



The species of *Eutatus* (Mammalia, Xenarthra): Assessment, morphology and climate

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ABSTRACT

From a systematic perspective, the genus *Eutatus* is in a complex situation. P. Gervais published the type species, *Eutatus seguini*. Later, F. Ameghino recognized *Eutatus brevis*, *Eutatus punctatus* and *Eutatus minutus*, whose diagnostic characters were not clearly defined. A.F. Bordas added a new species, *Eutatus ameghinoi*, and provided anatomical differences between this species and *E. seguini*, but did not compare it with the others previously recognized by Ameghino. For these reasons, Scillato-Yané only recognized for the Ensenadan, Bonaerian and Lujanian stages the type species *E. seguini* and synonymized the other four. On the other hand, *E. seguini* has been mentioned as occurring, if not exclusively, in the Ensenadan stage. However, an exhaustive review of earlier publications indicates that *E. seguini* is the *Eutatus* species occurring in the Bonaerian, Lujanian and Platan (middle Pleistocene to early Holocene) stages. Osteoderm characters, as well as endoskeletal elements, were compared between specimens assigned to the previously nominated species. A detailed analysis of osteoderms from homologous regions of the pelvic shield (internal and external morphology) was performed to identify significant differences that would allow recognition of the eventual species of this genus. Materials from the Chapadmalalan, Marplatan (Vorohuean), Ensenadan and Lujanian stages were selected. An equivalent comparative study was made on the osteoderms of *Chaetophractus villosus* (Euphractinae, Euphractini) to assess the range of intra-specific morphological variations. Differences were found between osteoderms from different stratigraphical provenance. According to the new nomenclatural situation proposed here, *E. seguini* is limited to the Bonaerian, Lujanian and Platan stages, and a new species is recognized for the Marplatan (Vorohuean, Sanandresian) and Ensenadan stages. The morphological changes in osteoderms of different *Eutatus* species may be correlated with paleoclimate variations, because these changes consist of variations in the amount and extension of cavities that would have held hair follicles and the development of cavities that would have been filled with adipose tissue, probably acting as thermal insulation.

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1. Introduction

Eutatus Gervais, 1867 is a genus whose record in the Pampean region extends from the Chapadmalalan (late Pliocene) to the start of the Platan (early Holocene) stages.

It is also, by far, the best represented dasypodid in the Plio-Pleistocene fossil record: armors, skulls and postcranial elements have been recovered. However, finding the armors associated with skulls or abundant postcranial elements are rare and, so far, no convincing taphonomic explanation has been provided for this

phenomenon. In fact, most of the specimens of this genus preserved in collections are a few unarticulated osteoderms, or isolated endoskeletal elements. This has led to the creation of some nominal species of the genus based on rather poor materials, which in some cases are not even homologous between the different nominal taxa.

The systematic status of genus *Eutatus* can be summarized by stating that the recognition of assigned species is quite complex. In 1867, Paul Gervais erected the new genus and species (type), *Eutatus seguini*, with descriptions based on endoskeletal remains only. At that time, he announced that another work would follow with the description of osteoderms, but this paper was never published. Later, Florentino Ameghino (1881, 1889), on the basis of osteoderm morphology, recognized three new species: *Eutatus*

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brevis Ameghino, 1881, *Eutatus punctatus* Ameghino, 1881 and *Eutatus minutus* Ameghino, 1889. Similarly, in 1932 A.F. Bordas added a new species, *Eutatus ameghinoi*, and provided a differential anatomical comparison of the latter with *E. seguini* but, remarkably, he omitted any comparison with the three species that Ameghino had recognized earlier. In fact, it is not clear from his work whether he recognized the validity of these three species. Later, Scillato-Yané (1980, 1982) chose to recognize only the type species, *E. seguini* Gervais, 1867, for the Ensenadan (early to middle Pleistocene), Bonaerian (middle Pleistocene) and Lujanian (late Pleistocene–early Holocene) stages of Argentina and he synonymized the other four species.

Such varying opinions about the genus and its contents led to great confusion about which species occurred in given stratigraphic levels, to the point that *E. seguini* was actually proposed as guide taxon for the Ensenadan stage/age (Ameghino, 1889: 871–872).

2. Abbreviations

AMNH, American Museum of Natural History (New York, U.S.A.), FML, Instituto “Miguel Lillo”, Universidad Nacional de Tucumán (Tucumán, Argentina), IFG, Museo Florentino y Carlos Ameghino, Universidad Nacional del Litoral (Rosario, Santa Fe, Argentina), LARBO-UNMDP, Laboratorio de Arqueología, Facultad de Humanidades, Universidad Nacional de Mar del Plata (Mar del Plata, Buenos Aires, Argentina), MACN, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Ciudad Autónoma de Buenos Aires, Argentina), MLF, Museo de Ciencias Naturales “Florentino Ameghino” (Las Flores, Buenos Aires, Argentina), MCNL, Museo de Historia y Ciencias Naturales del “Club de Pesca Lobería” (Lobería, Buenos Aires, Argentina), MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata (La Plata, Buenos Aires, Argentina), MMCIPAS, Museo y Centro de Investigaciones Paleontológicas de Salto (Salto, Buenos Aires, Argentina), MMCNCD, Museo Municipal de Ciencias Naturales Carlos Darwin (Punta Alta, Buenos Aires, Argentina) MMCNMH, Museo Municipal de Ciencias Naturales (Monte Hermoso, Buenos Aires, Argentina), MMP, Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, (Mar del Plata, Buenos Aires, Argentina), MMPH, Museo Municipal de Punta Hermengo (Miramar, Buenos Aires, Argentina), MNHN-PAM, Museum national d’Histoire naturelle (Paris, France), MPV, Museo Paleontológico de Valencia (Valencia, Spain), PIMUZ, Paleontological Institute und Museum Universität Zürich (Zurich, Switzerland).

3. Materials and methods

3.1. Materials

MLP: 16-146, 16-221, 16-225, 38-X-2-1, 42-IX-1-2, 47-XI-8-1, 49-XII-6-64, 52-IX-28-8, 52-IX-28-9, 52-IX-28-10, 52-IX-28-19, 52-IX-30-28, 52-IX-30-82, 52-X-2-27, 52-X-2-44, 52-X-2-84, 52-X-2-99, 52-X-3-56, 54-VI-19-5, 54-VI-19-9a, 55-X-17-2, 59-VI-19-9a, 59-XI-10-1, 62-VII-27-3, 62-VII-27-108, 62-VII-27-127, 62-XI-27-4, 69-VII-22-5, 69-VIII-1-4, 69-VIII-1-5, 69-VIII-1-6, 69-VIII-1-8, 69-VIII-4-1, 69-VIII-4-4, 69-VIII-5-1, 69-VIII-5-2, 69-VIII-5-5, 69-VIII-6-1, 69-VIII-6-2, 69-VIII-6-3, 69-VIII-8-3, 69-VIII-8-6, 69-VIII-8-7, 69-VIII-9-1, 69-VIII-9-2, 69-VIII-9-3, 69-VIII-9-4, 69-VIII-13-5, 69-VIII-19-1, 69-VIII-22-1, 69-VIII-22-2, 69-VIII-22-4, 69-VIII-22-5, 69-VIII-22-6, 69-VIII-22-13, 69-VIII-22-14, 69-VIII-25-8, 69-VIII-25-12, 69-VIII-25-20, 69-VIII-26-5, 69-VIII-29-9, 69-IX-5-3, 69-IX-8-15, 69-IX-8-17, 69-IX-9-7, 69-IX-9-10, 69-XII-26-5, 70-III-10-2, 70-XII-1-2, 70-XII-23-1, 70-XVI-23-3, 71-X-17-10, 80-VIII-13-2, 80-VIII-13-56, 81-VII-20-6, 82-IV-10-1, 84-II-6-1, 86-VI-23-6, 86-XI-20-3, 89-X-1-1,

91-IV-5-182, 91-IV-5-183, 91-IV-5-238, 91-IV-15-39, 91-IV-15-40, 91-IV-15-43, 91-IV-15-47, 91-IV-15-48, 91-IV-15-51, 91-IV-15-53, 91-IV-25-1, 91-IV-25-66, 91-IV-25-81, 91-IV-25-86, 91-IV-25-90, 91-IV-25-149, 91-IV-30-4, 91-IV-30-5, 91-IV-30-8, 91-IV-30-38, 91-IV-35-1, 94-II-1-67, 94-V-1-10, 95-X-2-1, 95-XII-1-26, 00-VIII-5-1.

MACN: 511, 982, 985, 986, 1122, 1123, 1124, 1125, 1126, 1127, 1128, 1129, 1130, 1131, 1132, 1133, 1134, 1135, 1136, 1137, 1138, 1139, 1140, 1142, 1143, 1144, 1145, 1309, 1634, 1635, 1636, 1638, 1742, 1743, 1744, 1746, 1747, 1820, 1825, 1914, 1942, 1982, 1985, 1988, 1999, 2210, 2268, 2273, 2277, 2340, 2436, 2772, 2809, 5121a, 5169, 5189, 5238, 5264, 5514, 5547, 5572, 5580, 5631, 5675, 5697, 5698, 5715, 5803, 5804, 5829, 5851, 5852, 5870, 5909, 5914, 6035, 6255, 6256, 6383, 6388, 6389, 6520, 6650, 6881, 6910, 6951, 7031, 7039, 7069, 7095, 8612, 8614, 8628, 8789, 8796, 8823, 8824, 8964, 9207, 10064, 10097, 10160a, 10177, 10417, 10425, 10845, 11071, 11073, 11112, 12015, 12400, 13225, 13268, 13587, 13737, 13833, 13967, 14057, 14058, 14060, 14075, 14076, 14077, 14080, 14081, 14082, 14965, 15709, 16639, 17401, 17469, 17998, 19195, 19211.

AMNH: 11231, 11232; FML: 755, 1213, 1318, 1340, 1347, 1424; IFG: 73, 100, 131, 367, 1074, 1082, 1161, 1165, 1179, 1195; LARBO-UNMDP: 154, 155, 156, 157, 156, 157, 158, 159, 160, 161, 162, 163; MCNL: 6.21; MLF: 454; MMCIPAS: 2901-3068; MMCNCD: 85-34-I-D; MMCNMH: 85-7-1; MMP: 63-S, 130-S, 171-S, 1212; MMPH: 0031, 0053; MNHN-PAM: 273; MPV: 50-64; PIMUZ A/V: 415, 416, 419, 420.

3.2. Methods

To assess the validity of the species of genus *Eutatus*, as many materials as possible from the abovementioned collections were studied. After reviewing the specimens, a detailed analysis of osteoderms, including external and internal morphology, was undertaken in order to identify significant differences that would allow interspecific differentiation for the genus. Osteoderms were selected (instead of skulls or postcranial elements) because most of the species have been recognized on the basis of external characters. In any case, few endoskeletal remains are associated to dermal shields or osteoderms, and the available skulls and postcranial elements are not enough to allow comparison of homologous areas. At the same time, osteoderms occur frequently along the entire temporal range of the genus, which allows association of morphological changes with age and stratigraphy, and verification of the existence of any overlap among the different morphotypes. Thus, the morphological groups identified (species) have greater support and significance.

Among the different regions of the dorsal armor of *Eutatus*, the pelvic shield was selected for the more detailed study of osteoderms, not only because of the greater availability (fossil record frequency) of these elements, but also because the identification of homologous zones is more reliable in this region.

Osteoderm characters were compared for the specimens assigned to the previously nominated species of genus *Eutatus*. A similar comparative study was performed for specimens of the living *Chaetophractus villosus* (Euphractinae, Euphractini), to observe and assess the range of intraspecific morphological variation. This living species was selected based on the facts that the tribe Eutatini is extinct and that, among the living forms, the Euphractini are the most similar to the former in morphology and, according to some authors, also the phylogenetically closest clade (Patterson and Pascual, 1968; Scillato-Yané, 1980; McKenna and Bell, 1997).

In addition to the methods habitually used to study external morphology of osteoderms of armored xenarthrans (macroscopic observation, measurements, etc.), the internal structure was

investigated using seriated sections to extract as much information as possible. The osteoderms were cleaned using 100 volumes hydrogen peroxide as a 1/10 dilution in distilled water to remove the sediment lodged in pores, foramina and cavities. Then, they were included in colored polyester resin and placed in a vacuum chamber to ensure perfusion of each sample. Once the resin solidified, each preparation was progressively ground using a grinder/polisher metallographic disk. Digital photographs were taken at every 200 μ on average between grinding stages. The observations were compared with the results of previous works on the histology of *C. villosus* osteoderms (Fernández, 1931; Krmpotic et al., 2005, 2008), in an attempt to recognize homologous structures in the osteoderms of *Eutatus*.

Because some fossils could only be studied through photographic images, all the materials were measured using the software program Image J v.1.40a in order to minimize measuring errors.

With respect to endoskeletal remains, their study resulted very complex because generally these materials are not quite complete, thus rendering the comparison of homologous areas unfeasible. Nevertheless, some differences were found in femora collected from the Ensenadan and later stages. The third trochanter is in a higher position in the femora from the Ensenadan materials with respect to the condition in femora from upper levels. In order to quantify this variation, the distance between the third trochanter and the distal trochlea was measured and divided by the distance between the greater trochanter and the third trochanter. The variation coefficient for this index was calculated. The same analysis was made for the femur of *C. villosus*, and lower variation of this index was observed in this taxon compared to the femora of different species of *Eutatus* (Table 1 and Figs. 1 and 2).

4. Assessment of previously designated species

Based on the most recent studies, which have been made using more abundant materials and new research approaches, an attempt is made here to clarify the systematics of this genus. The species *E. brevis* was recognized on the basis of a specimen deposited in the American Museum of Natural History, AMNH-11231, consisting of a partial skull, postcranial remains, isolated dorsal shield osteoderms, a fragment of pelvic shield, and caudal sheath osteoderms. According to Ameghino (1889: 872) this species is one third smaller than *E. seguini* and its skull has only eight upper molariforms (a characteristic that so far has not been verified for any other *Eutatus* individual). This skull has at least eight molariforms, but it is important to note that its entire anterior region has been reconstructed, which makes it extremely difficult to determine the actual number of molariforms given that the absence of the first one could be due to an incorrect reconstruction. This specimen is 24 cm in total length, whereas the type of *E. seguini* is 26 cm long; thus, it is not one third smaller (as stated by Ameghino, 1889: 872). Taking into account the range of intraspecific variation for this

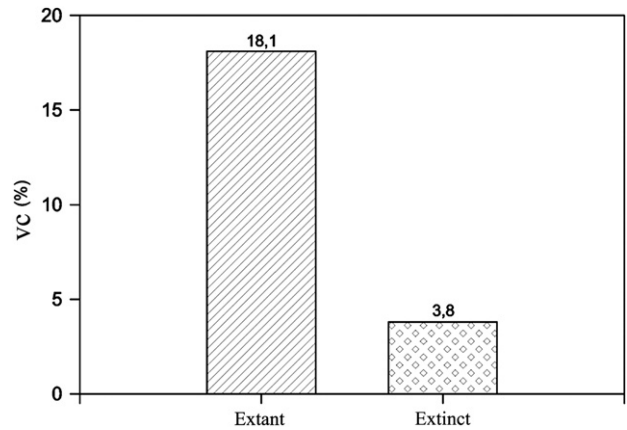


Fig. 1. Variation coefficient on the femur of different species of *Eutatus* compared with variation coefficient on the femur of *Chaetophractus villosus*.

variable in living species (see Carlini and Scillato-Yané, 1996 for *C. villosus* and *Euphractus sexcinctus*, and also Wible and Gaudin, 2004, for *E. sexcinctus*) such a difference falls within the variation range of these living species. With respect to the osteoderms, the empirical evidence belies Ameghino's assertion that "las placas que constituyen la coraza son notablemente más pequeñas" [the plates forming the armor are notably smaller] (in comparison with those of *E. seguini* sensu Ameghino, 1889: 872). The osteoderms from *E. brevis* are completely similar to those of *E. seguini* in terms of size, considering the following: (1) the measurements indicated by Ameghino (1889: 872) for the osteoderms of *E. brevis*, (2) the measurements of specimen N° 69-VIII-22-1 MLP (fragments of shield osteoderms labeled as belonging to *E. brevis* by Ameghino himself) and (3) the measurements of osteoderms from the pelvic shield N° 69-IX-9-10 MLP, from the "Pampean" of Laguna Vitel Buenos Aires Province, illustrated by Lydekker (1894, pl. XLI, fig. 1) and attributed to *E. brevis* by Ameghino (see Ameghino, 1895–1920). All the abovementioned considerations indicate that no characters exist that support the validity of this species.

With respect to *E. minutus*, Ameghino (1889: 873) only described mobile osteoderms, highlighting in his comparison with other species

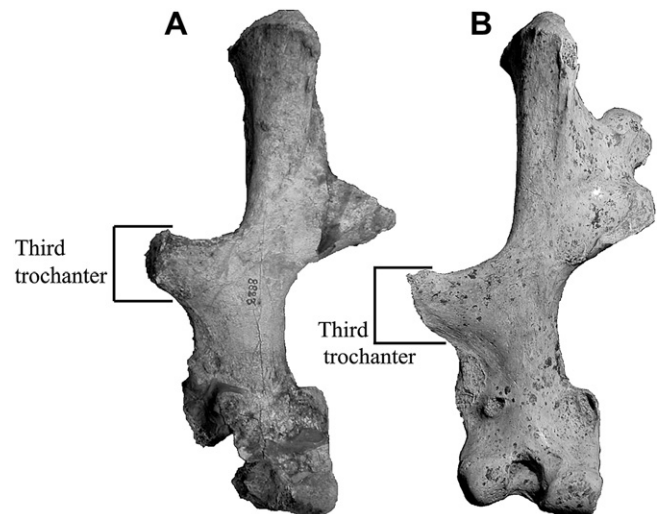


Fig. 2. A: Femur from the Ensenadan stage and B: femur from the Bonaerian stage. Not to scale.

Table 1

T3T = Distance between the greater trochanter and the third trochanter.
TM3T = Distance between the third trochanter and the distal trochlea.

<i>Eutatus</i>	T3T/TM3T	<i>C. villosus</i>	T3T/TM3T
MACN-2436	0.72	MLP-15.X.98.3	1.25
MACN-8823	1.04	MLP-30.XII.02.69	1.27
AMNH-11231	0.82	MLP-785	1.17
MMCI PAS 2101	0.85	MLP-795	1.23
MPV 64-50	1.17	MLP-911	1.16
MNH PAM 273	0.85	MLP-29.IV.99.4	1.24
		MLP-1271 d	1.14
		MLP-1300 d	1.17
		MLP-XI d	1.22

a great size difference (smaller), but morphologically similar to those of *E. punctatus*, and only differing in the presence of a double row of hair follicle foramina. The only materials referred by Ameghino to *E. minutus* (MACN 1133–1140), a species assumed to be similar in size to the living *E. sexcinctus*, are mobile band osteoderms. After thorough morphological study, these osteoderms appear not to belong to an animal smaller than *E. seguini* (sensu Ameghino, 1889), but instead to correspond to the first mobile bands of the dorsal shield of the latter species, where the osteoderms are much smaller than those from the succeeding bands. *Eutatus* does not have a complete scapular shield, but a rudimentary structure limited to the sides of the armor; thus, the medial region of the body, located between the cephalic shield and the pelvic shield, is covered by rows of mobile bands which are very variable in size. This makes it problematical to use size differences between isolated mobile osteoderms as the only diagnostic character, without precise indication of their position within the shield. With respect to the double row of hair follicle foramina commented by Ameghino, this feature cannot be observed in the previously referred materials. Consequently, there are no true anatomical differences to support this nomination, which ultimately arose from the comparison between non-homologous shield regions.

In 1933, A.F. Bordas described *E. ameghinoi* on the basis of anatomical differences in the skull, cephalic shield and postcranial skeleton with respect to *E. seguini*. The type material is a skull, MACN-986, from Chascomús (Buenos Aires Province). One of the differences mentioned by Bordas (1933) is the position of the infraorbital foramen, which would be between the 4° and 5° molariform in *E. ameghinoi*, and at the level of the 5° molariform in *E. seguini*. However, considering the location of this foramen in numerous skulls of *C. villosus* studied here, it is evidently variable, occurring at the level of M6 or between M5 and M6, presenting the same range of variation as would exist between *E. ameghinoi* and *E. seguini*. Another difference between the two species highlighted by Bordas (1933) concerns the arrangement of the dental series, which would be parallel (in *E. ameghinoi*) or divergent posteriorly (in *E. seguini*). To begin with, this character cannot be observed in the holotype of *E. ameghinoi*, because the dental rows are incomplete and the skull is somewhat deformed. Furthermore, in the skulls of *Eutatus* studied, the dental series tend to be slightly divergent posteriorly, and no significant difference was found in all the cases where this feature could be quantified. According to Bordas, the outer auditory meatus is more vertical in *E. ameghinoi* than in *E. seguini*; it must be noted that, first, this region is not preserved in the holotype of *E. ameghinoi*; and on the other hand, the study of several *C. villosus* specimens shows that there is some intraspecific variability in the position of this meatus, so that the use of this character as diagnostic becomes highly doubtful. Concerning the cranial vault, which according to Bordas (1933) is somewhat more flattened in *E. ameghinoi* with respect to *E. seguini*, this is yet another character that shows intraspecific variation in *C. villosus*. With respect to the differences mentioned by this author for the cephalic shield (narrower and posteriorly vaulted in *E. ameghinoi*, as well as some outline details), these are hardly verifiable, since the cephalic shield that Bordas assigned to *E. seguini* and used for comparison is not complete. There is a fragment of anterior skull (MACN 5803) which Bordas attributed, without much basis, to *E. ameghinoi*, and which is associated to endoskeletal remains (humerus, ulna, femur, tibia–fibula, and astragalus), in which this author recognized and described morphological features to support his species. These materials were not identified in the MACN collection, and consequently it was not possible to verify the certainty of his observations. However, the description and figures presented by Bordas (1933), combined with comparisons of numerous *Eutatus* materials, indicate that none of the characters mentioned by this author as

diagnostic are in fact significant. To sum up, the validity of this species is severely questioned, given that the supposed differences which support its nomination probably fall within the normal range of intraspecific variability of *E. seguini*.

The Bonaerian *E. punctatus* is the only one of the species described by Ameghino (1881) which, after this careful review, presents anatomical characters that support its separation from the Ensenadan species of *Eutatus*. Ameghino (1881: 310) characterized this species mainly on the basis of the large foramina of the exposed surface. With respect to its size, Ameghino's first assessment is that it is similar in size or even more robust, than *E. seguini* (Ameghino, 1881: 310); later (Ameghino, 1889: 872) he states that its "tamaño superior al del *E. brevis* igualando casi al tamaño de *E. seguini*" ("size is greater than that of *E. brevis*, almost equal to that of *E. seguini*"). From this, it may be deduced that he did not perceive a truly evident size difference between *E. punctatus* and the Ensenadan species. Concerning the morphology of osteoderms, Ameghino (1889: 872) asserts that those of *E. punctatus* are distinguished from those of other species by having a central figure that is more elongated and as high/thick as the peripheral figures, surrounded by large foramina. The geographical provenance of the remains of this species are the coastal cliffs of Río Salado (Buenos Aires Province) (Barrancas del Río Salado Provincia de Buenos Aires, Argentina) and the vicinity of La Plata [alrededores de La Plata (Ameghino, 1889)].

The type species, *E. seguini*, poses an unexpected situation, because its stratigraphical provenance is not the one that had always been accepted (v. Krmpotic and Scillato-Yané, 2007). In fact, ever since 1889 (Ameghino, 1889: 871), *E. seguini* has been mentioned as a species occurring, if not exclusively, in the Ensenadan stage. Given this situation, it is especially relevant that Paul Gervais recognized this species in 1867 based on remains from the Río Salado (Buenos Aires Province), which were collected by François Seguin and purchased by the Museum National d' Histoire Natural (Paris) in 1856. The fossil outcroppings of the Río Salado correspond to the Bonaerian ("Pampeano superior" of Ameghino, 1881) and the Lujanian ("Pampeano lacustre" of Ameghino, 1881) stages. To date, no taxon has been recorded from those outcroppings that could indicate an older age. Consequently, the holotype of *E. seguini* must be middle to late Pleistocene, or even early Holocene, in age. All the species correctly attributed to *Eutatus* so far, come also from the Bonaerian and Lujanian stages, namely: *E. brevis* Ameghino, 1881, *E. punctatus* Ameghino, 1881, *E. minutus* Ameghino, 1889 and *E. ameghinoi* Bordas, 1932. Likewise, all of these species are synonyms of *E. seguini* (v. supra). Thus, it becomes necessary to recognize a new species for the abundant *Eutatus* specimens from the Ensenadan, as well as for those from the Marplatán (Vorohuean and Sanandresian) stages which are conspecific; this work designates this species.

5. Osteoderm features and their systematic significance: intra- and interspecific variability

The armor of both *C. villosus* and the species of *Eutatus* include the following parts: 1) cephalic shield, 2) dorsal shield, 3) caudal sheath and 4) isolated osteoderms from other areas, such as those occurring in the integument of the limbs or ventral trunk. The dorsal shield can be divided into: a) scapular shield, which is rudimentary and limited to the flanks in *Eutatus*, and well developed in *C. villosus*, b) several mobile bands, and c) pelvic shield. In this study, the pelvic shield osteoderms were selected for analysis because of the abovementioned greater availability of complete materials corresponding to this region of *Eutatus*.

The osteoderms of *Eutatus* species are strongly rugose due to the presence of numerous foramina and small grooves. The

ornamentation of the exposed surface consists of a central figure, limited anteriorly by cranial figures and laterally by lateral figures. The sulci that demarcate the central figure do not reach the posterior margin of the osteoderms, so that this figure becomes less distinct toward the posterior end. The anterior half of the plaque bears the foramina of the exposed surface, located at the intersection between the sulcus around the central figure with those that bound the peripheral figures. Large hair follicle foramina appear at the posterior margin of the osteoderm. This great development of hair foramina has been mentioned as one of the most distinctive features of the Eutatini (e.g. Burmeister, 1883; Hoffstetter, 1958). The ventral surface of the osteoderms is smooth, with large irregularly scattered perforations.

Osteoderms from the pelvic shield of both *C. villosus* and *Eutatus* were carefully studied in order to distinguish characters with systematic value at the species level from others that may presumably vary among individuals of the same species. To address this issue, a comparative study of homologous portions of the pelvic shield was undertaken. The osteoderms from this area were analyzed both qualitatively and quantitatively. The qualitative characters considered were: a) convexity of the central figure, b) lateral figures more distinct or more diffuse toward the caudal area, and c) relative size of foramina on the exposed surface and of hair follicle foramina. The quantitative characters studied were: a) measurements (length, width), b) number of foramina on the exposed surface, c) number of anterior peripheral figures, d) number of lateral peripheral figures, and e) number of hair follicle foramina.

As a result of this analysis, the specimens of *Eutatus* were grouped into three relatively homogeneous and chronologically successive clusters: (a) one from the Chapadmalalan, (b) a second one from the Vorohuean (Marplatan) and Ensenadan, and (c) a third one from the Bonaerian–Lujanian stages. This study includes the groups (b) and (c); more empirical information is being collected about group (a) for a future more detailed study. In group (b), the foramina on the exposed surface appear as fine punctuations, variable in number (sometimes difficult to distinguish due to the presence of numerous small sulci and perforations that give the surface its characteristic rugose appearance), the most frequent number of hair foramina areas is 5, and the central figure is a little wider. In section, each osteoderm show well developed gland reservoirs, arranged singly or in pairs, and located antero-posteriorly, following the wear plane, with one or two thin ducts; the cavities for hair follicles only occur on the middle-posterior part of the osteoderm (Figs. 3A, B and 4A, B). In group (c), the foramina on the exposed surface are well marked, ranging in number primarily between 5 and 6, generally with 4 hair follicle areas, and a central figure slightly narrower compared to the previous group. Internally, the foramina on the exposed surface continue as large diameter gland ducts. Within the thickness of the osteoderm, well developed gland reservoirs are arranged in groups of up to three, located antero-posteriorly, following the wear plane (these reservoirs may even coalesce and be partially fused to each other); the cavities for hair follicles take up a larger proportion of the osteoderm compared to the previous group, extending anteriorly and determining a transverse protuberance on the ventral surface of the osteoderm (Figs. 3C, D and 4C, D).

The Chapadmalalan materials cannot be included in any of the abovementioned groups and are currently under evaluation.

6. Systematics

Superorder XENARTHRA Cope, 1889
Order CINGULATA Illiger, 1811

Superfamily DASYPODOIDEA Gray, 1821

Family DASYPODIDAE Gray, 1821

Subfamily EUPHRACTINAE Pocock, 1924

Tribe EUTATINI Bordas, 1933

Genus *Eutatus* Gervais, 1867

Type species: *Eutatus seguini* Gervais, 1867 (p. 2).

Synonyms: *Euphractus* Ameghino, 1882 (part: 41, nec Wagler, 1830).

Dasyus Ameghino, 1889 (part: 864, nec Linné, 1758).

Diagnosis (emend. Scillato-Yané, 1982): Large size, comparable to that of *Priondotes giganteus*. Head shield osteoderms with marked sculpturing, consisting of a raised central figure and tubercle-shaped peripheral figures. Scapular shield rudimentary, limited to the lateral parts of the armor, although more developed than in the other Eutatini. The right and left half of each pelvic shield band not forming a smoothly curved transversal girdle, but meet in the sagittal area forming an obtuse angle with the apex directed forward (this arrangement being unique among the Dasypodidae so far). The surface of osteoderms is more rugose than in *Chasicotatus* and *Doellotatus*. Central figure more convex and delimiting sulci deeper than in *Doellotatus*. In the mobile osteoderms, the posterior margins prolonged beyond the row of foramina further than in any other Eutatini. Internally, osteoderms present three well differentiated zones from dorsal to ventral. The external and internal zones are formed by compact bony tissue. The intermediate zone is the most developed and presents bony lamellae arranged around large cavities. These cavities would have been occupied by hair follicles, glands and adipose tissue. Zygomatic arch extremely robust. Tympanic bulla relatively small. Length of upper premental space approximately equal to total length of dental series. Most common dental formula 9/9. Last 4 or 5 upper and lower molariforms sometimes more elongated, presenting two lobes.

Chronological and stratigraphical distribution: late Pliocene–early Holocene (Chapadmalalan, Vorohuean, Sanandresian, Ensenadan, Bonaerian, Lujanian and Platan Ages/Stages).

Geographical distribution: Argentina (Buenos Aires, Santa Fe, Entre Ríos, Córdoba, Santiago del Estero, and Tucumán Provinces) and Uruguay (Fig. 5).

Eutatus pascuali n. sp. (Fig. 7)

Derivatio nominis: honoring Dr. Rosendo Pascual

Holotype: Quite complete dorsal armor, cephalic shield, skull, MMP S-171. Provenance: “Playa Bristol”, Mar del Plata, Buenos Aires Province. Ensenadan stage.

Paratype: IFG: 73. Provenance: “Toscas del Río de La Plata”, Buenos Aires city.

Hypodigm: the holotype, plus the following, IFG: 131; MMP: 1212; MACN: 8823, 10425, 10845, 11073; MLP: 52-X-2-27, 62-VII-27-3, 69-IX-5-3, 70-III-10-2; MPV 50-64.

Assignable materials: MLP: 52-IX-30-28, 54-VI-19-9a, 55-X-17-2, 69-VIII-1-3, 69-VIII-1-8, 82-IV-10-1, 95-XII-1-26, 95-XII-1-28; MACN: 1635, 1636, 1746, 1747, 1825, 1914, 1982, 1988, 1999, 2268, 5514, 5675, 5803, 5829, 5852, 6520, 6881, 8789, 8796, 10097, 10177, 12400; IFG: 100; MMP: 63-S, 130-S.

Synonymy: *Eutatus seguini* Ameghino, 1889 (part., nec Gervais, 1867).

Diagnosis: Large-sized Eutatini, comparable in size to *E. seguini*, but more robust than the latter. Size and thickness of osteoderms are similar to those of *E. seguini*. Osteoderms from anterior central region of pelvic shield with exposed surface foramina much smaller than those of *E. seguini* and appearing as fine punctuations. Generally, 5–6 hair follicle foramina. Central figure of osteoderms is wider. Osteoderms with well developed gland reservoirs, arranged in up to 2 antero-posteriorly at the wear plane, with one or two thin ducts; the cavities for hair follicles only extend onto the middle-posterior part of the osteoderm (Figs. 3A, B and 4A, B). Femur with

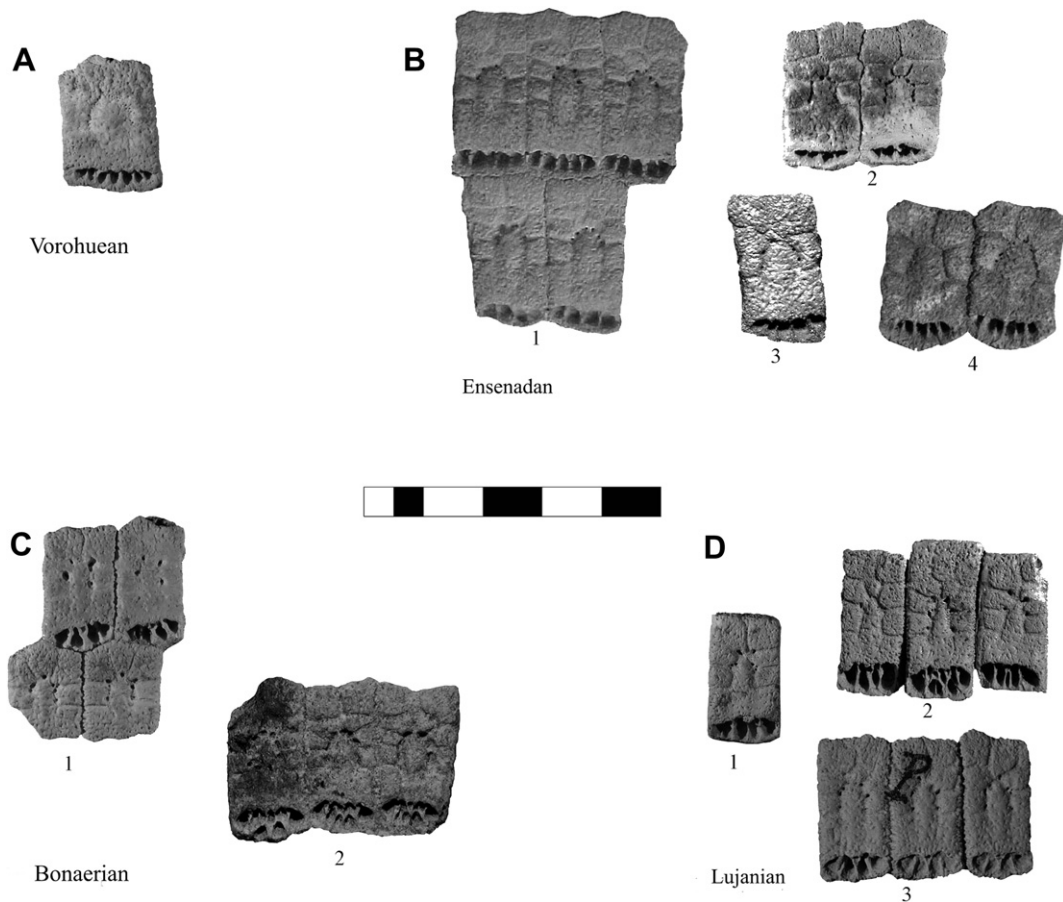


Fig. 3. Osteoderms from homologous regions of the pelvic shield. A: *Eutatus pascuali*, MLP: 70-III-10-2. B: *E. pascuali* (1) MMP: S-171, (2) MMP: 1212, (3) MLP 69-IX-5-3, (4) MACN 5238. C: *E. seguini* (1) MLF: 454, (2) IFG: 1179. D: *E. seguini* (1) and (2) MLP: 0-VIII-5-1, (3) MLP: 69-VIII-19-1.

third trochanter higher than in *E. seguini*, distance from third trochanter to greater trochanter always smaller than distance from distal trochlea to third trochanter (Fig. 2).

Chronological and stratigraphical distribution: Vorohuean, Sanandresian, Ensenadan stages (Fig. 6) (late Pliocene middle Pleistocene).

Geographical distribution: Argentina (Buenos Aires Province).

Eutatus seguini Gervais, 1867

Holotype: Skull, cervical vertebrae, left and right humeri, left and right radii, left ulna, carpals and phalanges of both forefeet, left and right femora, left tibia–fibula, metatarsals, phalanges of both hindfeet. MNHN-PAM: 273. Provenance: Río Salado, Buenos Aires Province, Argentina

Hypodigm: The holotype plus MLP: 38-X-2-1, 52-IX-28-19, 52-IX-28-50, 52-X-2-99, 69-VIII-19-1, 69-VIII-22-1, 69-IX-9-10, 00-VIII-5-1; MACN: 1122-1132, 2436, 2772, 6035, 10160a, 10417, 19211; AMNH: 11231; IFG: 1082, 1179; MLF: 454; MCNL: 6.21; MMCIPAS: 2901-3068; PIMUZ A/V: 0420, 0415.

Assignable materials: 52-IX-30-82, 62-VII-27-107, 69-VIII-1-5, 69-VIII-22-14, 71-X-17-10, 80-VIII-13-56, 86-XI-20-3, 91-IV-15-51, 97-II-1-45; MACN: 6255, 6256, 986, 1133-1140, 2273, 5121a, 2277, 5715, 16638; IFG 1074; LARBO-UNMDP: 154-163.

Synonymy: *Eutatus brevis* Ameghino, 1881

Eutatus punctatus Ameghino, 1881

Diagnosis: Large-sized Eutatini. Size and thickness of osteoderms are similar to those of *E. pascuali* n.sp. Osteoderms from anterior central region of pelvic shield with exposed surface foramina larger than those of *E. pascuali* n.sp., mainly 4–6 in

number. Generally 4 hair follicle foramina (5–6 in *E. pascuali* n.sp.); hair foramina more developed on the exposed surface than in *E. pascuali*, occasionally even with some subdivision that defines 2 rows. Central figure of osteoderms is narrower than in *E. pascuali* n.sp. Osteoderms with maximum 3 gland reservoirs per wear. Gland ducts large in diameter, one or two per gland reservoir. Internally, the cavities for hair follicles surpass half of the total length of the osteoderm anteriorly, sometimes modifying the ventral surface of the osteoderm as a protuberance (Figs. 3C, D and 4C, D). Femur with third trochanter lower with respect to that of *E. pascuali*; distance from third trochanter to greater trochanter always greater than distance from third trochanter and distal end trochlea (Fig. 2).

Chronological and stratigraphical distribution: Bonaerian, Lujanian and Platan stages (middle Pleistocene–early Holocene) (Fig. 6).

Geographical distribution: Argentina (Buenos Aires, Santa Fe and Entre Ríos Provinces).

7. Paleoclimatic context

The main climate changes occurred in the time laps that includes the biochron of *Eutatus* may be summarized as follows. The early Pliocene was marked by a warm trend, until 3.2 Ma when the rise in δO^{18} values reflected the beginning of extensive glaciations in the Northern Hemisphere (Zachos et al., 2001). The glacial and interglacial cycles brought about significant changes in the environmental conditions of the Pampean and Patagonian regions (Rabassa et al., 2005). For the Pampean region, cold environmental conditions

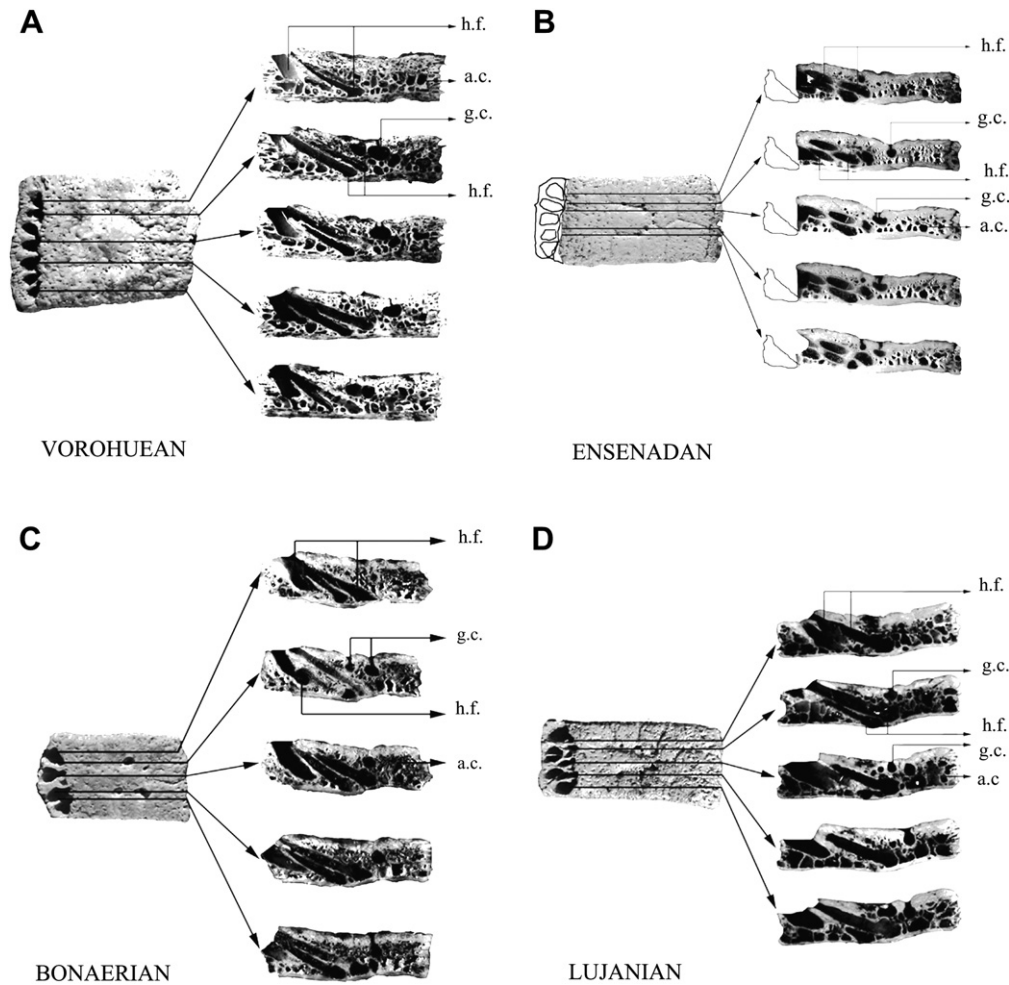


Fig. 4. Osteoderms of pelvic shield and their respective longitudinal sections. A: *Eutatus pascuali* MLP: 70-III-10-2. B: *E. pascuali* MMP: S-171. C: *E. seguini* MLP: 454. D: *E. seguini* MLP: 00-VIII-5-1. g.c.: gland cavity, a.c.: adipose tissue cavity, h.f.: hair follicle cavity. Not to scale.

are only recorded after 2.6 Ma BP in the most recent Marplatan (Sanandresian) stage, for which several glacial events have been recognized; before 3 Ma, environmental conditions were always warmer than those of the late Pleistocene interglacial periods, according to the global isotope records (Rabassa et al., 2005). In the Marplatan (late Sanandresian) stage, and in the earliest Ensenadan deposits of the Pampean region, several mammalian general indicative of cold arid climate are recorded and, simultaneously, some indicators of warm and probably humid conditions cease to be recorded in this area (Cione and Tonni, 2001). This event is simultaneous with the establishment of well calibrated glacial advance in southern Argentina (Cione and Tonni, 2001, and references cited therein). The climatic conditions in the Pampean area during the early Pleistocene (Ensenadan stage) were relatively humid and warm according to the record of mammals and the lithology (Nabel et al., 2000). The late Ensenadan stage holds the last records for the Pampean region of large mammals indicative of warm humid conditions (e.g. Tapiridae) (Cione and Tonni, 2001; Cione et al., 2007). With respect to the glaciation events for the early Ensenadan stage, recurrent glaciations are acknowledged in Patagonia, but only one is recognized in the geographical areas studied here (Rabassa et al., 2005). In contrast, the late Ensenadan stage is characterized by the great extension of the Patagonian glaciers during the Great Patagonian Glaciation (GPG) that would have taken place between 1.168 and 1.016 Ma BP (Rabassa et al., 2005).

After the Jaramillo event (between 1.0 and 0.78 Ma BP), the fossil beds from the late Ensenadan to the Lujanian stages include mammals that indicate cold arid condition, except those that suggest a humid and probably warm pulse during the Bonaerian stage (Tonni and Cione, 1994; Tonni et al., 1999; Cione and Tonni, 2001).

The loess sedimentation at the beginning of the Brunhes Chron (0.78 Ma BP), with the marked immaturity of minerals, abundant fresh plagioclases, volcanic glass, carbonate globules and calcretes, as well as the mammalian fauna, suggest cold and arid climatic conditions (Nabel et al., 2000). Furthermore, as previously mentioned, the Bonaerian stage probably starts with a warm event, based on faunal and geologic evidence that corresponds to an interglacial period at approximately 0.4 Ma (Verzi et al., 2004; Cione et al., 2007 and literature cited therein). Sensu Droxler et al. (2003), the terrestrial record also suggests that the Marine Isotope Stage (MIS) 11 could represent the longest, and perhaps warmest, interglacial stage in the past 500 ka (see also Merino et al., 2007 for *Noctilio* sp.). Small glaciations and the Gotiglacial 1 event take place during the Bonaerian stage (Rabassa et al., 2005).

The Lujanian stage starts with interglacial conditions recognizable in the fauna at 130 ka BP (Cione et al., 2007, and literature cited therein). Mammals indicative of arid and/or cold climate are recorded in the outcroppings of the Guerrero Member (Tonni et al., 1999, and literature cited therein). The Guerrero Member deposits

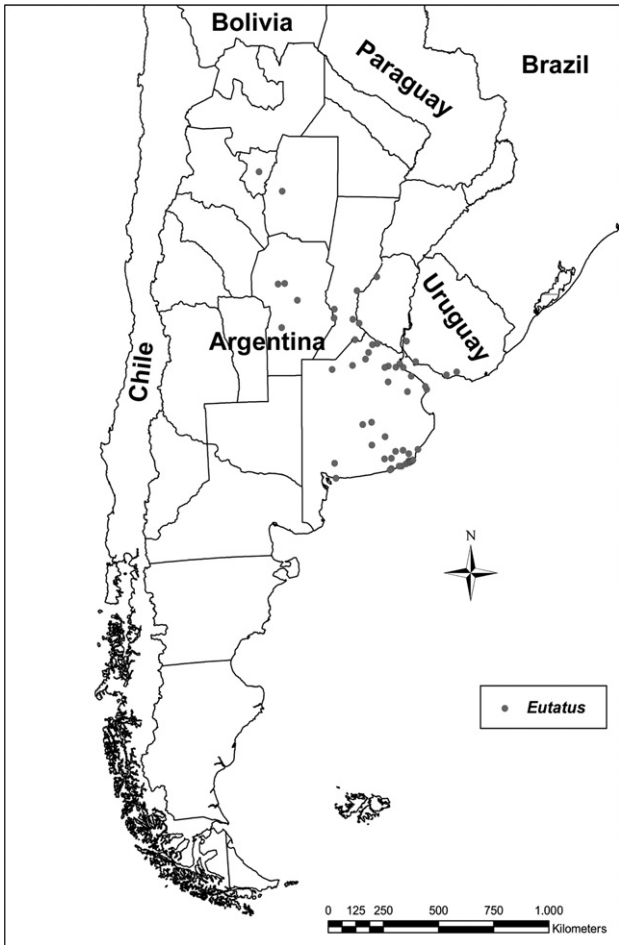


Fig. 5. Map showing the distribution of *Eutatus*.

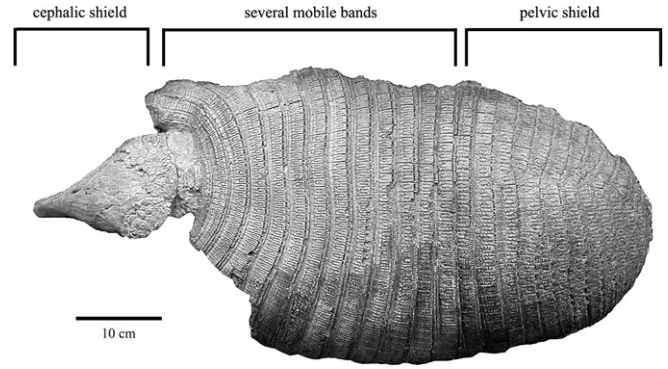


Fig. 7. Holotype of *Eutatus pascuali* MMP: S-171.

would span the 21–10 ka BP period; the faunal evidence suggests arid conditions during the entire deposition of this unit (Tonni et al., 2003) and the presence of Patagonian fauna suggests temperatures lower than the current ones (Tonni et al., 1999). Based on sedimentological data, Iriondo and García (1993) proposed that

climate conditions similar to those current for Patagonia extended 750 km further north during the late Pleistocene, until 8.5 ka BP. This arid event, previous to 10 ka, is at least partially coincident with the Younger Dryas event (Tonni et al., 2003; Rabassa et al., 2005). Fossil pollen studies corroborate the presence of plant communities adapted to arid environmental conditions during the late Pleistocene–early Holocene (Quattrocchio and Borromei, 1998). Between 11 ka and 13 ka BP, the presence of sterile pollen samples could be related to marked continental conditions resulting from a lower sea level (Quattrocchio and Borromei, 1998). Before 10.5 ka BP, according to another study based on the analysis of pollen samples, the climate is interpreted to have been sub-humid to dry, with precipitation in the Pampean region being 100 mm lower than the current levels (Prieto, 1996). Iriondo (1999) stated that, between 14 ka and 8.5 ka BP, the Pampean region is characterized by an arid climate with predominance of SW winds. The glaciations of this period could have begun at around 85 ka BP; the events recognized include the Gotiglacial II and the Last Great Glaciation (LGG) which reached its peak (known as the Last Glacial Maximum, LGM) toward 25 ka BP and ended at about 16 ka BP (Rabassa et al., 2005).

8. Discussion

Given that no stratigraphical superposition has been recorded thus far between the two recognized species, several isolated remains have been tentatively assigned to *E. pascuali* n. sp. or *E. seguini*, based on their stratigraphical provenance.

With respect to the species *E. minutus* Ameghino, 1882 (nomen nudum), *Dasyptus major* Ameghino, 1889 (= *Euphractus major* Ameghino, 1882) and *E. ameghinoi* Bordas, 1932, which were erected on the basis of a few osteoderms (not from the pelvic shield) or skeletal parts that cannot be compared using the diagnostic criteria followed in this work, they cannot be assigned to *E. seguini* or to *E. pascuali* n. sp. with any certainty. Furthermore, none of the materials used for the diagnosis of these species present characters that could question their validity. Lastly, considering that there is no known stratigraphic overlap between *E. seguini* and *E. pascuali* n. sp., and that the materials of *E. minutus*, *D. major* and *E. ameghinoi* come from levels above the Ensenadan stage, these could be specimens of *E. seguini* and are provisionally considered as such.

Based on the analyses made in the present work, as well as in other aspects anticipated in Krmptotic and Scillato-Yané (2004, 2007) and Krmptotic et al. (2004, 2007), two *Eutatus* species can be recognized for the late Pliocene–early Holocene: 1) *E. pascuali* n. sp., from the Vorohuean (late Pliocene) and Ensenadan (early to middle Pleistocene) stages, and (2) *E. seguini*, from the Bonaerian (middle

Ma	CHRONOS	POLARITY	EPOCH	SOUTH AMERICAN AGES	BIOZONES	
1	C 1	[Black bar]	PLEISTOCENE	HOLOCENE	PLATAN	<i>Lagostomus maximus</i>
				LUJANIAN		<i>E. (A.) neogaeus</i>
2	C 2	[Black bar]	PLEISTOCENE	BONAERIAN		<i>Megatherium americanum</i>
				ENSENADAN		<i>Mesotherium cristatum</i>
3	C 3	[Black bar]	PLEISTOCENE	MARPLATAN	SANANDRESIAN	<i>Ctenomys chapadmalensis</i>
					VOROHUEAN	

Fig. 6. Chronology, South American Ages, and Biozones (modified from Cione and Tonni, 2005).

Pleistocene), Lujanian (late Pleistocene–early Holocene) and Platan (in its early Holocene) stages. Thus far, no chronological overlapping of the two valid *Eutatus* species has been recorded; therefore *E. pasquali* n.sp becomes an exclusive taxon for the Ensenadan stage of the Pampean region, and *E. seguini* for the Bonaerian, Lujanian and Platan stages.

Although the brief review presented earlier in this work highlights only part of the complex climate changes, the morphological changes found in the osteoderms of *Eutatus* species could be related to environmental changes. The osteoderms of the different recognized species show variation in the morphology and number of gland reservoirs. The osteoderms from the Marplatán (Vorohuean)–Ensenadan stages contain within the depth of the osteoderm, well developed gland reservoirs, arranged in up to two anteroposterior levels, with one or two thin ducts; the cavities for hair follicles are limited to the middle–posterior part of the osteoderm. In contrast, in the osteoderms from upper levels (Bonaerian and Lujanian stages), the gland ducts are wider, some osteoderms have a maximum of three anteroposterior levels of gland reservoirs (which may be even coalescent and partially fused to each other), and the cavities for hair follicles occupy a greater volume than in Ensenadan osteoderms, extending forward and occasionally producing a transversal protuberance on the ventral surface of each osteoderm.

In living dasypodid species, the osteoderms are typically covered by horny scales. It is probable that the glands found in the osteoderms (sebaceous and associated sweat glands) produce a substance to protect the horny scales from extreme desiccation, especially in dry environments. Among the living species studied (Fernández, 1931; Krmpotic et al., 2005, 2008; Hill, 2006; Vickaryous and Hall, 2006; Ciancio et al., 2007), the ones with greatest glandular development are those from more arid areas. In addition, greater pilosity is observed in armadillos that inhabit colder regions compared to those that occur in more benign climates. The osteoderms of genus *Eutatus* from the Lujanian stage, which were included in the paleohistological study, come from the Guerrero Member, during which most authors agree that climate conditions were dry and cold; thus, the greater development of glands and pilosity would be important. In the case of the materials from the Vorohuean–Ensenadan stages, linking the morphological changes with climate conditions becomes more difficult because this was a long period that included many climatic fluctuations; however, in contrast with the previous period, this interval shows warmer and more humid periods.

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