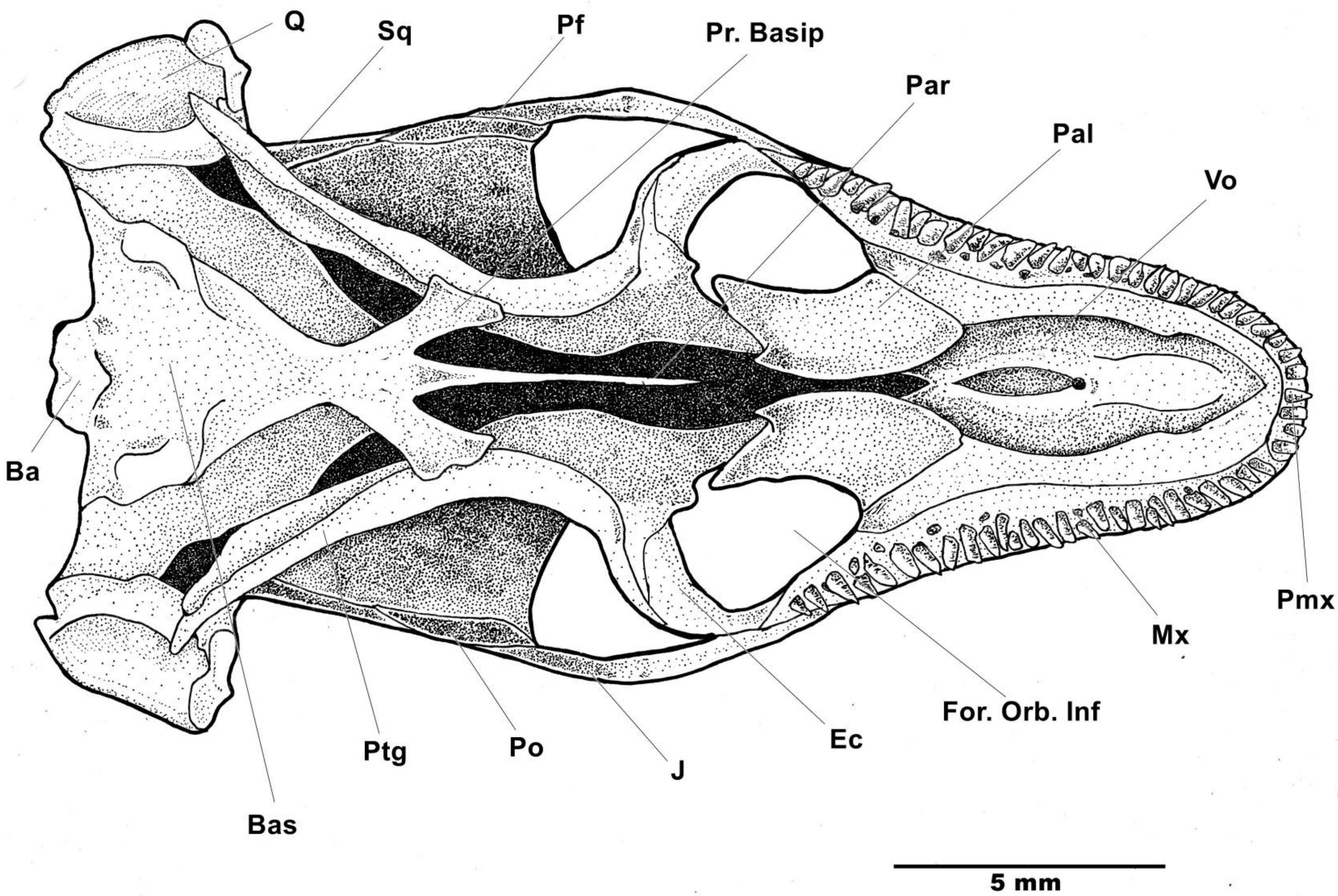

FIG. A1.4 – Illustration of the skull of *Trachylepis atlantica* MNRJ 26877 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

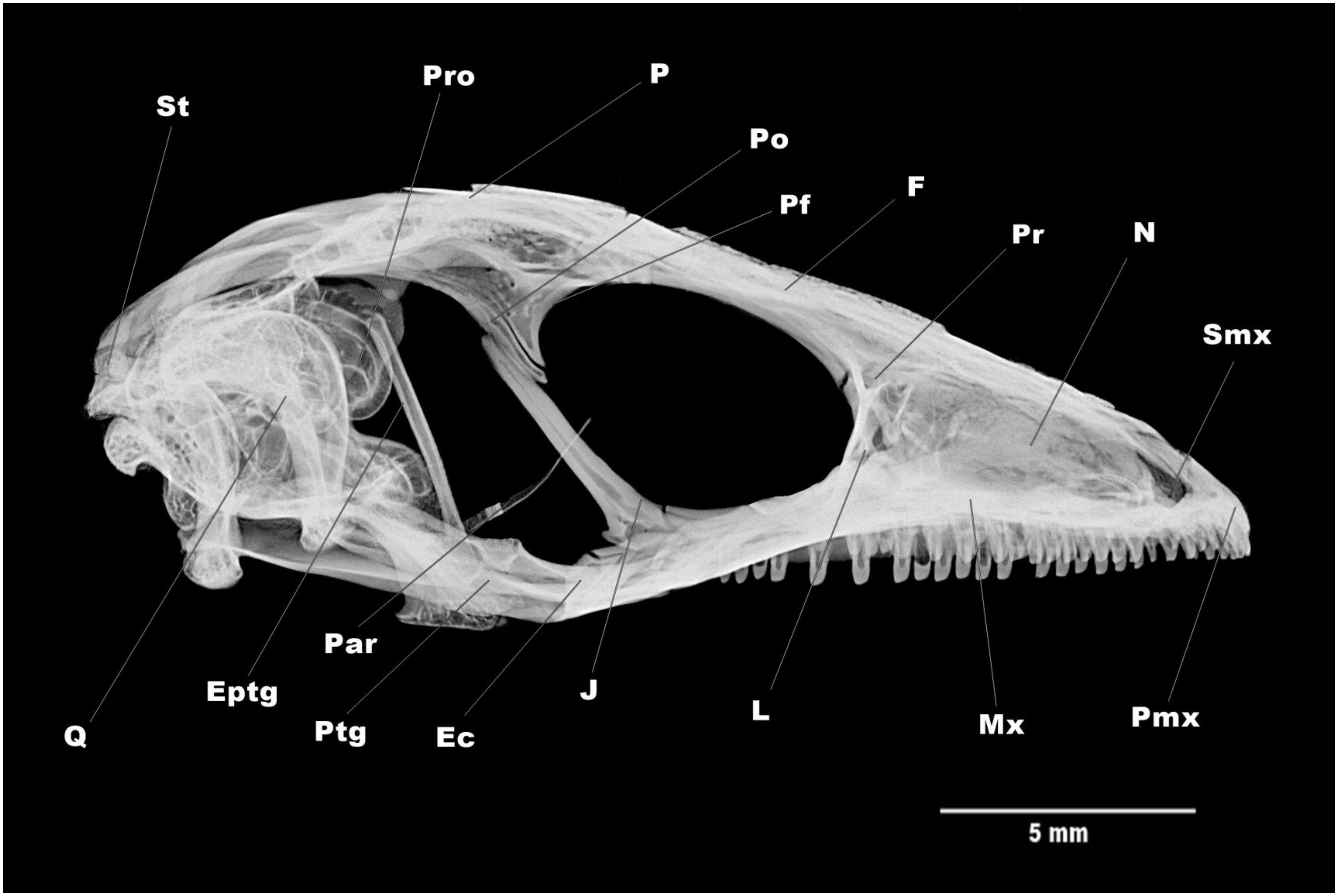

FIG. A1.5 – Radiography of the skull of *Trachylepis atlantica* MNRJ 26877 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; St - supratemporal.

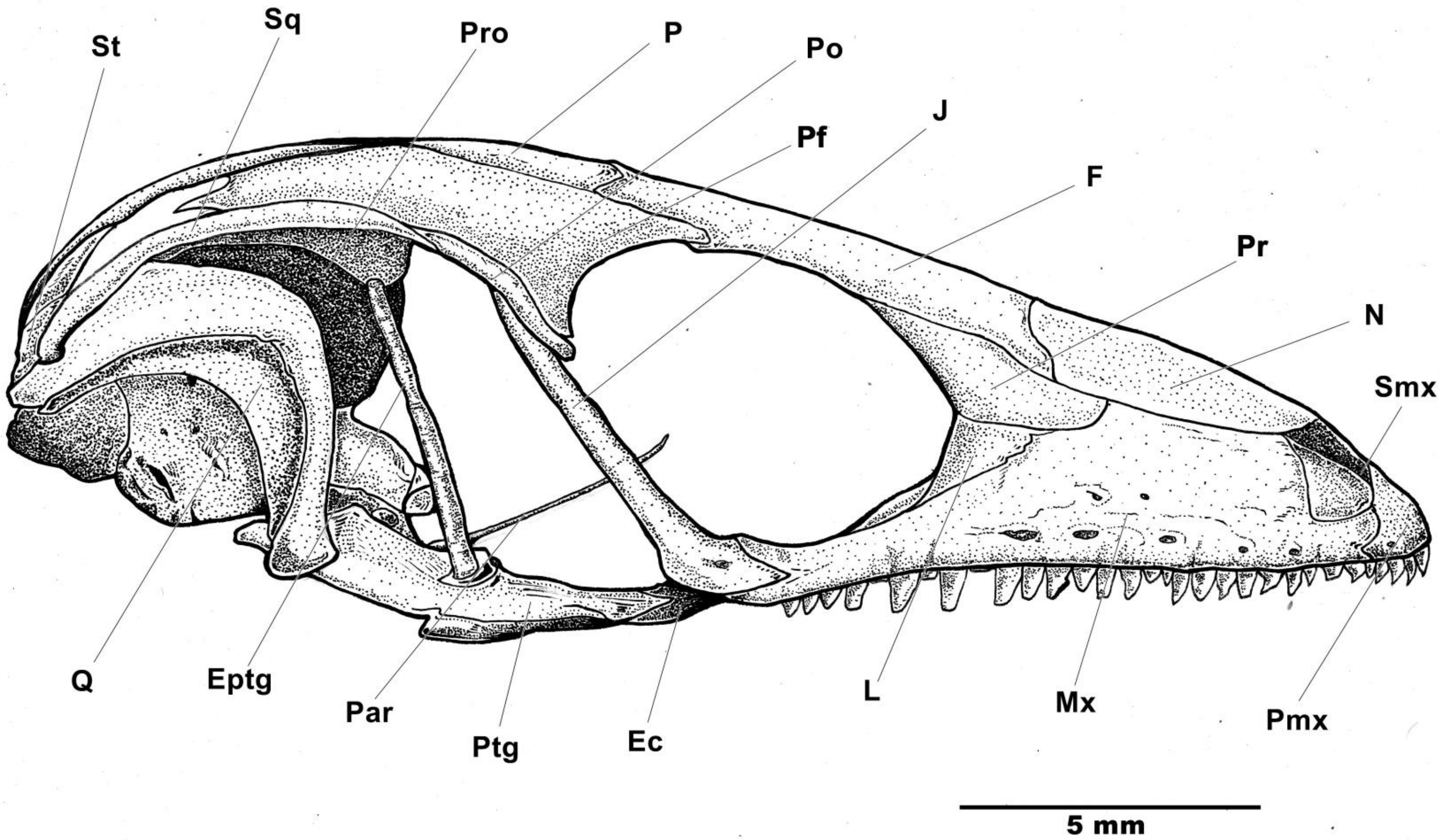

FIG. A1.6 – Illustration of the skull of *Trachylepis atlantica* MNRJ 26877 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; Sq – squamosal; St - supratemporal.

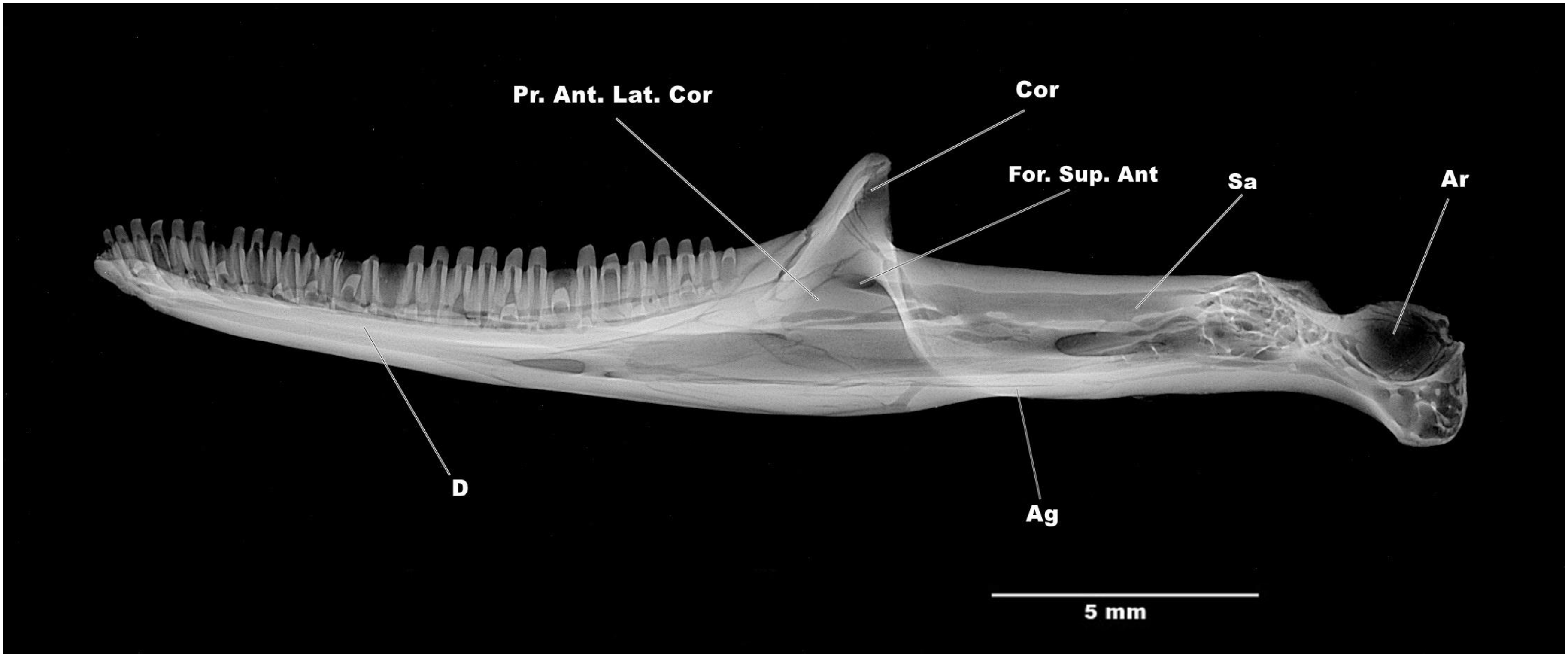

FIG. A1.7 – Radiography of the mandible of *Trachylepis atlantica* MNRJ 26877 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Sup. Ant – foramen supra-angular anterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

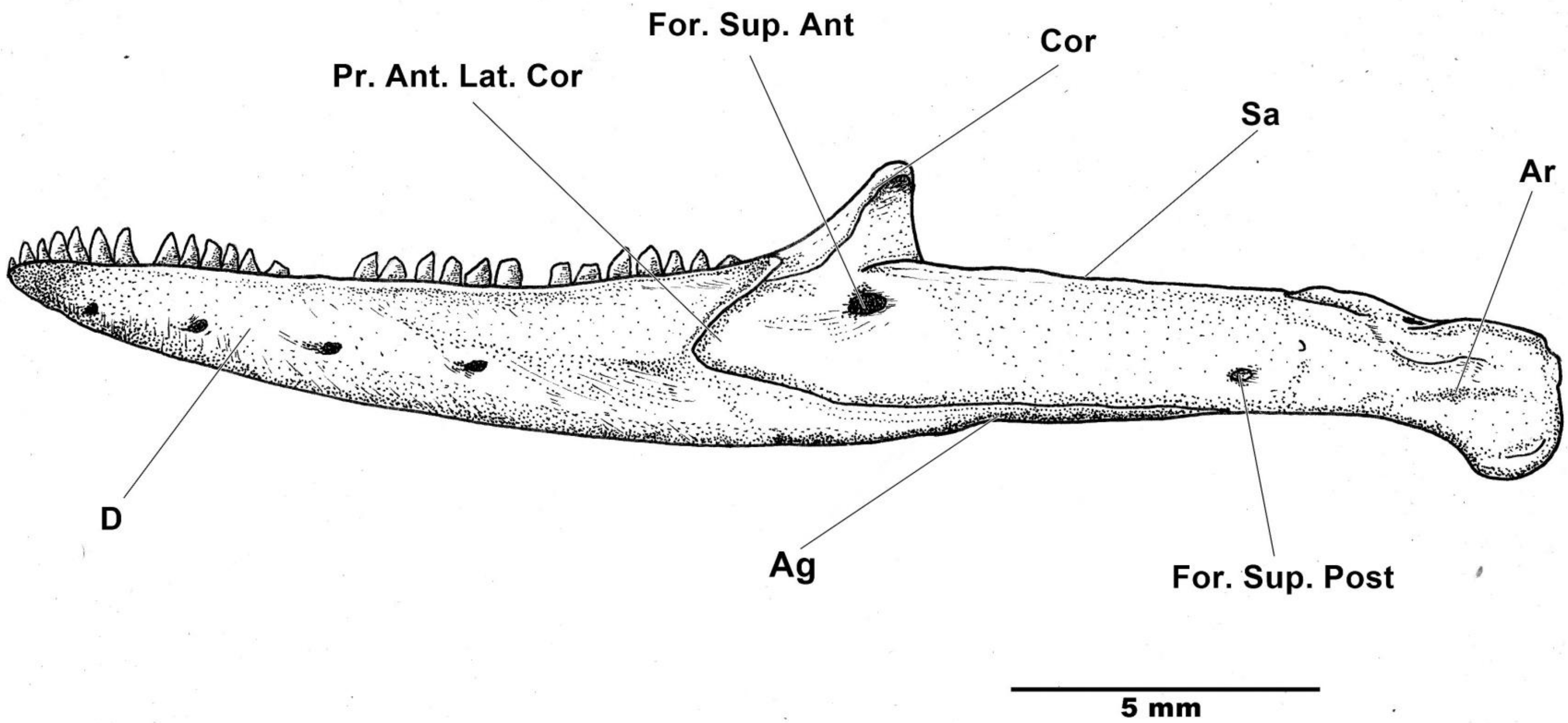

FIG. A1.8 – Illustration of the mandible of *Trachylepis atlantica* MNRJ 26877 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Supra. Ant – foramen supra-angular anterior; For. Sup. Post – foramen supra-angular posterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

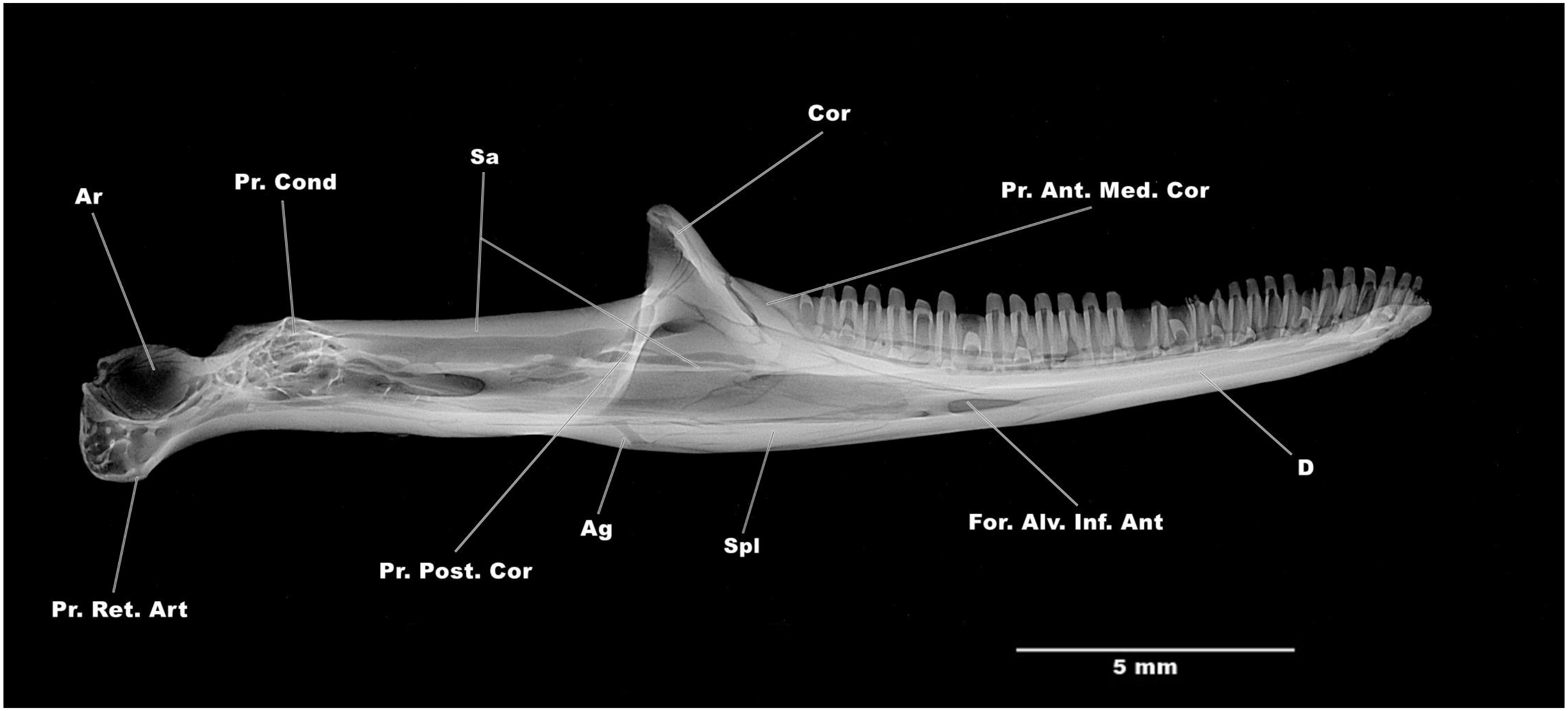

FIG. A1.9 – Radiography of the mandible of *Trachylepis atlantica* MNRJ 26877 – Lingual view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial process of coronoid; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

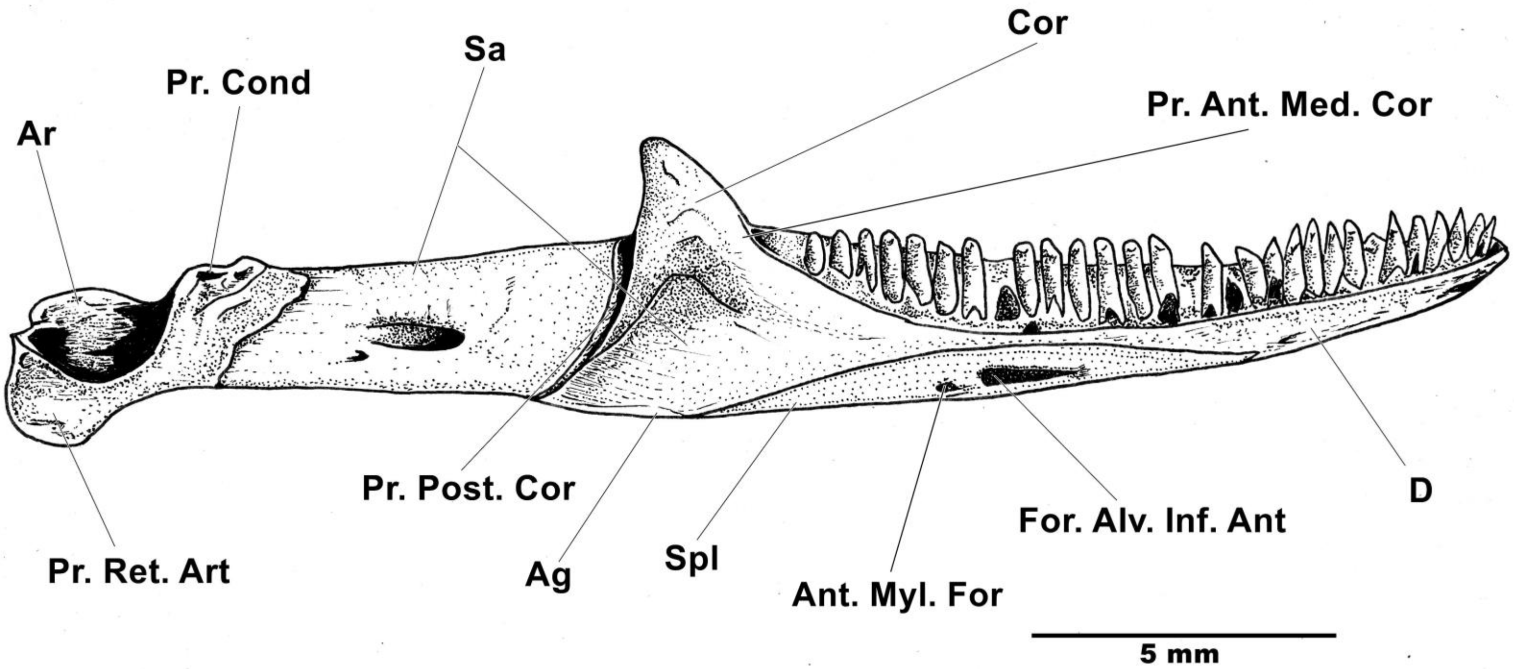

FIG. A1.10 – Illustration of the mandible of *Trachylepis atlantica* MNRJ 26877 – Lingual view

Ag – angular; Ant. Myl. For – anterior mylohyoid foramen; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial coronoid process; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

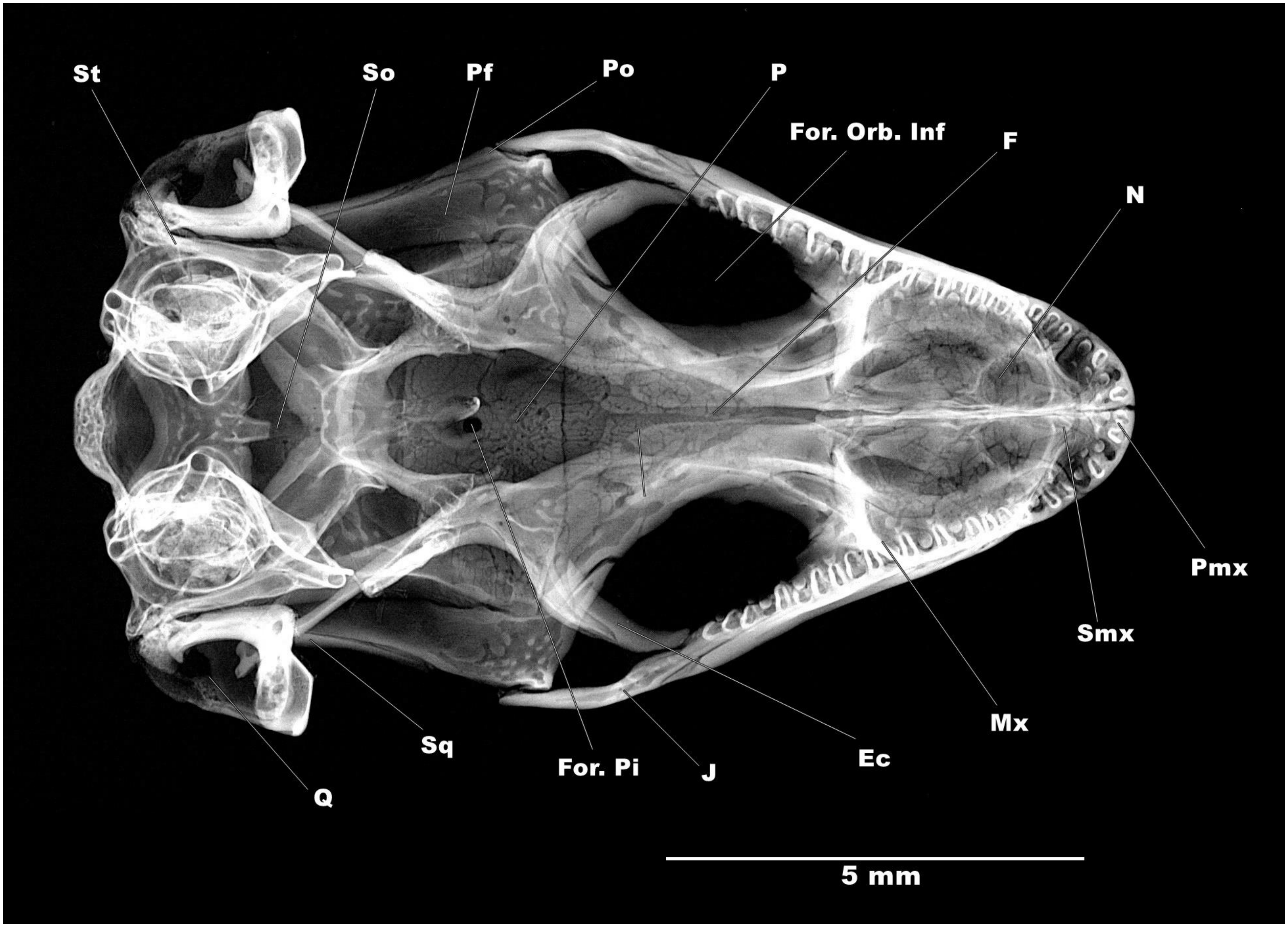

FIG. A2.1 – Radiography of the skull of *Mabuya agilis* MNRJ 14259 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

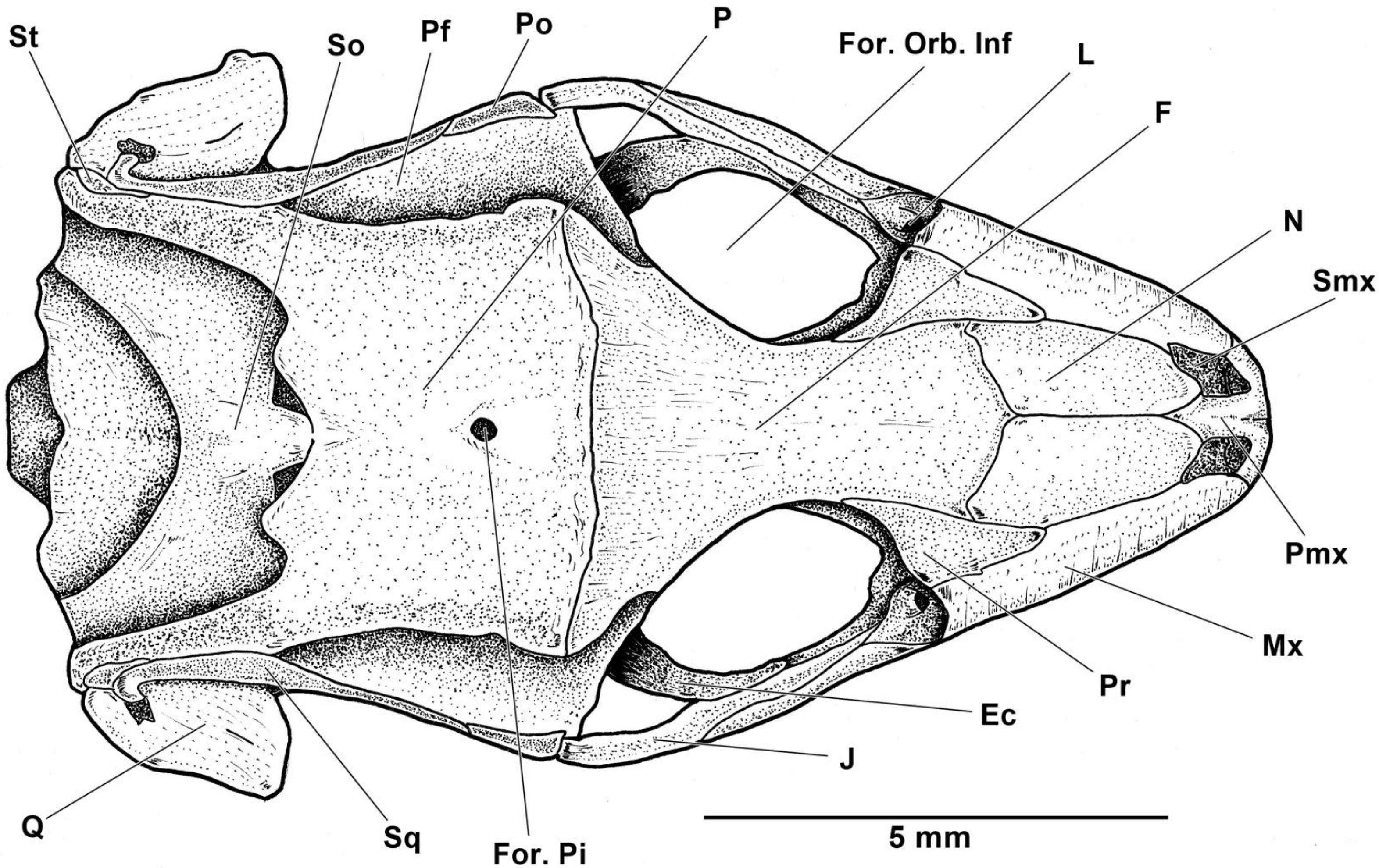

FIG. A2.2 – Illustration of the skull of *Mabuya agilis* MNRJ 14259 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; L – lacrimal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Pr – prefrontal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

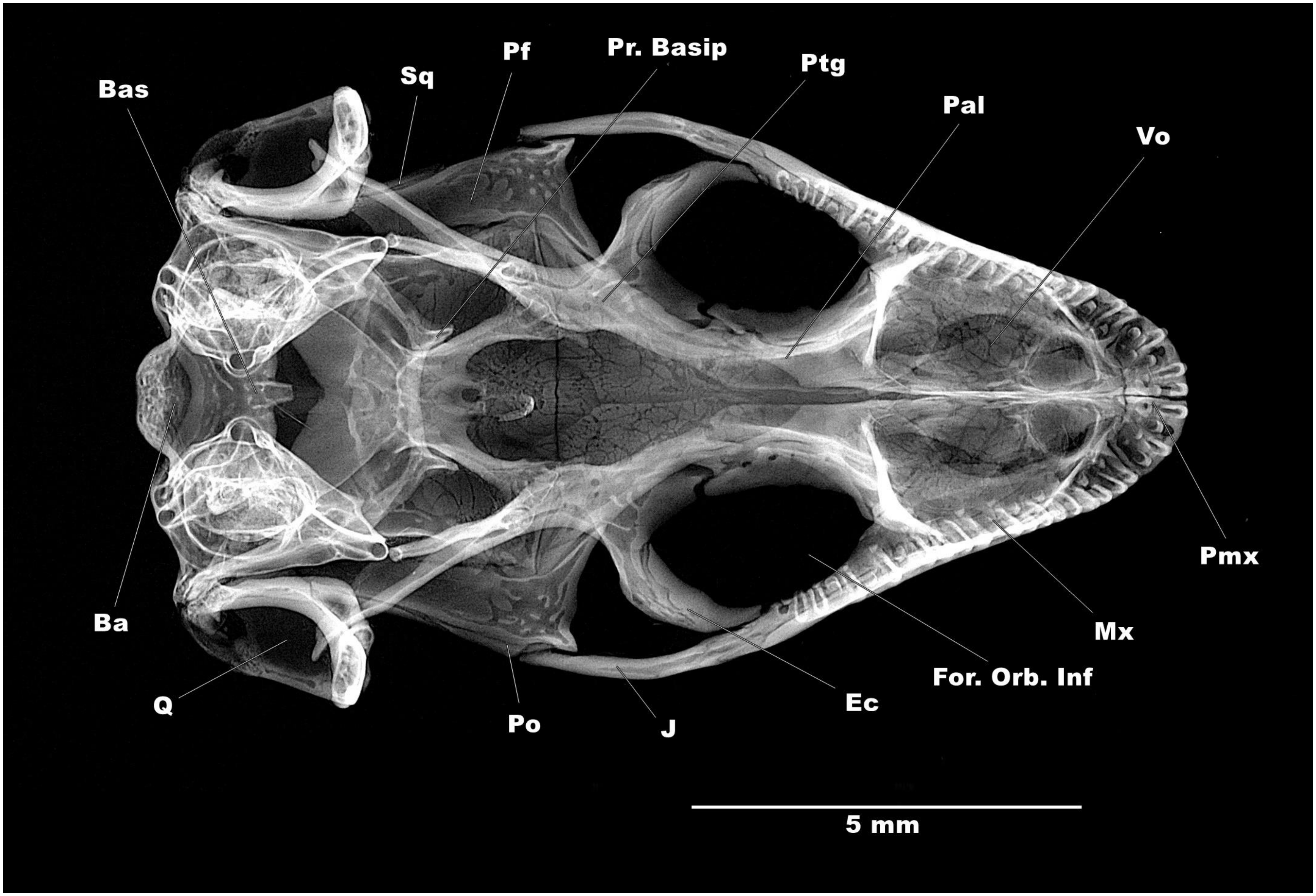

FIG. A2.3 – Radiography of the skull of *Mabuya agilis* MNRJ 14259 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

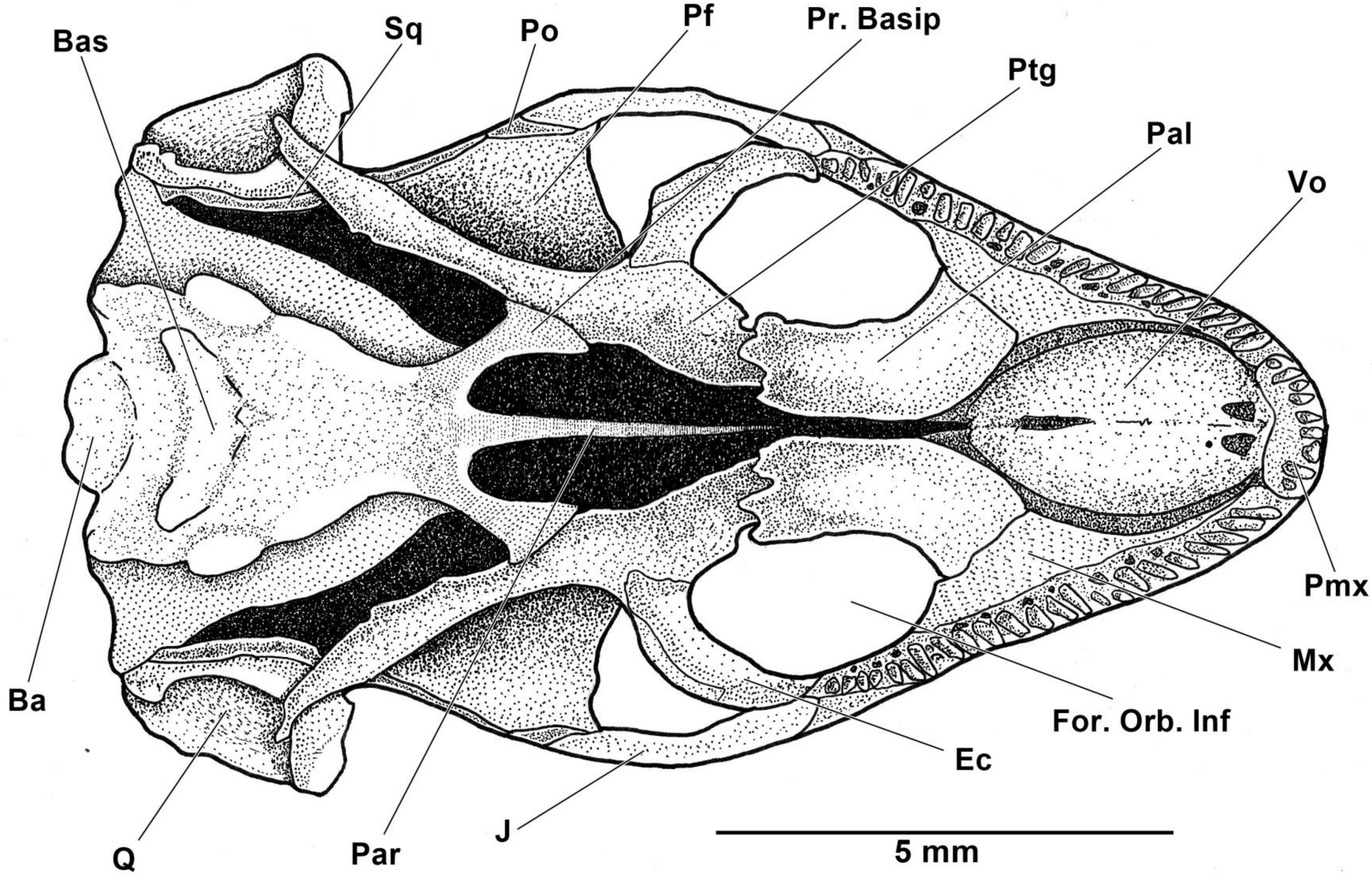

FIG. A2.4 – Illustration of the skull of *Mabuya agilis* MNRJ 14259 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

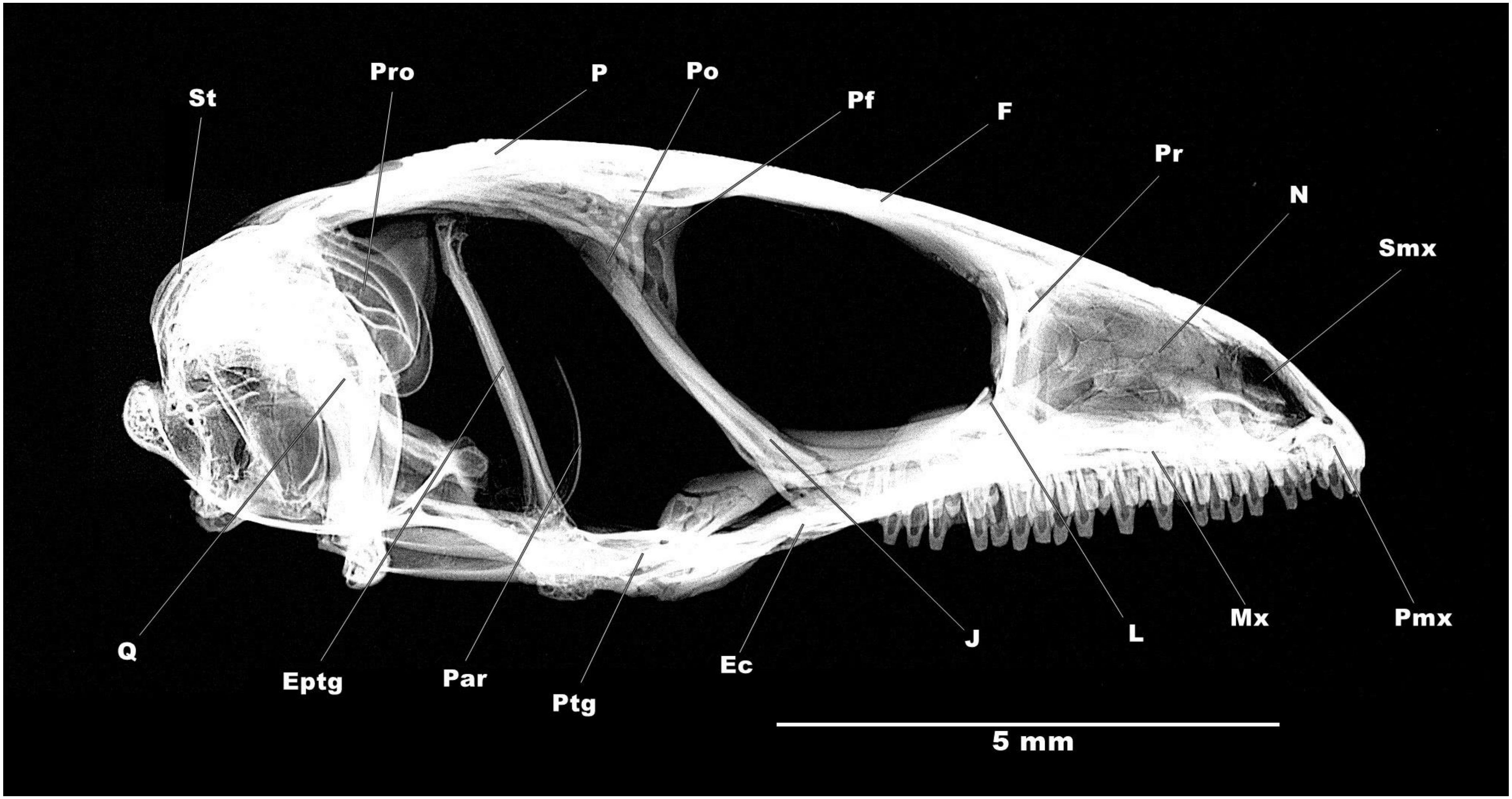

FIG. A2.5 – Radiography of the skull of *Mabuya agilis* MNRJ 14259 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; St - supratemporal.

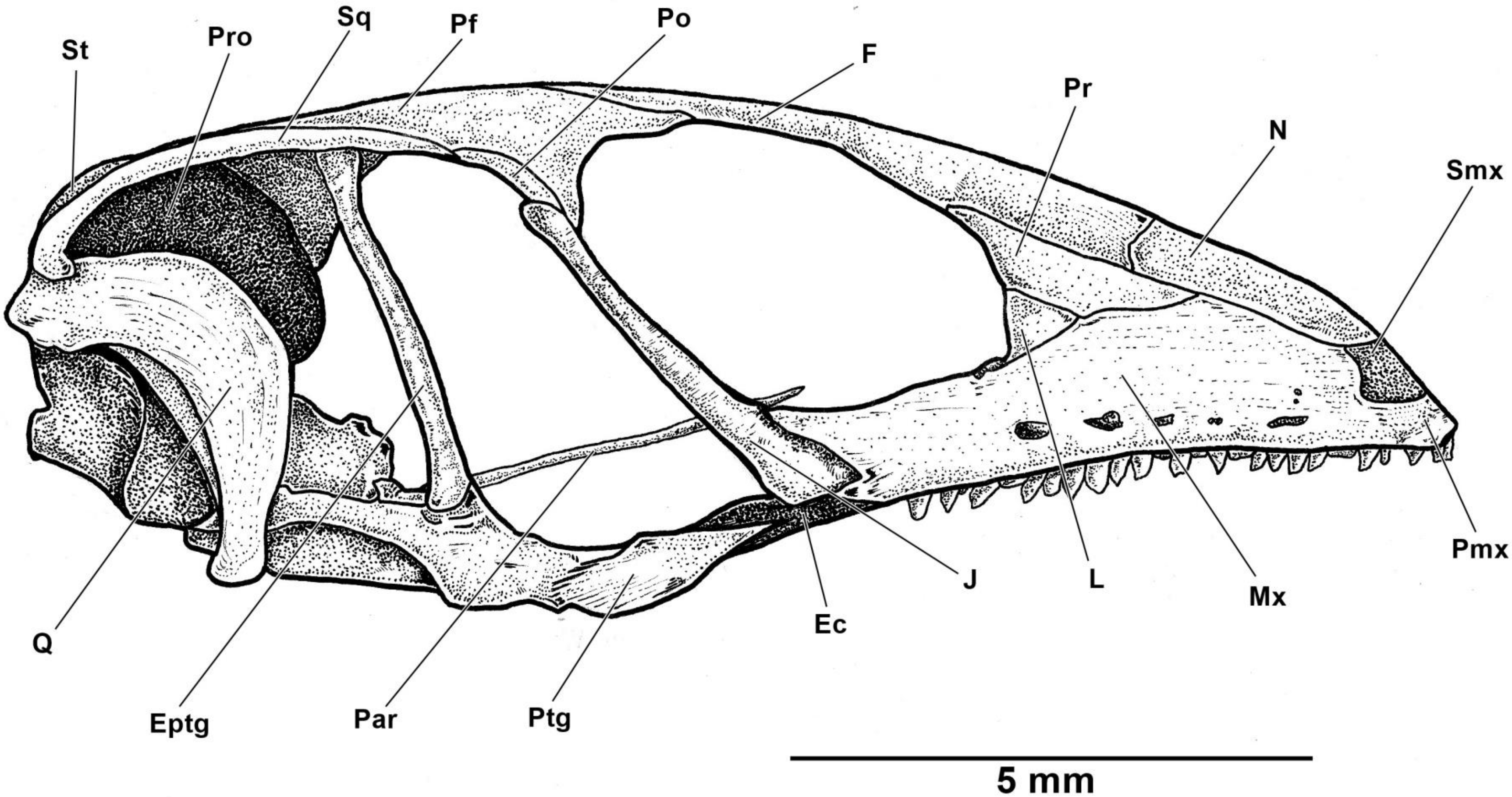

FIG. A2.6 – Illustration of the skull of *Mabuya agilis* MNRJ 14259 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; Sq – squamosal; St - supratemporal.

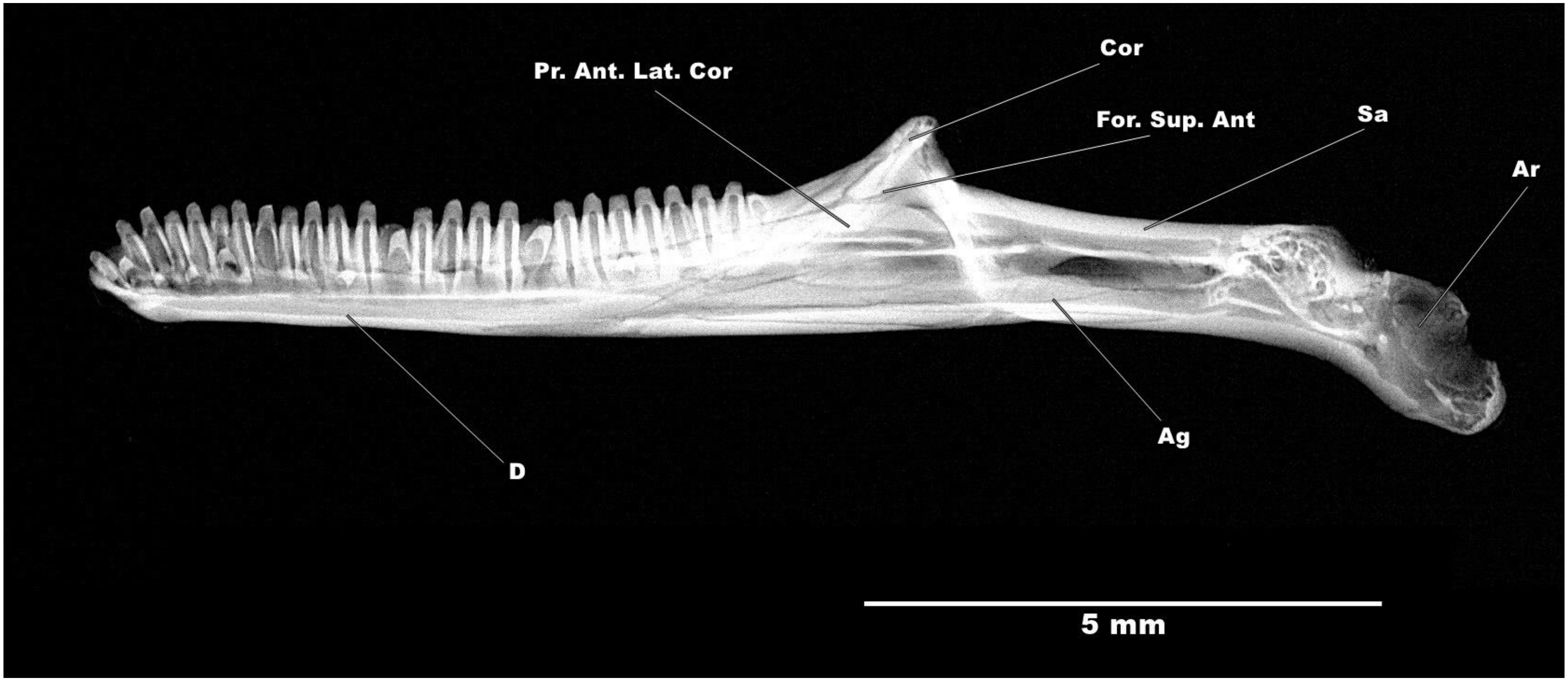

FIG. A2.7 – Radiography of the mandible of *Mabuya agilis* MNRJ 14259 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Sup. Ant – foramen supra-angular anterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

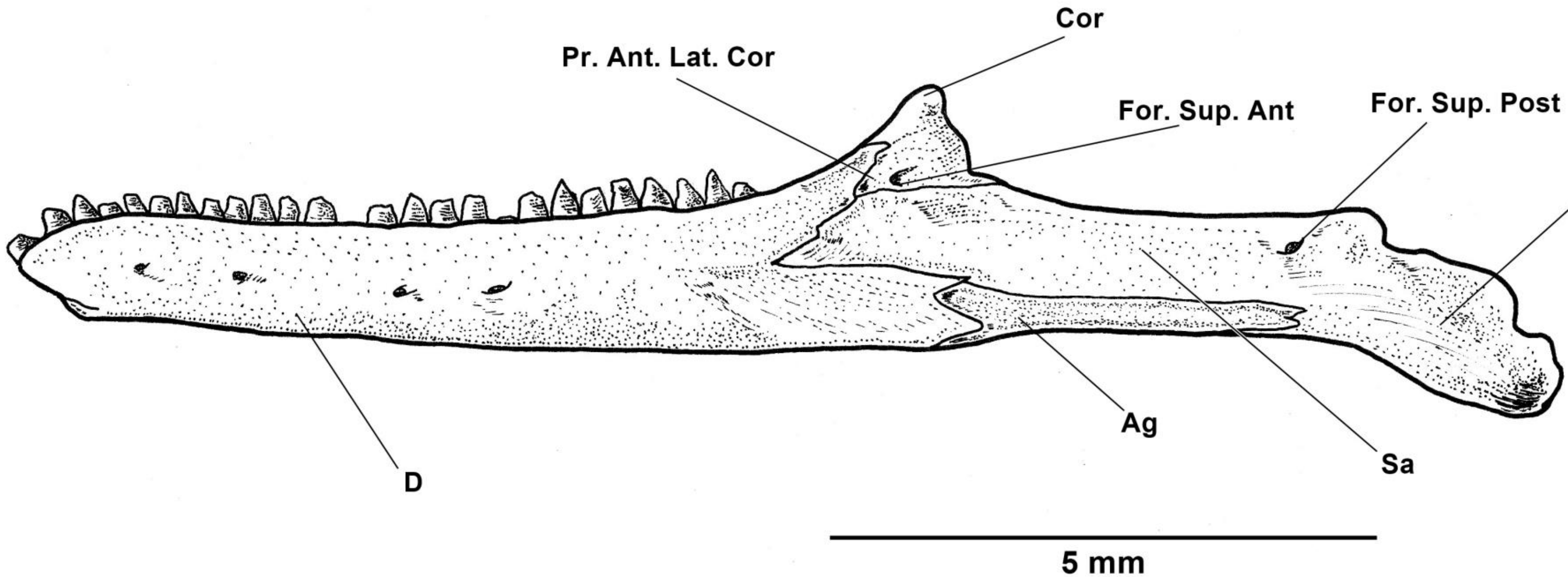

FIG. A2.8 – Illustration of the mandible of *Mabuya agilis* MNRJ 14259 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Supra. Ant – foramen supra-angular anterior; For. Sup. Post – foramen supra-angular posterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

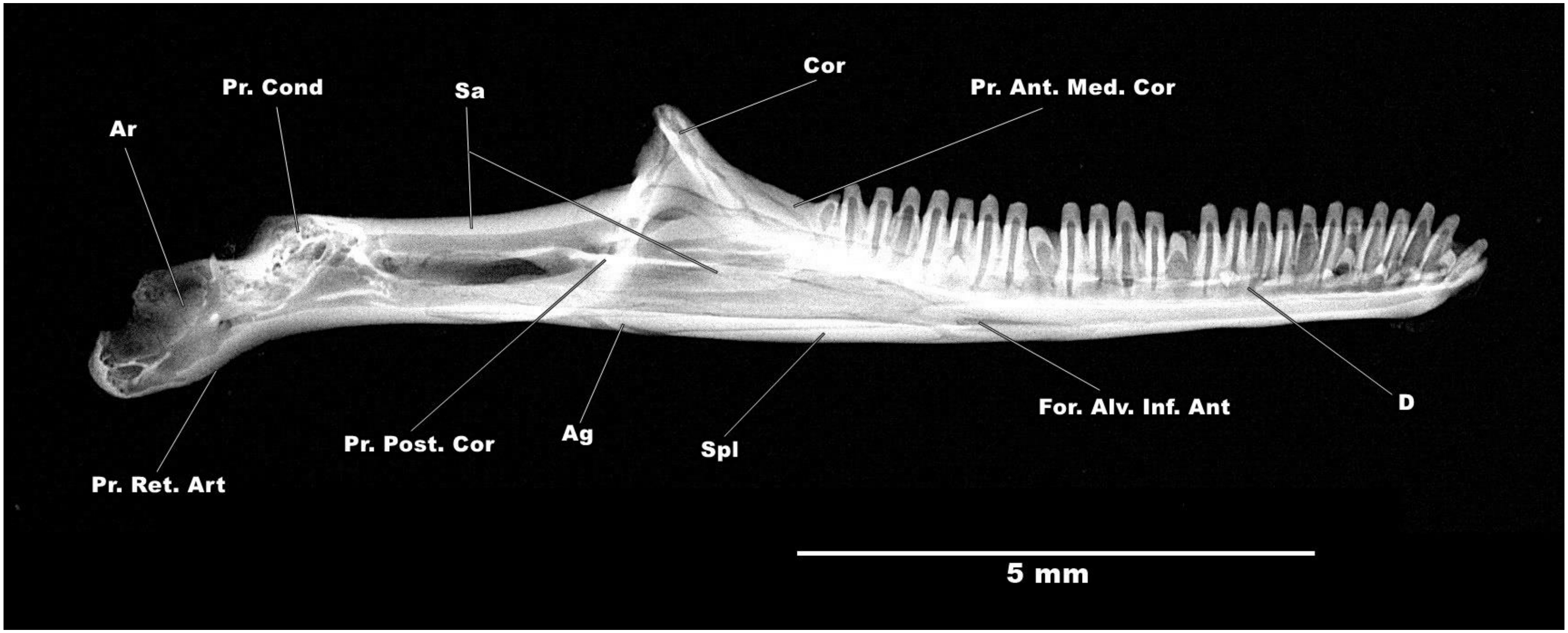

FIG. A2.9 – Radiography of the mandible of *Mabuya agilis* MNRJ 14259 – Lingual view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial process of coronoid; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

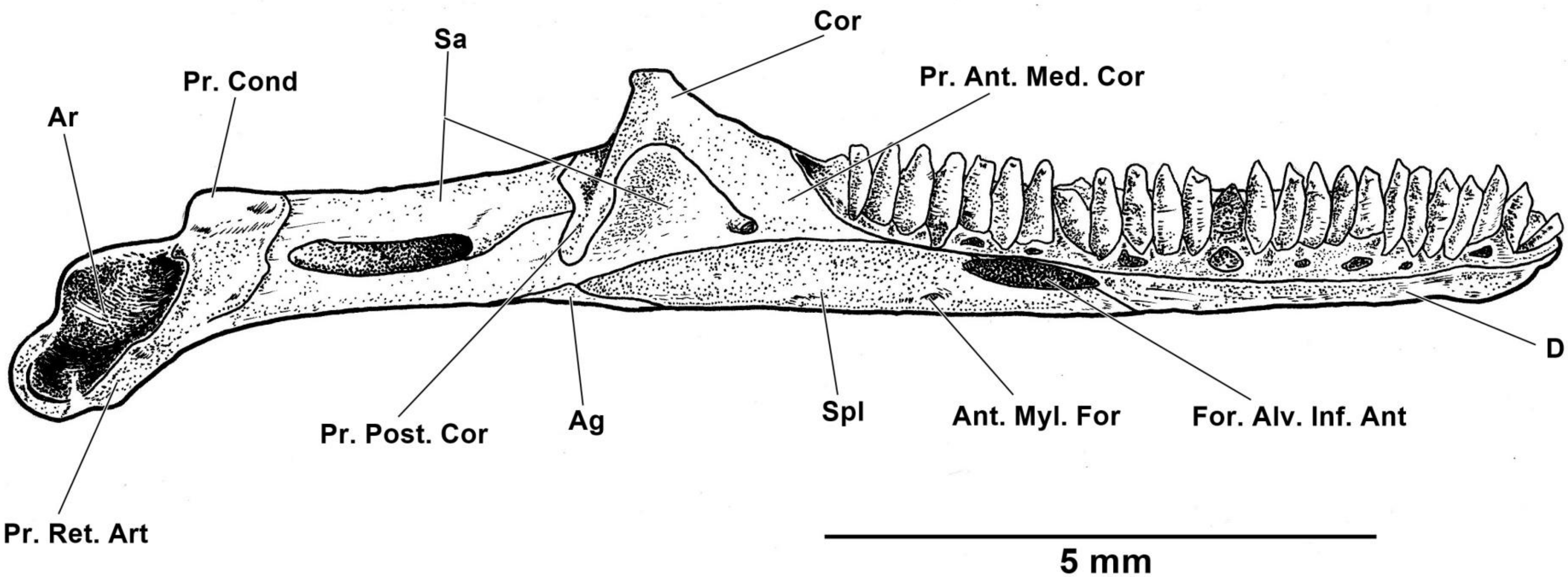

FIG. A2.10 – Illustration of the mandible of *Mabuya agilis* MNRJ 14259 – Lingual view

Ag – angular; Ant. Myl. For – anterior mylohyoid foramen; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial coronoid process; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

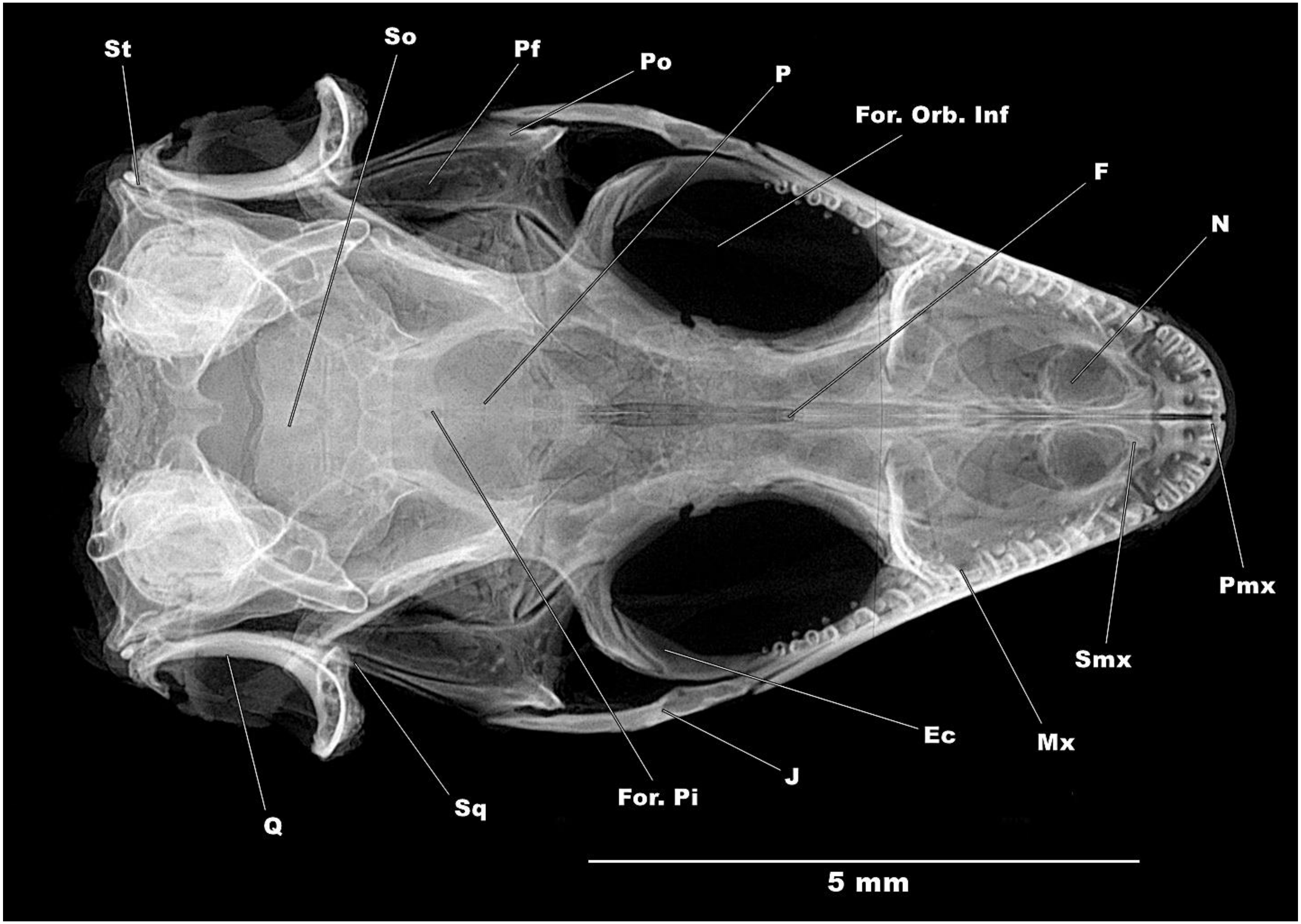

FIG. A2.11 – Radiography of the skull of *Mabuya dorsivittata* MNRJ 27106 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

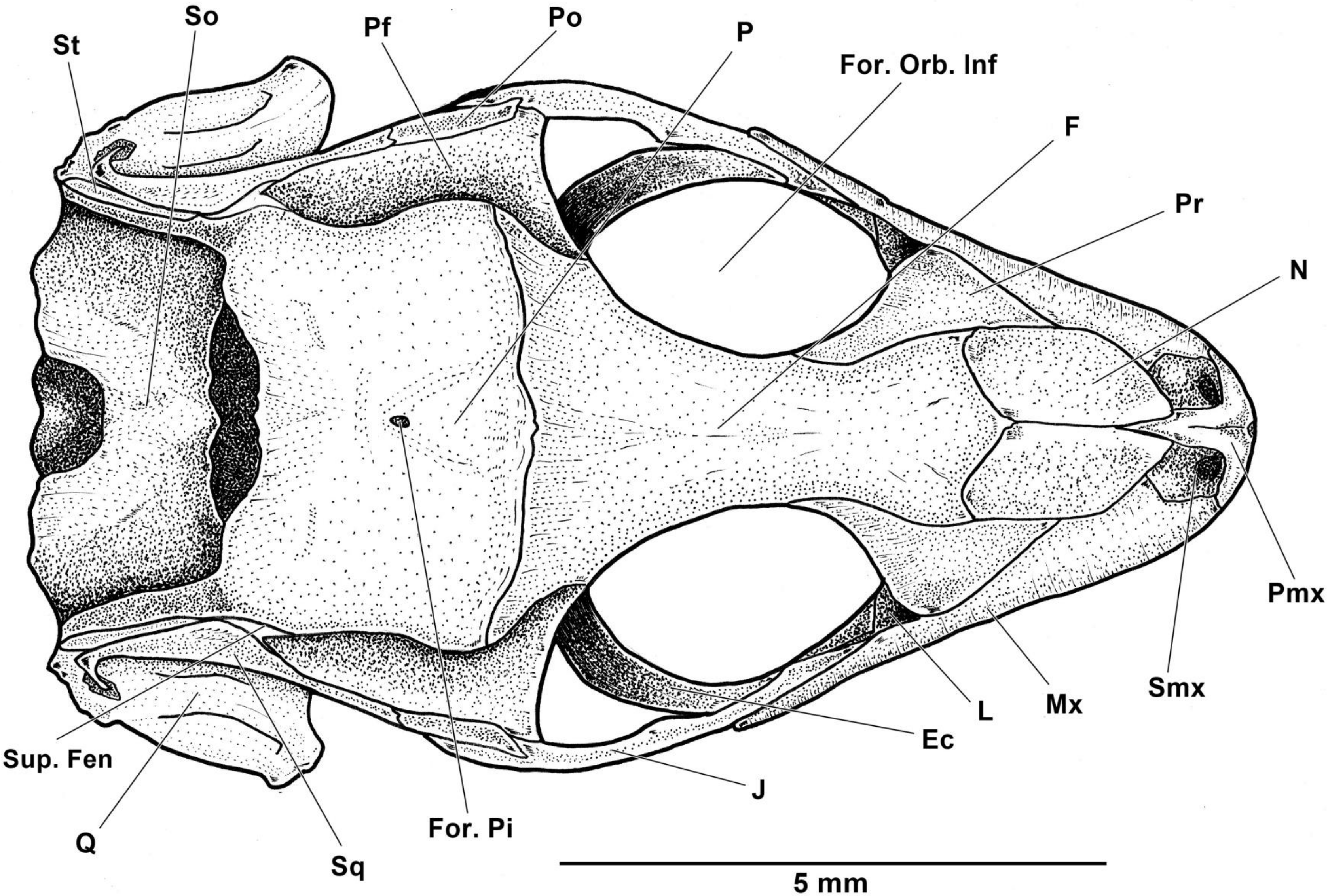

FIG. A2.12 – Illustration of the skull of *Mabuya dorsivittata* MNRJ 27106 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; L – lacrimal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Pr – prefrontal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal; Sup. Fen – supratemporal fenestra.

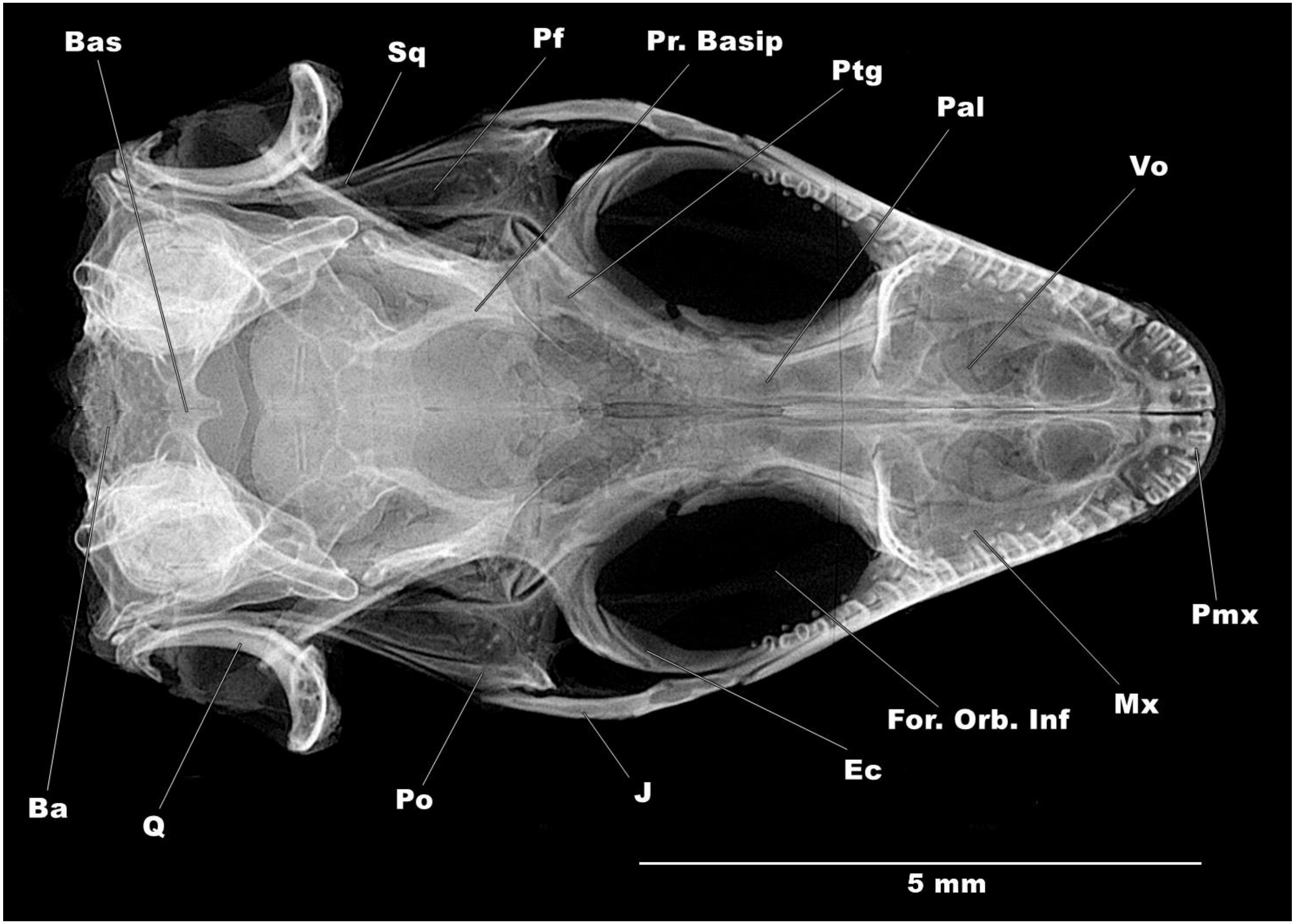

FIG. A2.13 – Radiography of the skull of *Mabuya dorsivittata* MNRJ 27106 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

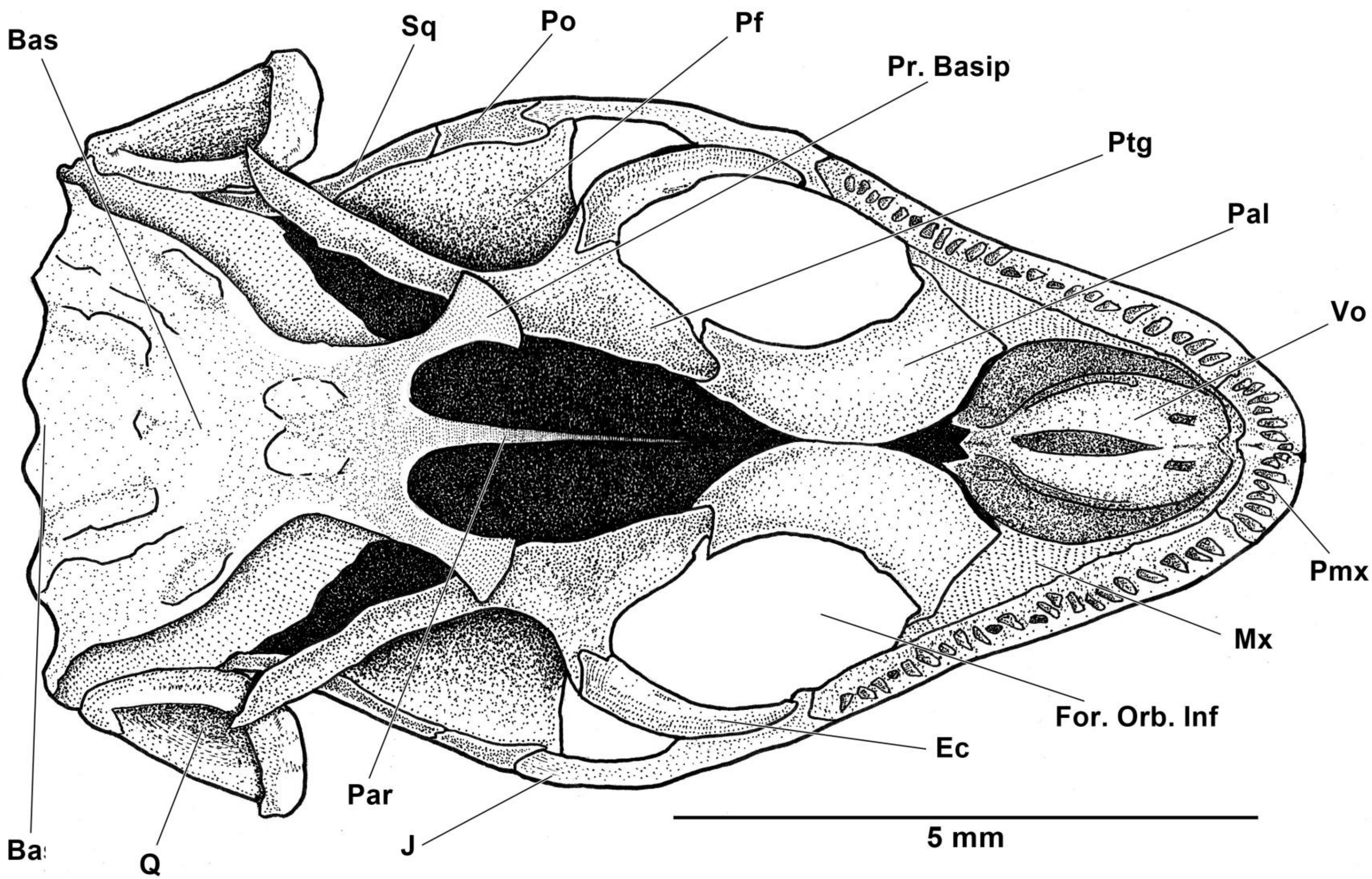

FIG. A2.14 – Illustration of the skull of *Mabuya dorsivittata* MNRJ 27106 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

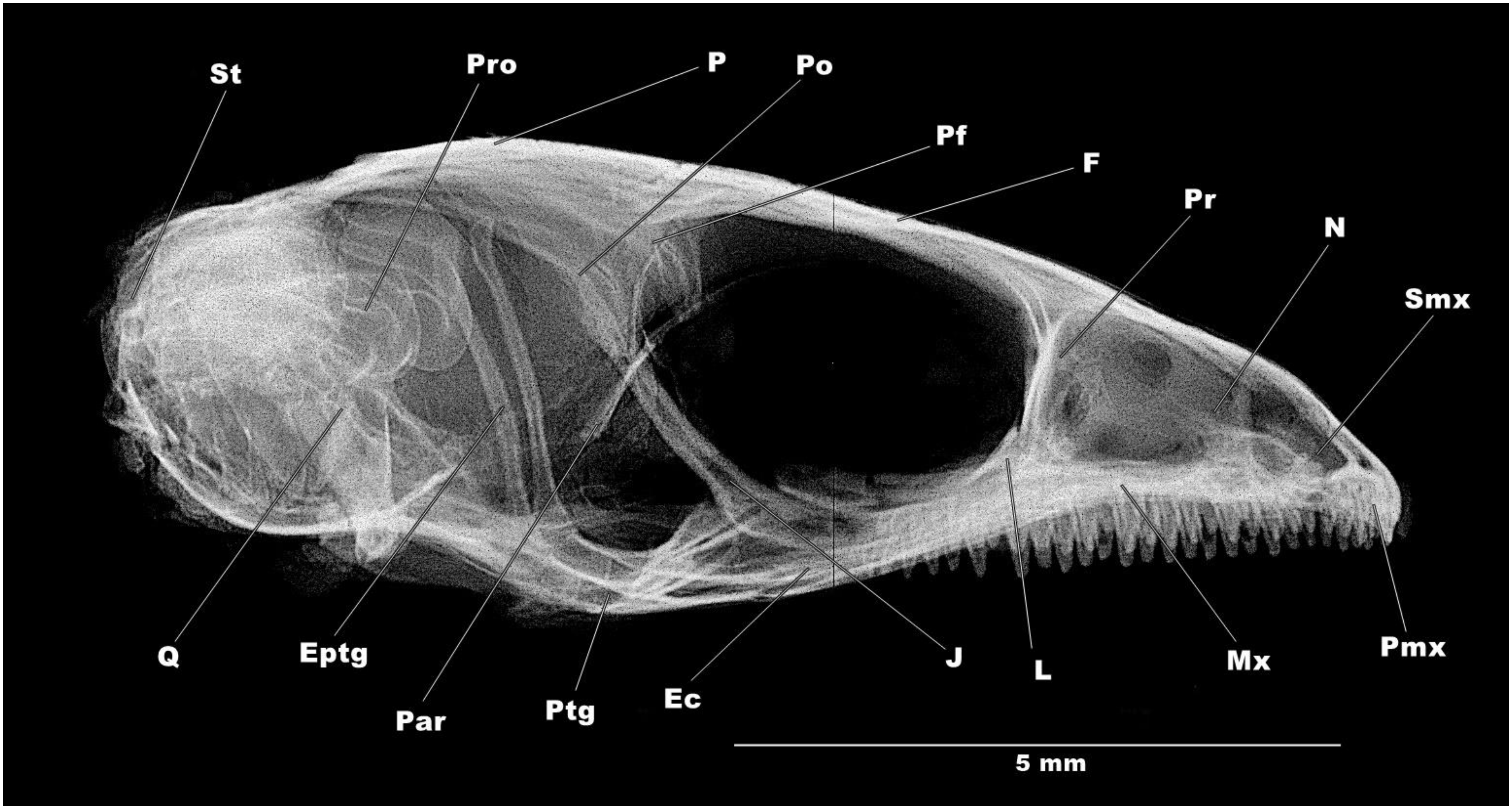

FIG. A2.15 – Radiography of the skull of *Mabuya dorsivittata* MNRJ 27106 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; St - supratemporal.

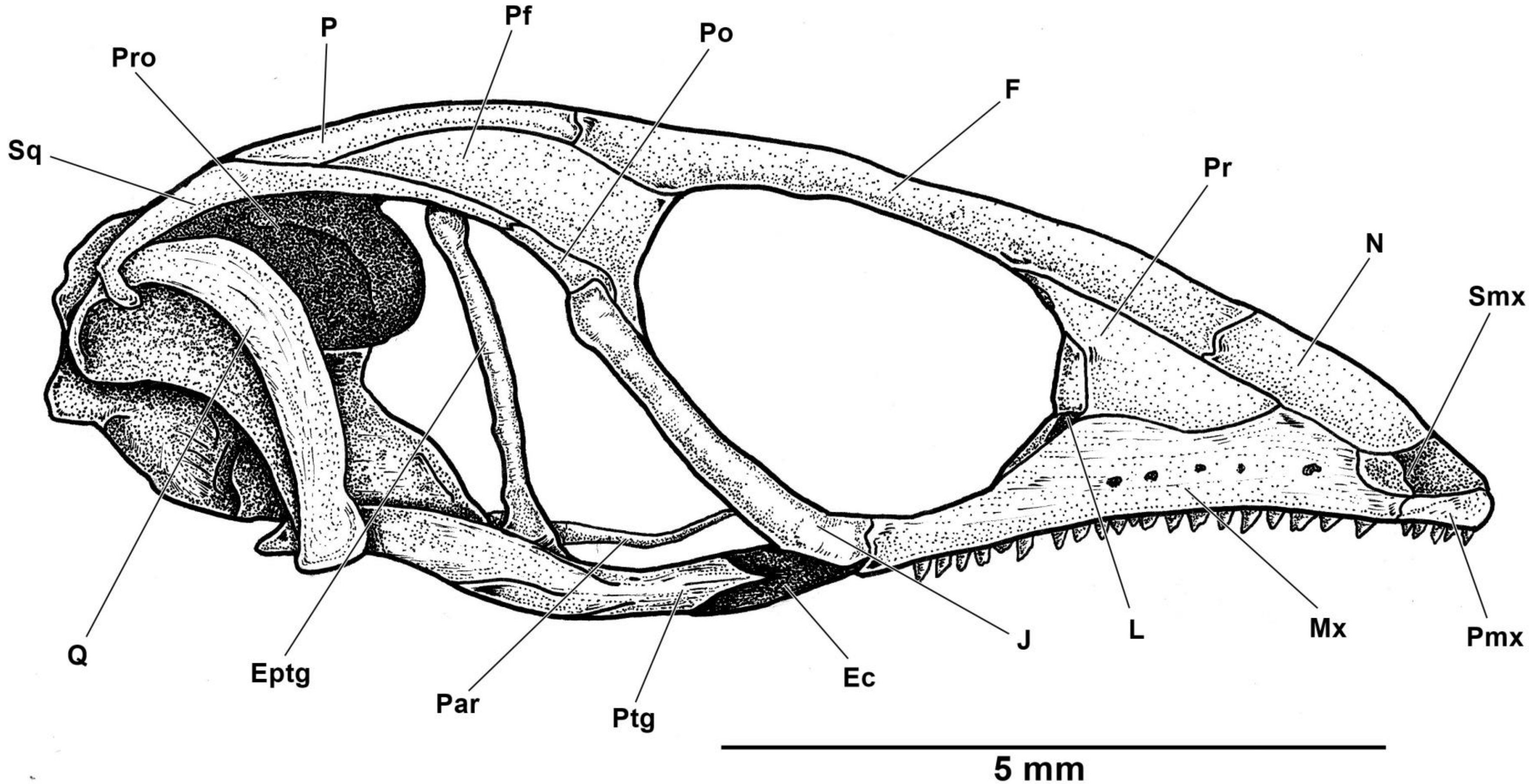

FIG. A2.16 – Illustration of the skull of *Mabuya dorsivittata* MNRJ 27106 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; Sq – squamosal.

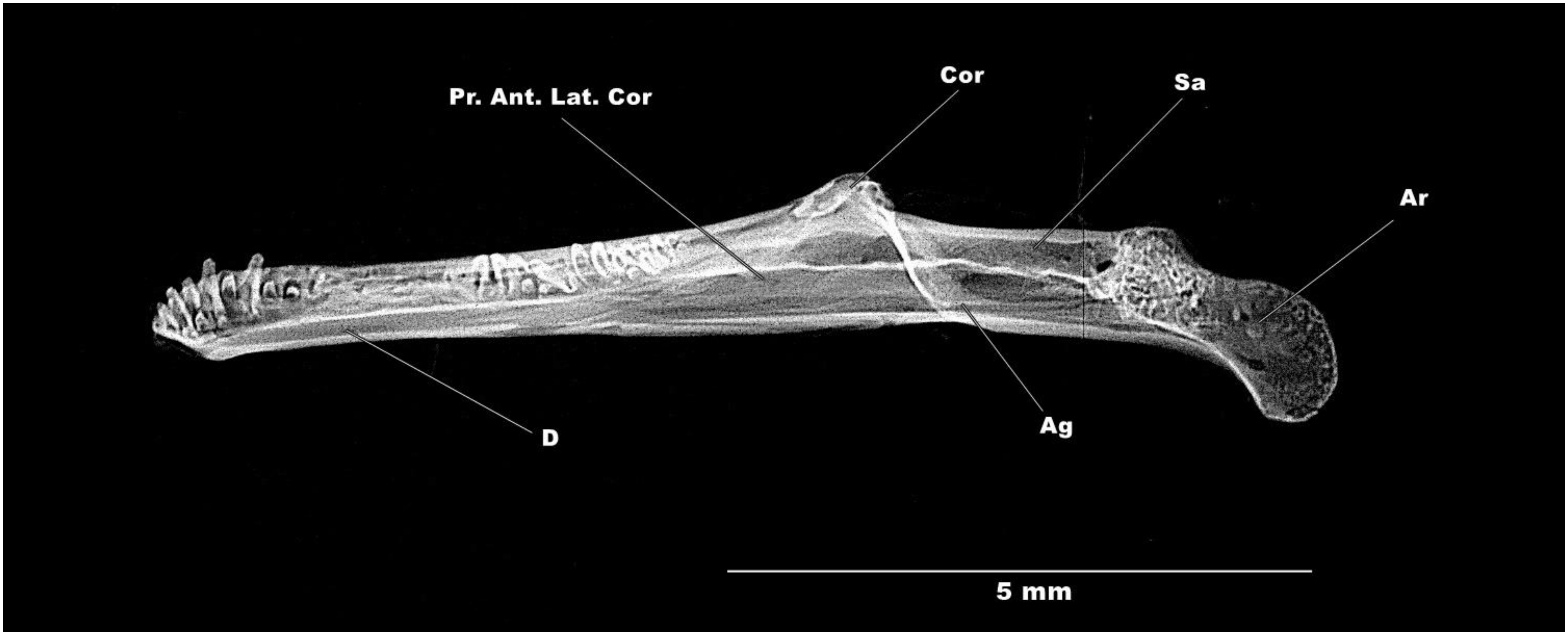

FIG. A2.17 – Radiography of the mandible of *Mabuya dorsivittata* MNRJ 27106 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

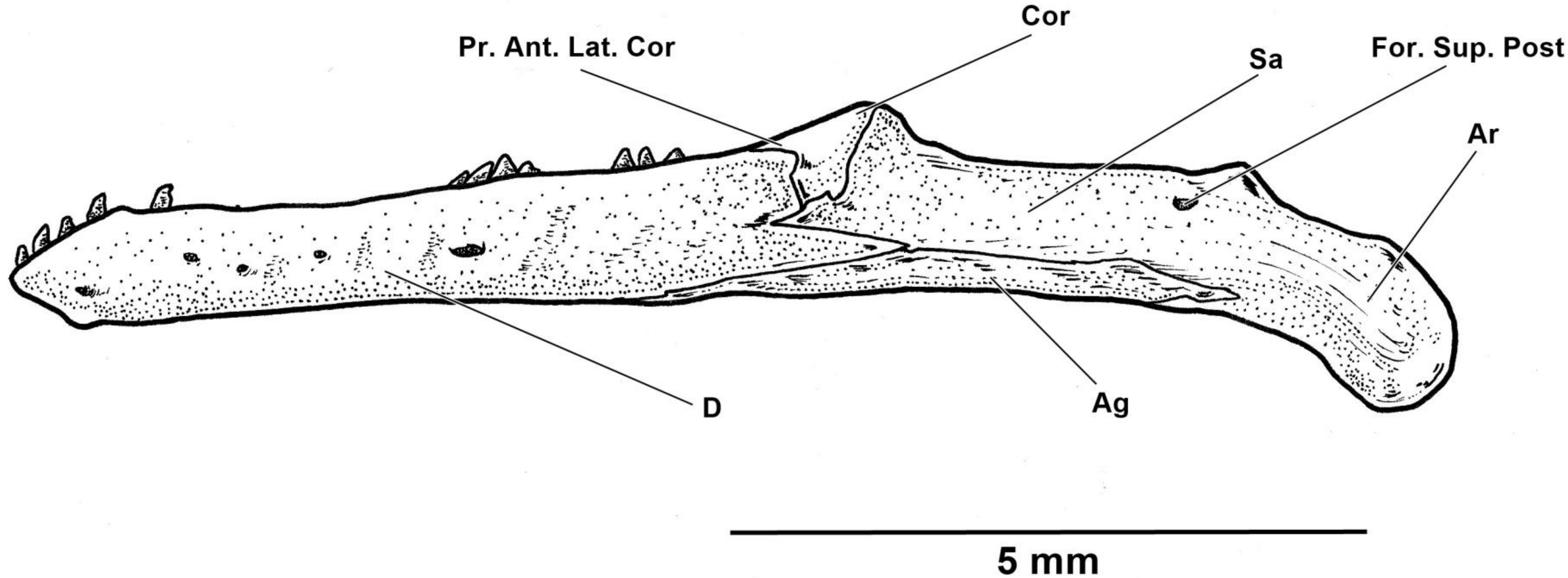

FIG. A2.18 – Illustration of the mandible of *Mabuya dorsivittata* MNRJ 27106 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Sup. Post – foramen supra-angular posterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

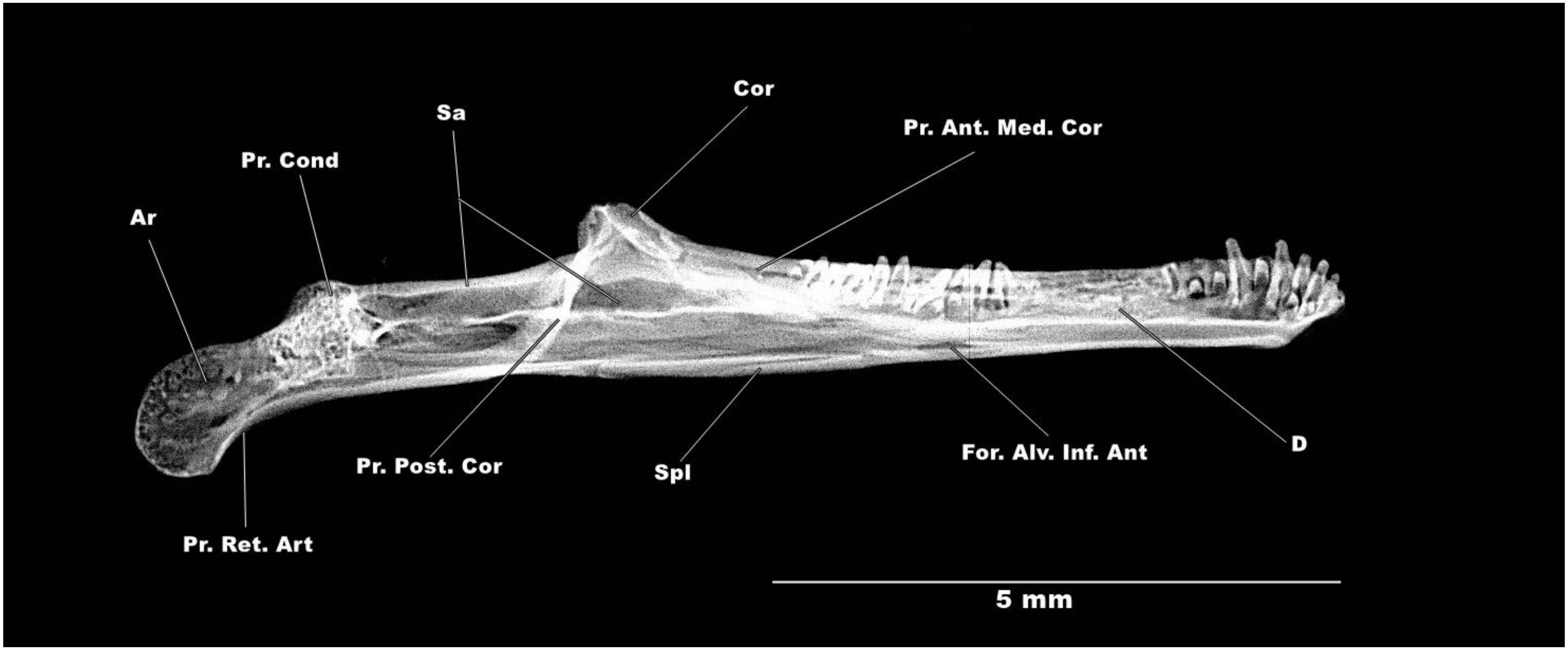

FIG. A2.19 – Radiography of the mandible of *Mabuya dorsivittata* MNRJ 27106 – Lingual view

Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial process of coronoid; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

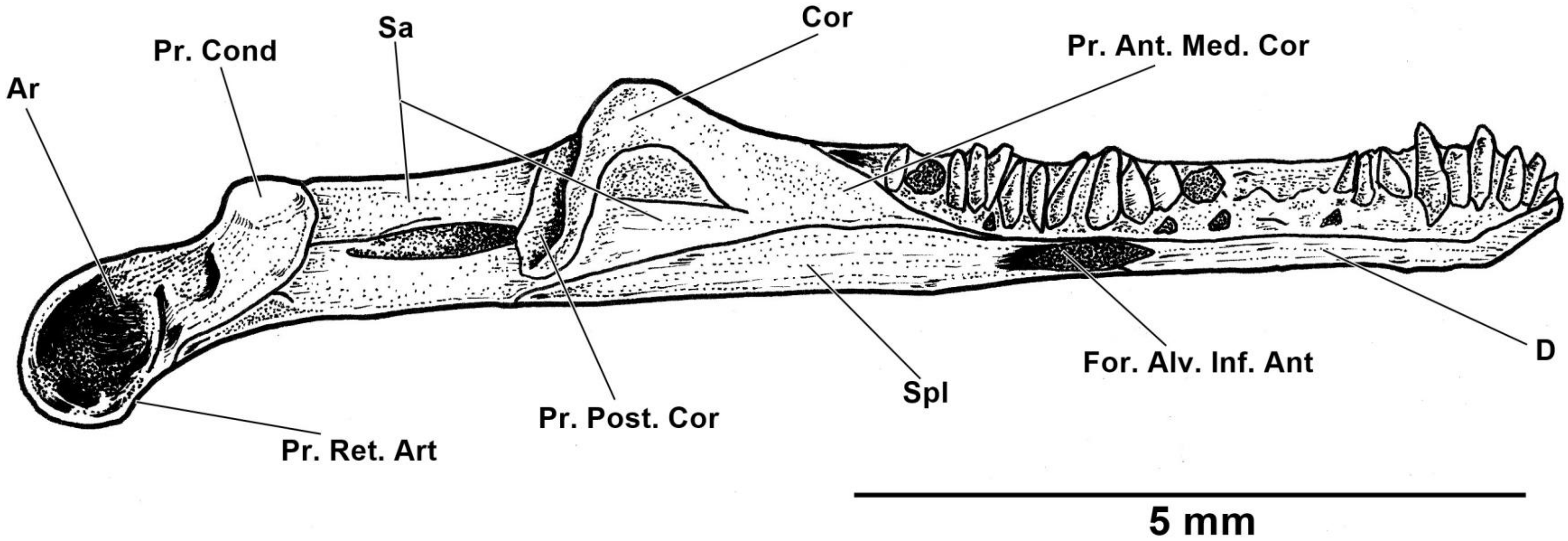

FIG. A2.20 – Illustration of the mandible of *Mabuya dorsivittata* MNRJ 27106 – Lingual view

Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial coronoid process; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

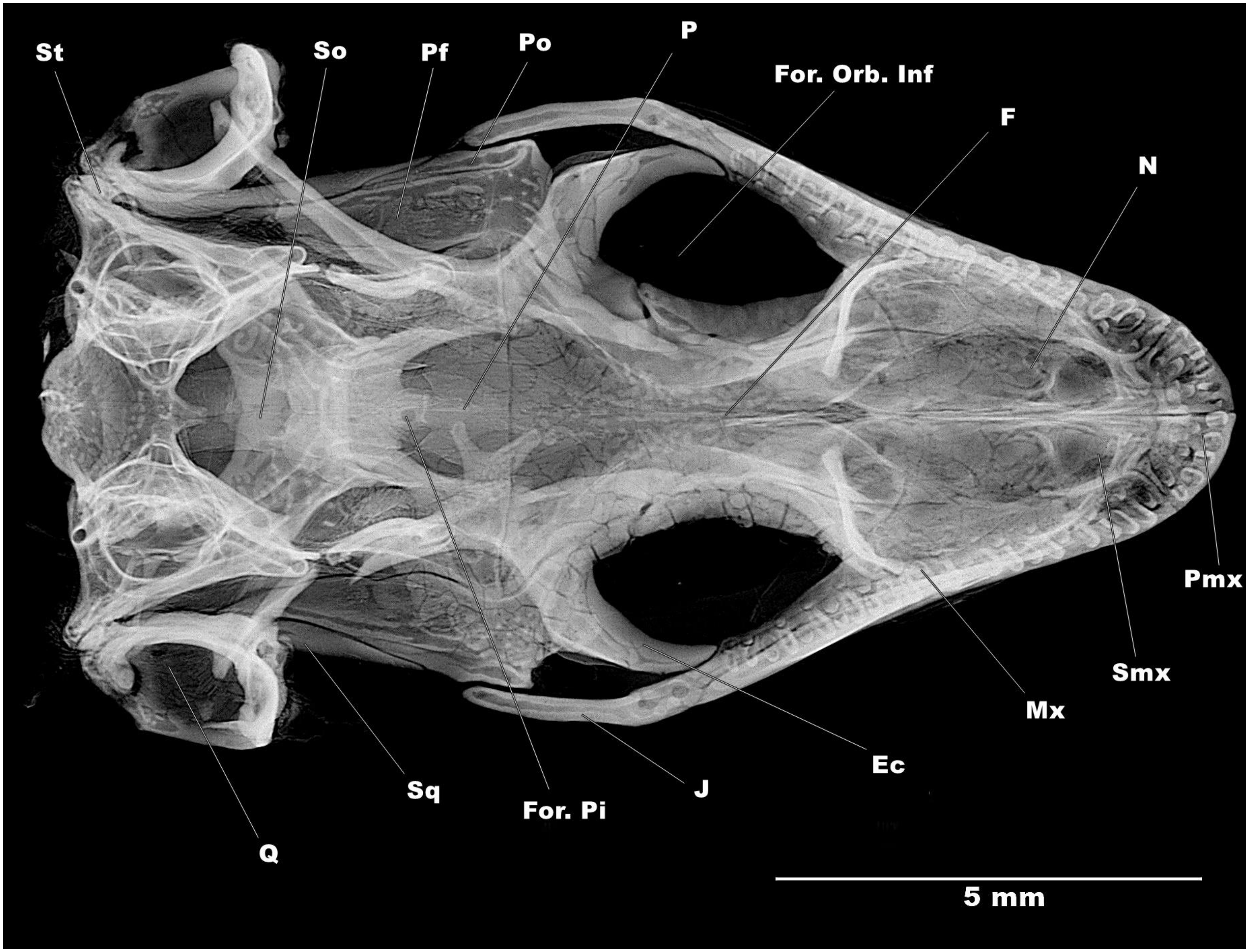

FIG. A2.21 – Radiography of the skull of *Mabuya frenata* MNRJ 6811 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

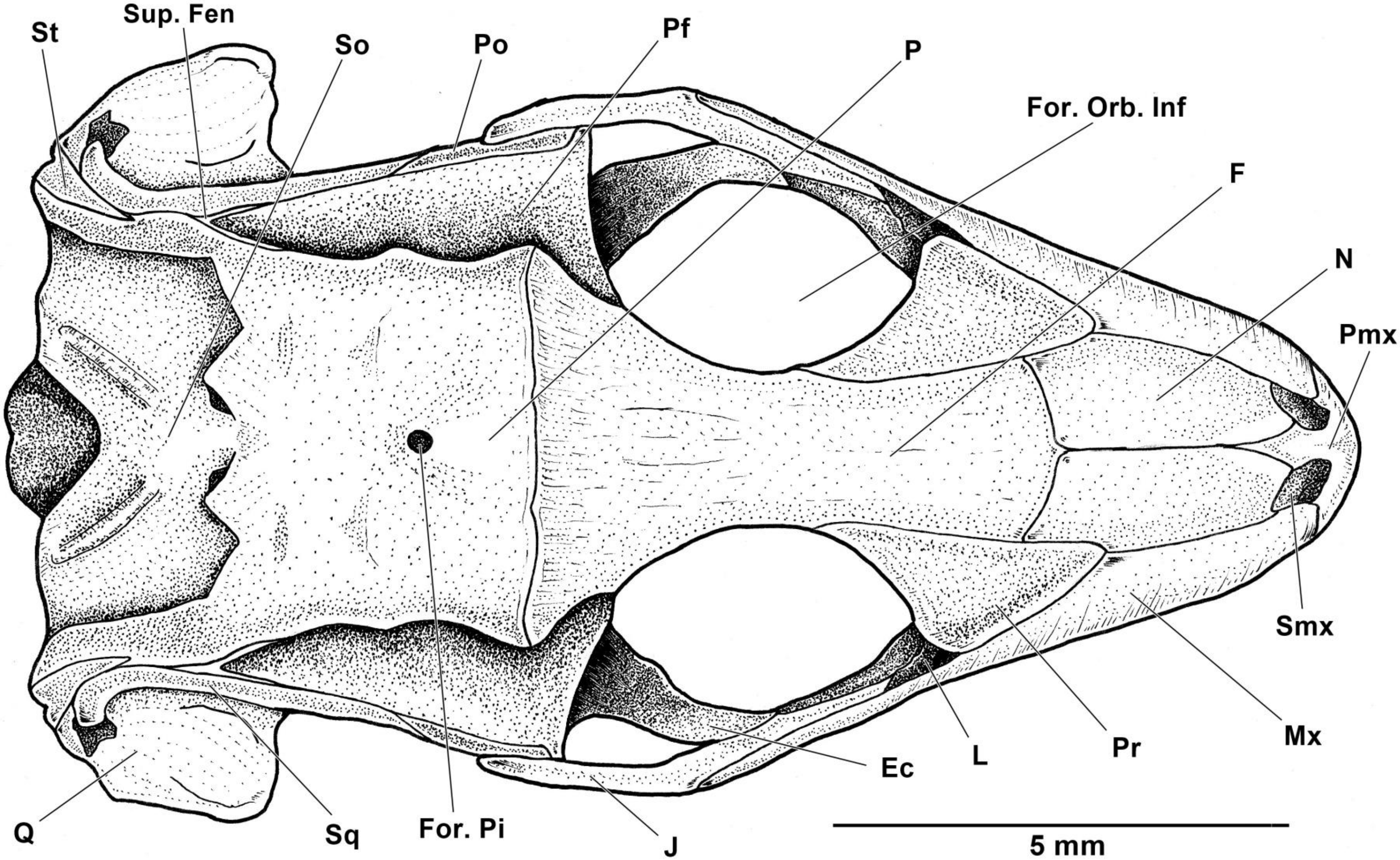

FIG. A2.22 – Illustration of the skull of *Mabuya frenata* MNRJ 6811 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; L – lacrimal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Pr – prefrontal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal; Sup. Fen – supratemporal fenestra.

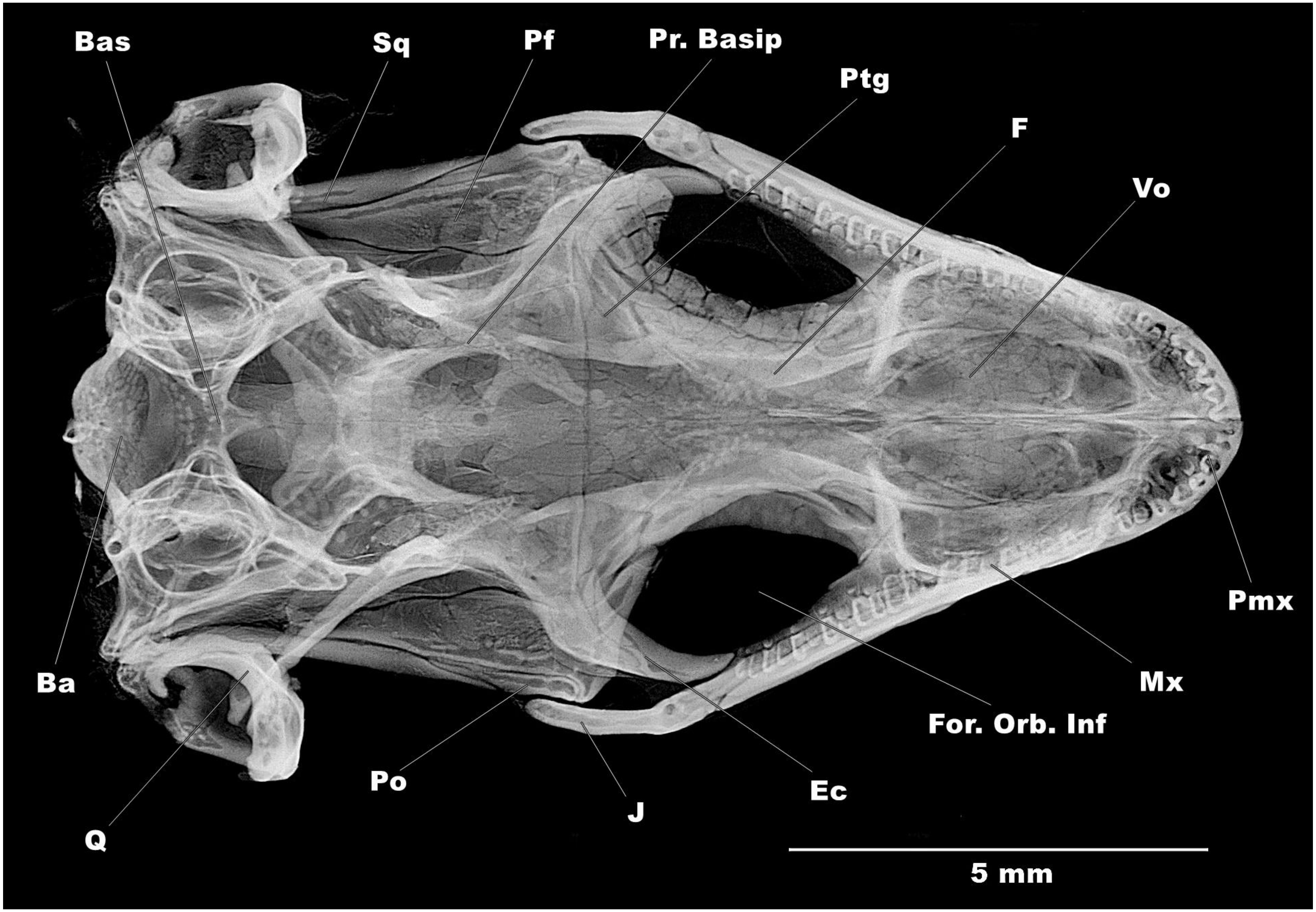

FIG. A2.23 – Radiography of the skull of *Mabuya frenata* MNRJ 6811 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

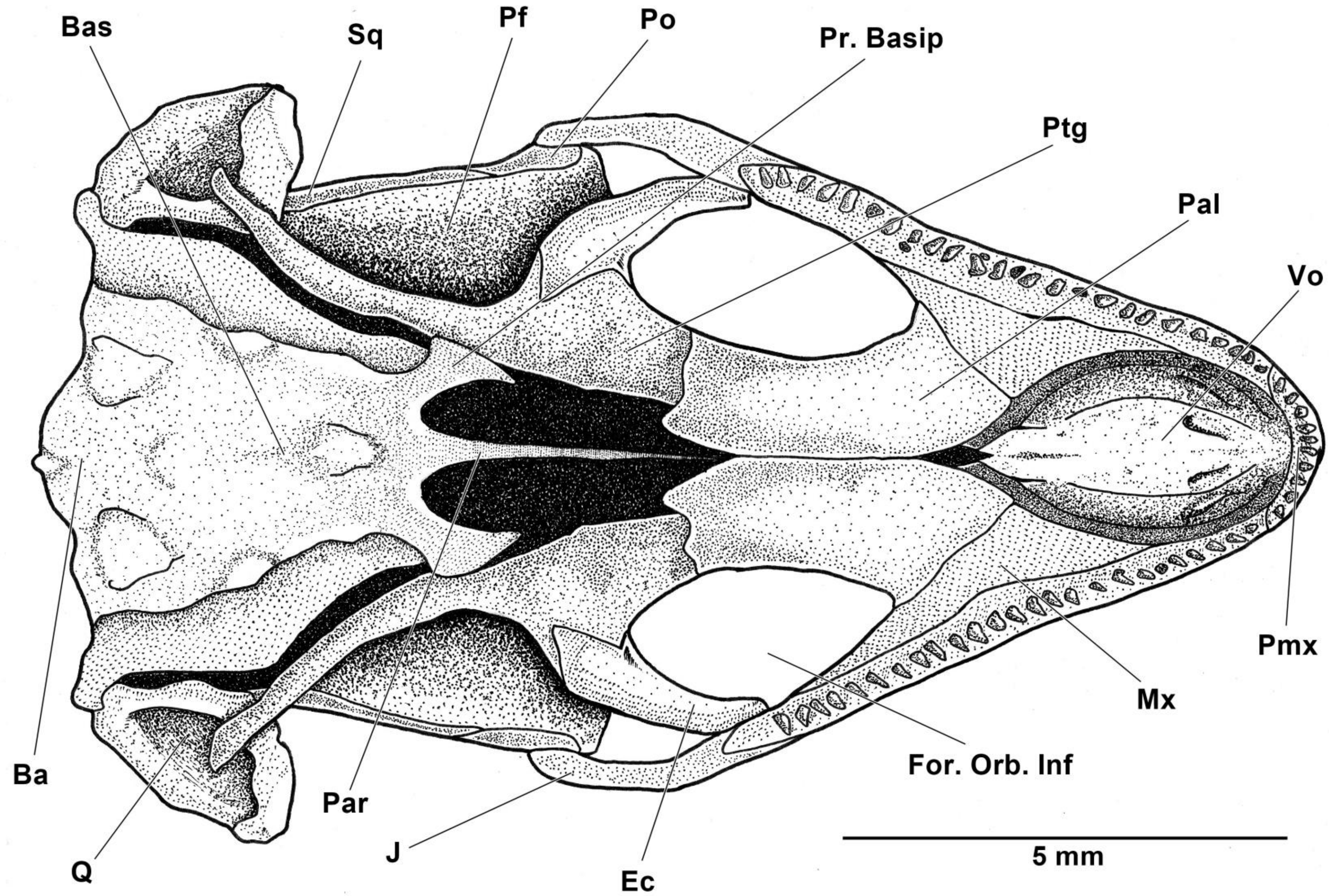

FIG. A2.24 – Illustration of the skull of *Mabuya frenata* MNRJ 6811 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

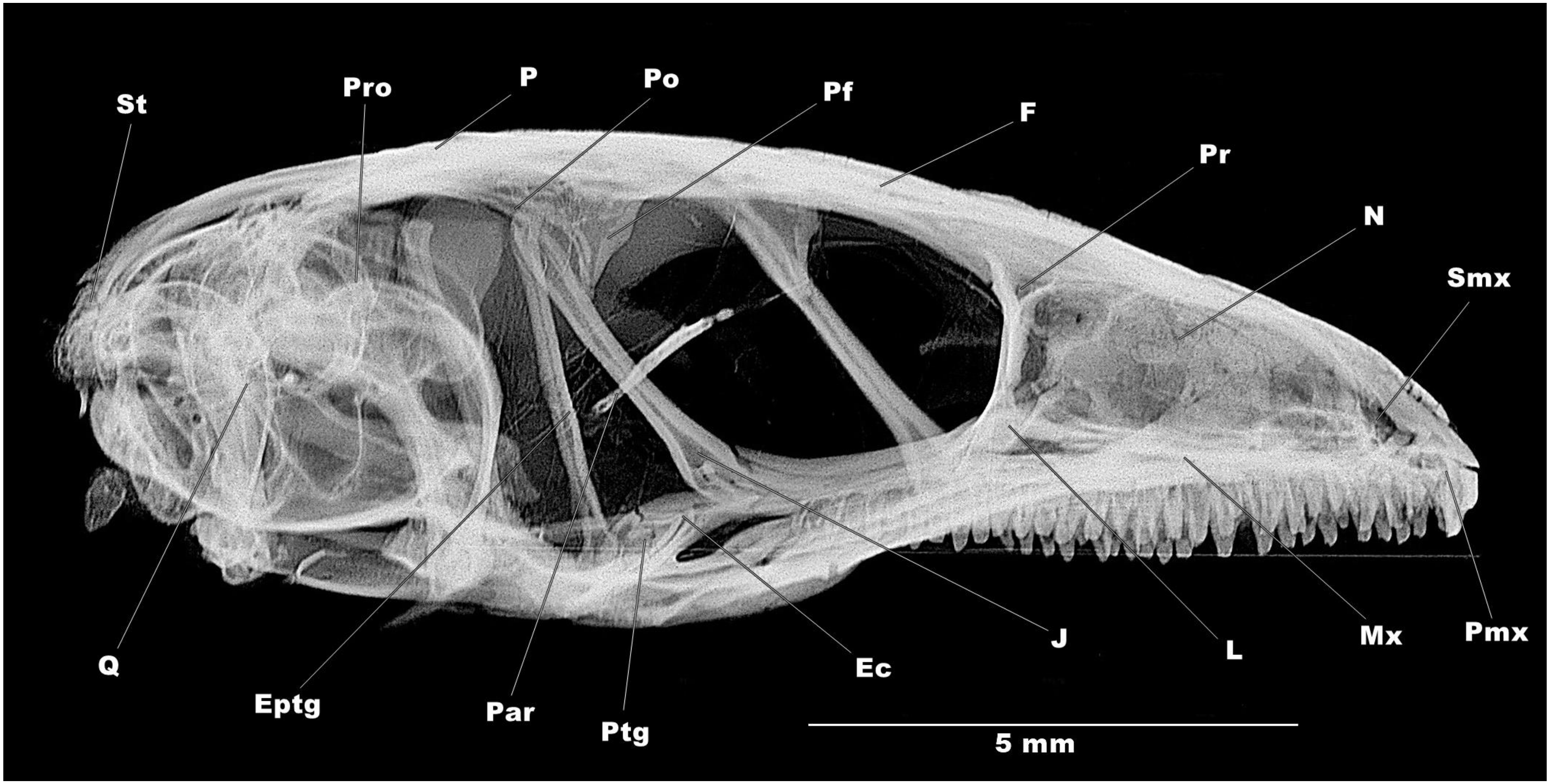

FIG. A2.25 – Radiography of the skull of *Mabuya frenata* MNRJ 6811 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; St - supratemporal.

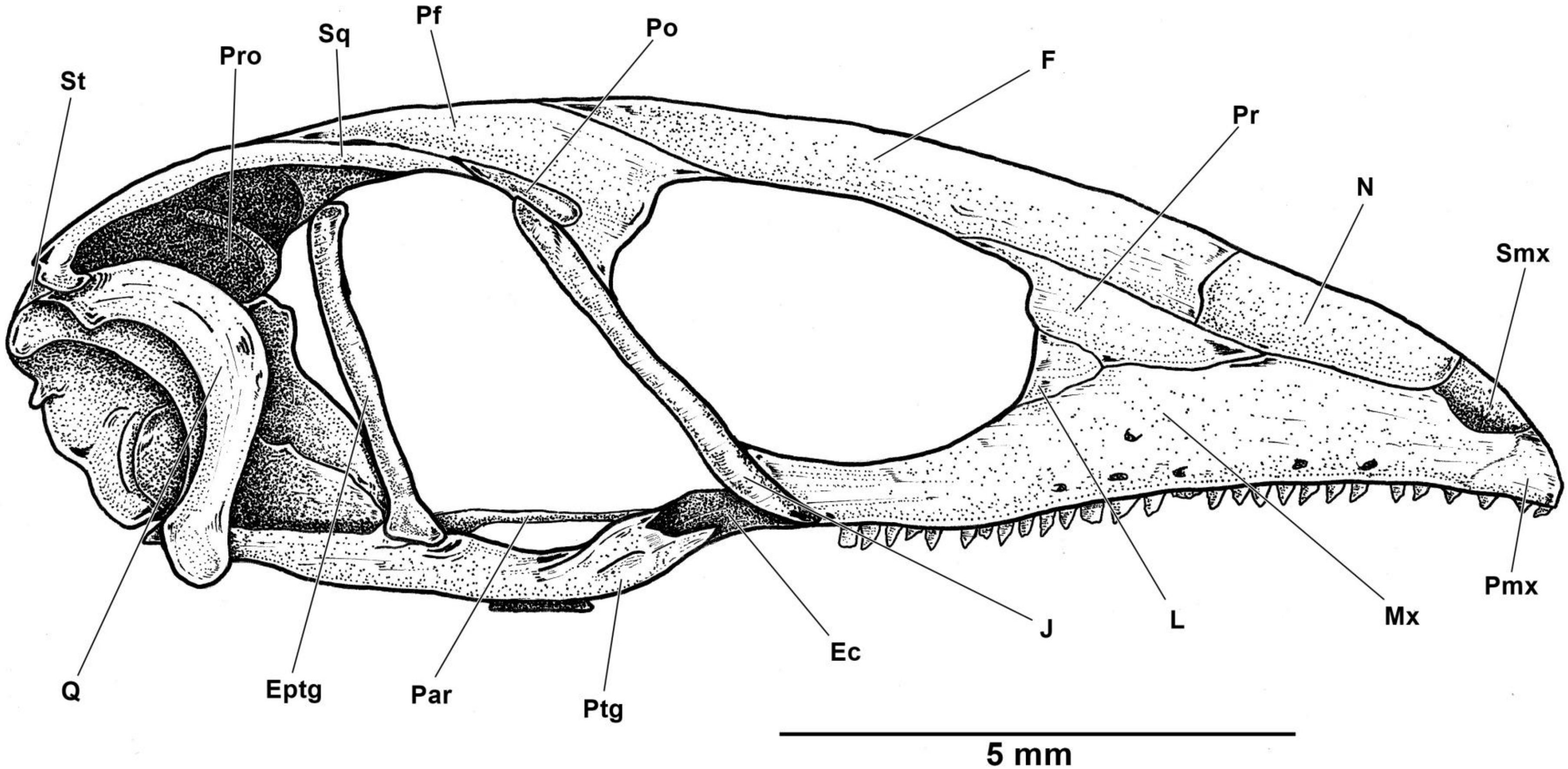

FIG. A2.26 – Illustration of the skull of *Mabuya frenata* MNRJ 6811 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; Sq – squamosal; St **-** supratemporal.

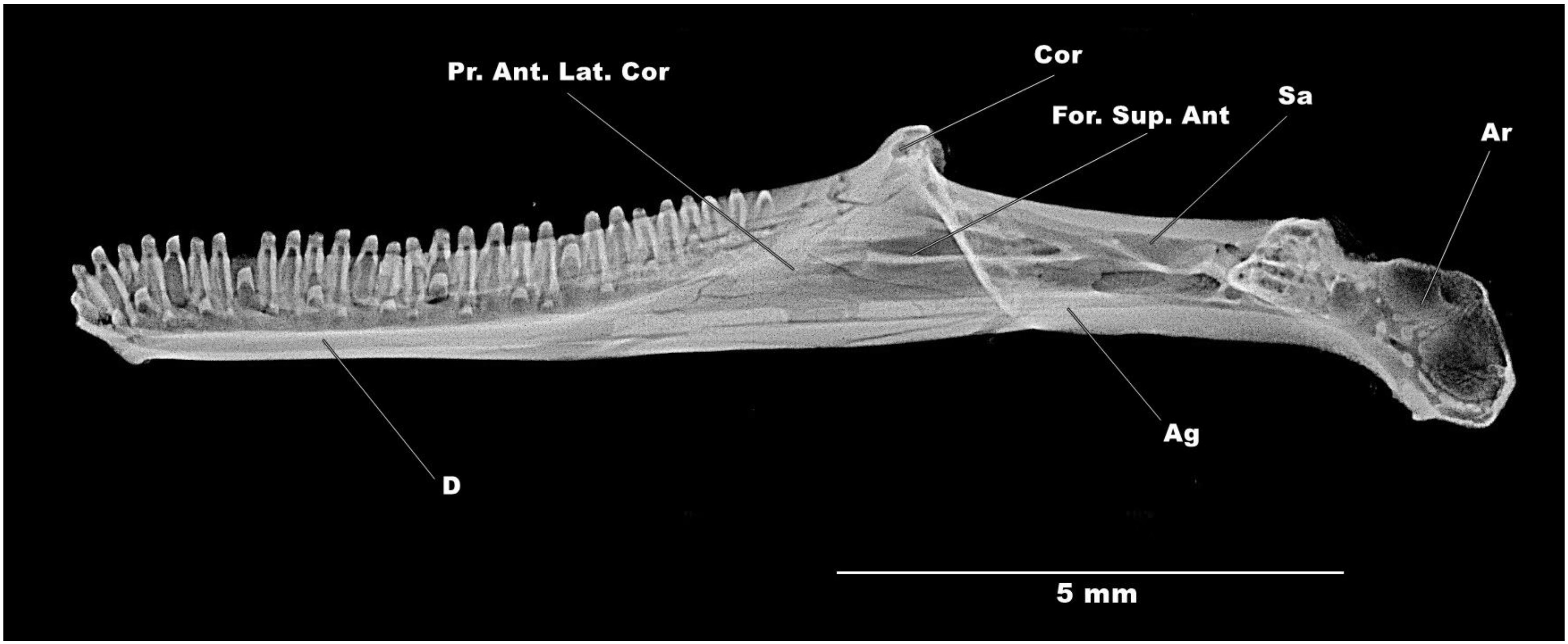

FIG. A2.27 – Radiography of the mandible of *Mabuya frenata* MNRJ 6811 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Sup. Ant – foramen supra-angular anterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

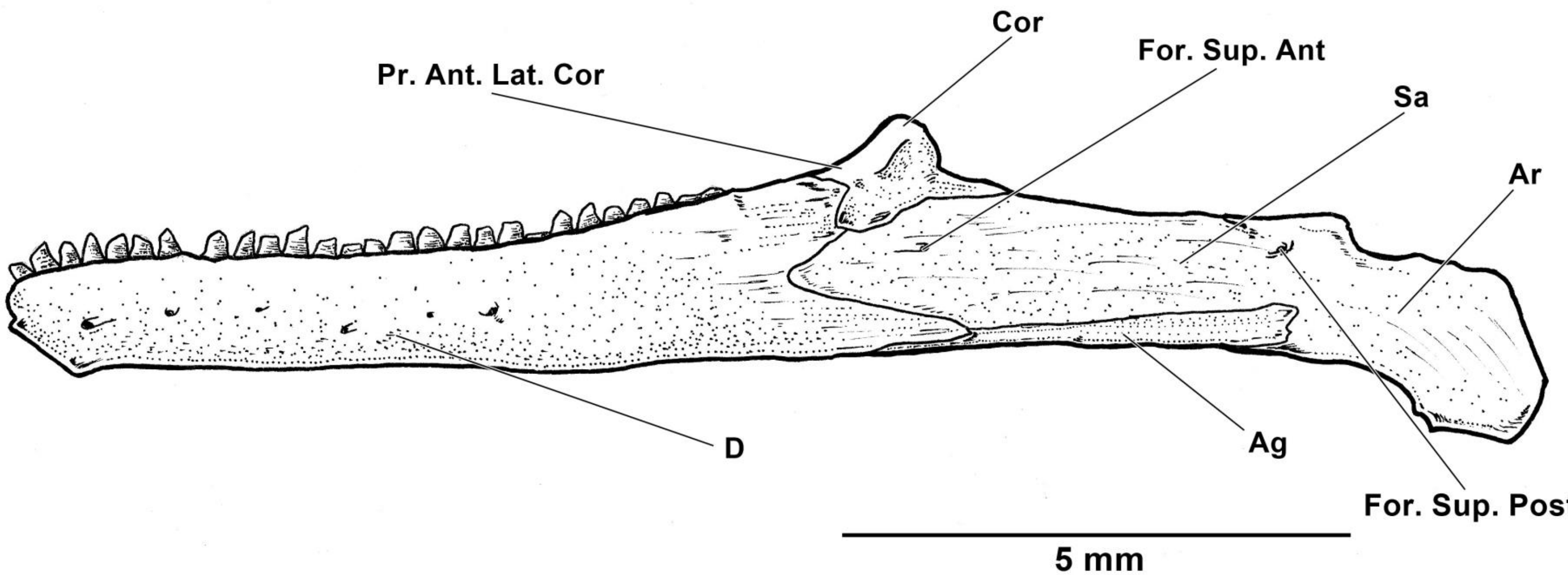

FIG. A2.28 – Illustration of the mandible of *Mabuya frenata* MNRJ 6811 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Supra. Ant – foramen supra-angular anterior; For. Sup. Post – foramen supra-angular posterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

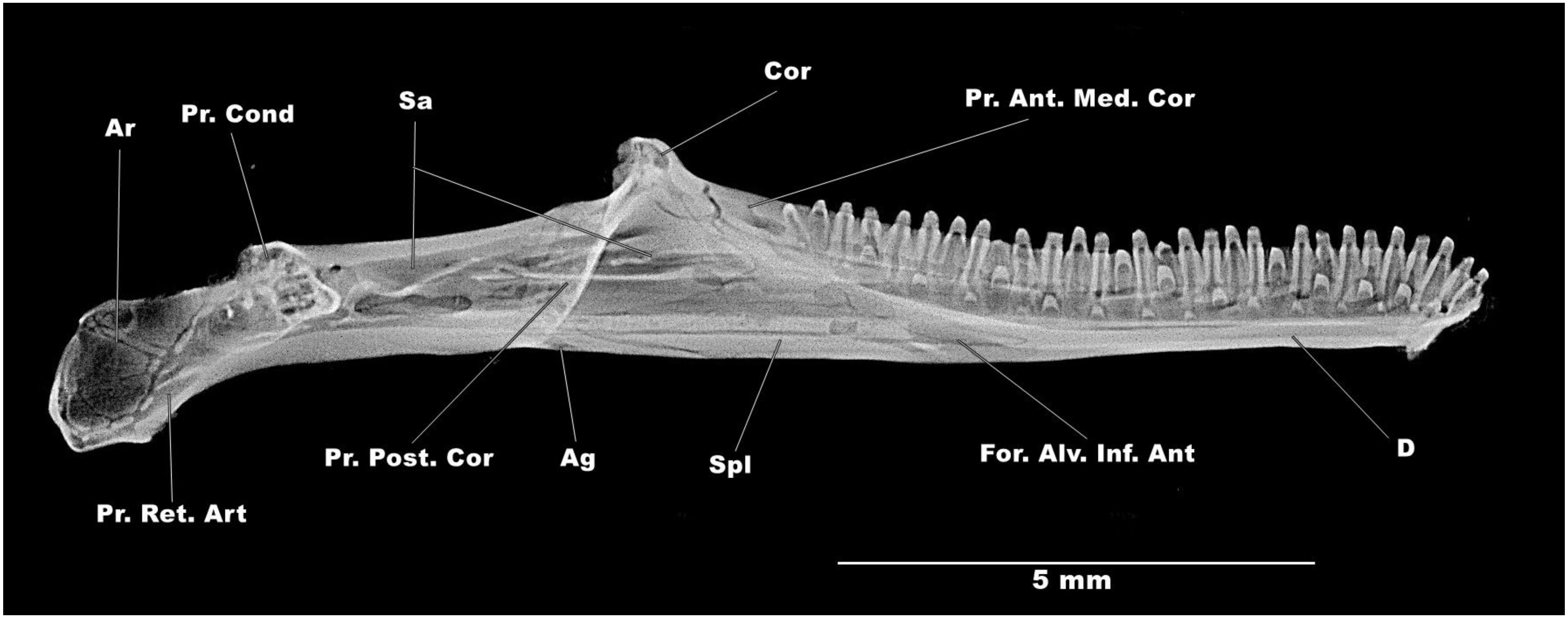

FIG. A2.29 – Radiography of the mandible of *Mabuya frenata* MNRJ 6811 – Lingual view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial process of coronoid; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

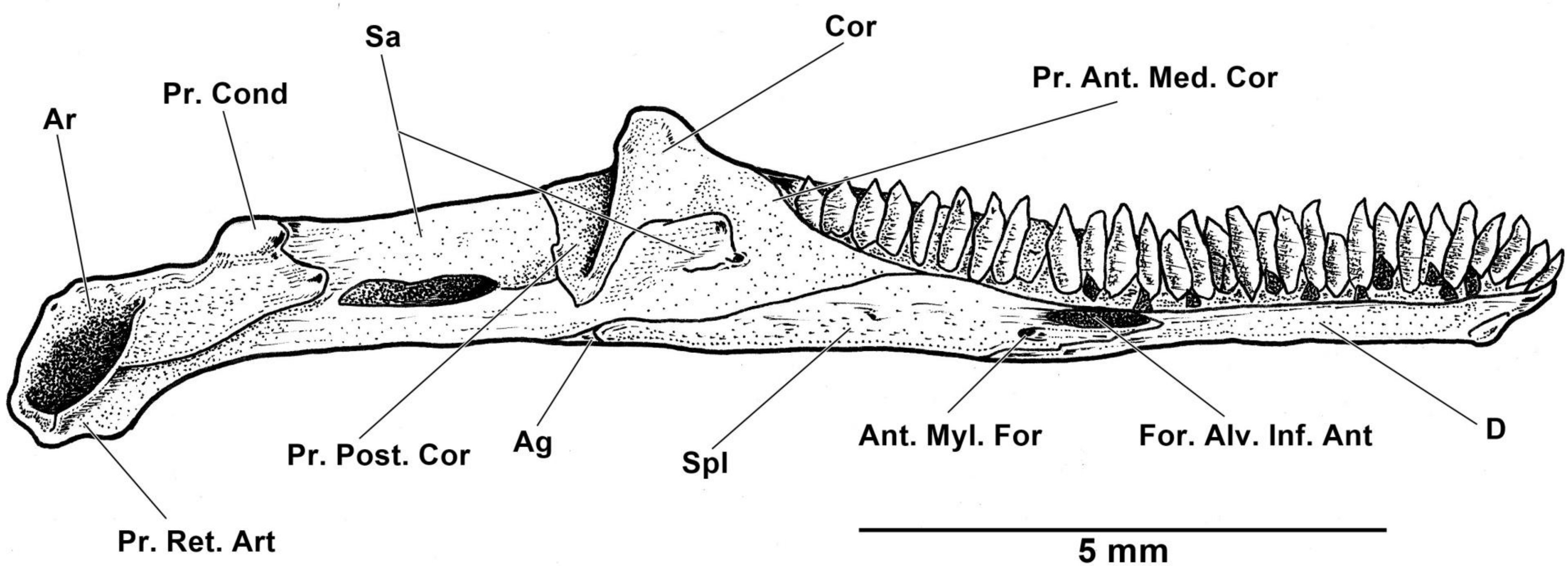

FIG. A2.30 – Illustration of the mandible of *Mabuya frenata* MNRJ 6811 – Lingual view

Ag – angular; Ant. Myl. For – anterior mylohyoid foramen; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial coronoid process; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

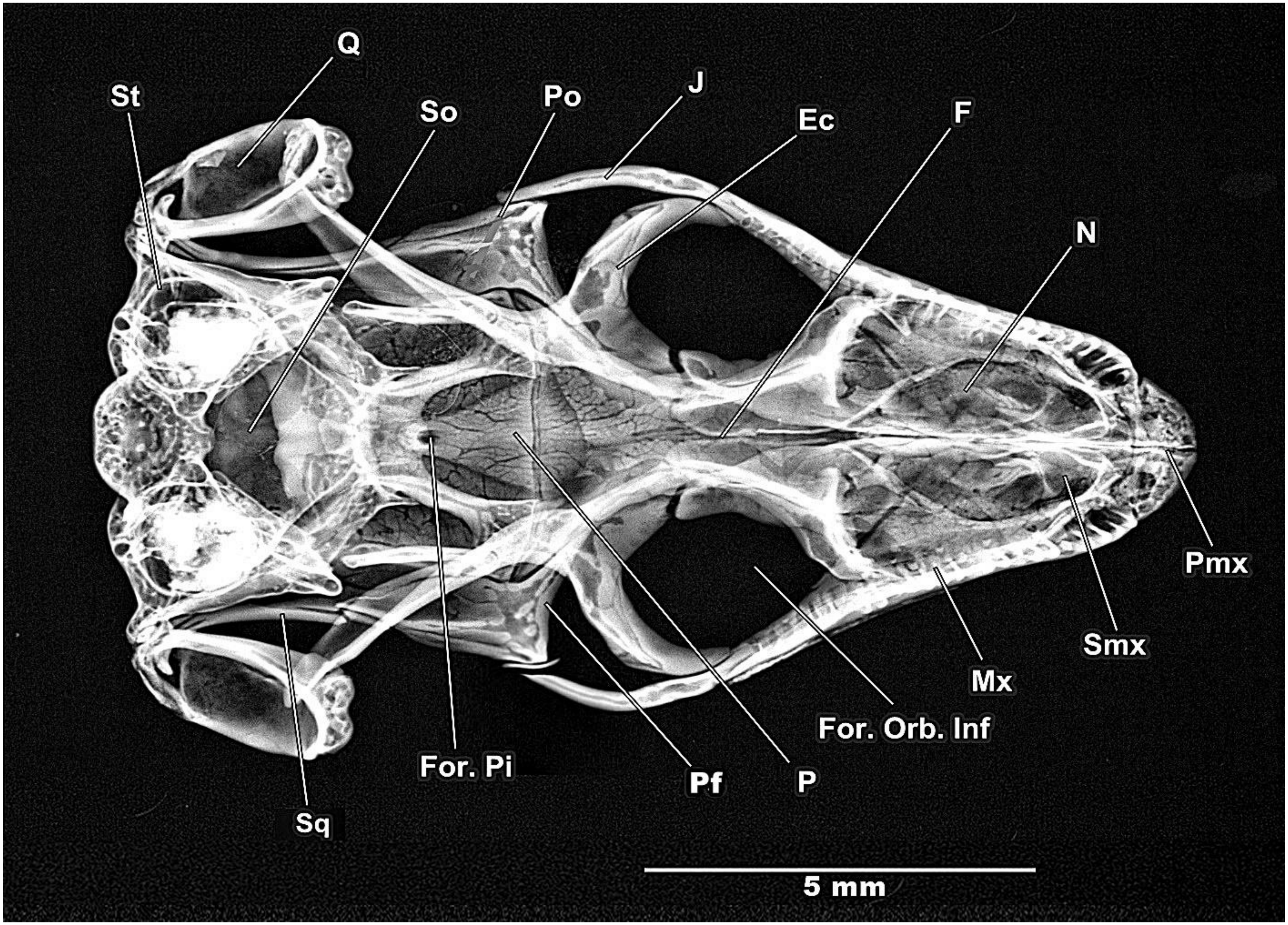

FIG. A2.31 – Radiography of the skull of *Mabuya macrorhyncha* MNRJ 17390 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

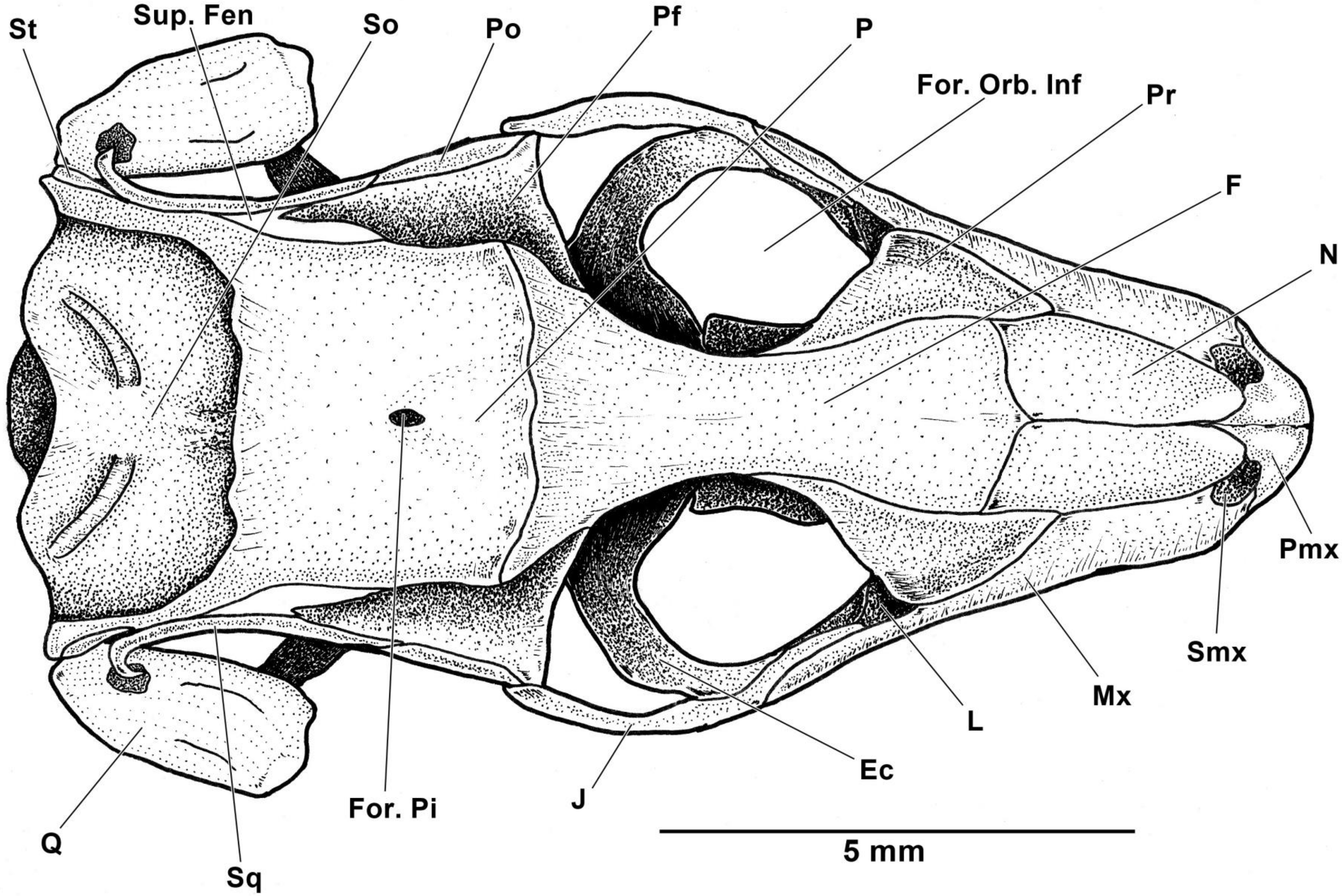

FIG. A2.32 – Illustration of the skull of *Mabuya macrorhyncha* MNRJ 17390 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; L – lacrimal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Pr – prefrontal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal; Sup. Fen – supratemporal fenestra.

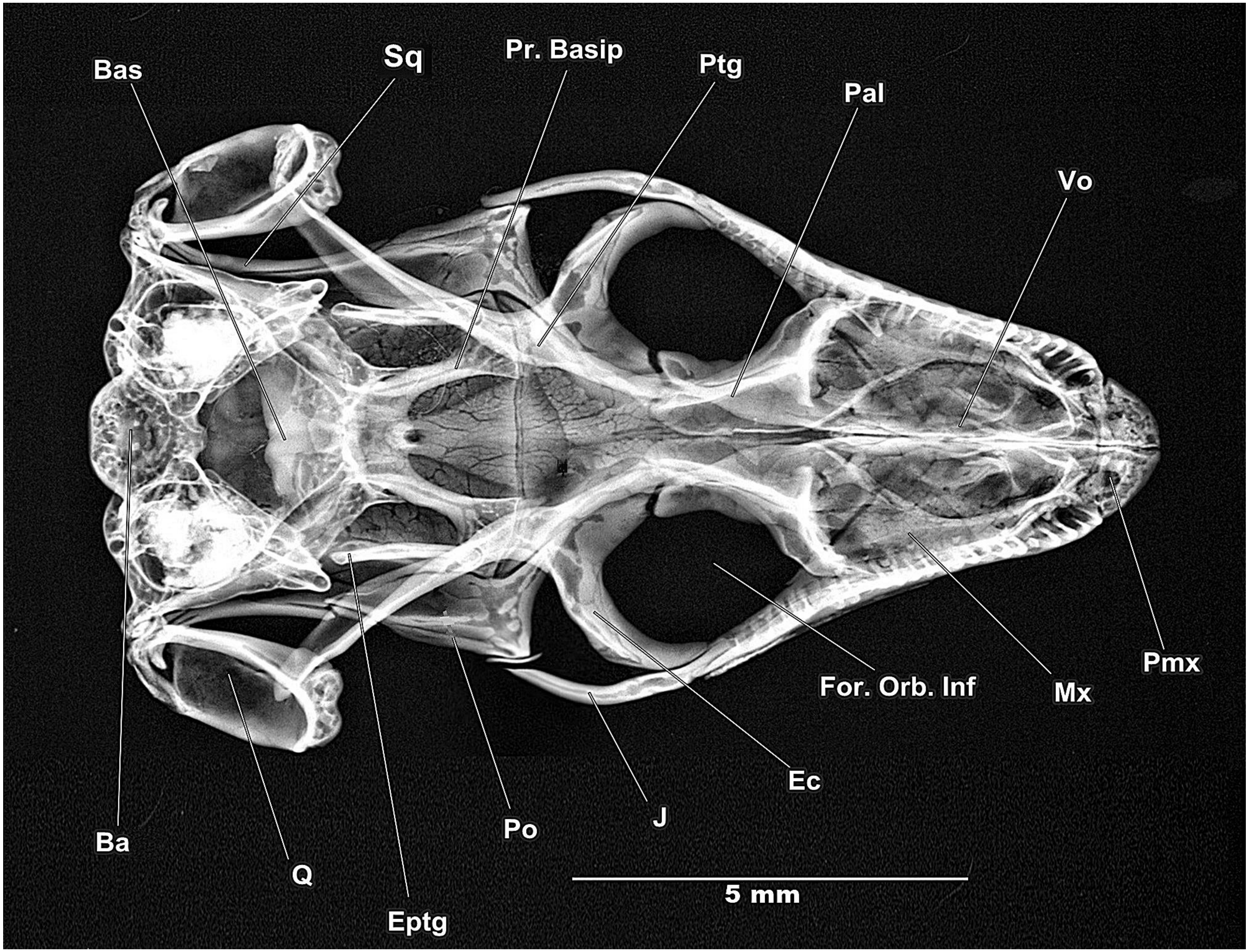

FIG. A2.33 – Radiography of the skull of *Mabuya macrorhyncha* MNRJ 17390 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

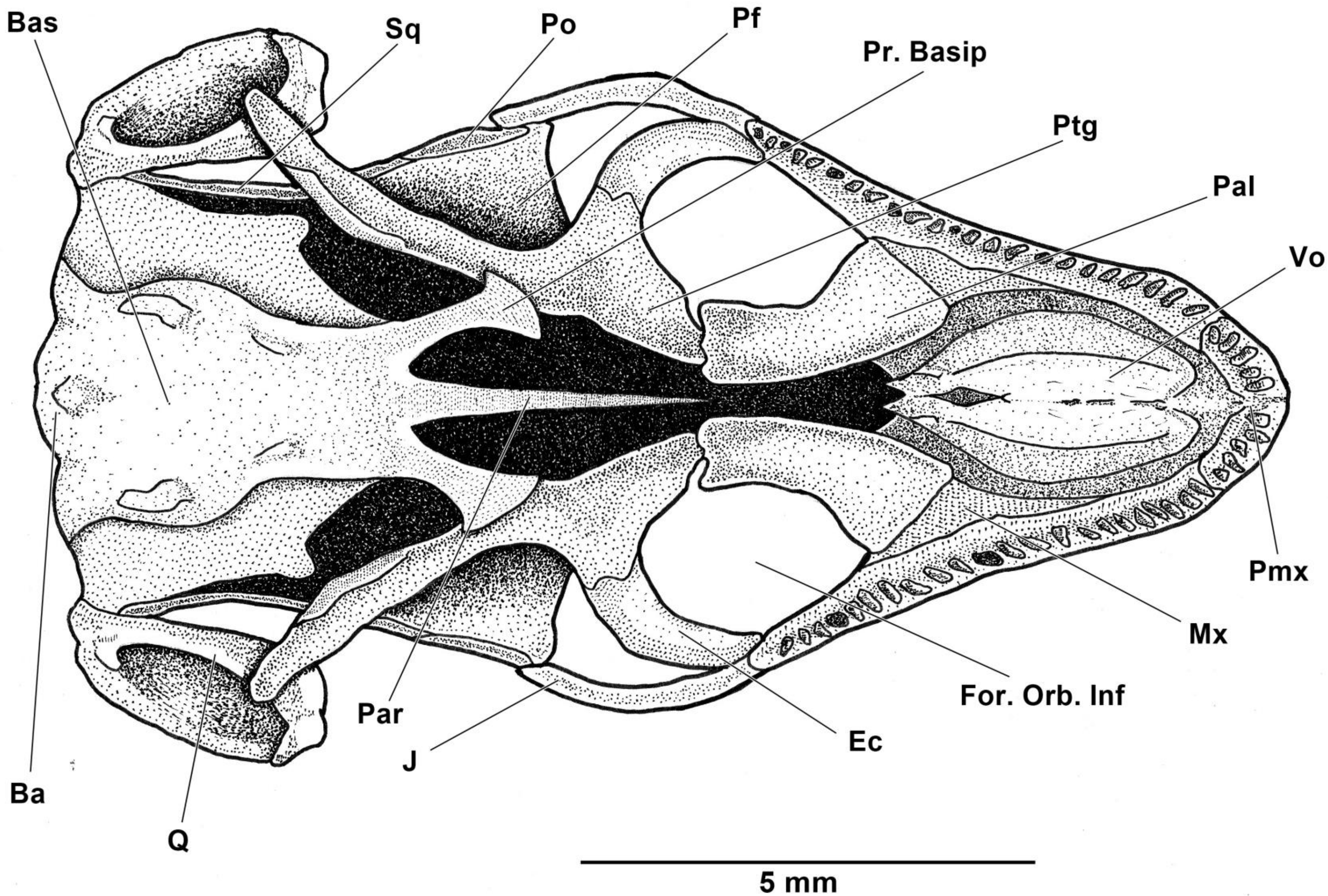

FIG. A2.34 – Illustration of the skull of *Mabuya macrorhyncha* MNRJ 17390 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

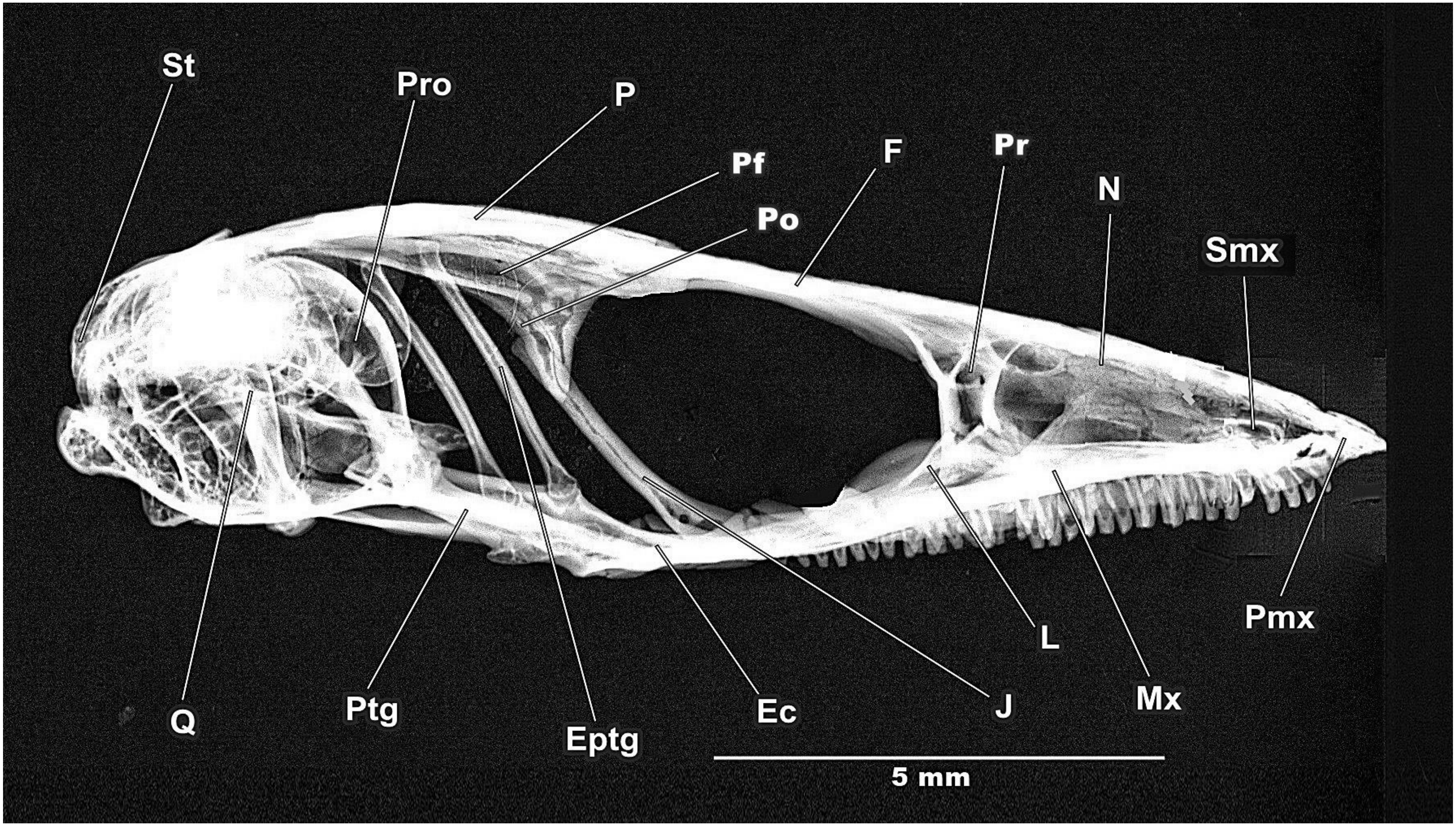

FIG. A2.35 – Radiography of the skull of *Mabuya macrorhyncha* MNRJ 17390 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; St - supratemporal.

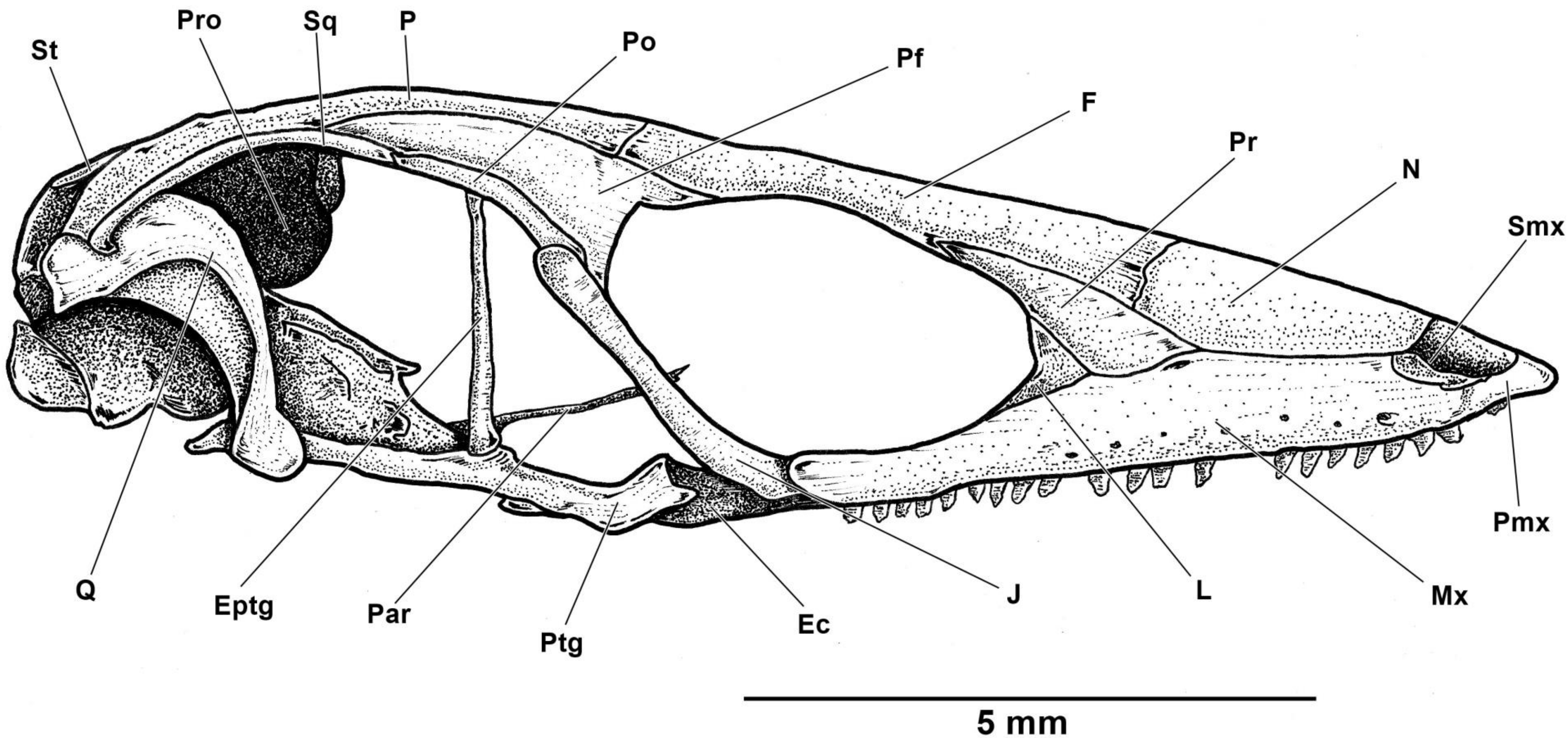

FIG. A2.36 – Illustration of the skull of *Mabuya macrorhyncha* MNRJ 17390 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; Sq – squamosal; St - supratemporal.

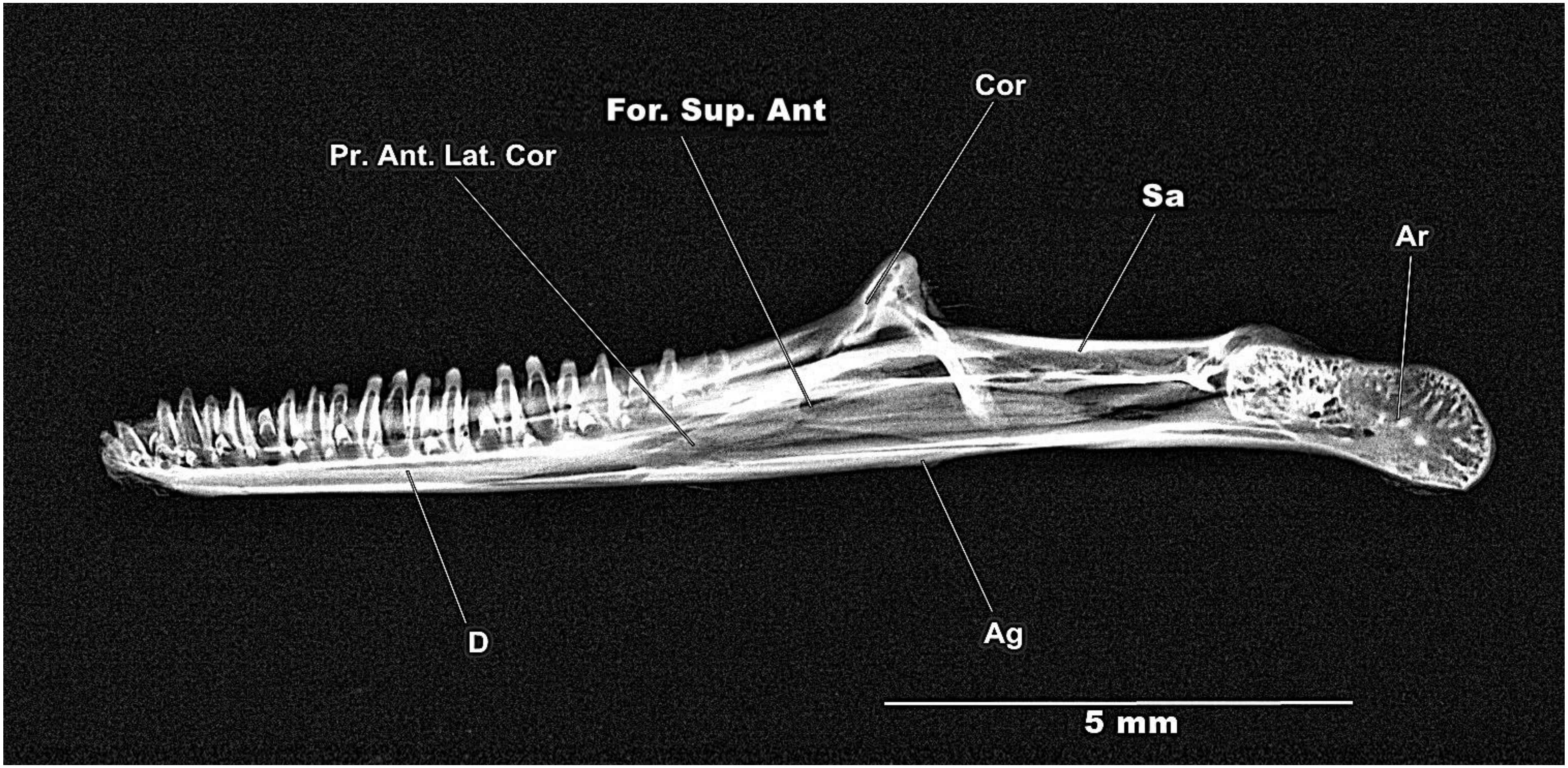

FIG. A2.37 – Radiography of the mandible of *Mabuya macrorhyncha* MNRJ 17390 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Sup. Ant – foramen supra-angular anterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

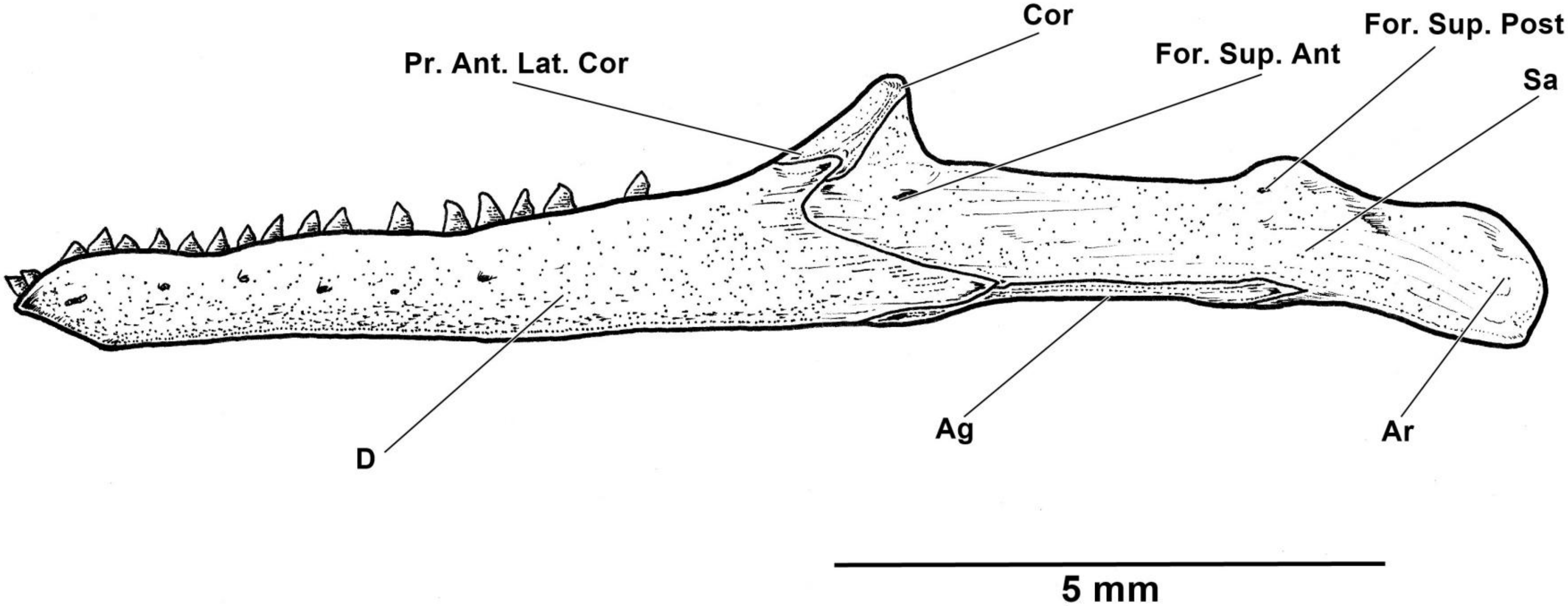

FIG. A2.38 – Illustration of the mandible of *Mabuya macrorhyncha* MNRJ 17390 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Supra. Ant – foramen supra-angular anterior; For. Sup. Post – foramen supra-angular posterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

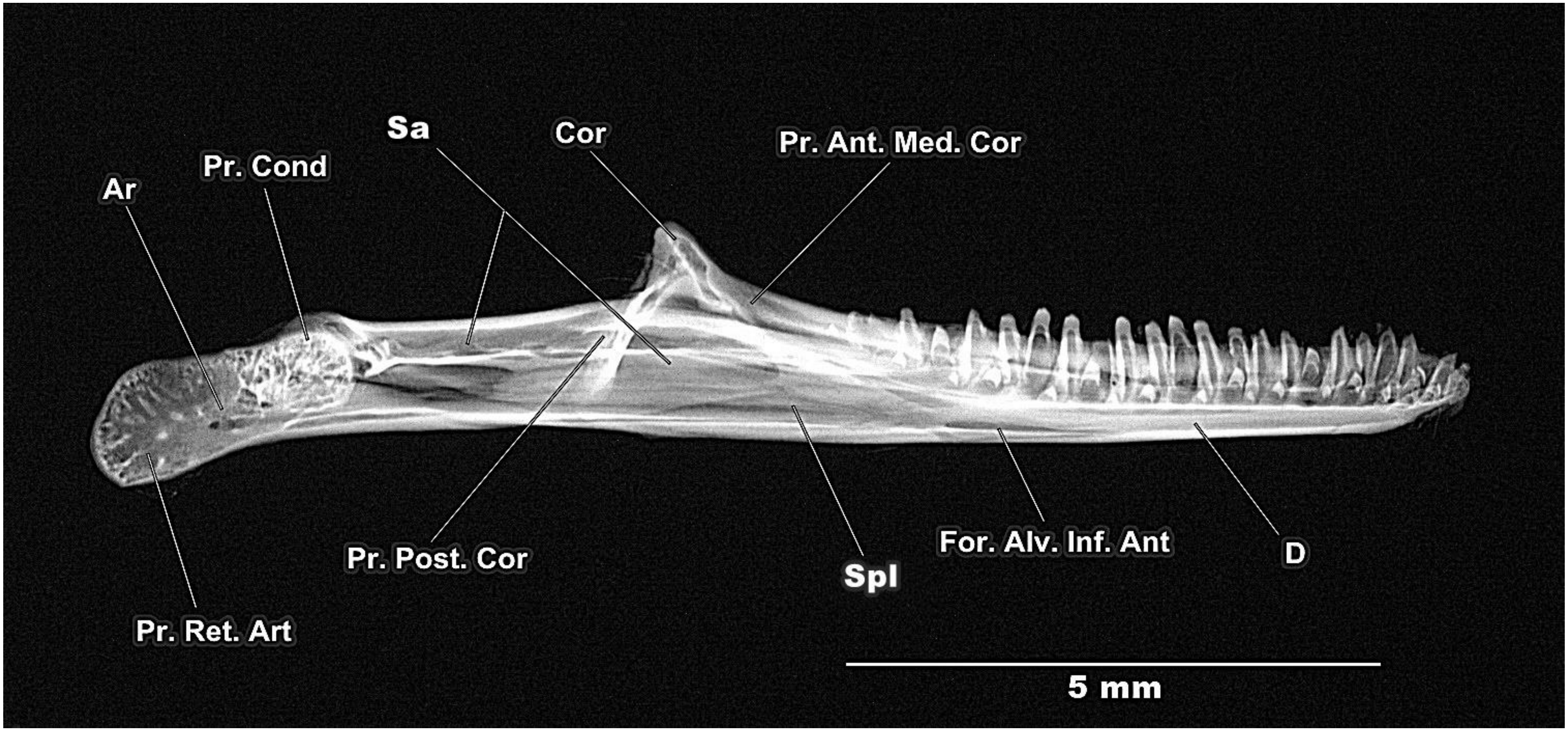

FIG. A2.39 – Radiography of the mandible of *Mabuya macrorhyncha* MNRJ 17390 – Lingual view

Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial process of coronoid; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

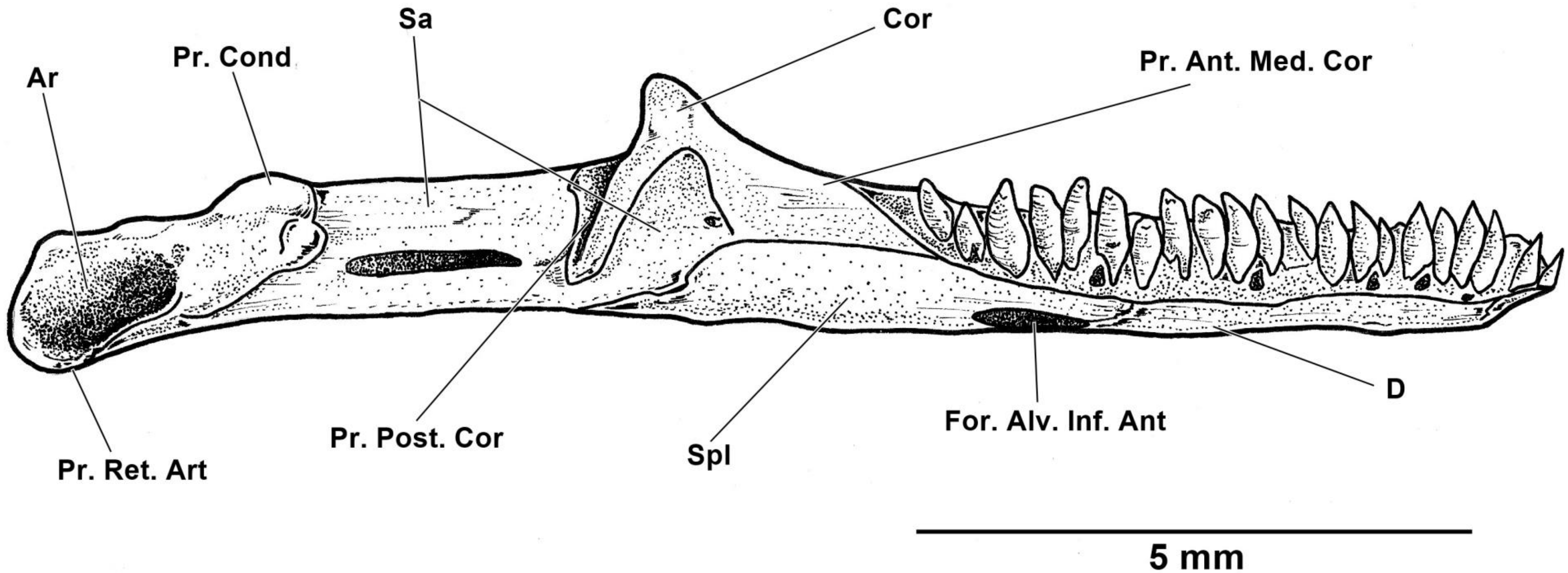

FIG. A2.40 – Illustration of the mandible of *Mabuya macrorhyncha* MNRJ 17390 – Lingual view

Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial coronoid process; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

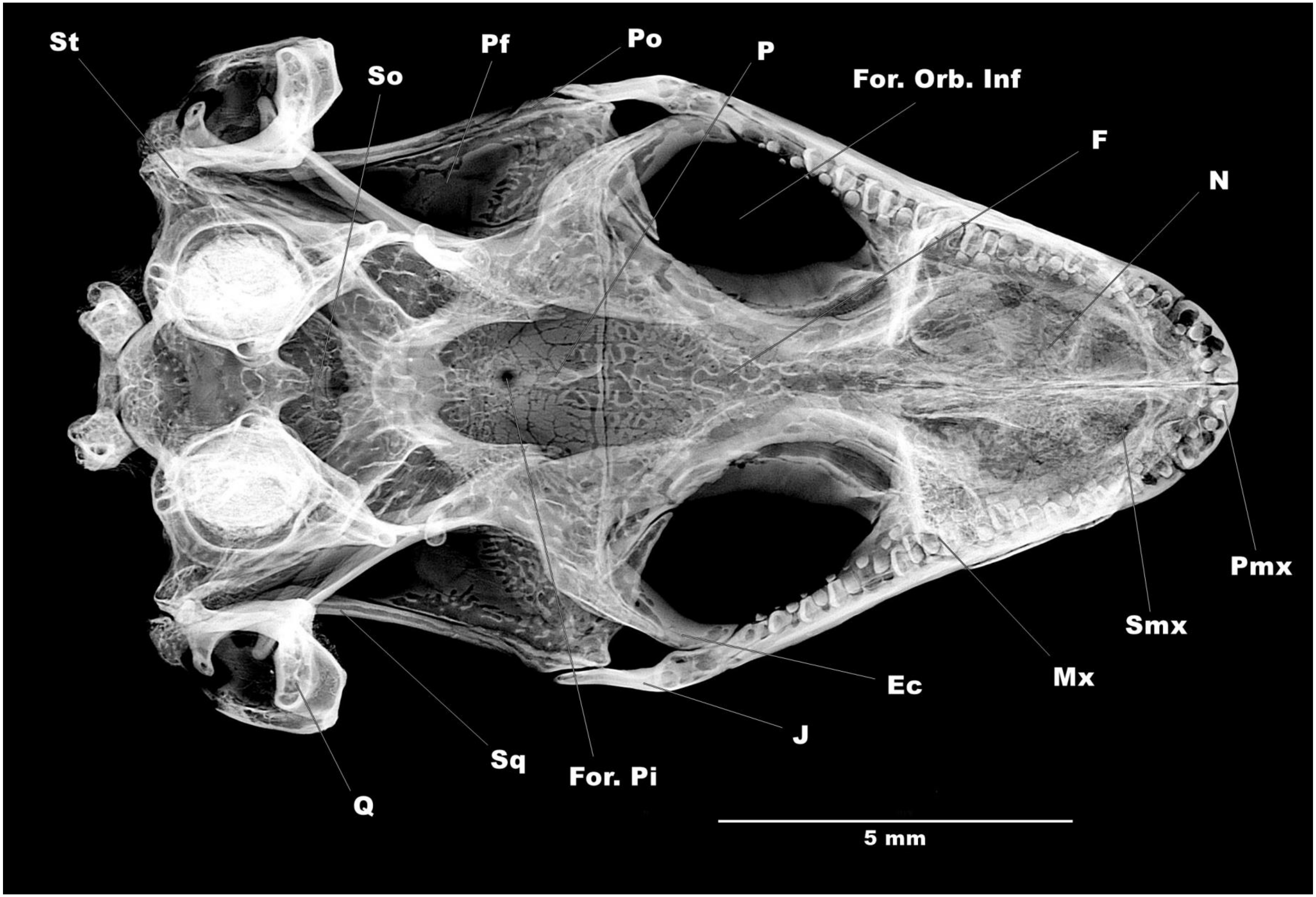

FIG. A2.41 – Radiography of the skull of *Mabuya nigropunctata* MNRJ 26876 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal.

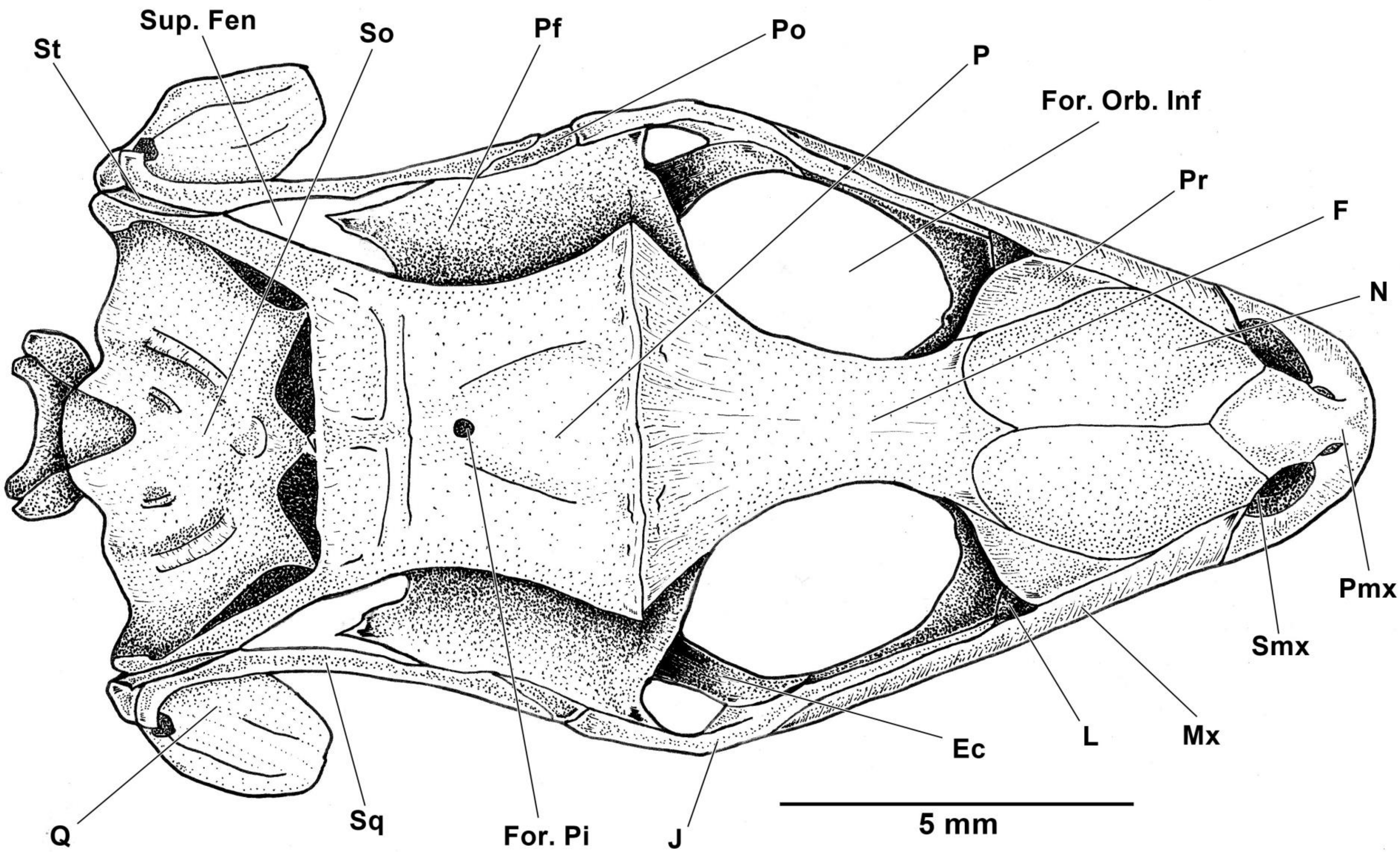

FIG. A2.42 – Illustration of the skull of *Mabuya nigropunctata* MNRJ 26876 - Dorsal view

Ec – ectopterygoid; F- frontal; For. Orb. Inf – foramen orbital inferior; For. Pi – foramen pineal; J – julgal; L – lacrimal; Mx – maxilla; P – parietal; Pmx – premaxilla; N – nasal; Pr – prefrontal; Po – postorbital; Pf – postfrontal; Q – quadrate; Smx – septomaxilla; So – supraoccipital; Sq – squamosal; St – supratemporal; Sup. Fen – supratemporal fenestra.

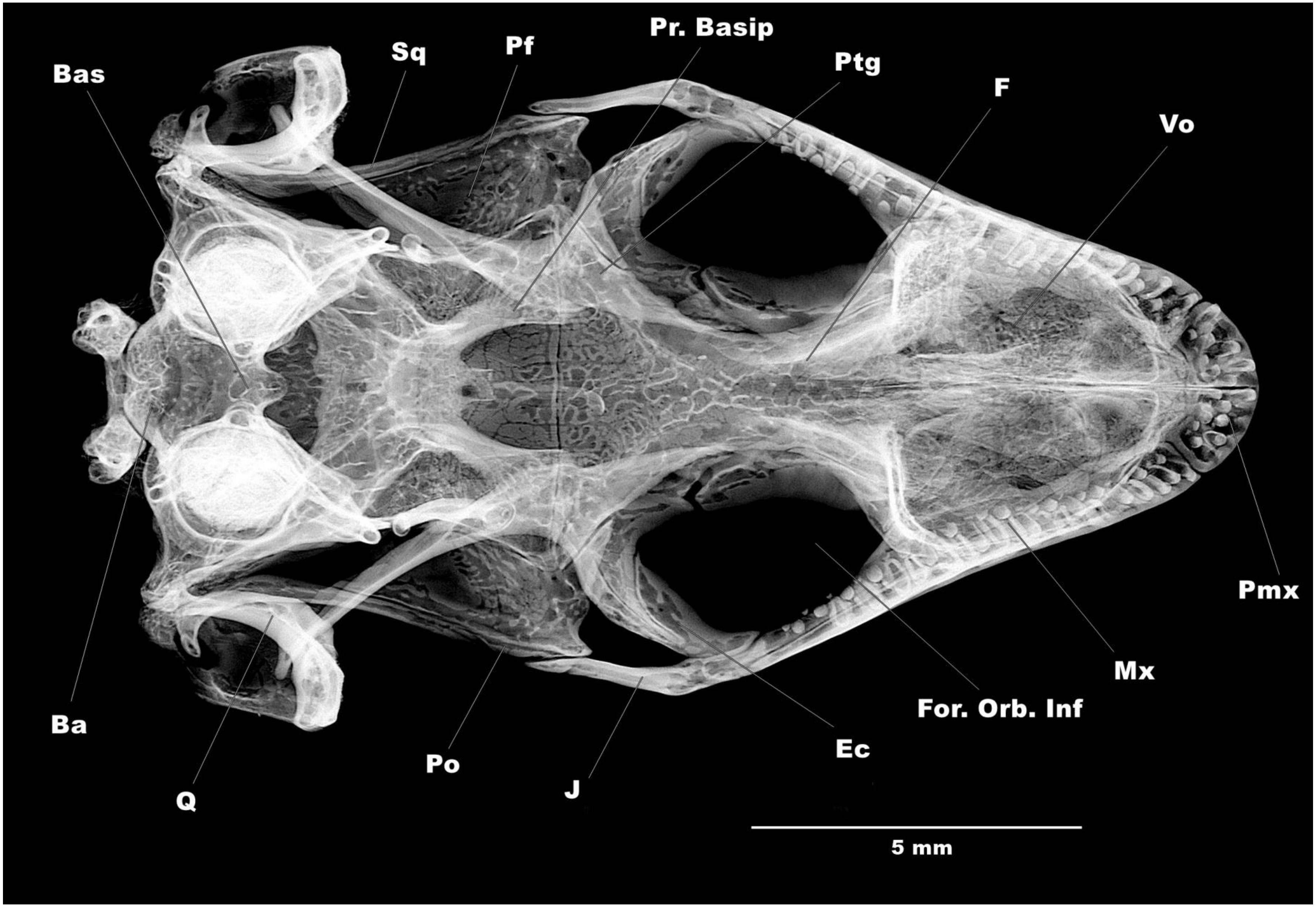

FIG. A2.43 – Radiography of the skull of *Mabuya nigropunctata* MNRJ 26876 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

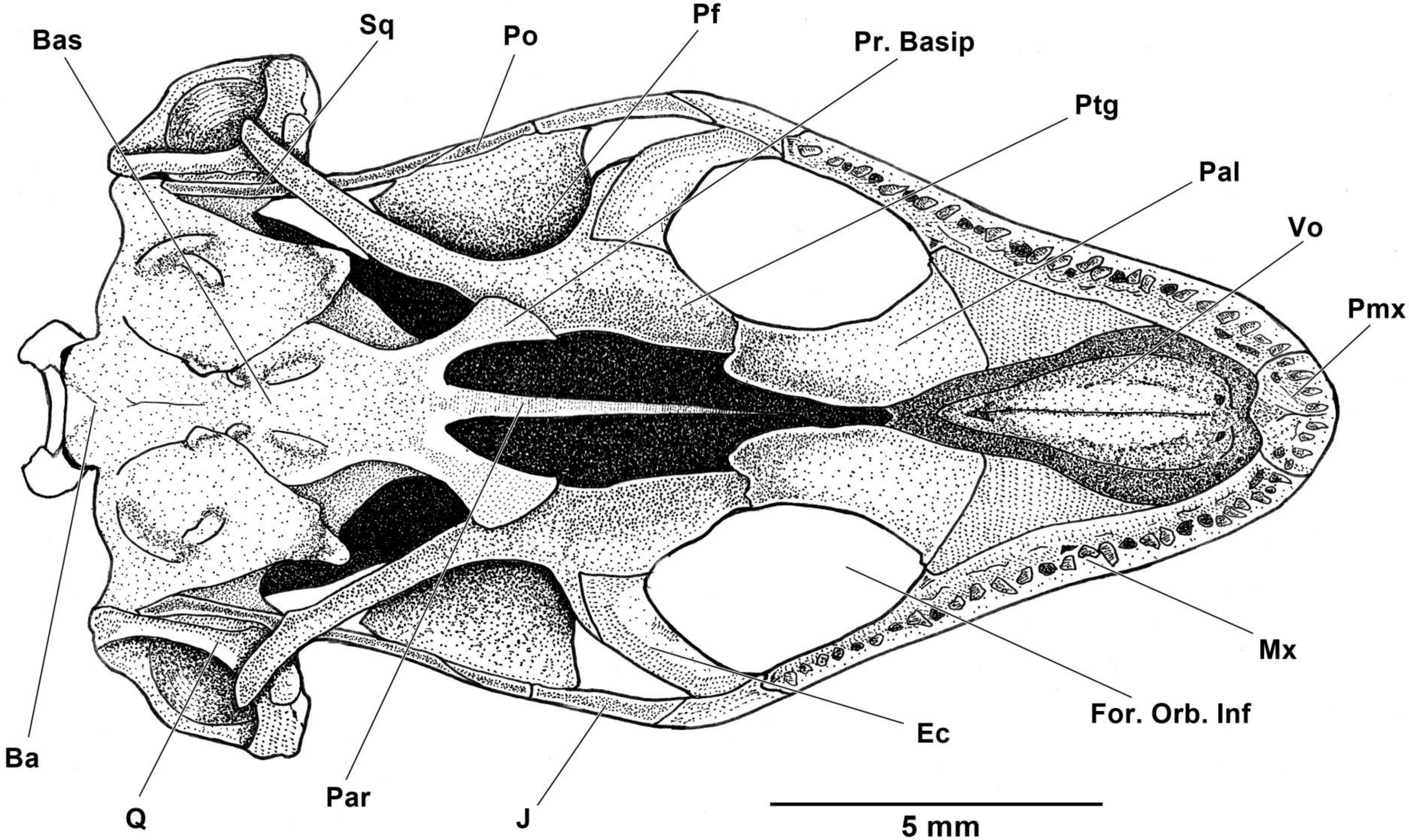

FIG. A2.44 – Illustration of the skull of *Mabuya nigropunctata* MNRJ 26876 - Ventral view

Ba – basioccipital; Bas – basisphenoid; Ec – ectopterygoid; For. Orb. Inf – foramen orbital inferior; J – jugal; Mx – maxilla; Pal – palatine; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Po – postorbital; Ptg – pterygoid; Pr. Basip –basipterygoid process; Q – quadrate; Sq – squamosal; Vo – vomer.

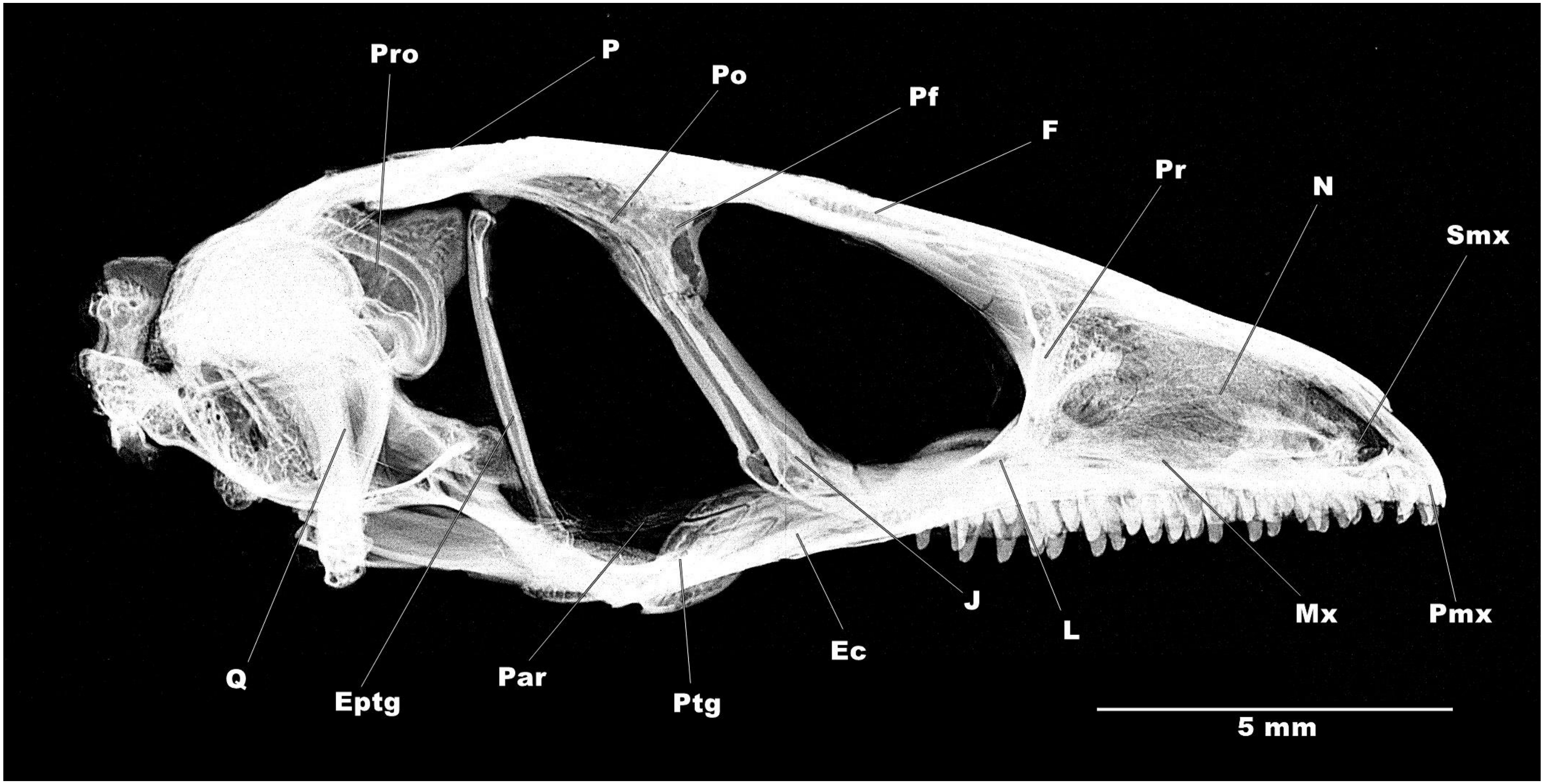

FIG. A2.45 – Radiography of the skull of *Mabuya nigropunctata* MNRJ 26876 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla.

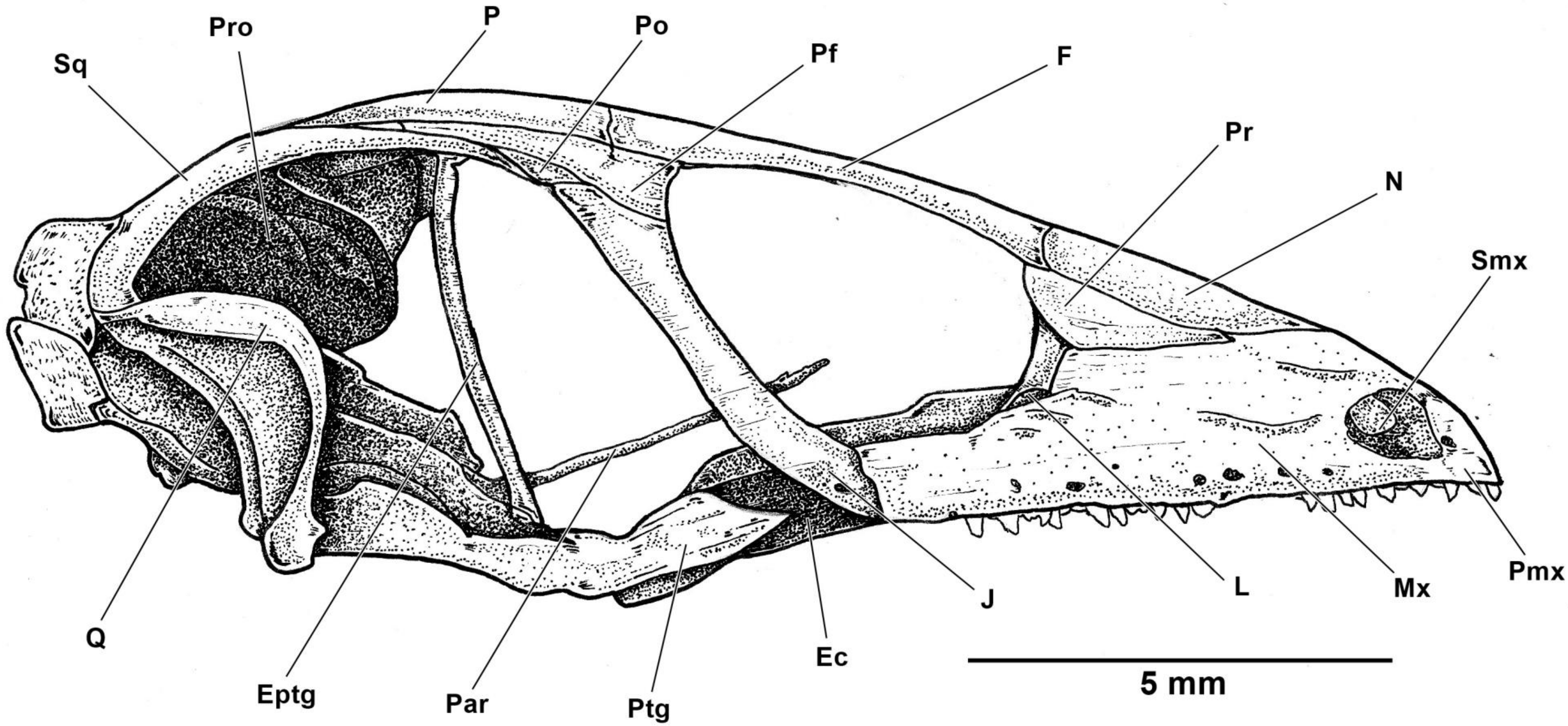

FIG. A2.46 – Illustration of the skull of *Mabuya nigropunctata* MNRJ 26876 - Lateral view

Ec – ectopiterygoid; Eptg – epipterygoid; F – frontal; J – jugal; L – lacrimal; Mx – maxilla; N – nasal; P – parietal; Par – parasphenoid; Pf – postfrontal; Pmx – premaxilla; Pr – prefrontal; Po – postorbital; Pro – prootic; Ptg – pterygoid; Q – quadrate; Smx – septomaxilla; Sq – squamosal.

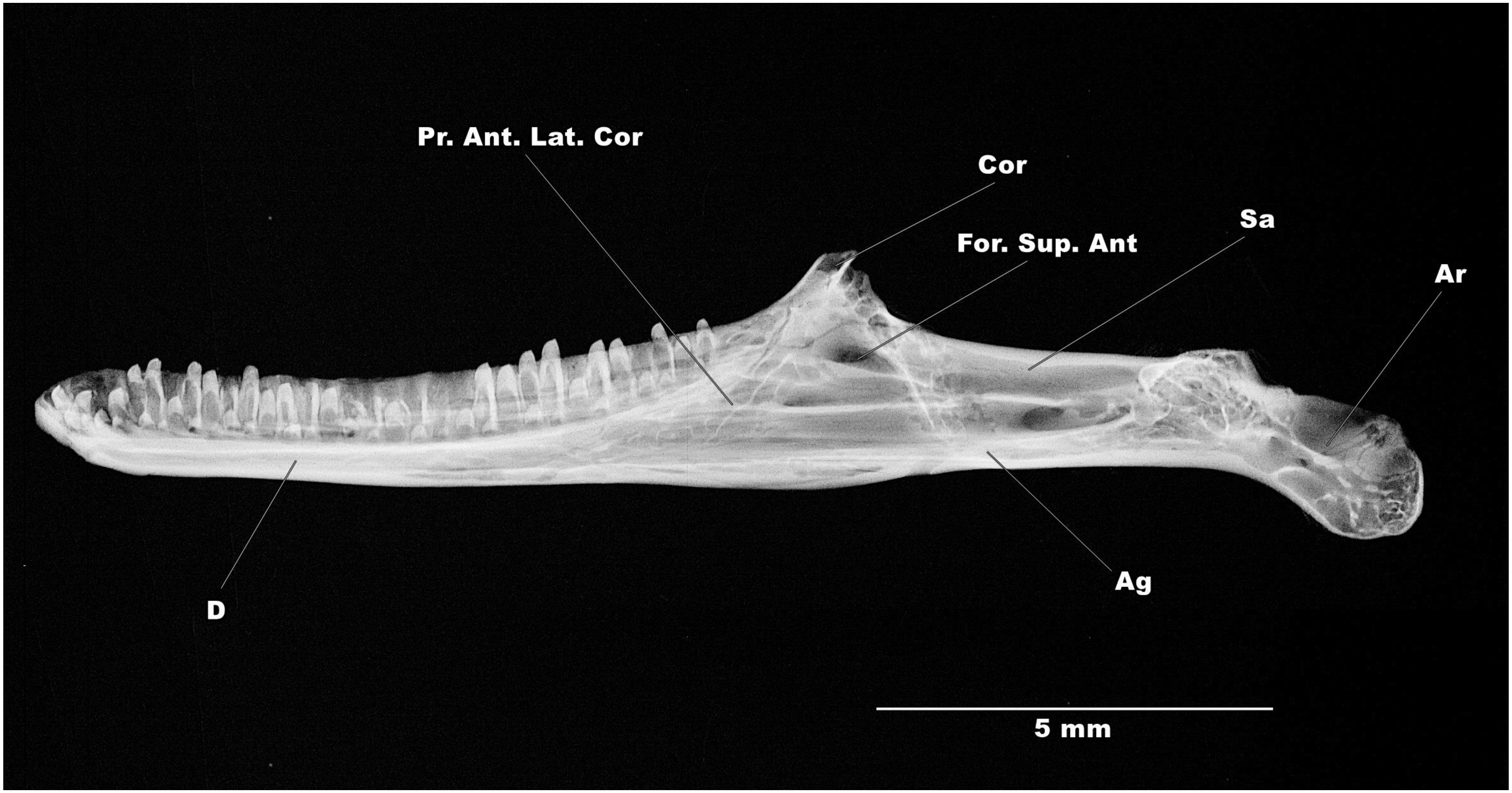

FIG. A2.47 – Radiography of the mandible of *Mabuya nigropunctata* MNRJ 26876 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Sup. Ant – foramen supra-angular anterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

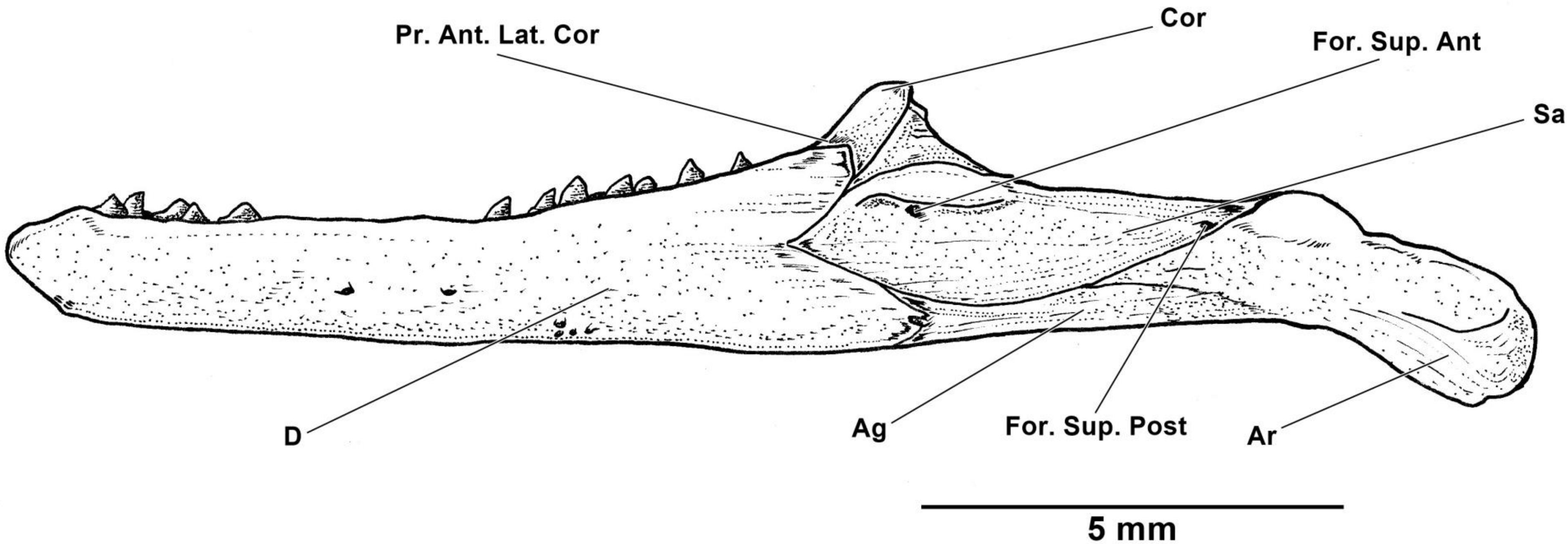

FIG. A2.48 – Illustration of the mandible of *Mabuya nigropunctata* MNRJ 26876 – Lateral view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Supra. Ant – foramen supra-angular anterior; For. Sup. Post – foramen supra-angular posterior; Pr. Ant. Lat. Cor – process anterior lateral of coronoid; Sa – supra-angular.

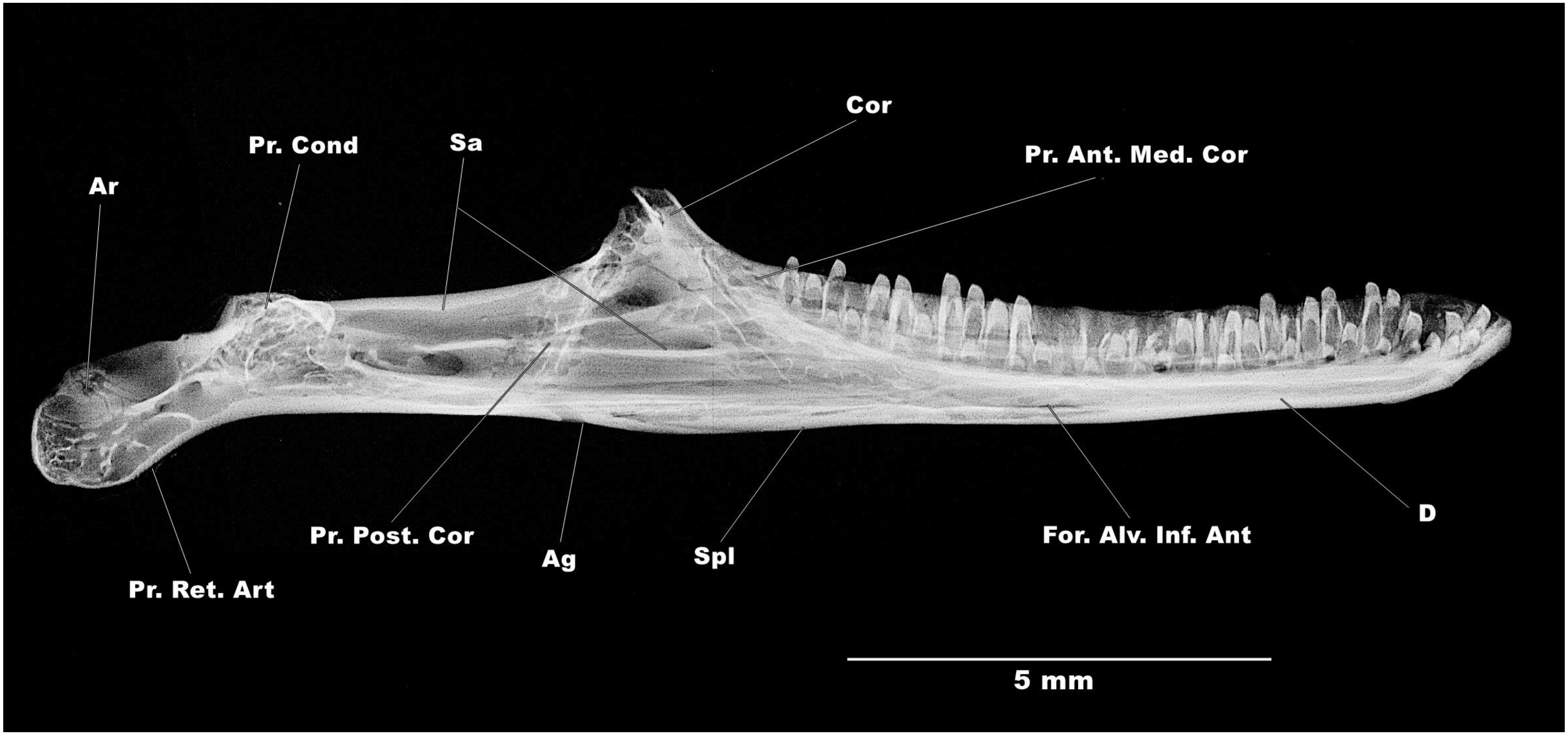

FIG. A2.49 – Radiography of the mandible of *Mabuya nigropunctata* MNRJ 26876 – Lingual view

Ag – angular; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial process of coronoid; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.

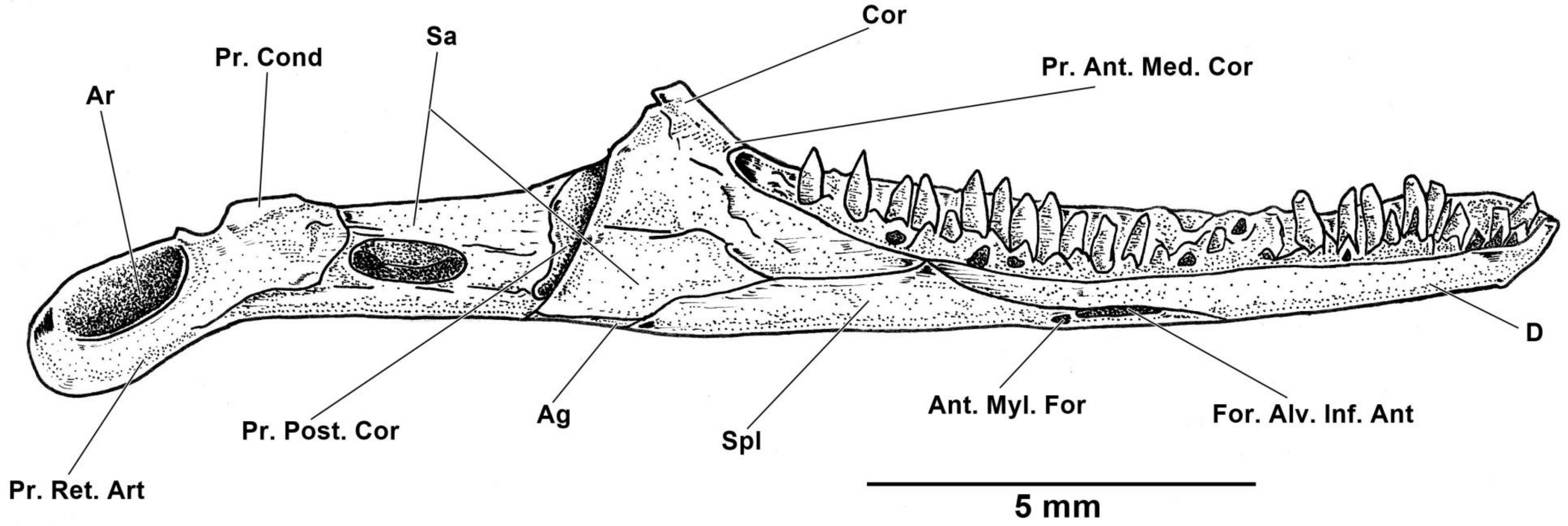

FIG. A2.50 – Illustration of the mandible of *Mabuya nigropunctata* MNRJ 26876 – Lingual view

Ag – angular; Ant. Myl. For – anterior mylohyoid foramen; Ar – articular; Cor – coronoid; D – dentary; For. Alv. Inf. Ant – anterior inferior alveolar foramen; Pr. Ant. Med. Cor – anterior medial coronoid process; Pr. Cond – condilar process; Pr. Post. Cor – posterior process of coronoid; Pr. Ret. Art – retroarticular process; Sa – supra-angular; Spl – splenial.