Journal of Threatened Taxa

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ARTICLE

REDESCRIPTION OF *LEPOSTERNON OCTOSTEGUM* (DUMÉRIL, 1851), WITH AN IDENTIFICATION KEY FOR BRAZILIAN *LEPOSTERNON* SPECIES, REMARKS ON MERISTIC METHODOLOGY, AND A PROPOSAL FOR PHOLIDOSIS NOMENCLATURE (SQUAMATA: AMPHISBAENIDAE)

José Duarte de Barros-Filho, Marco Antonio de Freitas, Thais Figueiredo Santos Silva, Mariana Fiuza de Castro Loguercio & Maria Celeste Costa Valverde

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Redescription of *Leposternon octostegum* (Duméril, 1851), with an identification key for Brazilian *Leposternon* species, remarks on meristic methodology, and a proposal for pholidosis nomenclature (Squamata: Amphisbaenidae)

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Abstract: The amphisbaenian *Leposternon octostegum* (Duméril, 1851) is redescribed based on newly collected material from the state of Bahia, Brazil. Species validity was confirmed, and comparisons made to other *Leposternon* species and to the scarce literature available on *Leposternon octostegum* taxonomy. Aspects of meristic annuli methodology are reviewed, and nomenclatural adjustments for some scales are proposed. To place this information in its taxonomic context, a species identification key for the Brazilian species of the genus *Leposternon* is provided. The present redescription contributes to a better understanding of Amphisbaenia taxonomy, thus also enabling the design of more adequate conservation and management strategies for the species belonging to this group.

Keywords: Amphisbaenia, Bahia, Brazil, *Leposternon octostegum*, meristic methodology, pholidosis nomenclature, taxonomy.

INTRODUCTION

Amphisbaenia is a group of fossorial reptiles (Gans 1978). Since the last taxonomic checklist by Gans (2005), new species descriptions and more strict taxonomic revisions modified the number of recognized living species from 202 to 194, 72 occurring in Brazil (cf. Uetz & Hošek 2018). South American amphisbaenians include the genus *Leposternon* Wagler, 1824, belonging to the family Amphisbaenidae (Gans 1971a). Except for *L. microcephalum*, recorded from Argentina, Bolivia, Paraguay and Uruguay, and *L. bagual*, endemic in Argentina, the other nine species are known only to occur in Brazil, where they are distributed from the south of the Amazonas River to the extreme meridional State of Rio Grande do Sul (Gans 1967, 1971a, 2005; Ribeiro et al. 2018) in almost all phylogeographic regions (cf. Ribeiro et al. 2008, 2018).

Leposternon, along with the African *Dalophia* and *Monopeltis* and North American *Rhineura* genera, are considered the most specialized burrowing amphisbaenian group, due to their shovel-like head shape, among other characteristics (Gans 1960, 1968, 1974, 1978). The 11 recognized *Leposternon* species are *L. microcephalum* Wagler, 1824, *L. scutigerum* (Hemprich, 1829), *L. octostegum* (Duméril, 1851), *L. polystegum* (Duméril, 1851), *L. infraorbitale* (Berthold, 1859), *L. wuchereri* (Peters, 1879), *L. kisteumacheri* Porto, Soares & Caramaschi, 2000, *L. cerradensis* Ribeiro, Vaz-Silva & Santos-Jr., 2008, *L. maximus* Ribeiro, Nogueira, Cintra, Silva Jr. & Zaher, 2011, *L. bagual* Ribeiro, Santos-Jr. & Zaher, 2015, and *L. mineiro* Ribeiro, Silveira & Santos-Jr., 2018.

The species *L. octostegum* was described from a single specimen (MNHN 7055, holotype) collected in "Brésil" (Duméril 1851). While a few historical records of the species are mentioned in literature, these have been largely plagued with inconsistencies and omissions that greatly reduce their taxonomical value (cf. Barros-Filho et al. 2013). This short literature essentially includes the original description of *L. octostegum* from Duméril (1851), a *Leposternon* revision by Strauch (1881) and the fundamental work of Gans (1971a) on *Leposternon* taxonomy.

During 2003 and 2006, new specimens were collected near Salvador City, in the state of Bahia, northeastern Brazil, allowing for comparisons with the holotype and confirmation of species validity. We can now provide a summary of external morphological variations for the species and detailed shield descriptions, to complete the concise original ones and to offer a more precise understanding of observed sample variations. These were the main objectives of this study, but we also found the need for more precision regarding certain details of the traditional *Leposternon* and amphisbaenian meristic methodology, and also propose a review of some nomenclatural pholidosis terms. Finally, to place this species redescription in its taxonomic context, we also provide a species key for the Brazilian *Leposternon* species (*L. bagual* endemic in Argentina, with osteological diagnostic characters, was not included).

MATERIAL AND METHODS

Specimens were collected (License 0018/2003 – NUFAU/IBAMA/BA) at Aterro Metropolitano Centro (12.858⁰S & 38.370⁰W), Salvador City, and at Arembepe County (12.697⁰S & 38.324⁰W), in the municipality of Camaçari, state of Bahia, Brazil, in June and November 2003 (Fig. 1). Three specimens were damaged by bulldozers but were useful for most comparisons conducted herein.

Collected specimens were anesthetized with ether, fixed in 4% formalin and preserved in 70% alcohol. The color of the specimens was edited for better exposure of details, except for Image 23, showing the coloration in live and preserved specimens. Drawings were made by Leandro dos Santos Lima Hohl, obtained from photographs, except for Fig. 2A (by José Duarte de Barros-Filho). Images (all the photographs) by José Duarte de Barros-Filho.

Measurements were made with dial calipers to the nearest 0.01mm and taken with a ruler to the nearest millimeter. Sex determination, whenever possible, was achieved by dissection or hemipenial eversion. Specimens were dissected or X-rayed for vertebral (body+caudal) counts (Table 1). The species key is based on both firsthand observations and bibliographic references (Gans 1971a; Porto et al. 2000; Ribeiro et al. 2008, 2011, 2018). *Leposternon octostegum* and *L. scutigerum* specimens examined or cited in this study are housed in the following collections (acronyms follow Sabaj-Pérez 2010 when possible): MCP (Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Brazil), MNHN (Museum National d'Histoire Naturelle, Paris, France), MZUEFS (Museu de Zoologia da Universidade Estadual de Feira de Santana, Bahia, Brazil), MZUSP (Museu de Zoologia, Universidade de São Paulo, Brazil), NMW (Naturhistorisches Museum, Wien, Austria) and ZUFRJ (Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Brazil, now at
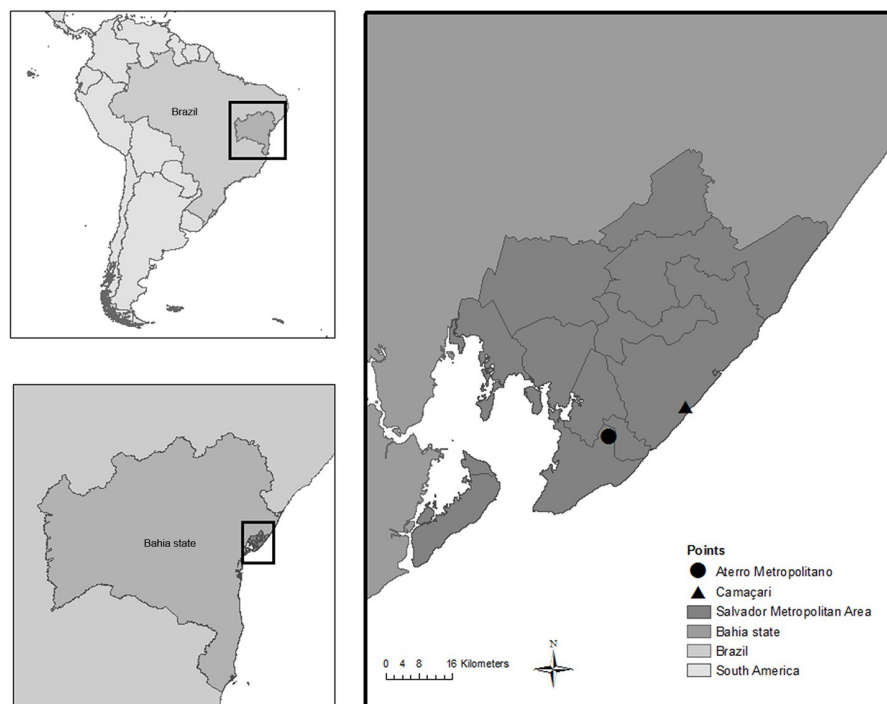
Museu Nacional do Rio de Janeiro). The material used for comparison of counting methodologies and for the analysis of the pholidosis nomenclature are listed in Appendix 1 (*L. microcephalum* and *L. scutigerum* specimens used herein and also by Gans 1971a, Ribeiro et al. 2008, 2011) and Appendix 2 (other amphisbaenians and Lacertilia).

Count methods and pholidosis nomenclature

Gans (1971a: 385) emphasizes that "The segmentation pattern of *Leposternon* differs markedly from that shown in the species of *Amphisbaena*. Consequently, it is necessary to use a slightly different counting and description system from that most recently detailed by Gans (1966)". Indeed, the need for adaptations was verified herein, including for some proposals made by Gans (1971a). Therefore, the methodology of half-annuli counts and some of the pholidosis nomenclature terms used in this study differ to some extent from previous publications. To justify these new proposals, it is important to comment on them before presenting the redescription. The obtained data were compared with appropriate literature and with other *Leposternon*, amphisbaenian and lacertilian species (Table 2, Appendix 1 and 2).

Count methodology

The standard methodology for "postpectoral annuli"
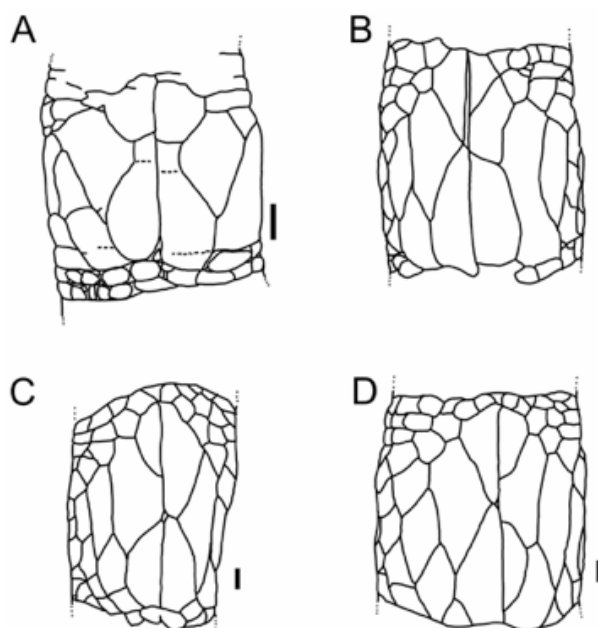
Figure 2. Pectoral shield patterns. *Leposternon scutigerum*, (A) ZUFRJ 1730; *Leposternon octostegum*, (B) ZUFRJ 1749, (C) MZUEFS 653 and (D) MZUEFS 657. Scale bars = 1mm.

counts essentially followed herein was established by Vanzolini (1951) and Gans & Alexander (1962), on the amphisbaenian ventral left side. This standardization, used for all genera, has particular importance for *Leposternon*. As Gans (1971a, 1977) points out, the

Table 1. Measurements and meristic data for *Leposternon octostegum*. Abbreviations: AL (anterior lateral annuli, right/left sides), PPVL (postpectoral annuli, ventral and right sides), PPVR (postpectoral annuli, ventral and left side), PPDL (postpectoral annuli, dorsal and left side), PPDR (postpectoral annuli, dorsal and right side), L (lateral annuli, right/left sides), C (caudal annuli, counted in the ventral left side from the cloaca to the tip of the tail), PFS (postcloacal flap shields), VAS (ventral annuli scales, counted for five adjacent annuli at midbody), DAS (dorsal annuli scales, counted for five adjacent annuli at midbody), HW (maximum head width, measured at ocular region), BW (body width, measured at half of body length), CW (maximum caudal width, measured at is base), SVL (snout-vent length), CL (caudal length), TL (total length), V (number of vertebrae, body plus caudal), S (sex).

Specimens	AL	PPVL	PPVR	PPDL	PPDR	L	C	PFS	VAS	DAS	HW	BW	CW	SVL	CL	TL	V	S
MNHN 7055	15/16	382	379	376	372	6/6	13	19	23-26	29-32	6.1	8.5	7.8	337	11	348	140+12	-
MNHN 2007.0023	16/16	366	359	370	363	5/6	12	23	26-27	26-29	7.1	8.9	8.5	373	14	387	134+11	male
MNHN 2007.0024	16/15	369	358	367	363	5/5	14	23	24-25	27-28	6.1	7.3	7.5	323	12	335	137+14	female ?
MZUEFS 652*	13/13	15+n +194	15+n +195	n+ 207	n+ 204	4/4	13	21	23-26	28-32	6.3	9.3	8.7	29+n+2-	11	244+n	121+15	female
MZUEFS 653*	16/16	189+ n	190+ n	192+ n	193+ n	-	-	-	25-27***	30-31***	4.8	6.9***	-	126+n	-	126+ n	64+n	-
MZUEFS 654*	15/14	236+ n	245+ n	244+ n	246+ n	-	-	-	25-29***	30-31***	5.6	6.8***	-	150+n-	-	150+ n	79+n	-
MZUEFS 655*	14/14	331+ n	323+ n	327+ n	327+ n	-	-	-	25-26***	28-32***	5.7	6.5***	-	225+n-	-	225+ n	117+n	female
MZUEFS 656	18/17	370	370	381	370	4/4	14	19	24-28	27-31	7.2	7.6	8.3	374	14	388	140+11	male
MZUEFS.657	17/17	369	379	374	367	4/4	12	19	23-24	28-30	5.3	6.1	5.8	238	9	245	100+n	-
MZUEFS.695	16/15	372	374	379	378	6/5	12	21	23-25	28-31	6.4	9.2	8.2	329	11	340	134+12	female ?
MZUEFS.696**	16/16	357	357	361	357	4/5	14	20	26-29	30-33	7.1	9.0	8.5	354	15	369	140+12	male
ZUFRJ.1713**	17/18	363	337	383	367	5/5	14	19	24-25	25-28	3.9	4.3	4.3	150	5	155	42+n	-
ZUFRJ 1714**	15/16	375	374	384	383	5/6	13	18	24-28	25-28	4.5	5.7	4.8	232	9	241	138+9	-
ZUFRJ.1715**	14/14	379	370	397	392	5/5	15	17	24-27	24-28	5.1	6.5	5.4	283	12	295	140+15	female
ZUFRJ.1716**	17/17	381	386	385	384	5/6	14	18	25-28	26-27	4.9	6.9	6.3	320	9	329	114+n	-
ZUFRJ.1748	17/15	359	356	360	358	5/5	13	22	24-25	28-30	6.6	9.3	7.5	368	13	381	142+11	-
ZUFRJ.1749	13/13	353	348	357	354	4/5	14	22	24-26	24-27	6.6	8.6	7.2	344	12	356	113+n	female

* Dissected specimens
** Specimens from Arembepe county, Municipality of Camaçari (all others are from Salvador City)
*** Values taken near half-body length of the damaged specimen

Table 2. Compared counts of post-pectoral ventral half-annuli (PPVLeft or PPVRight body side) for specimens of *Leposternon octostegum*, *L. microcephalum*, and *L. scutiegrum* examined in this paper and in Gans (1971a), Ribeiro et al. (2008, 2011). The cited bibliography do not give individual counts, but the species minimum-maximum counts (min-max), except for the *L. octostegum* holotype (Gans 1971a).

GANS (1971a)	This paper
Leposternon microcephalum (N = 19) Rio de Janeiro sample	
(PPVL 181–226)	(PPVL 197–216)
MNRJ 1762	203
MNRJ 1767a	213
MNRJ 1767b	207
MNRJ 1755a	197
MNRJ 1755b	198
MNRJ 1768	200
MNRJ 1774	204
MNRJ 1778a	216
MNRJ 1778f	209
MNRJ 1783	197
MNRJ 3261	204
MNRJ 3262	199
MNRJ 3264	203
MNRJ 3265	208
MNRJ 3266	207
MNRJ 3267	204
MNRJ 3268	208
MNRJ 3269	202
MNRJ 3270	197
Leposternon octostegum (N=1) Brazil	
(PPVL) MHNP 7055 (holotype):378	(PPVL) 382
Ribeiro et al. (2008)	**This paper**
Leposternon microcephalum (N = 30) Brazil sample	
(PPVR 186–254)	(PPVL 193–244)
MNRJ 7469	244
MZUSP 1249*	196
MZUSP 2426*	200

MZUSP 2676*	198
MZUSP 6394*	199
MZUSP 6397*	202
MZUSP 6398*	198
MZUSP 6399*	204
MZUSP 6466*	201
MZUSP 6488*	196
MZUSP 6518*	203
MZUSP 6578*	200
MZUSP 7677*	204
MZUSP 8284*	214
MZUSP 13762*	198
MZUSP 65390*	198
MZUSP 77013*	218
MZUSP 77014*	215
MZUSP 77031*	209
MZUSP 77037*	226
MZUSP 77038	204
MZUSP 77039	205
MZUSP 77040	235
MZUSP 77042*	210
MZUSP 77043	193
MZUSP 77515*	213
MZUSP 77527	204
MZUSP 77532	202
MZUSP 77536*	221
ZUFRJ 1490	203
Leposternon scutigerum (N=3) Rio de Janeiro sample	
(PPVR 250–278)	(PPVL 256–262)
MZUSP 2519*	262
MZUSP 7075*	261
ZUFRJ 289*	256

*Also in Ribeiro et al. (2011).

dorsal counts of *Leposternon* are usually higher and more variable than the ventral counts (Gans 1971a: 386—"…the dorsal counts of certain populations were significantly higher than the ventral counts."; "…the dorsal count is more variable and it is appropriate to discuss the addition of dorsal half-annuli rather than the dropping out of accessory ventral ones."). And some differences between the left and right sides' counts are the normal condition, as the practice of laboratory examination clearly shows (this is implicit in Gans 1971a: 386 - "Left and right counts did not show any **major** differences..."—bold by the authors). Thus, dorsal counts are not a good standard, due to their higher variability, but right or left counts are perfectly comparable and useful; however, besides Papenfuss (1982), only the description papers of Ribeiro and contributors (2008, 2011, 2015, 2018) emphasize the dorsal and the right side counts. It seems that our results using standardized ventral counts are preferable for their stability. At the same time, the data regarding the right counts in Ribeiro et al. (2008, 2011) are, as explained, comparable to our results and other bibliographical data. In fact, the counts on the right side were based on the statement of Gans (1971a) that counts on left or right sides do not make any significant difference to the

characterization of the species (Síria Ribeiro, pers. comm. v.2018). So, it is implicit the understanding that data of Ribeiro and contributors are comparable with literature. That is why their data was also used, including in the Key.

Gans (1971a: 387) states that "The postpectoral annuli of *Leposternon* are remarkably irregular and the intercalated half-annuli do not start at the lateral sulci, but often begin either dorsal or ventral to these". These "intercalated half annuli" pose a problem for counts, because they can be represented by variable conditions, as having a total of only one or two segments, instead of having just one or few segments less than a "normal (= complete)" half-annulus. Of course, there are many intermediate situations between these two conditions, and successive counts on a same specimen can show different results (cf. Gans 1971a: 386).

Ribeiro et al. (2008) presented the data of postpectoral counts as "n" complete plus "n" incomplete half-annuli in the species description, but we are of the opinion that a definition of a "complete" or "incomplete" half-annulus is necessary. The complete half-annuli – or, better saying, quarter of annuli, see below – are supposed to have the segments of their extremities touching adjacent sulci, however, since the shape of segments in the extremities of the half-annuli can be somewhat variable, it is not so easy to precise this condition, particularly in twisted specimens. Herein, we also counted as "complete" all half-annuli which, despite having one or few (depending on the proportions) segments less than a "normal" one, are separated from the sulci just by the meeting of the extremities of their two bordering half-annuli.

It is important to highlight that, in practice, we are dealing with counts of a quarter of each annulus: the four longitudinal body sulci (dorsal, ventral and laterals) define four regions. However, as the right and left counts, especially ventrally, are almost the same (cf. Gans 1971a), the literature refers to the counts as ventral or dorsal half-annuli. The standard counts are in the ventral left side – a quarter of annulus – and, ideally, the information about the other quarters must be indicated in descriptions. Table 1 explicits these data.

Gans (1971a: 387) suggests that the anterior lateral counts should be increased by the half-annuli placed between "the *angulus oris* and the first annulus passing back of the enlarged head shields"; however, the anterior laterals, sensu Gans (1971a), are body annuli (i.e., not related to the head), and these half-annuli are clearly in the head region. As such, these half-annuli are treated herein as "temporal", "postemporal", or "occipital".

The first anterior lateral row defined by Gans (1971a: 387) includes the dorsal occipital shields, as understood from the following definition: "Anterior laterals (…) are counted from the first annulus (often reduced to two or three segments flanking the middorsal line) posterior to the last of the highly keratinized dorsal head shields (…)". But ventrally, these "reduced two or three segments" are more related to the gular region than the pectoral region, and the occipital area is a cephalic, not body, region (as is the pectoral area). Thus, these segments are not counted herein together with the anterior laterals, and are referred to simply as the "occipital row". The occipital shields can be poorly expressed or even totally absent in some amphisbaenian forms. In these cases, the most posterior enlarged head shields are the parietals.

Gans (1971a: 387) states that caudal annuli "are counted from the first complete (ventrally not reduced) postcloacal annulus up to and including the last complete annulus showing regular segments"; however, the observed first caudal annulus pattern in *Leposternon* is almost always characterized by a ventral medial concavity shaped by the posterior border of the postcloacal flap. The position of this annulus is definitively caudal, so it is included herein in the tail counts. Also included herein were the annuli towards the caudal tip, since the "last complete annulus showing regular segments" is a dubious definition. For instance, in amphisbaenians the terminal annuli often tends to a spiral (although this is not the common situation for *L. octostegum*), with irregular-shaped but clearly discernible segments. So, they are complete, although not "regular" annuli, and usually occupy a significant area of the tail. In addition, it is not easy to identify the last "regular" annulus and the first "irregular" one, a problem amplified in amphisbaenians by the frequent presence of intercalated incomplete half-annuli (see "dorsal and ventral postpectoral half-annuli" description below).

Thus, it is not justifiable to exclude the terminal annuli from the caudal counts. Even without the spiral pattern, the terminal annuli can generally be traced despite the irregular shape of their segments. Exceptions are natural or artificial damages or a naturally modified caudal tip (e.g., smooth). Hence, some tail counts may vary between the present data and the bibliography, although these differences are minimal and in no case may confuse species identification. For the sake of accuracy, and as the counts obtained with this methodology are perfectly comparable with published data, we propose the present count methodology as a standard.

The number of half-annuli segments (scales) were counted for five adjacent annuli at midbody.

Pholidosis nomenclature

Pholidosis nomenclature largely follows Gans (1971a). Adaptations include new definitions and naming of some scales and scale rows, and an original proposal for the Amphisbaenia nomenclature of "chin shields". The present proposal is naturally focused on *Leposternon* species but it is also applicable for the whole suborder. The reason for these modifications is that the nomenclature (and homology of scales) used for the Amphisbaenian pholidosis is still somewhat unclear, also regarding other Squamata (e.g., Loveridge 1941; Gans 1960). Different approaches have been used, mainly, but not only, for the cephalic shields (e.g. Strauch 1881; Gans & Alexander 1962; Gans 1971a; Vanzolini 1991; Porto et al. 2000; Thomas & Hedges 2006; Ribeiro et al. 2008; Pinna et al. 2010). Unsolved scale homologies between genera and species also add to the confusion (Gans 1971a).

The following points justify the present nomenclatural proposal:

1 - Direct observation that generally used names are not adequate for some scales (do not offer the better/right definition, and/or are historically a source of confusion), thus justifying the need for nomenclatural alterations. In this way Vanzolini (1991: 261) corrected a wrong nomenclature applied by Gans & Alexander (1962): "I do not think that 'malar' (i.e., zygomatic) should be used for a scale on the ventral side of the head". This applies for the naming of groups of associate scales, since associated names eventually tend to be confusing (e.g., "mental"/"genial" and associated scales);

2 - There are relevant classical precedents for the present proposal (e.g., Alexander 1966, Gans 1971a). More recently, scale nomenclatural changes in amphisbaenian literature were accepted and currently adopted (cf. Pinna et al. 2010 adopted by Pinna et al. 2014 & Roberto et al. 2014). These changes, as in the present paper, are understood as an improvement. We are of the opinion that, as the mentioned authors implicitly demonstrated, the terminological stability by itself, if not correctly correlated with the observed anatomy, has no reason to be followed. Consequently, previous dubious interpretations, once detected, must be questioned, and a more desirable terminology, coherent with the anatomical reality of the structures, can be proposed. We consider this as enough evidence, even without a homology analysis, and by no means an artificial resource (this would be a proposal not fit to reality, as were the "malar" scales of Gans & Alexander 1962 and Gans 1971a) or arbitrariness (with no evidence for the need for change, observed in the variety of questionable terms and uses already published on the subject).

3 - Nomenclature criteria: the papers of, for example, Pinna et al. (2010, 2014) and Roberto et al. (2014) explicitly do not base their nomenclatural changes on homology. We understand that homology is the basic criterion for naming morphological structures, and we essentially agree with the statement by Ribeiro et al. (2011): "...we believe that efforts should be invested in the search of more general hypotheses of homology regarding amphisbaenian cephalic shields"; however, there are cases when the homologies are undefined or even inconclusive, but at the same time the structures should be correctly indicated, and other criteria can perfectly be used, in face of evident wrong structure naming and/or persistent confusion of interpreting terms. This is especially significant if the renaming can aid future homological studies.

More importantly in the present case, we agree with the cautious stance adopted by Gans (1971a: 385) regarding *Leposternon* nomenclature and homology: "Any group of species showing fusions of cephalic shields incorporates the seeds of nomenclatural confusion. In 'homologizing' segments one must differentiate between segments that fuse or subdivide, in which case the overall spatial proportions are maintained, and those that shrink or expand, leading to a shift in the regions they occupy. (...) In other instances, such as the prefrontal subdivisions, we are unable to determine by what steps the observed patterns were produced. The present material [over 500 specimens of *Leposternon*] does not permit conclusions regarding presumptive homologies". The same author, on page 386, gives a practical example: "The term prefrontals is retained (...) but it must be recognized that they are only partially homologous to the prefrontals of *Amphisbaena* and similar forms". Thus, strict homologies can be very difficult to understand, and if they are undefined, they cannot be of compulsory use. Meanwhile, there is also no obligation to blindly follow a questionable nomenclature.

Lastly, it is important to mention that our nomenclature, if not focused strictly on homology, does not simply neglect it. One of the propositions brings a stronger base for homology studies in an area of the amphisbaenian head that was never, to the best of our knowledge, considered under this view (the "chin shields"). Regarding most of the other terms, without disregarding those reported in the literature, they act only as guidelines for a better understanding of the head shield pattern disposition, besides bringing a consideration concerning exactly the clearly mistaken approach—also regarding homology—of some nomenclatural terms

used for amphisbaenian head pholidosis. Only in one case do we propose a strictly better descriptive usage, but for scales of no critical homology importance.

4 - Following the above considerations, the proposed nomenclature is the best one, as it uses adequate anatomical and semantic criteria for the scales, and takes into consideration morphological characteristics of the peculiar cephalic *Leposternon* features, which are somewhat different from *Amphisbaena,* for example. This last point is important for nomenclature, since particular aspects are typical of *Leposternon* and an explicative nomenclature can, eventually, prevent homology problems, as, for example, Gans (1971a: 386) indicates for the *Leposternon* azygous scale, not present in *Amphisbaena* and most of other amphisbaenian genera: "In order to avoid confusing homologies, the enlarged median shield is hereafter referred to as the azygous". It must be noted that "azygous" was a term elected by its proper condition of not forming a pair, not for any homological criteria, and is a very well established name in amphisbaenian literature (there is also a small azygous median shield in a group of the amphisbaenian genus *Cynisca*, in addition to the prefrontal and frontal scales, cf. Gans 1987). As mentioned above, our proposition is perfectly compatible with other Amphisbaenia; it is important only to emphasize that its application also takes into account *Leposternon* particularities.

Finally, there is another important point to contextualize our proposition. To better explain the guidelines for the present nomenclature, it seems necessary to first consider that the criteria for definition of cranial limits must take into account that, even within Craniata, the shape and disposition of the different parts of the organism can vary, so their identification must refer to their more typical elements and functions. Thus, the disposition of the typical cephalic region must include brain, eyes, nostrils, among others, although in Amphisbaenia the disposition of these elements is different from other organisms, such as humans, for example. That is why, for instance, the amphisbaenian gular area can be recognized as a gular area and not a cephalic area, even if well aligned horizontally and under (not behind) the skull—its gular function is clearly identified. Similarly the posttemporal scales are included in the cephalic area, as well as other head scales mentioned herein—they are elements of the cephalic region, by definition (i.e., anatomical position), and cannot be included in postcephalic annuli counts, independently of the particular interpretations in the literature. This topic is very relevant because the body architecture of amphisbaenians is greatly specialized (cf.

Gans 1974, 1978), and has to be correctly understood to undertake homological approaches and other comparisons with different organisms, as well as for the comprehension of the methodological decisions of this paper.

We add that the proposed terminology allows for the clarification of comparisons with previously disputed or inexact approaches of previously published data. For instance, in a seminal paper on Amphisbaenia nomenclatural and meristic standardizations, Gans & Alexander (1962: 78) propose that, for *Amphisbaena,* the first anterior body annulus must include head shields, "Parietal (occipital of some authors)". In the following literature description of Amphisbaenia, this point of view was largely adopted, with variations in shield nomenclature (e.g., Pinna et al. 2010), however, for morphological and homological perspectives, it is not reasonable that scales clearly over the skull (cf. Alexander 1966: 210, relative position of skull and scales; Gans & Montero 2008) should be named as a body structure. Our proposal, in analyzing both dorsal and ventral components of the area between head and body, intends to contribute to also correct these discrepancies.

For the present nomenclatural purposes, the following scales deserve a close analysis:

Temporal and temporal rows

Usually defined as a group of three to five scales aligned in a vertical row immediately behind the ocular line and the last supralabial, and including those above the temporal scale in many amphisbaenian forms. Frequently, the first scales below the temporal, or the temporal itself, are behind the ocular, and the lowest ones behind the supralabial, being usually named "postoculars" and "postsupralabials" (e.g. Ribeiro et al. 2008; 2011; see also Gans 1965, "postocular row" for *Amphisbaena camura*). Vanzolini (1950), however, suggests that "postocular" is not always adequate, an observation followed by Gans (1971a - no reference to "postoculars" or "postsupralabials" scales in *Leposternon*). The reason is that, as mentioned by Gans (1971a: 386), "A variable number of segments is also found in the temporal region. It appears as if the variability of this region is again very large, and it is suggested that the variability results from the overlap of the functional influence extending caudad from the snout and that extending anteriorly from the body (and indeed from the pectoral region)". In other words, variations in scale number and position are frequent in this area, for Amphisbaenia in general (José Barros-Filho pers. comm. v.2001) and certainly for *Leposternon* (e.g.,

see illustrations in Gans 1971a). Indeed, not always can the scales of this row be identified as postoculars and postsupralabias; many times a particular scale is in a position where it can be indifferently named as one or another, or none, a problem for nomenclature and homologies.

At the same time, there is a clear homogeneity for this row's localization pattern, regarding the amphisbaenian cephalic Bauplan (even if there are not discrete temporal scales, as in *L. scutigerum*). Thus, we herein propose the use of "temporal row" for descriptions, detailing when pertinent which of the scales are in an unmistakable postocular or postsupralabial position. In the descriptions, the "first temporal scale" is defined as the one from top to bottom (and depending on the species will be above, or correspond to, the postocular position), and the others descend as "two", "three", etc.

A similar approach is described in Pinna et al. (2010: 45–46) for *Amphisbaena*: "temporals are scale rows between parietals and supralabials or post-supralabials; numbers of temporals may vary (two in Fig. 1C and D against three in Fig. 1A and B); the postocular (sensu Gans & Alexander 1962) is here considered a temporal". This is certainly of significance, since the use of "temporals" for the scales of this row, adapted to the specific amphisbaenian Bauplan, is a historical procedure also supported by classical amphisbaenian (and descriptive *Leposternon*) papers (e.g., Duméril 1851; Peters 1879; Boulenger 1885; Barbour 1914; Smith 1946; Gans & Alexander 1962; Gans 1971a; Ribeiro et al. 2008, 2011, 2015; Pinna et al. 2010, 2014; Roberto et al. 2014; Teixeira Jr. et al. 2014). The term "temporal" is used not only for Amphisbaenia, since its use in Squamata is very old (e.g., Duméril & Bibron 1839; Peracca 1897 for Serpentes; Barbour 1914), even if, regardless of homological aspects, it must be considered that Squamata do not have temporal bones (Cope 1900; Romer 1956; Höfling et al. 1995), although posterior supratemporal ones can be identified (Romer 1956).

Therefore, "temporal" is a valuable and useful topological reference. In fact, a direct identification of the temporal scale (and region) within the Amphisbaenia skull architecture can lead to difficult problems concerning homology. This occurs because the temporal scale position would have to be related with (at least) one of the following bones: frontal, tabulosphenoid, parietal (cf. Barros-Filho 2000; Gans & Montero 2008) - and even this could vary, due to different adaptations of the Amphisbaenia skull (e.g. Trogonophidae, Gans 1960; *Amphisbaena* = "*Anops*" group, Vanzolini 1999) and head scale arrangements (e.g. the large fusions of *Cynisca* scales, Gans 1987). A homology analysis in this

situation can prove not only hard to be understood, but also extremely confusing concerning practical naming of scales.

It is certain that future research will reveal a clearer picture, but considering the lack of trustworthy homological data, the nomenclatural discordances, the stressed adaptive condition for this group of scales and its variability, it seems more sensible and useful to identify them simply as temporal and temporal row, for easier comparisons within Amphisbaenia and to Squamata.

Another convenience of this procedure is that the temporal row (and sometimes the postemporal and occipital ones, see below) incorporates the "postsupral abials"/"postinfralabials", which are defined differently between authors (e.g., Vanzolini 1950; Pinna et al. 2010; Ribeiro et al. 2008). The problem also exists for other genera and species that have scales in this "postlabial" region, which are aligned with the gular area below and one of the head cephalic shields above (temporals, occipitals), i.e., not the first body annulus as standardized by Gans & Alexander (1962) (cf. Alexander 1966 for *Blanus*; Gans 1971b for *Amphisbaena* of "*Aulura*", "*Bronia*" and "*Mesobaena*" groups; Broadley & Gans 1978 for *Chirindia*; Gans & Kraklau 1989 for *Geocalamus* and *Loveridgea*). The first body annulus must be considered, in all amphisbaenians, only after the last recognized head shields, where the skull effectively ends (cf. Alexander 1966).

The importance of this nomenclature also concerns the definition of the postemporal scale row, which includes some scales of disputed interpretation within Amphisbaenia (e.g., in *Leposternon* and *Amphisbaena* spp., see below).

Postemporal row

A vertical row with variable number of segments may be present behind the temporal row and before the occipital row (see below), at least in *Leposternon* species. It has been suggested by Gans (1971a) that these postemporals must be included in the anterior lateral counts, an inaccurate approach. Postemporals are not anterior laterals (which are body scales), as they are located in the cephalic region (laterally) and continue towards the gular region (ventrally). Also, they cannot be considered true temporals, due to their more posterior position and as they are in an area of lateral folding movement of the head, which is not characteristic of the temporal region. The logical way is to name them posttemporals, an unequivocal reference point.

Occipitals and occipital rows

A pair of dorsal medial segments immediately after the azygous (e.g., *L. octostegum*) or the parietals (most other Amphisbaenia), and the scales lateral to this pair, vertically arranged down to the gular region. These shields seem to have been included in the anterior lateral counts by Gans (1971a) however, ventrally they are not related to the pectoral (body) region, but to the gular region. Thus, the annulus that includes them cannot be counted as the first anterior lateral, oriented to the pectoral region. As such, it is referred herein as the occipital row, which is immediately followed by the first "anterior lateral" row. It is assumed herein that they are not merely reduced parietals, which as they are usually bigger shields, but are more likely to have been fused with the other great dorsal head shields to form the azygous (in *L. octostegum*); it is also important to consider that in *L. octostegum* and the other *Leposternon* species the parietals tend to laterally follow the orientation of the temporal/postemporal rows (i.e., the arrangement of the cephalic shields), while the occipital row aligns posteriorly with the gular region. Naturally, the occipital area is posterior to the parietal one (also in other Amphisbaenia). Furthermore, in the original description, Duméril (1851) had already named these shields "occipitals" (see also Steindachner 1867; Boulenger 1885; Gans 1971a).

"Chin region"

For this group of scales we propose not only redefinitions and adaptations as above, but a new nomenclature.

We performed a reevaluation of the nomenclature of the scales of the so called "chin region" of amphisbaenians. This included the scales confined by the genial (= mental), the infralabial scales and the gular region. We found that the terms historically utilized to name these scales are basically derivations of the terms "genial" or "mental". The correct definition of "gen*ys*" (Greek; or Latin "mentum" = chin) refers to "The anatomical frontal portion of the mandible, also known as the mentum, that contains the line of fusion of the two separate halves of the mandible (symphysis menti)" (Biology Online 2005). This is a concept shared for both human and animal anatomy (Testut & Jacob 1947; International Committee on Veterinary Gross Anatomical Nomenclature 2012; Medicalency 2014). Informal usages led to the application of this term also for the correspondent external, lower extremity of the face, below the mouth; and, in Zoology, often for the external surface below the lower jaw or between its branches (cf. Vanzolini 1991). In other words, the same name is applied

for different regions with different characteristics.

Thus, we propose the name "intermandibular" (Latin "inter" = between and "mandibula" = mandible) for the area confined by the genial (= mental), the infralabial scales and the gular region. The mandible bones encircle this region, being an unequivocal reference for anatomical or homological purposes. The name of the scales restricted to this area will be then related to the term "intermandibular".

Observation

The definitions for intermandibular scales below (Fig. 4) contemplates Amphisbaenia in general, but for the sake of simplicity the observations are mainly for *Leposternon* and *Amphisbaena*.

Lateral intermandibulars are all the scales touching/bordering the infralabials.

Central intermandibulars are the scales immediately behind the postmental (or the mental, in the forms of mental fused with postmental, e.g., *L. octostegum*); these may appear in more than one row (frequently one to three in *Amphisbaena*); laterally limited by the lateral intermandibulars; posteriorly delimited by the posterior intermandibular row.

Medial intermandibulars are the scales that may appear between the central and lateral intermandibulars; these are more frequent in *Leposternon* and usually absent in *Amphisbaena*.

Posterior intermandibular row includes the scales disposed transversally between the last lateral intermadibular scales on each side, and behind the central and medial intermandibular scales. More than one may occur, or it can be absent. It corresponds to the "postmalar row" as cited by Gans & Alexander (1962) except for two lateralmost scales, herein identified as the last lateral intermandibulars (which are frequently larger than the other "postmalar" scales).

Gular row is usually not well identified in *Leposternon*, due to the arrangement of the gular folds and the postintermandibular row, but in *Amphisbaena* corresponds in the majority of the cases to the "first body annulus" of Gans & Alexander (1962), which includes typical dorsal head scales (e.g., occipitals or parietals).

The only reference found to use "intermandibular" with the same term and area was in the report by Komárek (2012: 145–156, Fig. 1-1), in a work conducted on with mice, but of course there is no mention to scales.

For the scales bordering the intermandibular region (e.g., infralabials) there is no need to change the current names, however, adaptations are necessary for the scales touching the gular region ("posterior intermandibular

row" and "gular row", see description). For the sake of standardization, we maintain "mental" and "postmental" (e.g., Gans 1971a; Porto et al. 2000; Ribeiro et al. 2008), a very well-established term with a Latin origin (the official anatomical language), and so is preferable to "genial", of Greek origin. The name "symphysal" (Vanzolini 1991) is not adequate, since it refers to the anterior mandibular symphysis, which is not present e.g., in Serpentes, and, thus, hampers homologies.

This standardization also seems advisable since the terms "mental" and "postmental", "genial" and "postgenial" and their derivations (e.g., "lateral genial", among others), in addition to not being correct for some scales, have been repeatedly used with different criteria, which results in great nomenclatural confusion. For instance, Broadley et al. (1976) used "postmental (genial)" for *Monopeltis* and *Dalophia* spp. In a more recent example, Costa et al. (2015), in describing *A. mettalurga*, used "mental", "postmental", "postgenial", "malar" and "postmalar row" simultaneously, following the nomenclature reported by Gans & Alexander (1962) and Teixeira Jr. et al. (2014). This is a historical but incorrect use of "postmental" and "postgenial" simultaneously, both being synonymous and referring to different scales. The same apply to "malars", which presumably was proposed (Gans & Alexander 1962) – inadequately – as the bone structure of reference for these shields.

It is interesting to note that, until now, only the mental/postmental disposition offered a reliable source of homology for the scales of the intermandibular area, due to previous variable/erroneous approaches. The present novel nomenclature for this group of scales is simple to be applied, semantically and anatomically correct, and, thus, facilitates homological analyses for Amphisbaenia and Squamata. In addition, it can be easily compared with published data. We offer the following very brief bibliography (enough as an example) for term and images comparison of scales from the intermandibular region in Squamata (similar words and meaning in English, French, Italian, Latin, Portuguese and Spanish):

Lacertilia – terms: mental, postmental(s), sublabials, gular(s) (sometimes used incorrectly, since the gular region cannot be identified with the region between the more anterior infralabial scales), symphysal, postsymphysal, chin shields and scales between chin shields, chin scales, genials; or they can simply be unnamed and not even mentioned. In: e.g., Boulenger (1885); Vanzolini et al. (1980); Rocha et al. (2000); Avila-Pires (1995); Meneghel et al. (2001); Rodrigues et al. (2001, 2006); Nogueira & Rodrigues (2006); Hoskin

(2014); Nicholson & Köhler (2014); Doughty et al. (2015); Troncoso-Palacios et al. (2016).

Amphisbaenia – terms: symphysal, postsympysal, mental, postmental, submental(s), postmental (= "median chin shield of some authors", Gans & Alexander 1962), genial, lateral genial, median genial, postgenial, postmental row, postgenial row, intergenials, malars, postmalar row, chin shields, lateral chin shields, "other shields posterior to the median chin shield", unnamed, sublabials, gulars (inadequately). In: e.g., Strauch (1881); Boulenger (1885); Cope (1900); Barbour (1914); Loveridge (1941); Witte & Laurent (1942); Smith (1946); Vanzolini (1950); Gans (1960); Alexander (1966); Saiff (1970); Broadley et al. (1976); Broadley & Gans (1978); Gans (1987); Gans & Kraklau (1989); Broadley & Broadley (1997); Broadley & Measey (2016).

Serpentes – terms: mental(s), postmentals, symphysal, chin shields, median gular, gular rows, gulars (inadequataly), genials. In: e.g., Peracca (1897); Amaral (1926); Dunger (1966); Downs (1967); Vanzolini et al. (1980); Zaher & Caramaschi (1992); Scrocchi & Cruz (1993); Thomas & Fernandes (1996); Hoogmoed (1997); Ota et al. (1999); Meneghel et al. (2001); Marques et al. (2002); Fernandes et al. (2004); Franco et al. (2006); Shea (2015).

"Anterior and posterior laterals"

These terms were proposed by Gans (1971a) for the group of half-annuli respectively dorsal to the pectoral and cloacal *Leposternon* shields. Effectively, they are partially lateral, but mainly dorsal – the lateral sulci are the parameter for dorsal and ventral half-annuli counts in the same paper. Thus, "lateral" is not the best option. As they are associated to undisputed structures (pectoral and cloacal regions), "anterior" and "posterior" are in this case less descriptive (as is "supra", due to the presence of lateral scales). We propose the standardization of "contrapectoral half-annuli" and "contracloacal half-annuli" for respectively "anterior" and "posterior" "laterals". As Greathouse (2012) explains, the term "contralateral" (Latin *contra* = against; i.e., opposite to) is a strictly relative direction (not defined by a fixed axis), so there is no homology concepts for this term, thus being truly descriptive but also not interfering in homological analysis. In addition, homology is not a critical point in the present case.

RESULTS

Leposternon octostegum (Duméril)
Amphisbaena octostega (Duméril)

Lepidosternon octostegum Duméril, 1851, p. 150–151. *Terra typica*: "Brésil". Holotype: MNHN 7055.

New material (N = 16): MNHN 2007.0023, MZUEFS 696 (adult males); MZUEFS 652, 655, ZUFRJ 1749 (females); MNHN 2007.0024, MZUEFS 653, 654, 657, 695, ZUFRJ 1748 (unidentified sex) all collected on 05 November 2003 by José Duarte de Barros-Filho, Marco Antônio de Freitas, Danilo Pacheco Cordeiro and Franco Henrique Andrade Leite; and MZUEFS 656 (male), collected on July 2003 by Marco Antônio de Freitas – all specimens are from Aterro Metropolitano Centro (12.858°S & 38.370°W), at sea level), Salvador City, state of Bahia, Brazil. ZUFRJ 1715 (female) and ZUFRJ 1713, 1714, 1716 (unidentified sex) collected on 04 June 2006 by Marco Antônio de Freitas at Arembepe county (12.697°S & 38.324°W), at the Municipality of Camaçari, state of Bahia, Brazil.

Diagnosis

A species of *Leposternon* with an enlarged, polygonal azygous shield atop the head, which, however, does not exclude the discrete prefrontals, oculars and first temporals shields of the dorsal cephalic area posterior to the rostronasal; one large supralabial and one large infralabial shield on each side of mouth; a large mental shield (postmental shield absent, probably fused with the mental shield); 353–382 ventral, postpectoral half-annuli.

Definition

A slender, medium-sized (388mm maximum adult total length) form of *Leposternon*, with an enlarged, polygonal azygous shield atop the head; in dorsal view, the rostronasal, the prefrontals, the oculars, the first temporals and a small pair of occipitals are also clearly discernible; one large supralabial and one large infralabial; mental and postmental shields, probably fused; three pairs of enlarged shields along the midline, with left and right asymmetries: the anterior pair forms a rough stretched pentagon pointing backwards, the second pair has irregular polygons tending to a medial suture in an "X" disposition and the posterior pair showing polygonal transversely elongated shields, larger caudad than rostrad; 353–382 ventral, 357–397 dorsal postpectoral half-annuli; 24–33 dorsal half-annuli scales; 23–29 ventral half-annuli scales; 12–15 caudal annuli; a short, cylindrical and round ending tail; 121–142 precloacal

vertebrae; absent precloacal pores and autotomy. Living specimens have a pale grizzled background coloration, with none or inconspicuous sparse, diminute and irregularly distributed dorsal brownish pigments, more concentrated in the second half of the body (Image 23A). Alcohol preserved specimens display a more pale brown (beige) brownish or whitish background coloration, and the pigments are more subtle. The sample from Municipality of Camaçari exhibited a different coloration, with marked brownish blotches or dorsal pigment dots evident along most of the body and in the tail.

Distinguishing features from one another (data in parenthesis) *Leposternon* species

Leposternon octostegum can be distinguished from all congeners by the combination of one supralabial and one infralabial shield, and a large single mental shield. The main evident differences between *L. octostegum* and all other *Leposternon* species, except *L. scutigerum* is the pectoral pattern with three pairs of enlarged unusually-shaped shields along the midline, with left and right asymmetries (see "Other remarks on congeneric comparison" below), and the dorsal shield head pattern with the great azygous shield occupying most (circa 55%) of the total area. Furthermore, *L. octostegum* has three rows of shields atop the head, including rostronasal, prefrontals, azygous, oculars and first temporals (eight main shields, the reason of the specific epithet etimology, cf. Duméril 1851), while *L. scutigerum* has two rows of dorsal head shields, represented by the rostronasal and azygous shields. *Leposternon octostegum* also differs from *L. scutigerum* by having 353–382 ventral postpectoral half-annuli (246–305). In addition to the cephalic and pectoral patterns, *Leposternon octostegum* further differs from other *Leposternon* species by the following combination of characteristics: it differs from *L. wuchereri* by having 353–382 ventral postpectoral half-annuli (233–265), 23–33 dorsal half-annuli scales (16–19) and 23–29 ventral half-annuli scales (16–21), from *L. infraorbitale* by having 353–382 ventral postpectoral half-annuli (201–275), a maximum adult body width of 9.3 mm (30mm or more; usually around 25mm) and live dorsal adult coloration of a pale grizzle background with brownish scale pigments, discrete or not (yellowish or whitish background with dark scale pigments), from *L. microcephalum* by having 353–382 ventral postpectoral half-annuli (186–254) and live dorsal adult coloration of a pale grizzle background with brownish scale pigments, discrete or not (usually a grayish background with dark scale pigments), from *L. polystegum*, *L. kisteumacheri*, *L. cerradensis*, *L. maximus* and *L. mineiro* by having no precloacal pores (two; 2–4

in *L. polystegum* and *L. cerradensis*), from *L. polystegum* by having 353–382 ventral postpectoral half-annuli (244–324), from *L. kisteumacheri* by having 353–382 ventral postpectoral half-annuli (246–264) and live dorsal adult coloration of a pale grizzle background with brownish scale pigments, discrete or not (bright yellow), from *L. cerradensis* by having 353–382 ventral postpectoral half-annuli (302–349), 23–33 dorsal half-annuli scales (32–37), and 23–29 ventral half-annuli scales (30–36), from *L. maximus* by having 353–382 ventral postpectoral half-annuli (408–448) and live dorsal adult coloration of a pale grizzle background with brownish scale pigments, discrete or not (pinkish), from *L. mineiro* by having 353–382 ventral postpectoral half-annuli (270–280).

Other remarks on congeneric comparisons

The pectoral shield pattern is very typical and useful for the identification of *Leposternon* species (cf. Gans 1971a), but seems not to be a diagnostic character for *L. octostegum*, as a similar pattern occurs in *L. scutigerum* (Image 11; Fig. 2A). However, the pairs of main shields are more regular in the latter species, while asymmetries in shape, size and/or position are the natural condition in *L. octostegum*. Nonetheless, *L. scutigerum* ZUFRJ 1730 (Fig. 2A to comparisons) has a close asymmetric situation, so it seems advisable not to use pectorals as a diagnostic character.

Furthermore, the pectoral pattern of *L. octostegum* (three pairs of enlarged, unusually-shaped shields along the midline, with left and right asymmetries, see below) is completely distinct from the ones present in *L. wuchereri* (parallel enlarged shields), *L. infraorbitale* and *L. microcephalum* (general "V" shaped shield arrangement) and *L. polystegum*, *L. kisteumacheri*, *L. cerradensis*, *L. maximus* and *L. mineiro* (diamond shaped shields).

There is a general trend for the elongation of the posterior dorsal half-annuli scales in *Leposternon* (José Barros-Filho pers. comm. v.2001), i.e., the scales tend to be longer instead of larger from near the head to near the tail (compare Images 8 and 18); but this trend, in a more rectangular than "squared" shape, seems relatively more accentuated in *L. octostegum*. In addition, the lateral sulci of *Leposternon* species most commonly do not begin immediately behind the pectoral region as in *L. octostegum*.

Variation in the analyzed samples

Table 1 summarizes the variations among the examined specimens. Additionally, the specimens from the Municipality of Camaçari show some minor morphological differences, such as an eventual

suggestion of scale fusions with the azygous, but not enough to characterize a different species. The most evident divergence of the Camaçari sample is the coloration pattern, although this is probably due to an ontogenetic variation (see Discussion).

It was also possible to use the published data regarding four other *L. octostegum* specimens cited by Ribeiro et al. (2008: 20; 2011: 182, Fig. 4B; 2018: 58) in the comparison to *L. cerradensis* and *L. maximus* (MCP 18192, MCP 1893, MZUSP 96349 - Brazil, State of Bahia, Municipality of Camaçari; MZUSP 96350 - Brazil, State of Bahia, Salvador City). The variations of these four specimens from the present *L. octostegum* sample (in parenthesis) are: maximum postpectoral ventral half-annuli 390 (382), minimum postpectoral ventral half-annuli 342 (353), 11 caudal annuli (12–15) and 144 precloacal vertebrae (121–142). The counts of maximum postpectoral dorsal half-annuli 398 (397) and minimum postpectoral dorsal half-annuli 353 (354) are very similar.

In *Leposternon*, the dorsal postpectoral counts are usually greater than the ventral counts (Gans 1971a), as is also true for *L. octostegum*, however, this difference is less striking in some *L. octostegum* specimens (cf. Table 1).

Description

A slender, medium-sized *Leposternon*, with 388mm of maximum adult total length, and maximum body width of 9.3mm at midbody. Body vertebrae 121–142. Measurements and meristic data are summarized in Table 1.

Shields of the dorsal half of the head (Images 1–5)

Rostronasal: Large, roughly semicircular (base: posterior) in dorsal and ventral views. Laterally, its posterior suture forms a triangle of approximately 45° pointing backwards, contacting the prefrontal superiorly and the supralabial inferiorly. Dorsally, at the midline, the transversal suture is deformed by the anterior portion of the azygous, in a triangular or more concave shape; a short middle depression (e.g., Image 1A) or straight sulcus (e.g., Image 1B) usually projects anteriorly from this deformation, but it never reaches the azygous tip. The ventral nares are essentially semicircular, their bases at a near 45⁰ angle from the longitudinal body axis; their medial-anterior rounded portions are protected by a semicircular flap, in a depression (i.e., the flaps are in a plane below the medial-rounded rims plane). A right line of weak suture is variably evident from the posterior extremity of each of the narial bases to the anterior mouth rim, indicating a probable ontogenetic fusion of
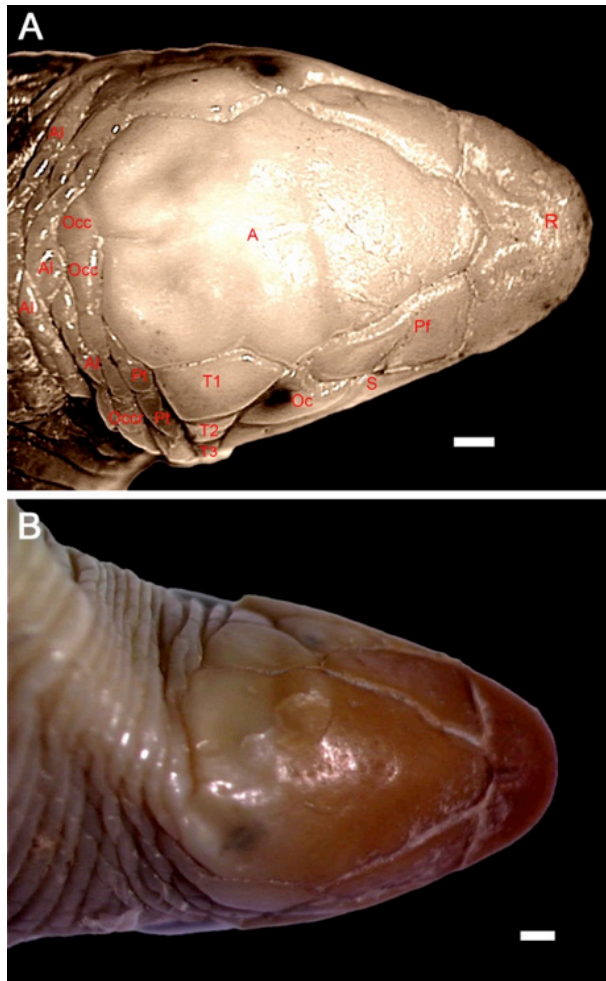
Image 1. *Leposternon octostegum*. Dorsal head shields.
(A) MZUEFS 695, (B) MNHN 7055 holotype. Legends: A - azygous; Cp - contrapectorals; Oc - ocular; Occ - occipitals; Occr - occipital row; Pf - prefrontal; Pt - postemporal; R - rostronasal; S - supralabial; T1, T2, T3 - temporal 1, 2, 3 of the temporal row. Scale bars = 1mm.
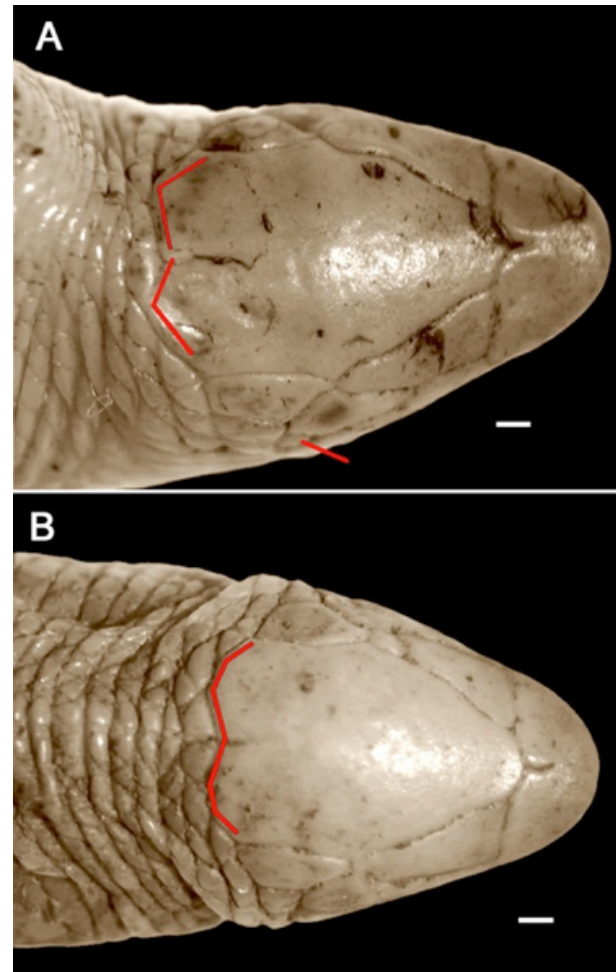

Image 2. *Leposternon octostegum*. Azygous suture variations. (A) ZUFRJ 1716 from Camaçari. Red bars showing the typical posterior "W" azygous suture. The isolated red line points out the extra shield (see *Oculars* description). (B) ZUFRJ 1749. Red bars showing the posterior "W" azygous suture with two more angles. Scale bars = 1mm.

scales involved in the rostronasal shield formation.

Azygous: Very large, occupying most of the dorsal head surface (circa 55% of total area and circa 80% of head length). At first glance, it seems pentagonal in shape, with a near triangular anterior and near squarish posterior contour (a similar impression was registered by Duméril (1851) in the original description). Nonetheless, the pattern is more complex when examined in detail. It anterior portion is actually not triangular; only the most rostral tip, which is inserted in the rostronasal shield, has a more "V" shape (tip not rounded as in the holotype in 13 of 17 specimens; no relation to collecting place or sex). The two "V" lines are anteriorly straight, but run backwards as slight undulated lines (convex and concave successively). They reach the greatest distance between each other at the level of the ocular shields

and continue backwards as the posterior lateral sutures. These are almost parallel with each other but can also display undulations or angulations; they dorsally delimit the first temporals on each side. The caudal suture of the azygous is the continuation of these posterior lateral sutures; it is transversely oriented but not as a straight line. Instead, the caudal suture has angulations, with the typical pattern being a stretched "W" (Image 2A).

The azygous's polygon, including the "V" and "W" sutures or other angulations, usually shapes a decagon (N = 8, the most typical conformation). Other patterns can occur, such as, for example, two more angles in "W" forming a dodecagon (Image 2B); or an octagon if instead of the "V" suture there is a rounded one. Other possible polygons include angulations of the posterior lateral sutures (Image 1A).
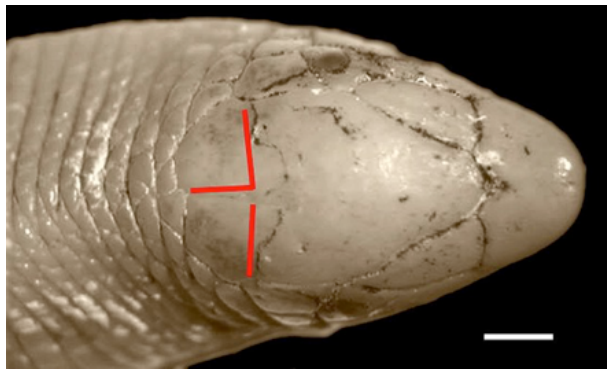
Image 3. *Leposternon octostegum* ZUFRJ 1714 from Camaçari. Red bars indicating that posterior "T" suture remains in the azygous shield. Scale bar = 1mm.
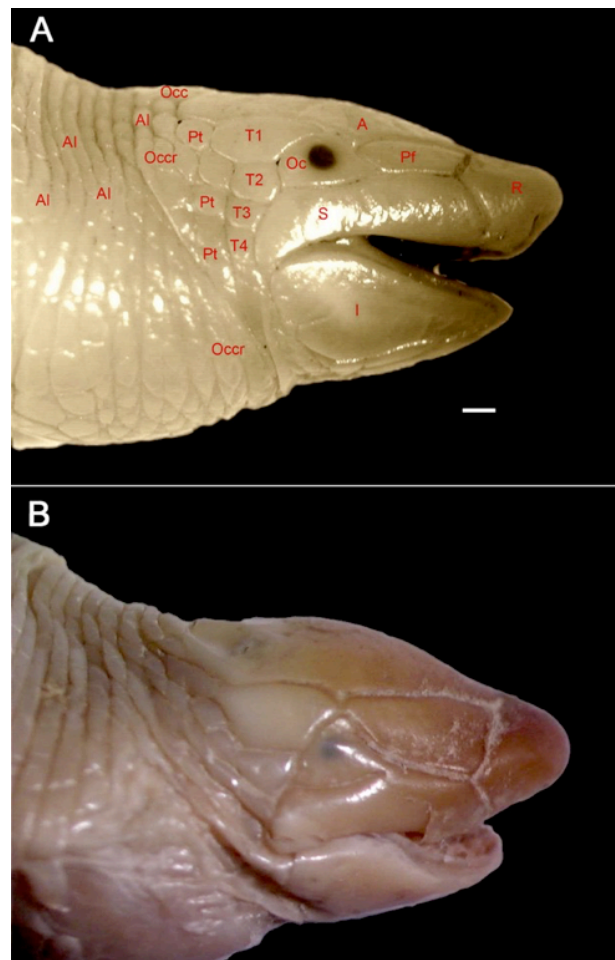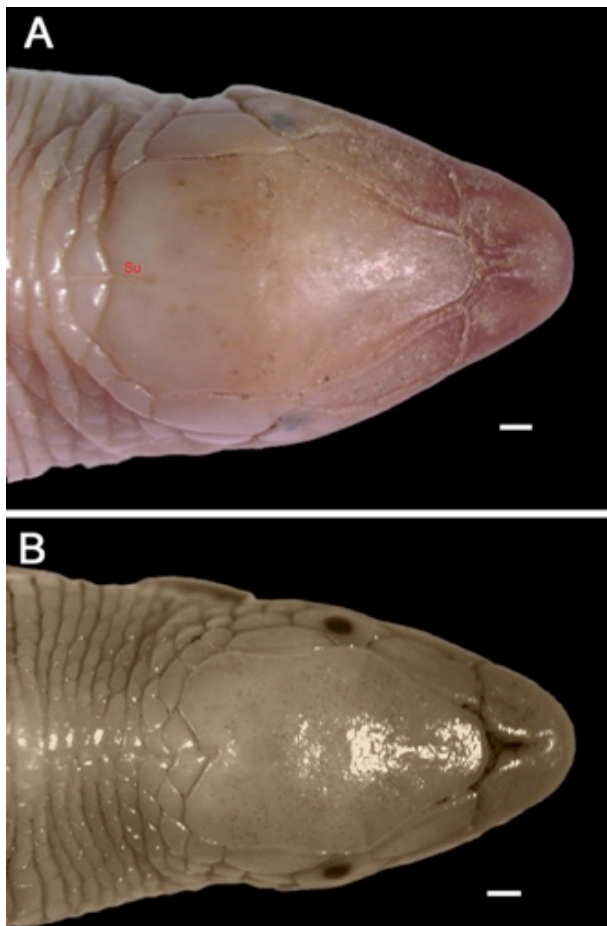

Image 4. *Leposternon octostegum*. (A) MZUEFS 653, posterior azygous sulcus present. (B) ZUFRJ 1713 from Camaçari, posterior azygous sulcus not expressed; note the rounded anterior part of the azygous, the modified"W" suture and small pigmentation. Su – posterior azygous's sulcus. Scale bars = 1mm.

Image 5. *Leposternon octostegum.* Lateral head shields. (A) ZUFRJ 1713 from Camaçari. (B) MNHN 7055 holotype. Legends: A – azygous; Cp – contrapectorals; – infralabial; Oc – ocular; Occ – Occipitals; Occr – occipital row; Pf – prefrontal; Pt – postemporals; R – rostronasal; S – supralabial; T1, 2, 3, 4 – Temporals. Scale bars = 1mm.

In the posterior half of the azygous shield of specimen ZUFRJ 1714, 1716 and 1749 (Image 3), the remains of a pair of elongated rectangular scales, corresponding to the probable fused frontals (with each other and the azygous), can be better noted by a faded "T" (or similar) shaped suture line. In almost all specimens a somewhat elongated sulcus (the posterior portion of the longitudinal "T" trace, touching the "W" caudad suture) is clearly seen in the midst of the posterior portion of the azygous shield (Image 4A). It is aligned with the inter-occipital suture that follows behind the azygous.

Prefrontals: In dorsal view, they are the larger shields on the top of the head after the azygous and rostronasal shields. They form an irregular trapezium with curved corners, despite the general "triangular" appearance, especially in the dorsal view. The base of the "triangle" is relatively short, sutured transversally with the rostronasal shield. The longest, dorsal suture with the azygous shield is undulated, as described above. The

ventral suture with the single supralabial is an almost straight line parallel with the mouth line, which then tilts upwards posteriorly, suturing with the ocular and giving it the shape of a trapezium. The prefrontals may contact the first temporal shield above the ocular shield (Image 4A), but usually do not (Image 4B).

Oculars: roughly irregular pentagons, the ventral (and longest) suture to the supralabial is usually slight curved or alternatively being almost straight. The anterior suture, with the prefrontal, is inferiorly concave. The posterior suture, with the two upper temporal shields, is somewhat convex. A point of contact (or very small line) can occur superiorly to the azygous, between the prefrontal and first temporal shields. The Camaçari sample shows oculars shaped almost as trapezia; in ZUFRJ 1713, 1715 and 1716 these "trapezoidal" oculars touch a small extra "infraocular" shield posteriorly and inferiorly, shaped as a trapezium or a triangle, in at least one side of the head (Image 2A). The extra shield is inserted between the ocular, the supralabial and the temporal row.

Supralabials: A single and large supralabial on each side of the head, shaped as a stretched irregular pentagon. Sutures: anteriorly as a backslash ("\") with the rostronasal; superiorly with the prefrontals and oculars, respectively, usually with different angulations with each one, and posteriorly with the temporal row, in an almost convex line. The inferior edge of the supralabial is curved, clearly concave near the angulus oris.

Temporal row: The vertical temporal row on each side of the head lies immediately behind the ocular and last supralabial line, and usually has four scales (rarely three or five). These scales will be here referred as first through fourth temporals, from top to bottom. The first temporal is the largest scale in the row and is longer longitudinally compared to vertically. Its shape varies from a rough trapezium to an irregular polygon with five or six sides. The anterior suture with the ocular is concave; the superior suture with the azygous is slightly undulate; the posterior suture with the postemporal rowscale(s) (see below) is curved or angulated; and the inferior suture with the second temporal is approximately a straight line. The second temporal is usually trapezoidal, almost square-shaped, higher than longer, always with the superior margin being the longest – sometimes appearing as an almost longitudinal rectangle. It is anteriorly sutured with the ocular, or with ocular and supralabial, by curved or straight lines. The inferior and posterior sutures are straight lines, respectively with the third temporal scale and postemporal row. The third and fourth temporals are usually disposed as a rough vertical

rectangle, cut by a backslash ("\") that forms the suture between them. They are usually higher than longer, suturing (curved or straight lined) anteriorly with the supralabial (third supralabial rarely in contact with the ocular, see above) and posteriorly with the postemporal row. Minor variations in scale shape, number (up to three small supernumerary scales) and disposition can occur involving the temporal row region, from third temporal down to the angulus oris.

Postemporal row: One to three lateral vertical rows of somewhat irregular shaped scales, confined anteriorly between the temporal row, the dorsal half-annulus that includes the occipitals posteriorly, the azygous superiorly and the gular region inferiorly.

Occipitals and occipital row: A pair of occipital shields is discrete at the midline, sutured with the azygous posterior margin. They are trapezoidal in shape, sometimes almost triangular, usually transversely elongated and of about same area, but a little larger than the immediate lateral and posterior scales. They are sutured medially with each other on a straight line on this side of the trapeziums, which have the narrower vertex laterally oriented. This sagittal suture is aligned posteriorly with the dorsal sulcus and anteriorly with the midst sulcus of the posterior portion of the azygous. The occipitals are in the center of a dorsal half-annulus, composed of somewhat irregular scales (varying in shape, rounded, polygonal or elongated). The occipital row ends inferiorly at the limit of the gular/pectoral region

Shields of the ventral half of head (Images 6–7, Fig. 4)

Mental: This is the biggest ventral head scale, after the infralabials. This shield anteriorly forms the central edge of the mouth. It is about two times longer than wide, with the general appearance of an elongated heptagon. The posterior end is triangular and inserted between the central intermandibulars. Vestiges of up to four sutures can be seen, including what would probably be an individualized postmental shield. The sutures are (probably) the result of ontogenetic development, and are not clearly noticeable in only two of the 17 specimens. The mental scale is laterally sutured, almost straight, from front to rear, with the infralabials, the lateral intermandibulars, and the medial intermandibulars, respectively.

Infralabials: An enormous scale on each side of the mouth, most certainly resulting from the fusion of two shields. The evidence is the presence of a very discrete, but usually not very long sulcus, beginning more or less at the middle of the posterior infralabial shield margin, but ending inside the area of the same shield (Image 7).
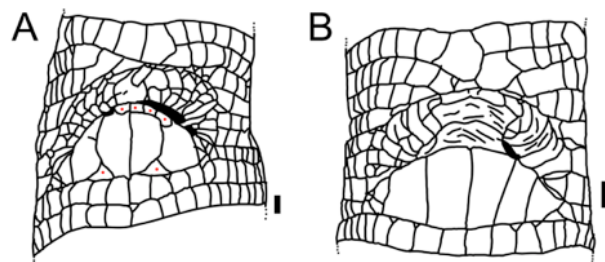
Figure 3. *Leposternon octostegum*. Cloacal flaps. (A) ZUFRJ 1749, with supplementary shields marked in red. (B) ZUFRJ 1715, without any supplementary or extra shields. Scale bars = 1mm.
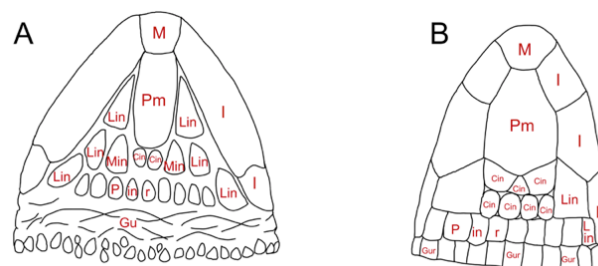

Figure 4. *Leposternon* spp (A) and *Amphisbaena* spp (B). Squematic drawing displaying the ventral head shields. Legends: Cin - central intermandibulars; Gu - Gular region; Gur - Gular row; I - infralabials; Lin - lateral intermandibulars; Min - medial intermandibulars; Pinr - postintermandibular row.

The infralabials have a general triangular appearance, but with undulated sides. They form most of the inferior mouth edge, except for the rostral tip, occupied by the mental scale. They are laterally sutured, from rostrad to caudad, respectively, to the mental and the lateral intermandibulars, in straight or slightly undulated lines; and posteriorly in undulated lines (or, alternatively, straight lines forming angles), with the first of the irregular and narrowed half-annulus that can be present in the gular region.

Lateral intermandibulars: One (usually)**,** two or rarely three (Image 7) on each side; if two, aligned longitudinally. The one, or the anterior of the two, is shaped like an elongated trapezium, with the narrower vertex inserted rostrad between the mental and the infralabial scales. Laterally sutured throughout their length with the infralabial, medially and rostrad with the mentals, medially and caudad with the central intermandibulars, in straight or slightly undulated lines. The second pair of lateral intermandibulars is shorter than the first, not elongated, trapezoidal or almost squared. They are at the level of the central intermandibulars, forming a transversal row with the latter. The lateral intermandibulars suture posteriorly with the postintermandibular row.

Central intermandibulars: One to three discrete scales, each shield triangular or trapezoidal in shape (some deformation can occur). Usually a pair is present, with the narrower vertex inserted rostrad between the mental and lateral intermandibulars, and a median scale slight posterior and between the pair. This median scale is sometimes easily discernible but too far from the mental shield (cf. Fig. 7), being included in the postintermandibular row (see description). The pair is limited laterally by the lateral intermandibulars, and the median scale is limited by the postintermandibular row. Posteriorly, they are sutured to the postintermandibular row.

Medial intermandibulars: In *L. octostegum* these are poorly expressed as very small irregular scales, or absent.

Posterior intermandibular rows: One, two, or rarely three rows of irregulary shaped shields, with a general semicircle arrangement, and the arch of the semicircle rostrad. The shields of the first row are usually enlarged, in a more or less fixed pattern: the median one is larger, almost round or oblong and the lateral ones are oblong, sutured laterally with infralabials, with elongated, almost rectangular, shields between them. The shields of the second/third rows are usually more weakly expressed.

This semicircle arrangement is usual for *Leposternon*, being well expressed or not. This occurs since, in contrast to *Amphisbaena*, the scales of these rows tend to converge anterior and medially in the specific *Leposternon* head *Bauplan* (against the more transversal and organized disposition of *Amphisbaena*). The last row is posteriorly followed by the folds of the gular region, where the definition of the irregular, weakly expressed shields and rows is sometimes vestigial.

Contrapectoral rows and pectoral region (Images 5 and 8–11, Fig. 2)

Contrapectoral rows: These dorsal half-annuli (13 to 18) extend from the first dorsal half-annulus immediately behind the occipital row to the last dorsal half-annulus which touches the modified ventral pectoral shields laterally. They possess two or three rostrad annuli, ventrally, corresponding to a transitional area (due to their postoccipital and gular position), with the shape and pattern of their shields not very distinctive from those of the gular region; they are irregular, polygonal or almost rounded shields, and the largest (or fusion of small shields, frequently triangular) are usually located at the midline.

Dorsally, the contrapectoral rows display rounded or somewhat oval scales (near the head), modified
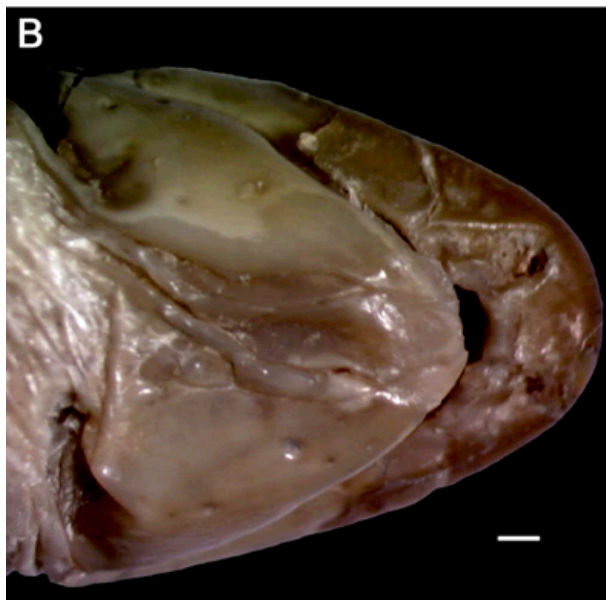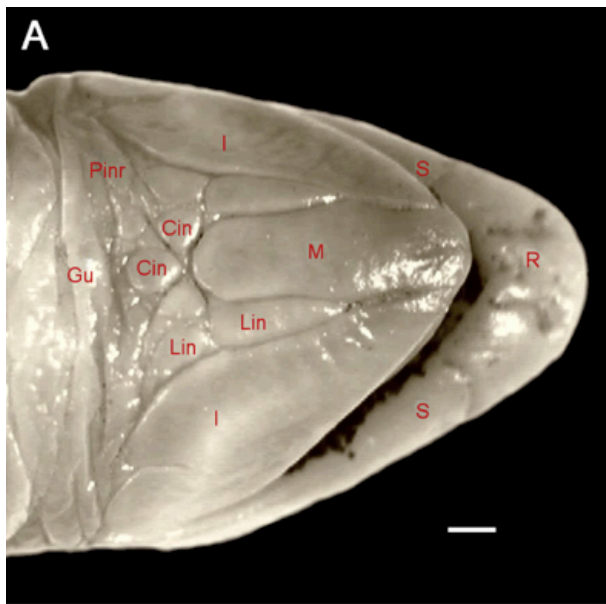
Image 7. *Leposternon octostegum* MZUEFS 654. Legends: Lin - additional anterior pair of lateral intermandibulars; Su - infralabial sulcus. Scale bar = 1mm.

Image 6. *Leposternon octostegum*. Ventral head shields. (A) ZUFRJ 1713 from Camaçari. (B) MNHN 7055 holotype. Legends: M - mental; Gu - gular region; I - infralabials; Lin - lateral intermandibulars; Cin - central intermandibulars; Pinr - postintermandibular row; R - rostronasal; S - supralabials. Scalebars = 1mm.

posteriorly into rectangular, squarish scales (Image 8). The medial dorsal sulcus begins in this region, well expressed or only discernible.

Pectoral region: The larger shields of the pectoral region have a very typical disposition pattern (Image 9), but the shape of each individual shield is highly variable. The three mediad pairs are the most characteristic: the anterior pair forms a rough stretched pentagon pointing backwards; the shields of the medial pair may or may not display sagittal contact; they are elongated, irregular polygons, with a marked tendency to suture diagonally both rostrally and caudally with the anterior and posterior pairs respectively, roughly in a "X"-shaped disposition. In addition, as their lateral sutures are elongated and closely parallel to the sagittal plane, the two shields are shaped similarly to a "bowtie". The posterior pair has polygonal elongated shields, usually wider caudad when compared to rostrad. The main variations are the contact of the anterior and posterior pairs, usually separated by the medial pair, the absence of the caudal part of the "bowtie" (i.e., transversal instead of diagonal suture with the posterior pair), and shield asymmetries (shape, size and/or position) (Image 10). Some fusions can occur. Rounded margins and/or shorter length are seen in the posterior pair of specimen MNHN 7055 (holotype), MNHN 2007.0024, and ZUFRJ 1714 (Image 9). Usually, the shields of the anterior pair are trapezoidal, but can display more or less than four sides, or rounded margins; the shields of the medial pair are irregular polygons with - usually - five to seven sides; and the shields of the posterior pair are irregular polygons with - usually - five or six sides. These variations extend to the more laterally located modified pectoral shields, which also display a pattern. Their general disposition is of elongated and concentric rows on both sides of the central pairs. These rows, the more laterally located pectorals, are posteriorly confluent and anteriorly divergent, roughly in a "V" pattern. The more medially placed rows (the first lateral pectoral row), sutured with the three central pairs, usually have three or four main shields. Of these shields, the more elongated and noticeable, sutured mainly with

Image 8. *Leposternon octostegum* ZUFRJ 1716 from Camaçari. Oval scales near the head (left side). Note the anterior dorsal body pigmentation, and squarish tendency of the contrapectoral (middle) and anterior postpectoral scales (right side). Scale bar = 1mm.
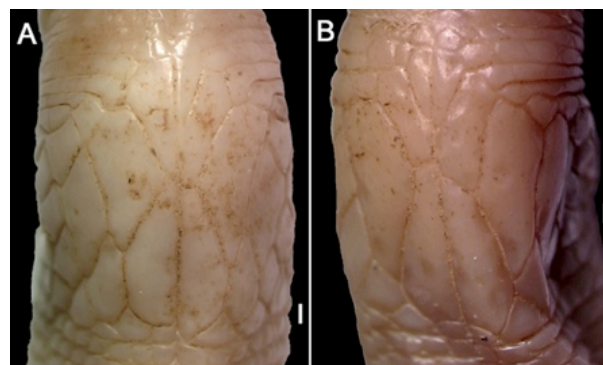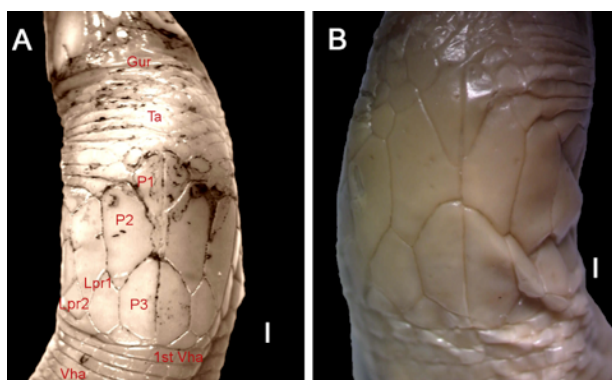

Image 10. *Leposternon octostegum*. Pectoral shield variations. (A) MZUEFS 654, anterior and posterior pectoral main pairs in contact, separating the shields of the medial pair. (B) MZUEFS 653, four instead of three main central shield pairs. Scale bars = 1mm.

Image 9. *Leposternon octostegum*. Pectoral region shields. (A) ZUFRJ 1714 from Camaçari. (B) MNHN 7055 holotype. Legends: Gur - gular region; Lpr1, 2 - lateral pectoral rows 1, 2; P1, 2, 3 - main pectoral shield pairs 1 (anterior), 2 (medial), 3 (posterior); Ta - transitional area; Vha - ventral postpectoral half-annuli; 1stVha - first ventral postpectoral half-annulus. Scale bars = 1mm.

the medial ("bowtie") pair, have the general appearance of a typical parallelogram (shorter sides inclined). It is anteriorly preceded by a few smaller typical parallelogram or irregular polygonal shields, and followed posteriorly by one or two smaller and usually irregular polygonal shields. The next (second) lateral row usually has four shorter main shields, with a general typical parallelogram appearance. The next two or three rows on each side are transitional areas to the dorsal contrapectoral half-annuli. They are composed of decreasing smaller shields of typical parallelogram, rectangular or squarish shape, in a regular half-annulus disposition.

Body sulci (Images 12–18)

The four typical amphisbaenian longitudinal sulci (the dorsal, laterals and ventral) usually well expressed

Image 11. *Leposternon scutigerum*. Pectoral shield pattern, NHMW 12375. Scale bars = 1mm.

in *Leposternon,* are present, although the ventral sulcus may be inconspicuous. They divide the animal's body in roughly four quarters. Three main patterns of sulci formation exist, with minor variations. In the first pattern, the disposition that characterizes the sulcus area, at the extremity of an annulus quarter, has scales inserted as a triangle between two equal extremities of a contacting quarter. This provides a zigzag sulcus appearance and is more typical of the dorsal sulcus (Image 12). A second pattern results from the simple alignment of adjacent scales in the sulcus region, forming a straight line (Image 13). This pattern is eventually undistinguishable from the adjacent longitudinal alignments. The straight-line pattern is more typical for the ventral sulcus. In the third pattern, very small scales of varying shapes fill the sulcus area (Image 14A). In this case, many folding lines are present between the scales. The more regular disposition of this kind comprises of a single scale divided by a pair of diagonal furrow lines that cut it into two more discrete triangles (anterior and posterior, united by one vertex) (Image 14B). The three patterns can occur along the same sulcus (Image 15). The ventral and lateral sulci begin immediately behind the pectoral region, more or less well expressed beginning in the first half-annulus rows. The dorsal sulcus begins immediately behind the occipitals, more or less well expressed already in the first contrapectoral rows. The ventral sulcus ends in the last ventral half-annulus. Except for dorsal or ventral scale alignment, sometimes well expressed, the sulci do not go beyond the cloacal level to the tail.

Dorsal and ventral postpectoral half-annuli (Images 8 and 13–18)

The meristic data are summarized in Table 1. There are 357–382 ventral postpectoral half-annuli, 397–357 dorsal postpectoral half-annuli, 24-33 dorsal half-annulus scales and 23–29 ventral half-annulus scales. Incomplete half-annuli are present, each consisting of a short row of transversal aligned scales that do not reach the normal half-annuli length and are inserted between them. The incomplete half-annuli are not included in the final counts and are few, usually four or less, rarely eight or 10, ventrally, and usually two or less, rarely seven or eight, dorsally (Images 15, 16). The shape of the scales of the half-annuli is always rectangular or squarish (Image 17), except for specializations for the sulci (see above), however, general shape trends within the body region are present: 1 – The dorsal scales tend to be longer instead of wider (Images 14B, 16), and the ventral scales tend to be wider instead of longer, especially the scales delimiting the ventral sulcus (Image 13). A transitional area occurs

below the lateral sulci (Image 14A). 2 – Dorsally the first 30 or so postpectoral half-annuli have squarish scales (Image 8). The rectangles stretch backwards in most of the dorsum, and in the posterior body portion they are visibly thinner (Image 18).

Contracloacal rows, cloacal region and tail (Images 19–22, Fig. 3)

Contracloacal rows: Four to six (Table 1). Extra half-annuli may appear, touching the remainder of the lateral sulci. The scales are not differently shaped from the ones of postpectoral and ventral half-annuli (i.e., rectangular), except in the sulci areas (if expressed) and the cloacal base margins, where some kind of minor deformation may occur (e.g., triangle or polygon shapes).

Cloacal region: The cloacal region does not have pores. The precloacal flap is characterized by four main pairs of shields in a transversal row with the addition of small supplementary shields appearing in the same areas. The main eight shields are the large, almost rectangular longitudinal central pair, the large irregular pentagon medial pair, and the two smaller lateral pairs, with triangular or trapezoidal shields (Image 19). Minor variations in these pairs can occur in shape, size or proportions, however, three specimens differ in having one (MNHN 2007.0023, ZUFRJ 1716, on the left side) or two (MZUFES 656, one on each side) extra-large rectangular longitudinal shields between the central shields and the medial ones (Image 20A). The small supplementary shields that normally appear are located as: 1 – a thin row of small usually squarish shields below the central and medial pairs (Image 19); 2 – one or two small but very discrete shields, triangular or trapezoidal, with a vertex inserted between the below suture of a central and a medial shield (Image 20B); 3 – the correspondents of both anterior patterns in the upper side of the precloacal shields (Image 19); 4 – different combinations of all these patterns (Fig. 3A). The summary of these variations is a general trend in only partial manifestations of two additional fragmentally developed rows, both dorsally and ventrally, in the precloacal flap. The only exception is ZUFRJ 1715, without noteworthy supplementary or extra shields (Fig. 3B). The postcloacal flap is composed of short 17–23 longitudinal rows in a semicircular arch, bordering the posterior cloacal opening. The central and more caudad pair of rows is composed of widened scales. The other rows have diminished scales of a generally polygonal shape, the larger usually being the posterior scale in each row (Image 19).

Tail: The tail is short (circa 1/19 body length), cylindrical, with a rounded extremity (Images 20B, 21).
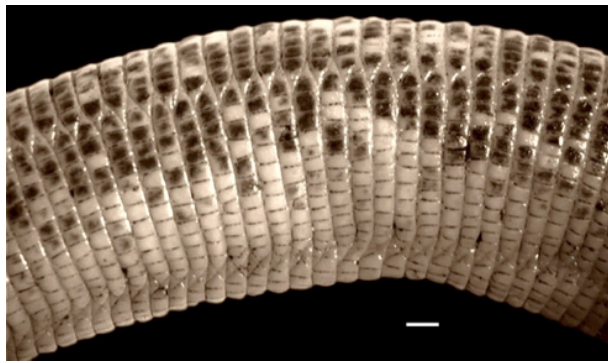
Image 12. *Leposternon octostegum* ZUFRJ 1716 from Camaçari. Zigzag dorsal sulcus formation and coloration. Head to left. Scale bar = 1mm.
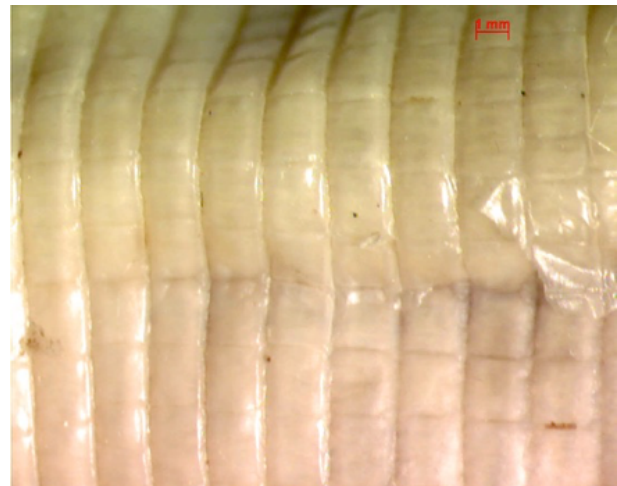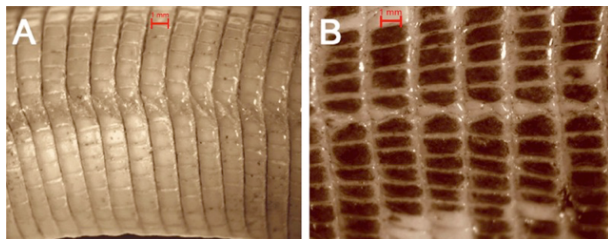

Image 14. *Leposternon octostegum*. Sulci patterns. (A) ZUFRJ 1748. Small scales filling the lateral sulcus region. Below the sulcus, note a transitional scale area, with more rectangular scales turning into lower more squarish ones. Head to right. (B) ZUFRJ 1716 from Camaçari. Dorsal sulcus filled with two main scales. Head to left.
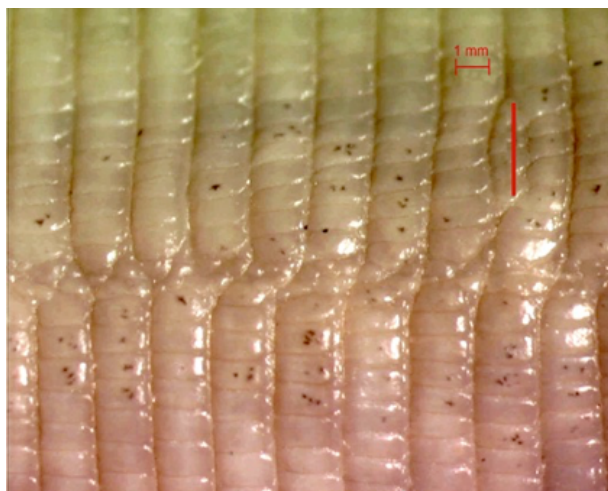

Image 16. *Leposternon octostegum* MZUEFS 654. Red bar showing an incomplete postpectoral scale row near dorsal sulcus. Note pigment disposition. Head to left.

Image 13. *Leposternon octostegum* MZUEFS 654. Ventral sulcus with aligned scales. Head to left.
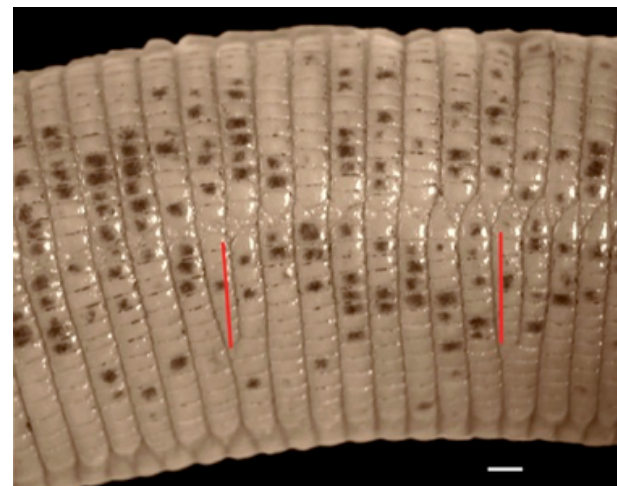
Image 15. *Leposternon octostegum* ZUFRJ 1714 from Camaçari. Dorsal sulcus defined by a zigzag arrangement (right), two main scales (center), and various small scales (left), all occurring simultaneously. The red bars shows examples of incomplete postpectoral scale rows. Head to right. Scale bar = 1mm.

The diameter is usually a little smaller than that of the body (Table 1). There is no autotomy annulus, nor sulci expression, besides the medial scale dorsal and ventral alignment. There is commonly no other regular scale alignment. Extra half-annuli may occur. The annuli count begins at the base of the most posterior margin of the postcloacal flap, even if the first ventral annulus is not complete at the sagittal plane, because its position is postcloacal (there is a tendency for a rostrad enlargement of the mid pair of scales of the second ventral annulus, which interrupts the first annulus by contacting the postcloacal flap). The counts include the tail tip, with

Image 17. *Leposternon octostegum* MNHN 7055 holotype. Dorsal sulcus and squarish or rectangular scales. Head to left. Scale bar = 1mm.
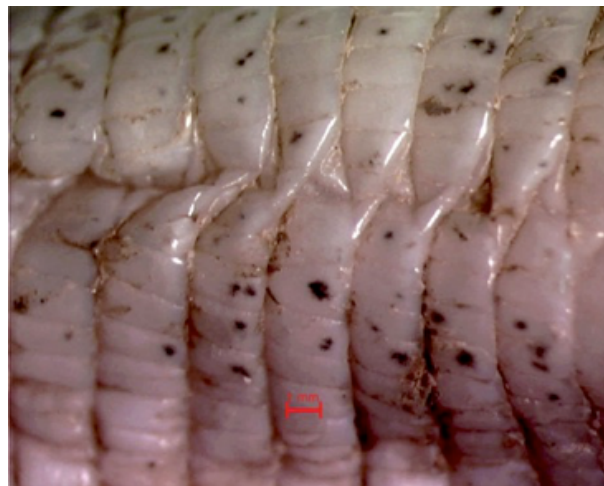

Image 18. *Leposternon octostegum* MZUEFS 652. Dorsal sulcus and thinner rectangular scales. Head to left.

the always recognizable, even if irregular, annulus. There are 12–15 caudal annuli present. The shape of the scales varies; dorsally and laterally they are more regular, longitudinal rectangles (Image 21A). The dorsal medial pair is usually larger than the rest. Approaching the tail tip, the scales tend to be squarish. Ventrally, the medial pairs are usually a little wider or more squarish than the lateral pairs, except for the first two or so. These tend to be trapezoidal or irregular pentagons (Images 20B, 21B). The last (i.e., posterior) five or so annuli display more scale shape variation. They can be irregular hexagons or pentagons (especially dorsally), with elongations, or shortening, and/or irregular polygonal forms in the extreme tip (Image 22). There are no scale fusions, but eventually the extreme scales show slightly attenuated limits.

Coloration (Images 2, 8, 12, 14–16, 18, 20–21 and 23)

Living specimens from Salvador City have a pale grizzled background coloration (cf. Image 23A), including head, pectoral region and tail. The head of the holotype is brownish (Images 1B, 5B, 6B, 23B), perhaps due to preservative artifacts. There is no marked head pigmentation, although diminute dots can be present (cf. Images 2, 4B). Body scale pigments are absent (MNHN 2007.0034 and MZUEFS 657; also MZUEFS 563, 654, however, these are mutilated specimens) or usually inconspicuous, represented by sparse, diminute and irregularly-distributed dorsal brownish dots, normally several dots per scale, also observed in the preserved specimens (cf. Images 14A, 16, 18). These are usually more concentrated in the second half of the body. The alcohol-preserved specimens show a more pale brown

(beige) or whitish background coloration, and the pigments are faded (Images 23B, C), however, even the holotype (MNHN 7055, from 1851) still retains some pigment blotches dorsally, at the corresponding cloacal area. Tails are depigmented, except for very few small sparse dots in MZUEFS 652, 696.

Three of four specimens from the Camaçari sample (ZUFRJ 1714, 1715, 1716) have a marked different coloration. In the preservative (they were not seen alive to obtain a color description), the background color is beige from head to tail and the pigmentation is more pronounced compared to all other specimens (Images 23D-F). There is no ventral coloration except for the tail of specimens ZUFRJ 1715 and 1716. Very few dorsal brownish dots may occur on the head (Image 2A). Immediately after the head, in the first 1/10 of the body, the dorsal brownish dots are less intense and scarcely distributed (Image 8). The rest of the dorsal body has an evident brownish pigmentation (Images 12, 14B, 15), that eventually reaches the lateral sulci, although not all scales are pigmented, nor are the spaces between annuli or scales (they seem to be in e.g. Image 12, however see comment on edited photographs in the Material and Methods section). The pigments can occupy the entire scale (e.g., Image 14B) or not (e.g. Image 15). The tail can display a ventral pigmentation of discrete blotches (Image 20B) or small dots (Image 21B), or none at all (ZUFRJ 1714). Dorsally, the tail has few pigmented scales, concentrated medially and rostrad, but some dots can appear near the tip (Image 21A). Specimen ZUFRJ 1713 is smaller than the others from Camaçari (and Salvador) and does not show any discernible pigmentation.
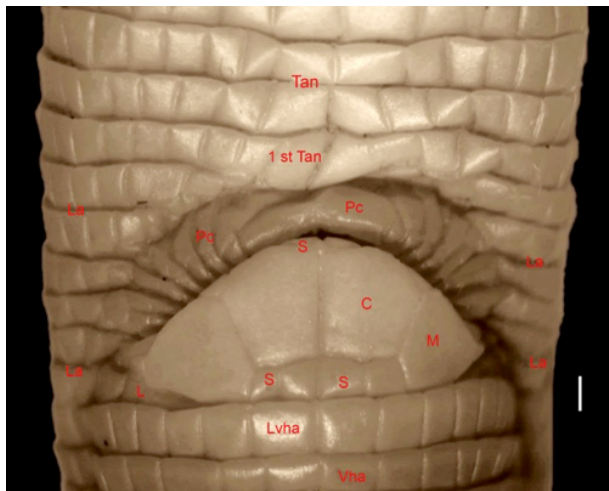
Image 19. *Leposternon octostegum* MNHN 7055 holotype. Cloacal region. Legends: C - shield of the central pair in the cloacal flap; Cc - contrapectoral rows; L - lateral shield of the cloacal flap; Lvha - last ventral postpectoral half-annulus; M - shield of the medial pair in the cloacal flap; Pc - postcloacal rows; S - supplementary shields; Tan - tail annuli; Vha - ventral postpectoral half-annulus; 1st Tan - first tail annulus. Scale bar = 1mm.
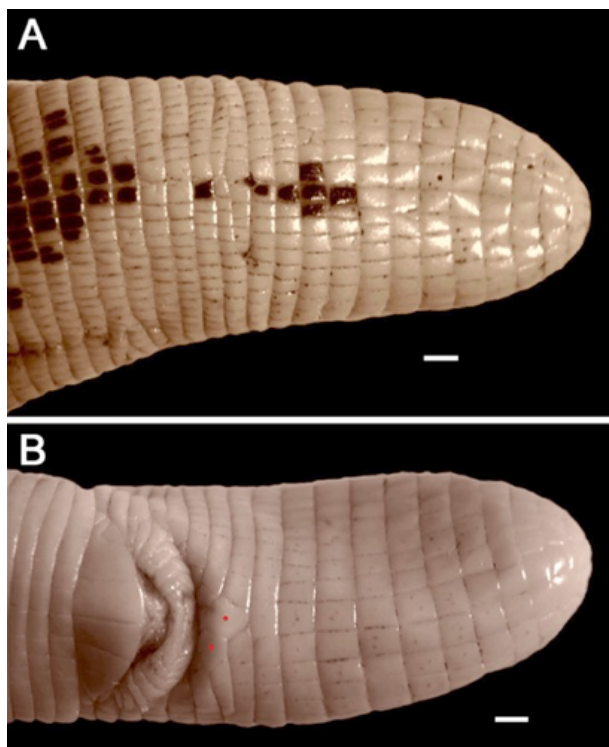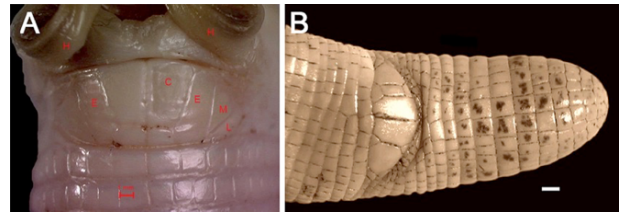

Image 20. *Leposternonoctostegum*. Cloacal region. (A) MZUEFS 656. Legends: C - shield of the central pair in the cloacal flap; E - extra shields; H - hemipenis; L - shield of the lateral pair in the cloacal flap; M - shield of the medial pair in the cloacal flap. (B) ZUFRJ 1716 from Camaçari. Tail shape and cloacal flap shield disposition. Note pigmentation pattern. Scale bar = 1mm.
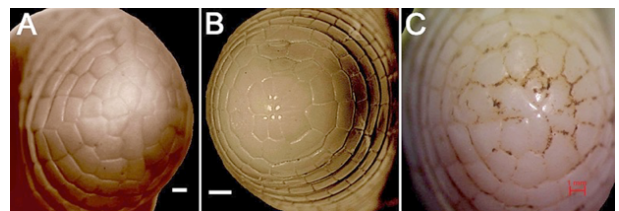
Image 22. *Leposternon octostegum*. Tail extremities. (A) MNHN 7055 holotype, with discrete, yet irregular, rows and scales. (B) MZUEFS 695, showing more attenuated scale sutures. (C) MZUEFS 652, showing regular scale rows until the very tip. Scale bars = 1mm.

Geographic distribution and habitat

Detailed data of *Leposternon octostegum* distribution and habitat are provided by Barros-Filho et al. (2013). The species is known only to occur in the state of Bahia, Brazil (Fig. 1).

DISCUSSION

The analysis conducted by Gans (1971a) retained the validity of *L. octostegum*, although the point of view of this author was based on a single specimen. The new data presented herein confirm that author's conclusions and provide detail on intraspecific variation.

Except for some nomenclatural changes and minor different counts or measurements, the original data (Duméril 1851) and posterior references (Peters 1879; Boulenger 1885; Gans 1971a) are well in general accordance with the holotype; however, Duméril (1851) was wrong in describing "straight lines" for lateral and posterior azygous sutures, and Boulenger (1885) in referring to a "small mental", "followed by a single rather small chin-shield" (there is only one big mental); Gans (1971a), with knowledge only of the holotype, mentioned the pectorals as "regular shields", but these display great individual variations (but there is a shield
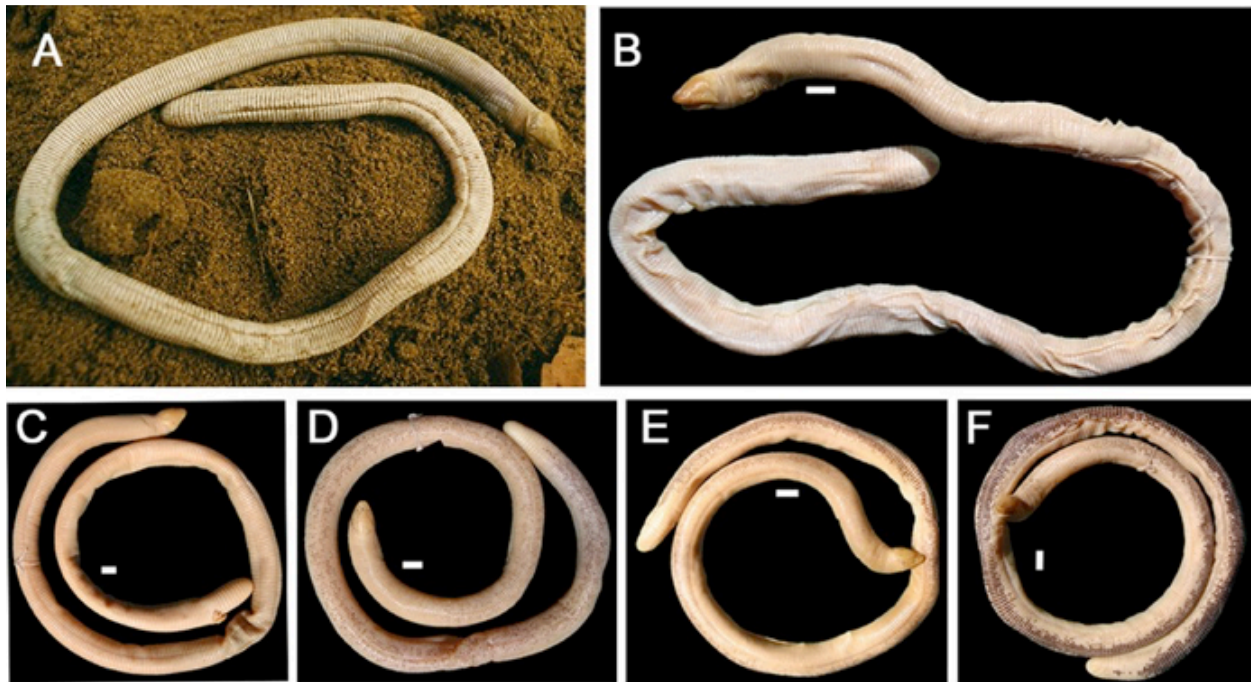

Image 21. *Leposternon octostegum*. Tail scales and pigmentation pattern of Camaçari specimens. (A) ZUFRJ 1716, dorsal view. (B) ZUFRJ 1715, ventral view; irregularly shaped scales marked in red. Scale bars = 1mm.

Image 23. *Leposternon octostegum*. Coloration. (A) Live coloration of newly captured specimen from Aterro Metropolitano Centro, near Salvador City, State of Bahia, Brazil; without scale; (B) MNHN 7055 holotype and (C) MNHN 2007.0023, color in preservative. (D) ZUFRJ 1714, (E) ZUFRJ 1715 and (F) ZUFRJ 1716 from Municipality of Camaçari, Arembepe County, color in preservative. Scale bars = 5mm.

arrangement pattern). Great discrepancy is found in the count by Gans (1971a), of 106 "body vertebrae" against the 121–142 counted herein. Even different X-rays or other methodological approaches cannot explain the problem (cf. Hoffstetter & Gasc 1969 : 174–175, "post-axial" plus "precloacal" vertebrae, the same as "body vertebrae" in the present study).

The annuli count methodologies used herein preserve the logic of the standards proposed by Gans (1971a) and improve them (e.g. desirable counts until the tip of the tail) by considering the particular morphology of amphisbaenian specimens. The reliability of this procedure was tested by comparing the counts reported by Gans (1971a) for the *L. octostegum* holotype (378 postpectoral annuli) with the count herein (379 ventral right postpectoral annuli) for the same specimen.

In addition, it is important to remember that the species do not display unique and exact counts, but indeed, variations - i.e., *L. octostegum* postpectoral ventral left annuli vary from 353 to 382. The same idea is expressed in Table 2, comparing counts of specimens analyzed in more than one paper. Gans (1971a) and Ribeiro et al. (2008, 2011) show only the range of these counts, but this range comfortably agree with the data presented herein for each specimen, highlighting that, even if there is some slight individual discrepancy with

literature data, they are insignificant for the purpose of comparisons.

A note regarding Table 2: In the study performed by Ribeiro et al. (2011) there is no mention of ventral postpectoral counts for other *Leposternon* species save *L. maximus*, which was being described in the paper; in this aspect, the authors only listed the material examined for comparison. The explanation is that, as stated by the *L. maximus* species diagnosis, "*Leposternon maximus* sp. nov. differs from all amphisbaenians by presenting 404–448 dorsal postpectoral half-annuli and 408–448 ventral postpectoral half-annuli". One species that reaches near counts is *L. octostegum* (Fig. 4: 182), with less than 400 left ventral postpectoral half-annuli. Again, the counts reported herein, despite the methodological differences, agree adequately with these observations.

Moreover, not only the sample used in this study, but also the large series of *Leposternon* spp. and Amphisbaenia of different genera and species have been analyzed, counted and identified by the present count methodology, for more than 30 years (Barros-Filho unpublished data) without any mistake or problem. In all pertinent cases, minimal count differences are far from causing confusion regarding species identification or description.

Therefore, we conclude that the count methodology

adopted herein absolutely does not damage or prevent comparisons with bibliographical data. Instead, it offers increased accuracy in this regard, with desirable adjustments for the methodology proposed by Gans (1971a) and Gans & Alexander (1962), thus allowing for more exact observations and being fully valid for comparative analyses with Amphisbaenia literature. That is why the new methodology is proposed herein, as well as the suggested modifications in pholidosis nomenclature, to be applied as new standards.

The pholidosis nomenclature proposed herein aims to contribute to an improvement of this still disputed subject in amphisbaenian studies. The authors are of the opinion that the propositions are fully justifiable and a necessity, due to the repetitive confusing usage of inadequate or simply mistaken terms. This applies especially for the terminology of the so called "chin shields", historically laden with synonymic terms for different scales.

With this aim, the specificities of the *Leposternon* and amphisbaenian Bauplan were considered, particularly concerning the cephalic region. The adopted names are more consistent with the location area of the respective shields. In fact, we identified very significant nomenclatural inconsistencies in this aspect. For instance, Gans & Alexander (1962) named the first body annulus one that dorsally includes typical head shields; this is also incompatible with the cranial elements that are supposed to support homological structure relations (cf. Gans & Montero 2008).

We recognize that the ideal approach for nomenclatural changes (connected to the definition of scales and scale rows and, consequently, with their counts) is the identification of homology between structures. Even if no homological analysis were available, there are solid reasons for the proposed modifications. As detailed in Material and Methods section, there are cases when homologies can be hard to determine (e.g., the amphisbaenian temporal region) but on the other hand, some applied historical terms are so wrong that there is really no sense in using them, just because they are in the literature. In these cases, other criteria, such as more consistent topological references, are improvements not only regarding description clarity, but also in facilitating the understanding of future homological studies.

To be effective and useful in this sense, however, we are of the opinion that new nomenclatural propositions should take into account the entire study group. For example the nomenclature suggested by Pinna et al. (2010), although certainly an improvement in some cases, restricted the analysis essentially to South American *Amphisbaena* species. This can make future comparisons within Amphisbaenia harder. The present proposals deal with morphological aspects that contemplate comparison bases for the entire suborder.

The proposed modifications are also easy to compare with published descriptions and illustrations (e.g., Castro-Mello 2003; Hoogmoed & Mott 2003; Thomas & Hedges 2006; Mott et al. 2008; Ribeiro et al. 2008, 2009, 2011, 2015, 2016, 2018; Strüssmann & Mott 2009; Pinna et al. 2010, 2014; Gomes & Maciel 2012; Roberto et al. 2014; Sindaco et al. 2014; Teixeira Jr. et al. 2014; Costa & Bérnils 2015; Costa et al. 2015; Broadley & Measey 2016), despite the variability of adaptations in amphisbaenians, and are a solid resource for the better understanding of nomenclatural and homological issues in this group.

The pigmentation differences observed in the Camaçari sample (coupled with smaller total length) suggests an ontogenetic color variation. The smaller specimen (ZUFRJ 1713, 150mm total length) shows no pigmentation, while the others (ZUFRJ 1714 – 232 mm, ZUFRJ 1715 – 283mm, ZUFRJ 1716 – 320mm total length) show increasing pigment intensity associated with total length. The larger specimens (and thus, supposedly older) from Salvador also tend to show more intense pigmentation than the smaller specimens (MZUEFS 657 with 245mm total length is not pigmented). Future collection of specimens will be needed to clarify issues regarding color variation by site and ontogeny.

An important aspect of correctly identifying species is the consequent support for their conservational status. *Leposternon octostegum* is a species with a relatively restricted geographical distribution and few known ecological data (cf. Barros-Filho et al. 2013). And, till recently, the species was based only on the holotype. Since much remains to be discovered with regards to the taxonomy and distribution of reptiles from Bahia and Brazil (e.g., Freitas et al. 2011, 2012a,b), and new shovel-headed Brazilian species are under present investigation (Ribeiro 2010), we understand that the redescription of *L. octostegum* will add to the clarification of the taxonomy of Brazilian amphisbaenians, and also contribute to its conservation and management strategies, largely overlooked in the country because (within other factors) taxonomic issues in this group remain unclear.

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Key to Brazilian *Leposternon* species*

1   A pair (rarely two) of very small precloacal pores, at the precloacal flap sides ……………………………….………….…………… 2
      – Precloacal pores absent ……………………………………………………………………………………………………… 6
2   Azygous smaller than frontals, which are almost rectangular and in longitudinal arrangement; preocular present ……………………
      ……….. *L. polystegum*
      Azygous somewhat or discretely larger than frontals; preocular absent ……………………………………………………………… 3
3   Three infralabials; less than 300 ventral postpectoral half-annuli …………………………………………………………………… 4
      – Two infralabials; more than 300 ventral postpectoral half-annuli ………………………………………………………………… 5
4   246-264 ventral postpectoral half annuli …………………………………………………………………………… *L. kisteumacheri*
      – 270-280 ventral postpectoral half annuli ………………………………………………………………………………… *L. mineiro*
5   Supraoculars present; 408-448 ventral postpectoral half-annuli …………………………………………………………… *L. maximus*
      – Supraoculars absent; 302-349 ventral postpectoral half-annuli ……….………………………………………………… *L. cerradensis*
6   Azygous by far the largest shield atop the head, covering nearly the entire head dorsum ………………………………………… 7
      – Azygous variably enlarged, but never covering almost the entire head dorsum ……….………………………………………… 8
7   Rostronasal and azygous are the only two main large shields in dorsal view; postmental shield present; 246-305 ventral
      postpectoral half-annuli ……………………………………………………………………………………......………… *L. scutigerum*
      – Rostronasal, azygous, prefrontals, oculars and first temporals clearly discrete in dorsal view; postmental shield absent; 353-382
      ventral postpectoral half-annuli …………………………………………………………………………………………… *L. octostegum*
8   Azygous very large (circa 25% of total head area), usually touching the rostronasal; the contact of the azygous with the rostronasal
      is always a point contact of the anterior "V" shape of the azygous, never a broad contact of the anterior azygous margin;
      a pair of very large rectangular, almost squarish frontals (together, occupying near the same head area of the azygous); parietals
      usually absent; four to six longitudinal, almost rectangular, main pectoral shields, in general in a parallel pattern …… *L. wuchereri*
      – Azygous variably large (but less than 25% of total head area), usually separated from the rostronasal by the prefrontals;
      parietals present, but may be partially (rarely totally) fused with the frontals; pectoral shields fused or not, disposed in a more
      or less discrete general "V" pattern, except for the medial ones …………………………………………………………………… 9
9   Adults very large, reaching more than 3 cm in mid-body diameter; yellow dorsal background coloration may be present in alive
      individuals; three supralabials at each side; usually one infraocular; pectoral shields may be large, but not fused or elongated;
      body scales small and squarish …………………………………………………………………………......…………………… *L. infraorbitale*
      – Adults sometimes large, but never reaching 3 cm in mid-body diameter (usually 1 to 2 cm); grayish dorsal background
      coloration in alive individuals; two supralabials at each side; infraocular absent; the pectoral large shields are usually fused
      and elongated, especially a medial pair; body scales rectangular …………….……………...…….…………………………… *L. microcephalum*

**Leposternon bagual* endemic from Argentina (cf. Ribeiro et al. 2015) is not included here. In addition, its diagnostic features are
osteological, and the type-series (four exemplars) shows obvious external morphological variations.

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Appendix 1. *L. microcephalum* and *L. scutiegrum* specimens examined in this paper ([1]) and in the studies performed by Gans (1971a) ([2]), Ribeiro et al. (2008) ([3]), (2011) ([3]).

Leposternon microcephalum (N = 49)
BRAZIL: MINAS GERAIS: Nova Ponte: MNRJ 7469[1,3]; *Sacramento*: MZUSP 77040[1,3]. *MATO GROSSO DO SUL: Anaurilândia*: ZUFRJ 1490[1,3]; *Porto Taboado*: MZUSP 77532[1,3]. *RIO DE JANEIRO: Angra dos Reis*: MNRJ 1762[1,2]; *Barro Branco*: MNRJ 1767a[1,2]; MNRJ 1767b[1,2]; *Duque de Caxias*: MNRJ 1774[1,2]; MZUSP 6394[1,3]; MZUSP 6397[1,3]; MZUSP 6398[1,3]; MZUSP 6399[1,3]; MZUSP 65390[1,3]; *Floriano*: MZUSP 578[1,3]; *Manguinhos*: MZUSP 7677[1,3]; MZUSP 8284[1,3]; *Miguel Pereira*: MZUSP 6539O[1,3]; *Parati*: MNRJ 1755a[1,2]; MNRJ 1755b[1,2]; *Petrópolis*: MNRJ 1778a[1,2]; MNRJ 1778f[1,2]; *Rio de Janeiro*: MNRJ 1768[1,2]; MNRJ 1783[1,2]; MNRJ 3261[1,2]; MNRJ 3262[1,2]; MNRJ 3264[1,2]; MNRJ 3265[1,2]; MNRJ 3266[1,2]; MNRJ 3267[1,2]; MNRJ 3268[1,2]; MNRJ 3269[1,2]; MNRJ 3270[1,2]; *Rio de Janeiro*: MZUSP 2426[1,3]; MZUSP 2676[1,3]; MZUSP 13762[1,3]. *SANTA CATARINA: Corupá*: MZUSP 1249[1,3]; MZUSP 6466[1,3]; MZUSP 6488[1,3]; MZUSP 6518[1,3]. *SÃO PAULO: Assis*: MZUSP 77038[1,3]; MZUSP 77039[1,3]; *Ilha da Queimada*: MZUSP 77031[1,3]; *Passa Quatro*: MZUSP 77527[1,3]. *São Carlos*: MZUSP 77536[1,3]. *São Paulo*: MZUSP 77013[1,3]; MZUSP 77014[1,3]; MZUSP 77037[1,3]; MZUSP 77042[1,3]; MZUSP 77515[1,3]. *Tupã*: MZUSP 77043[1,3].

Leposternon scutigerum (N=3)
BRAZIL: RIO DE JANEIRO: Rio de Janeiro: MZUSP 2519[1,3]; MZUSP 7075[1,3]; ZUFRJ 289[1,3].

Appendix 2. Amphisbaenia and Lacertilia specimens examined for comparisons of counts and/or shield nomenclature with *Leposternon octostegum*. Acronyms follow Sabaj-Pérez 2010 when possible: UnB (Universidade de Brasília, Brazil; UNESP-Rio Claro (Universidade Estadual Paulista, Campus de Rio de Claro, Brazil); UERJ (Universidades Estadual do Rio de Janeiro, Brazil; UFC (Universidade Federal do Ceará, Brazil); MHNCI (Museu de História Natural Capão da Imbuia, Curitiba, Brazil); MNRJ (Museu Nacional do Rio de Janeiro, Brazil); MPEG (Museu Paraense Emílio Goeldi, Brazil); MZUSP (Museu de Zoologia, Universidade de São Paulo, Brazil); ZUFES (Departamento de Zoologia, Universidade Federal do Espírito Santo, Brazil); ZUFRJ (Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Brazil, now at Museu Nacional do Rio de Janeiro).

AMPHISBAENIA (N = 213)
Amphisbaena dubia (N = 2): MZUSP 77054, ZUFRJ 996.
Amphisbaena mertensi (N = 13): UNESP-Rio Claro A51, A52, A54, A56-A58, 115, 126, 513, 530, 540; ZUFRJ 993-995.
Amphisbaena mitchelli (N = 2):MZUSP 828, 829.
Amphisbaena neglecta (N = 1):ZUFRJ 990.
Amphisbaena pretrei (n = 7):ZUFRJ520-526.
Amphisbaena roberti (n = 13): UNESP-Rio Claro A23 a A25, A53, A55, 70, 80, 356, 533, 541, 561; MZUSP 77072; ZUFRJ 992.
Amphisbaena vermicularis (N = 2):MZUSP 77067, 77077.
Amphisbaena vanzolinii (N =1):ZUFRJ 70.
Anops kingi (N =1): ZUFRJ 817.
Aulura anomala (N =1): ZUFRJ 826.
Leposternon infraorbitale (N = 6): MNRJ 4035, 4456; ZUFRJ 504, 538-539; UnB 3663.
Leposternon microcephalum(N =107): UERJ 29, 59, 108, 219, 144, 220, 234, 274-275, 296, 359, 359.1, 419, 424, 435, 595, 597; MHNCI 1398, 2780, 2941, 3034, 3538, 4223; MNRJ 1773, 4020-4033, 4264, 4487-4489, 4501; MZUSP 3345-3350, 3472, 6392-6393, 6395-6396, 6406, 6537, 6579, 6601, 6650, 7020, 7051, 7300, 7753-7755, 8282-8283, 8346, 13760-13761, 13763; ZUFRJ 29, 59, 240, 249, 280-281, 284-288, 299, 457, 462, 467-469, 483, 540-544, 639-640, 764, 797, 1001-1009.
Leposternon polystegum (N = 16): MPEG 6559, 6671, 7588 7602, 7597; UFC 204, 219, 298, 1467, 1646, 1802, 1839; ZUFRJ527-528, 938-939.
Leposternon scutigerum (N = 16): MNRJ 4036-4040, 4458, 4490-4492; ZUFRJ 289, 381, 530, 550, 798, 997, 1000.
Leposternon sp. (N = 6): MNRJ 4041-4046.
Leposternon wuchereri (N = 8): MNRJ 3892, 3893; MZUSP 8812; ZUFES 15/126, 15/181, 15/203, 15/208-15/209.
Loveridgea ionidesi (N = 3): MZUSP 2004-2006.
Monopeltis capensis capensis (N =1): MZUSP 58124.
Rhineura floridana (N =4): MNRJ 3188; MZUSP 3062, 3305-3307.
Trogonophis wiegmanni (N = 3): MZUSP 3199, 3200, 72807.

LACERTILIA (N = 6)
Bachia bresslaui (N =4): ZUFRJ 650-653.
Dibamus novaeguineae (N =1): MZUSP 68753.
Mabuya sp. (N =1): ZUFRJ 15.

Portuguese abstract: O anfisbênio Leposternon octostegum (Duméril 1851) é redescrito com base em novos exemplares coletados no Estado da Bahia, Brasil. É confirmada a validade da espécie e são feitas comparações com outras espécies de Leposternon e com a parca literatura relativa à espécie. Foram analisados aspectos merísticos e são propostos ajustes nomenclaturais para a folidose. Uma chave de identificação para as espécies de Leposternon é fornecida, de forma a melhor contextualizar estas informações taxonômicas. A conservação dos Amphisbaenia tem sido grandemente negligenciada, pois mesmo questões taxonômicas básicas para este clado permanecem indefinidas. A presente redescrição, contribuindo para o esclarecimento da taxonomia deste grupo, auxiliará no desenvolvimento de estratégias de conservação e manejo mais sólidas, tanto para L. octostegum quanto para todo o grupo dos Amphisbaenia.

Palavras-chave: Amphisbaenia, Bahia, Brasil, Leposternon octostegum, metodologia merística, nomenclatura de folidose, taxonomia.

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