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ARTICLE

SYSTEMATIC REVISION OF TROPICAL BRAZILIAN SCELIDOTHERIINE SLOTHS (XENARTHRA, MYLODONTOIDEA)

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ABSTRACT—The analysis of recently recovered ground sloth remains from Minas Gerais, Bahia, and Piauí (Brazil) results in a major reinterpretation of the Scelidotheriinae and Megalonychidae of tropical Brazil. Among the specimens collected from Lagoa Santa (Minas Gerais) by Lund during the first half of the 19th century are skeletal elements attributable to two scelidotheriine species, as Lund himself determined and Winge corroborated. This is in contrast to the interpretation of these remains as representing a scelidotheriine and the postcranial remains of a peculiar megalonychid, as most authors, following Hoffstetter, have believed. A new combination is proposed here for one of the species. Another scelidotheriine recently described from Piauí by Guérin and Faure is a synonym of this species.

INTRODUCTION

Scelidotheriinae were medium-sized mylodontid ground sloths. Their abundant remains indicate that they were common and widespread faunal elements of the South American Plio-Pleistocene. They possess lobate teeth with flattened grinding surfaces, as is general of mylodontids (McDonald and De Iuliis, 2008). Main differences from the other main mylodontid clade, the Mylodontinae, are that the skull is narrow and elongated and the dentition is subsequently transversely compressed (McDonald and Perea, 2002; Dantas and Zucon, 2007).

The monophyly of the Scelidotheriinae is robustly supported by at least 24 unambiguous synapomorphies, of which 6 are unique to the clade (Gaudin, 2004). However, several aspects of scelidotheriine systematics have not been satisfactorily resolved, such as the generic level taxonomy and the alpha taxonomy of remains principally from the Brazilian Pleistocene. Although both these aspects are considered here, the latter is the main focus of the current report.

The species of Scelidotheriinae discovered by Lund (1839a,b,c) in Lagoa Santa (Minas Gerais, Brazil) have a tortuous history. They were initially considered as megalonychids and various names have been applied to them (see Systematic Paleontology). Lund (1846) finally recognized that only two scelidotheriine species were present: *Scelidotherium owenii* Lund, 1846 and *Scelidotherium bucklandi* (Lund) Lund, 1846.

Gervais (1874) based *Valgipes deformis* on a calcaneum, MNHN 7384, recovered from caves in Curvelo (Minas Gerais) by the Danish fossil collector P. Claussen. Winge (1915) agreed with the scelidotheriine nature of the calcaneum, but Hoffstetter (1954:761) considered it "clairement différent de ceux de tous les autres gravigrades connus jusqu'à présent," and viewed it as a megalonychid worthy of its own subfamilial status. Paula Couto (1979) considered it as incertae sedis.

Reinhardt (1875) based *Ocnopus laurillardi* on a tibia-fibula that Lund (1846) had assigned to *S. bucklandi* and a tooth (ZMUC 1130) of a juvenile giant ground sloth (Megatheriidae) that Lund (1842) had identified as "*Megatherium laurillardi*" (= *Eremotherium laurillardi*). Reinhardt's mistake with regard to the assignment of this molariform has long been recognized. Cartelle and De Iuliis (1995, 2006) formally recongnized this molariform as the holotype of *E. laurillardi*, making *E. laurillardi* the valid name of the intertropical Panamerican giant ground sloth. We demonstrate below that the tibia-fibula belongs to a scelidotheriine.

In analyzing the material that Lund collected in Lagoa Santa and sent to Denmark, Winge (1915) also recognized two scelidotheriine species: *Catonyx giganteus* and *Scelidotherium magnum* (the equivalent of Lund's *S. bucklandi* and *S. owenii*, respectively). Hoffstetter (1954) drastically revised Winge's assessment of this material. According to this author, the species identified by Winge (1915) as *S. magnum* is distinct from this species (which had been described from Argentina), and should have been identified as *Scelidodon cuvieri* (Lund); the latter species is now placed in *Catonyx* (McDonald, 1987; see below). Hoffstetter (1954) considered Winge's (1915) *C. giganteus* invalid because it was based on an erroneous association of remains. According to Hoffstetter (1954), the skull, mandible, and teeth belonged to the scelidotheriine *S. cuvieri* (which Winge had recognized as *S. magnum*), whereas the postcranial skeletal remains belonged to a megalonychid. Winge (1915) assigned to *C. giganteus* the tibia-fibula that Reinhardt (1875) had attributed to *O. laurillardi* (see above). Hoffstetter (1954) thus proposed a new combination, *Ocnopus gracilis* (Lund) (see Systematic Paleontology).

According to Hoffstetter (1954), this species was known only from the postcranial remains that Winge (1915) had illustrated and two isolated molariforms (ZMUC 2154, 2406) from Lagoa Santa that Hoffstetter noted and assigned to the species. In support of his hypothesis, Hoffstetter (1954) cited the presence of these two molariforms, in addition to the purported megalonychid morphology of the postcranial remains. However,

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the presence of numerous skeletal remains of *O. gracilis* from the Lagoa Santa region (= *C. giganteus*; 26 individuals are represented in the Lund collection, according to Winge, 1915) suggests that if this species were a megalonychid, then numerous molariforms with typical megalonychid morphology should also have been recovered.

Hoffstetter's revision and opinions have been accepted by all subsequent authors (e.g., among other, Marshall et al., 1984; Cartelle, 1992). The peculiarities of the alleged megalonychid *O. gracilis* prompted Hoffstetter (1954) to propose a new subfamily Ocnopodinae, and to promote special status for *V. deformis*, the species described by Gervais (1874). Hoffstetter (1954) noted its overall axe-shaped tuber, reminiscent of that of *Megalonyx*, and therefore considered it, too, to be megalonychid.

An incomplete skull definitely pertaining to the Megalonychidae was recovered from a limestone cave in Iporanga (São Paulo, Brazil) during the 1970s. In an unpublished manuscript (CC, pers. obs.), C. de Paula Couto described this specimen and assigned it to *O. gracilis*. This was apparently the 'missing' skull of this species, confirming Hoffstetter's view of its megalonychid affinities.

The most recent development in Brazilian scelidotheriine taxonomy is the erection of *Scelidodon piauiense* by Guérin and Faure (2004) based on a skull, mandible and humerus from Piauí, Brazil. One may surmise from the discussion above that only one intertropical Brazilian scelidotheriine species, *S. cuvieri* (= *C. cuvieri*) has been recognized in the literature over the past half century, apart from the material described by Guérin and Faure (2004). This species has also had a long, disputed taxonomic history, described by Paula Couto (1973) as a nomenclatural nightmare. Indeed, it may have more synonyms (about 40) than any other mammal (Cartelle, 1995). It has already been noted that it was initially interpreted as a Megalonychidae by Lund (1839b,c and 1840a,b) and as a Scelidotheriinae by Owen (1842), Lund (1846), Winge (1915), and Hoffstetter (1954). Most recently, McDonald (1987) determined that the correct name is *C. cuvieri* (Lund) (rather than the more commonly accepted *S. cuvieri*), because he considered *Scelidodon* Ameghino, 1881 a nomen nudum to be replaced by *Catonyx* Ameghino, 1891. However, several authors have considered *Scelidodon* valid for species in Peru and Chile and have agreed that *Catonyx* is the valid name for Brazilian species (see Pujos, 2000; Guérin and Faure, 2004; Dantas and Zucon, 2007). In addition to Minas Gerais, *C. cuvieri* has been recovered from São Paulo, Bahia, Paraíba, Ceará, Piauí, and Paraná, the latter being the southernmost occurrence of this endemic Brazilian species (Cartelle, 1992; Dantas and Zucon, 2007).

Recent recovery of material that mirrors Lund's discoveries prompts us to suggest a profound reinterpretation of Brazilian Scelidotheriinae. This work aims to demonstrate that:

(1) the scelidotheriine species *C. cuvieri* (Winge's *S. magnum*) is valid, but the skull, mandible, and teeth assigned by Winge (1915) to *C. giganteus* do not belong to *C. cuvieri*, in contrast to Hoffstetter's (1954) proposal; (2) the species described by Lund (1846) as *S. bucklandi* and by Winge (1915) as *C. giganteus* is indeed a scelidotheriine, as these authors believed, rather than a megalonychid, as considered by Hoffstetter (1954) and subsequent authors. Its valid name differs from those given by Winge (1915) and Hoffstetter (1954); (3) the species *V. deformis*, founded by Gervais (1874), is neither a megalonychid nor even a valid taxon because the calcaneum (the holotype) belongs to Winge's *C. giganteus* (= *S. bucklandi* of Lund); (4) consequently, the postcranial remains of *C. giganteus*, considered by Hoffstetter (1954) as a megalonychid (improperly named *O. gracilis*), is a Scelidotheriinae, as defined by Winge (1915); (5) the megalonychid subfamily Ocnopodinae Hoffstetter, 1954, and the special status bestowed on *V. deformis* by this author should be rejected; (6) *Scelidodon piauiense* Guérin and Faure, 2004, is a synonym of the new combination proposed here.

Institutional Abbreviations—**MCL**, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **UFMG**, Museu de História Natural, Universidade Federal de Minas Gerais, Belo Horizonte; **ZMUC**, Zoologisk Museum Universitat Copenhagen, Copenhagen.

MATERIALS AND METHODS

This study is primarily a taxonomic revision rather than a cladistic analysis, although there are, clearly, phylogenetic implications. It is based almost entirely on the recently recovered material listed below. We have not included any comparative data from the literature on *C. cuvieri*, except for comparative measurements in Winge (1915), because the skull and molariform specimens from two different species were, for many years, erroneously considered conspecific, and such data might thus be unreliable. The material for the new combination proposed here for the species previously recognized as *C. giganteus* or *O. gracilis* is listed as referred material below. Material of *C. cuvieri* (= Winge's (1915) *Scelidotherium magnum* = Hoffstetter's (1954) *Scelidodon cuvieri*) used for comparative purposes includes: MCL 4265, skull and numerous skeletal elements of a single individual; MCL 4254, MCL 4259, skulls; MCL 22682 and 22683, posterior halves of skulls; MCL 22681 and 22686, anterior halves of skulls; mandibles; numerous postcranial elements, including humerus, radius, ulna, elements of the manus and pes, femur, tibia, and fibula; UFMG without number, nearly complete postcranial skeleton; and a cast of the partial calcaneum (MNHN 7384; holotype of *V. deformis*) figured by Hoffstetter (1954:761).

SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889
TARDIGRADA Latham and Davies in Forster, 1795
MYLODONTOIDEA (Gill, 1872)
MYLODONTIDAE Ameghino, 1889
SCELIDOTHERIINAE Ameghino, 1904
VALGIPES Gervais, 1874

Myrmecophaga Linnaeus: Lund, 1839a:571 (nomen nudum).
Megalonyx Harlan: Lund, 1839b:219 (partim).
Platyonyx Lund, 1840b:311.
Scelidotherium Owen: Lund, 1846:62 (partim).
Ocnopus Reinhardt, 1875:234 (partim).
Scelidodon Ameghino, 1881:307 (nomen nudum).
Catonyx Ameghino: Winge, 1915:144.
Scelidotherium Owen: Hoffstetter, 1954:748 (partim).

Type and Only Known Species—*Valgipes bucklandi* (Lund) Gervais, 1874

Diagnosis—As for type and only species.

VALGIPES BUCKLANDI (Lund, 1839) (new combination)
Scelidodon piauiense Guérin and Faure, 2004:41
Myrmecophaga gigantea Lund, 1839a:571 (nomen nudum).
Megalonyx bucklandi Lund, 1839b:219.
Megalonyx gracilis Lund, 1839b:219 (nomen nudum).
Platyonyx bucklandi (Lund): Lund, 1842b:196.
Scelidotherium bucklandi (Lund): Lund, 1846:62.
Valgipes deformis Gervais, 1874:32.
Ocnopus laurillardi (Lund): Reinhardt, 1875b:219 (partim).
Catonyx giganteus Winge, 1915:144.
Scelidotherium (*Parascelidodon*) *giganteum* (Lund-Winge): Hoffstetter, 1952:105 (partim).
Scelidodon (*Valgipes*) *cuvieri* (Lund): Hoffstetter, 1952:105 (partim).
Scelidodon (*Catonyx*) *cuvieri* (Lund): Hoffstetter, 1954:759 (partim).
Ocnopus gracilis (Lund): Hoffstetter, 1954:756.
Catonyx cuvieri (Lund): McDonald, 1839b:205 (partim).

TABLE 1. Skull and mandible measurements in mm (* = estimated).

SKULL	VL	RH	RW	HM1	HM5	POCW	OCW	PWM1	PWM5
Valgipes bucklandi									
MCL 4262	381	90	66	117	130	95	91	17	38
MCL 4264	-	85	69	109	126	101	90	27	37
MCL 4294	400	86	80	101	118	110	95	25	34
MCL 4295	397	83	76	130	150	90	85*	24	37
Catonyx cuvieri									
MCL 4259	358	86	122*	100	110	89	92	29	42
MCL 4265	365	-	104*	107	106	76	83	27	35
MCL 4278	388	92	86	108	111	90	89	25	-
MCL 22681	344	109	75	105	133	80	104	24	40

MANDIBLE	VLS	WMS	HBm1	HBm4
Valgipes bucklandi				
MCL 4262	136	47	77	83
MCL 4264	-	-	66	77
MCL 4293	-	-	65	80
MCL 4294	120	50	-	-
MCL 22427	143	40	80	88
MCL 22429	-	46	78	85
Catonyx cuvieri				
MCL 22684	117	51	56	70
MCL 22685	116	47	58	77
[1]Winge	119	50	68	79

[1]Winge (1915: pl. 35), measurements taken from a cast.

Abbreviations: **HBm1**, height of mandibular body at m1; **HBm4**, height of mandibular body at m4; **HM1**, height at M1; **HM5**, height at M5; **OCW**, orbital constriction width; **POCW**, pre-orbital constriction width; **PWM1**, Minimal palatal width between M1; **PWM5**, Minimal palatal width between M5; **RH**, rostrum height; **RW**, rostrum width; **VL**, maximal ventral skull length; **VLS**, maximal ventral length of symphysis; **WMS**, width at midlength of symphysis.

Holotype—A holotype was not formally designated. Hoffstetter (1954) noted that the right dentary figured by Lund (1839c:pl. 10, fig. 3) is the type of the species.

Referred Material—MCL 4264, MCL 4293, and MCL 4294, nearly complete skeletons; MCL 4262, skull and right dentary including symphysis; MCL 22426, anterior half of skull; MCL 22428, posterior half of skull; MCL 22427 and MCL 22429, mandibles; also numerous postcranial remains, including vertebrae, ribs, scapulae, humeri, radii, ulnae, manus elements, pelvis, femur, tibia, fibula, pes elements, and osteoderms housed in MCL and listed below. Winge (1915) reported that although the remains of *V. bucklandi* collected by Lund from Lagoa Santa corresponded to 26 individuals, there was little representation of the skull, vertebrae, girdles, and forelimbs. This material is housed in ZMUC. The new material analyzed here therefore greatly improves our knowledge of this species.

TABLE 2. Dentition measurements in mm, mesiodistal length/vestibulolingual width. **Abbreviations**: **M/m**, molariform; **TRL**, toothrow length.

UPPER TEETH	M1	M2	M3	M4	M5	TRL
Valgipes bucklandi						
MCL 4262	22/14	20/26	20/27	17/25	14/21	109
MCL 4264	23/12	20/23	15/25	17/23	16/19	108
MCL 4293	25/12	13/26	16/27	17/23	20/13	111
MCL 22426	26/15	21/22	17/24	19/23	21/13	117
Catonyx cuvieri						
MCL 4259	24/14	15/24	16/29	14/25	18/11	94
MCL 4265	24/11	18/24	17/25	11/22	17/9	95
MCL 22681	25/12	18/22	15/20	14/19	18/10	112
MCL 22686	18/9	12/23	11/24	17/24	22/11	104

LOWER TEETH	m1	m2	m3	m4	TRL
Valgipes bucklandi					
MCL 4293	36/15	14/31	14/31	37/20	118
MCL 22427	39/17	13/30	15/30	43/20	129
MCL 22429	38/17	14/28	15/31	38/16	124
Catonyx cuvieri					
MCL 4260	-	12/21	11/23	35/17	-
MCL 22684	30/17	14/27	15/23	34/15	106
MCL 22685	32/16	11/24	10/23	38/15	113

Diagnosis—Body size, based on measurements of homologous skeletal elements (Tables 1–3), similar to that of *C. cuvieri*, but with more gracile and elongated limbs. Skull narrows anteriorly; palate anterior to molariforms longer but with smaller premaxillae than in *C. cuvieri*. Mandibular symphysis tends to be more dorsally projected than in *C. cuvieri* and mandibular condyle is dorsal to molariform occlusal plane. Upper molariforms clearly triangular in section except for M1, which may lack the distinct lingual sulcus present in the other molariforms. Humerus as in other Scelidotheriinae (except *C. cuvieri*), with entepicondylar foramen; radius and ulna more elongated, narrower, and curved compared with those of *C. cuvieri*; manual ungual phalanges curved and narrow, with digits 1–3 bearing claws, in contrast to wide and uncurved ungual phalanges of *C. cuvieri*. Femur parallelogram-shaped in anterior view, elongated as that of *C. cuvieri* but mediolaterally narrower; patellar facet and tibial facets discontinuous, continuous in *C. cuvieri*; tibia and fibula fused proximally and distally in adults, but not fused in *C. cuvieri*; calcaneal tuberosity dorsoplantarly slightly flattened, but wide and with the distinct lateral crest characteristic of the calcaneum of scelidotheriines; pes pentadactyl with rudimentary digits I and V; ungual phalanges of digits II–IV clawed, with that of digit III longest. Osteoderms present, probably absent in *C. cuvieri*.

Distribution and Age—Endemic species of intertropical Brazil, recorded from the states of Minas Gerais (Lagoa Santa region and São João das Missões), Bahia (Iraquara and Nova Redenção), and Piauí (Coronel José Dias). The associated fauna indicates a latest Pleistocene age.

TABLE 3. Postcranial measurements in mm (* = estimated, ** = juvenile).

HUMERUS	ML	PW	DW	WDAS
Valgipes bucklandi				
MCL 4294	446	145	206	122
MCL 22453	551	130	209	108
MCL 22455**	388	121	175	101
MCL 22464	437	128	2002	111
Catonyx cuvieri				
MCL 4250**	359	142*	191	106
MCL 4292	355	135	170	102
MCL 22751	388	135	184	105
MCL 22752	360	121	168	102
MCL 22753	383	151	188	110
MCL 22755	390	137	180	107

RADIUS	ML	PW	DW
Valgipes bucklandi			
MCL 4293	391	56	85
MCL 4294	388	58*	104*
MCL 22464	382	57	93
MCL 22470	390	60	95
Catonyx cuvieri			
MCL 4265	300*	53	95
MCL 4297	314	54	103
MCL 22761	295	47	89

ULNA	ML	PW	DW
Valgipes bucklandi			
MCL 4293	436	128	44
MCL 4294	421	127	52
MCL 22464	429	115	56
Catonyx cuvieri			
MCL 4265	374	107	70
MCL 22753	376	112	59
MCL 22766	360	99	56
MCL 22769	383	116	61

FEMUR	ML	PW	MWM	DW
Valgipes bucklandi				
MCL 4264	403	190	142	163
MCL 4293	450	194	138	212
MCL 4294	419	211	134	217
MCL 22495**	378	202	119	188
Catonyx cuvieri				
MCL 4265	406	220	189	244
MCL 4298	439	220	174	225
MCL 22771	386	190	141	190
MCL 22794	405	201	172	219

TIBIA-FIBULA	ML	PW	DW
Valgipes bucklandi			
MCL 4264	309	178	179
MCL 4293	345	180	176
Catonyx cuvieri			
MCL 4265	320	190	202
MCL 20791	335	210	184

CALCANEUM	ML	MPH	MPW	MHTC	PMTC
Valgipes bucklandi					
MCL 4264	207	90	110	95	154
MCL 4293	219	85	100	102	157
MCL 4294	220	101	-	102	166
MNHN 7384	200	-	-	-	145
Catonyx cuvieri					
MCL 4265	200	88	98	106	117
MCL 4267	220	88	103	107	111
MCL 22783	180	82	93	88	93
MCL 22794	200	87	93	109	127

Abbreviations: **DW**, distal width; **MHTC**, maximal height at tuber calcis; **ML**, maximal length; **MPH**, maximal proximal height; **MPW**, maximal proximal width; **MWM**, minimal width at midlength; **PMTC**, width of posterior margin of tuber calcis; **PW**, proximal width; **WDAS**, width across distal articular surface.

DESCRIPTION

Cranial Skeleton

Skull—Winge (1915) reported that cranial remains of *V. bucklandi* included only fragments of the maxilla and palate, allowing him to observe only that the premaxillae articulated with the maxillae, and that the length between M1 and the premaxilla was greater than in *C. cuvieri*. For this analysis, seven skulls of *C. cuvieri* and six of *V. bucklandi* were available (see Materials and Methods). Although the skulls of the two species are very similar in length (Table 1), the skull of *C. cuvieri* is more tubular and, in posterior view, relatively wider than high compared to *V. bucklandi*. In lateral view the posterior half of the skull of *V. bucklandi* is more convex dorsally than in *C. cuvieri*. Anteriorly the rostrum is tapered, unlike the condition in *C. cuvieri*, and the palatal margin is less convex (Fig. 1A, B).

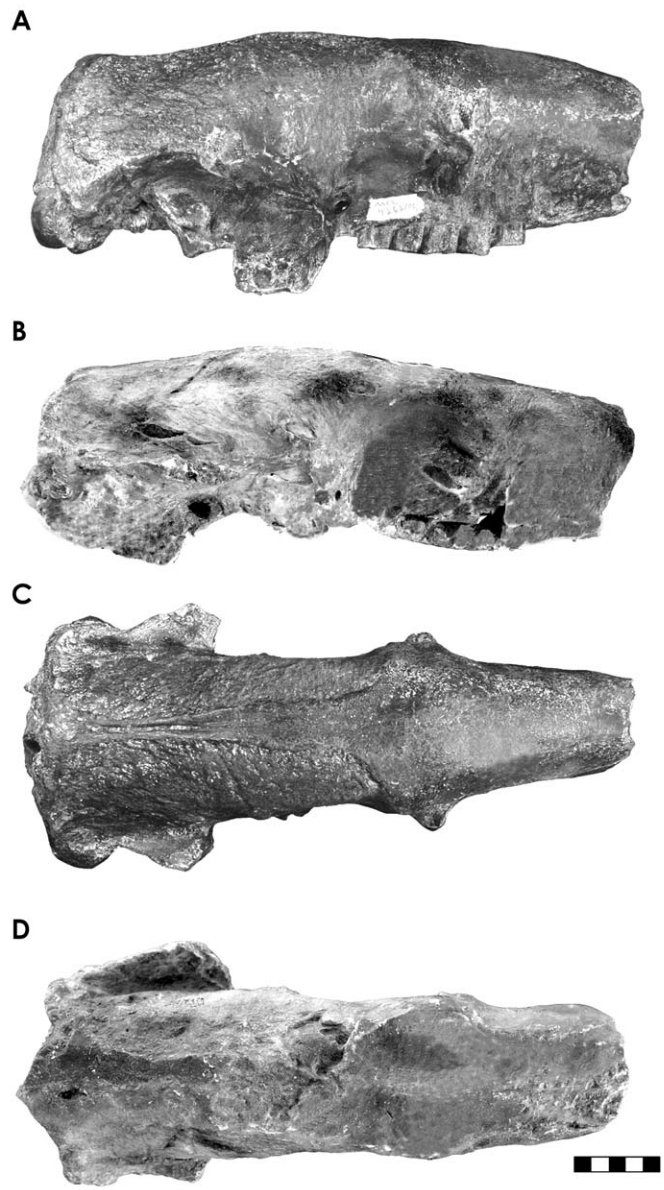

FIGURE 1. Skulls of scelidotheriines in right lateral (A–B) and dorsal (C–D) views. **A**, **C**, *Valgipes bucklandi*, MCL 4262/01; **B**, **D**, *Catonyx cuvieri* from Winge (1915:pl. 35). Scale bar equals 5 cm.

In dorsal view (Fig. 1C, D), the temporal lines are more robust in *V. bucklandi* than in *C. cuvieri*. The width across the pre- and the post-orbital constrictions are nearly equal in the latter species, whereas in *V. bucklandi* the pre-orbital constriction is more pronounced. The lateral walls of the rostrum converge anteriorly in *V. bucklandi*, but in *C. cuvieri* they diverge laterally from the constriction toward the anterior rostral margin. On the ventral surface of the skull, the palate is less longitudinally convex, the basicranium is wider and more convex, and the condyles are more robust in *V. bucklandi*.

There are differences between the species in the position of the cranial foramina on the lateral sphenoidal wall. In *C. cuvieri*, the anterior opening for the optic canal and the openings for the two sphenopalatine foramina are contained within a single depression, with the optic canal opening slightly posterodorsal to the sphenopalatine foramina. The opening of the combined orbital fissure and foramen rotundum lies approximately dorsal to the ventralmost extent of the pterygoid blade (i.e., the anterior edge of the pterygoid is well anterior to the opening).

In *V. bucklandi*, the openings for all these foramina are contained in a shallow depression, with the combined orbital fissure and foramen rotundum lying more anteriorly (approximately coincident with the level of the anterior edge of the pterygoid blade); the optic canal and sphenopalatine foramina are therefore much closer to the opening for the combined orbital fissure and foramen rotundum. This occurs even though the optic canal and sphenopalatine foramina are more anterior (much closer to the distal surface of M5) in *V. bucklandi*, than in *C. cuvieri*. Another difference is that in *V. bucklandi* the optic canal is more anterior as well, lying almost directly dorsal to the sphenopalatine foramina. Farther posteriorly, these differences mean that the distance between the combined orbital fissure and foramen rotundum and the foramen ovale is greater in *V. bucklandi* than *C. cuvieri*.

The premaxillae of MCL 4293 are very short, about equal in size to those of the nothrotheriid *Nothrotherium maquinense* (Lund) described by Cartelle and Bohórquez (1986), and half the length of those figured by Winge (1915:pl. 36, fig. 1) for *C. cuvieri*.

Mandible—Two nearly complete mandibles and four right dentaries of *V. bucklandi* and two mandibles and two dentaries of *C. cuvieri* are available for comparison. The mandibles of *V. bucklandi* and *C. cuvieri* are very similar morphologically (Fig. 2) and metrically (Table 1). The position of the posterior end of the ventral symphyseal margin relative to m1, used by McDonald (1987) to distinguish between various species of Scelidotheriinae, does not appear to be taxonomically significant in this case. In the six specimens of *V. bucklandi* for which this character is preserved, the position of the posterior end of the symphysis varies: it is anterior (MCL 4293 and MCL 4294), posterior (MCL 22429), or coincides with the mesial surface of m1 (MCL 4262, MCL 4264, and MCL 22427). The height of the mandibular body remains nearly constant in the alveolar region in *V. bucklandi*, whereas in *C. cuvieri* the body tapers anteriorly. Also, in *V. bucklandi* the ventral margin of the symphyseal region is more vertically oriented with respect to the alveolar margin of the body than in *C. cuvieri* (Fig. 2A, B).

McDonald and Perea (2002) noted that in *C. cuvieri* the mandibular condyle lies in the same plane as the occlusal surface of the molariforms. In *V. bucklandi*, as may be observed in Winge (1915:pl. 28, fig. 1; assigned to *C. giganteus*), the condyle lies dorsal to the occlusal plane, as is evident also in MCL 22427 and MCL 22429.

Dentition—The dental morphology in the specimens mentioned previously coincide with Winge's (1915) descriptions and figures for *C. giganteus* (= *V. bucklandi*). The differences between *V. bucklandi* (e.g., MCL 4262, MCL 4293, MCL 22.426) and *C. cuvieri* (MCL 4265, MCL 22681, and MCL 22686) are that cross-sections of M1–5 have less convex mesial margins, less concave distal margins, and less prominent lingual bilobation (a feature that diminishes from M2-M5) in *C. cuvieri* than in *V. bucklandi* (Fig. 2C, E, F). The teeth of these species are similar in size (Table 2).

Given the morphological similarity of the lower teeth of *C. cuvieri* and *V. bucklandi*, it is difficult to assign isolated lower teeth to one or the other species. A notable difference occurs in m1, the lingual surface of which is concave in *C. cuvieri*, but which bears a lobe on its central portion in *V. bucklandi* (Fig. 2 D, G).

Postcranial Skeleton

Osteoderms—Osteoderms have been recovered for some mylodontids, such as *Paramylodon harlani* (Owen, 1839b), *Mylodon darwini* Owen, 1839b, and *Mylodonopsis ibseni* Cartelle, 1991, but not for *Lestodon* Gervais, 1855 (Cartelle, 1992). Winge (1915:pl. 28, fig. 1) figured a right dentary of *C. giganteus* (= *V. bucklandi*) encrusted with numerous osteoderms that he attributed to this species. Several such osteoderms were recovered with MCL 4262 and MCL 4264, and hundreds with MCL 4293 and MCL 4294. These associations confirm Winge's assignment of the osteoderms to *V. bucklandi*. There are, in contrast, no records of osteoderms associated with the material of *C. cuvieri*, suggesting that osteoderms were not present in this species.

Vertebrae—The vertebral series is completely known from the several combined skeletons of *V. bucklandi*. The few slight differences between the vertebrae of this species and those of *C. cuvieri* render assignment of isolated elements to species difficult. Among the differences are that the transverse processes of the caudal vertebrae of *V. bucklandi* are more prominent, whereas the spinous processes of the thoracic vertebrae are more elongated and robust in *C. cuvieri*. Winge (1915) noted that the ribs of *V. bucklandi* are larger than those of *C. cuvieri*. This difference is not detectable in the present samples.

Scapula—In the scapula of *C. cuvieri* the coracoacromial bridge is more robust and projects more proximally and the glenoid cavity is narrower than in *V. bucklandi* (MCL 4294, MCL 22440, MCL 22441, MCL 22443, MCL 22446, and MCL 22464).

FIGURE 2. Right dentaries in lateral view (**A**, **B**) and occlusal outlines of dentition (**C**–**F**) of scelidotheriines. **A**, *Valgipes bucklandi*, MCL 4262/02; **B**, *Catonyx cuvieri*, from Winge (1915:pl. 35); **C**, *Valgipes bucklandi*, MCL 4293, upper right molariforms; **D**, *Valgipes bucklandi*, MCL 4293, left lower molariforms; **E**, *Valgipes bucklandi*, MCL 4262, right upper molariforms; **F**, *Catonyx cuvieri*, MCL 4265, right upper molariforms; **G**, *Catonyx cuvieri*, from Winge (1915:pl. 34, fig. 2), left lower molariforms. Scale bar equals 5 cm.

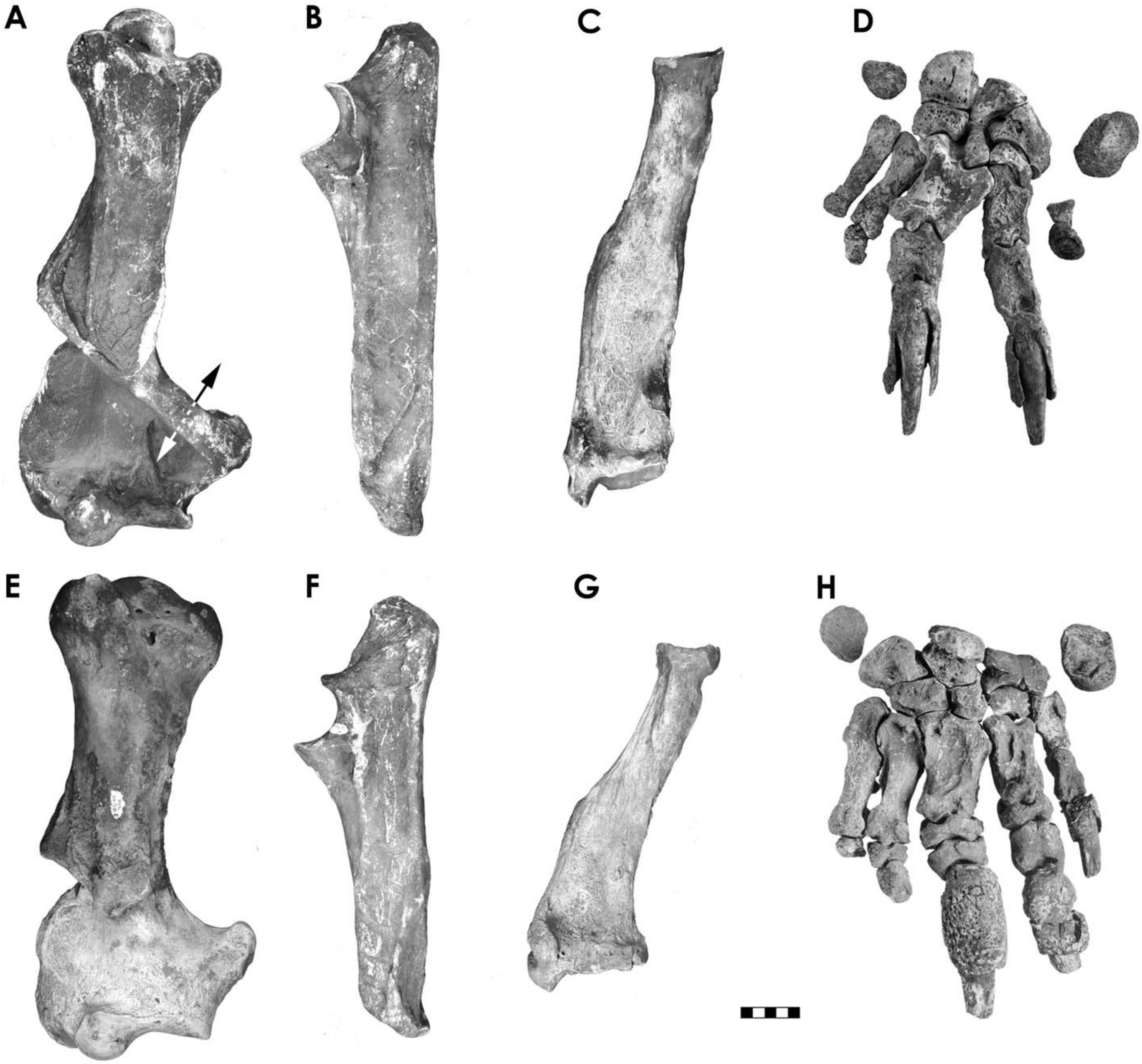

FIGURE 3. Upper limb elements of *Valgipes bucklandi* (above) and *Catonyx cuvieri* (below) including right humerus in anterior view (**A**, **E**), left ulna in lateral view (**B**, **F**), right radius in posterior view (**C**, **G**), and right manus in dorsal view (**D**, **H**). **A**, MCL 22453. Arrow shows path of entepicondylar foramen; **B**, MCL 22464; **C**, MCL 22470; **D**, MCL 4293. Mc I and the proximal phalanx are missing. Only the articular portion of the ungual phalanx is preserved; **E**, MCL 22751; **F**, MCL 22753; **G**, MCL 4297; **H**, from Winge (1915:pl. 34). Scale bar equals 5 cm.

Humerus—The ten available humeri of *C. cuvieri* lack an entepicondylar foramen, an absence that we consider diagnostic for this species. In contrast, each of the nine known humeri of *V. bucklandi* (two from MCL 4294, MCL 22445, and MCL 22464; one from MCL 22453, MCL 22454, and that figured by Winge (1915:pl. 30) possesses an entepicondylar foramen, as occurs in all other Scelidotheriinae. In the specimen figured by Winge (1915), the osseous bridge over the foramen is missing (Fig. 3A, E). Although there is overlap in size ranges, the humerus of *V. bucklandi* tends to be longer and more robust, particularly distally, than that of *C. cuvieri* (Table 3).

Radius and Ulna—The radius (thirteen are known: two from MCL 22464 and MCL 22470 and one from MCL 4293, MCL 4294, MCL 22461, MCL 22462, MCL 22465, MCL 22466, MCL 22467, MCL 22468, and MCL 22469) and ulna (six are known: two from MCL 22464 and one from MCL 4264 (partial), MCL 4293, MCL 4294, and MCL 22458 (partial)) of *V. bucklandi* are more elongated, curved, and narrower than those of *C. cuvieri* (five ulna and four radii) (Fig. 3B, C, F, G). The more elongated and narrow appearance may reflect a tendency toward greater length of these elements in *V. bucklandi* (Table 3). A notable difference is that the distal half of the radial shaft is more strongly deflected medially in C. cuvieri (Fig. 3C, G). Previously, only the distal epiphysis of the radius was known in *V. bucklandi* (Winge, 1915: pl. 30).

Manus—Nearly all elements of the manus (MCL 4293) of *V. bucklandi* (except Mc I and some sesamoids) and *C. cuvieri* are preserved (Fig. 3D, H). MCL 22493, belonging to *V. bucklandi*, includes the left and right manus missing the distal phalanges. The manus illustrated by Winge (1915:pl. 31, fig. 1) is incomplete and composite. In digits 1–3 the proximal and middle phalanges are fused. The ungual phalanges are narrow and gently curved palmarly, with that of digit 3 larger than of digit 2. In *C. cuvieri* the ungual phalanges are larger, nearly straight, with those of digits 2 and 3 almost equal in size. Furthermore, the proximal and middle phalanges of digit 3 remain separate. Among other differences, we note that the articular surfaces of Mc III for the magnum and unciform are separated in *V. bucklandi*, but contiguous in *C. cuvieri*. In the latter, the scaphoid and magnum contact each other via a single articulation, but two points of contact occur in *V. bucklandi* (Fig. 3D, H).

Femur—The femora of *V. bucklandi* (MCL 4264, MCL 4293, MCL 4294, MCL 22494 (juvenile), and MCL 22495 (juvenile)) are consistent with the morphology as figured by Winge (1915:pl. 32) (Fig. 4A). Compared with the femur of *C. cuvieri* (six are available for comparison), that of *V. bucklandi* has a more elongated parallelogram outline, a head that projects farther proximally and is more nearly hemispherical, and with a more prominent fovea for the round ligament (Fig. 4A, E). Another marked difference occurs distally, where the patellar trochlea is separated from the articular facets for the tibia. In *C. cuvieri* and other scelidotheriines, the patellar trochlea is contiguous with the facets for the tibia (Fig. 4B, F). Although femoral length is similar in these species, the femur tends to be wider in *C. cuvieri* (Table 3). The patella of *C. cuvieri* is thicker and wider than that of *V. bucklandi*.

Tibia-Fibula—Seven tibiae-fibulae of *V. bucklandi* are available: two for MCL 4264 and MCL 4293, one for MCL 4294 (incomplete), UFMG 94 (from a cave in the Lagoa Santa region), and the one figured by Lund (1846) and Winge (1915: pl. 32), which Reinhardt (1875) used as the holotype for *O. laurillardi*. Although similar in size (Table 3), in all the specimens of *V. bucklandi* the tibia and fibula are fused proximally and distally (Fig. 4C), whereas in *C. cuvieri* the two elements are not normally fused (Fig. 4G). The lateral malleolus is large and robust, whereas it is more medially projected and curved in *C. cuvieri*. Fusion is extensive, so that the interosseous region between the elements is smaller than in *C. cuvieri* when the elements of the latter are articulated (Fig. 4C, G).

As in other scelidotheriines and sloths in general, a cyamellar facet lies on the posteroproximal surface of the tibia near the margin of the lateral facet for the femur. The cyamella, the sesamoid of the tendon of the popliteal muscle, is preserved in MCL 4293 and is similar in size to the pisiform of the carpus.

Pes—The pes of *V. bucklandi* is well represented. MCL 4264 is missing only the cuboids and some phalanges. The right pes of MCL 4293 is almost complete, with the left lacking few elements (Fig. 4D). MCL 4294 preserves the calcaneum, astragalus, and Mt II and V. The calcaneum and both astragali of a very young individual (MCL 22500) are also preserved. There is thus no doubt about the morphology of the calcaneum of this species (Fig. 5A–G). These calcanea (two for MCL 4264, and one for MCL 4293, MCL 4294, and MCL 22500) are morphologically indistinct from that described and figured by Gervais (1874) and Hoffstetter (1954) as *V. deformis* (MNHN 7384, Fig. 5D–G). According to the latter, this calcaneum possesses marked peculiarities that led Ameghino (1889) to assign it erroneously to *Nothropus*, which was then considered a megalonychid. Hoffstetter (1954) concluded that it belonged to a Megalonychidae but that it could not be assigned to any of the already known subfamilies, and drew attention to the axe-shaped tuber calcis and the prominent crest that extends from the dorsal to plantar margins on the lateral surface of the tuber. A deep sulcus for passage of a tendon crosses the lateroplantar margin of the proximal end of the tuber (Fig. 5B). This region is broken (Fig. 5D, F) in MNHN 7384. Hoffstetter (1954) identified this calcaneum as megalonychid, despite noting that the prominent crest resembled that present in scelidotheriines and that the crest was not present in any other megalonychid species (Fig. 5 A, G).

The dorsal surface of the calcaneum bears a rounded articular surface, contiguous with the ectal facet, which according to Hoffstetter (1954:761) articulates "apparemment avec le péroné; on remarquera que ce dernier caractère le rend incompatible avec la tibia-péroné d'*Ocnopus*." This interpretation is incorrect. There is no contact here with the fibula. By articulating the calcaneum, astragalus, and tibia-fibula of MCL 4264 and 4293, we noted that the distance between the calcaneum and fibula precluded their contact, even though we tried to force the two together. The rounded articular surface, present in allthe available calcanea, could articulate only with a sesamoid. It is worth recalling (see above) that the tibia-fibula of *Ocnopus* to which Hoffstetter (1954) was referring is identical to all the tibiae-fibulae (of *V. bucklandi*) at our disposal.

Winge (1915) noted that the reason for the perceived extraordinary morphology of the calcaneum had to do with the fact that the proximal part and large portions of the internal [medial] surface were missing (Fig. 5D, G). He nonetheless recognized its scelidotheriine nature in assigning it to *S. magnum*. Unfortunately, Hoffstetter (1954) did not take Winge's observations into account.

Based on detailed comparison between a cast of the calcaneum on which Gervais (1874) erected *V. deformis* and the six calcanea of *V. bucklandi* at our disposal, it is clear that they are conspecific. The damage to the calcaneum (MNHN 7384) of *V. deformis* gives this (scelidotheriine) element the appearance of being megalonychid, and this is what induced Hoffstetter's error (Fig. 5D, E).

The astragalar morphology of *V. bucklandi* closely resembles that of *C. cuvieri*. Although several minor differences exist between these species (e.g., in the orientation of some articular facets), the deeply concave facets for the navicular and cuboid demonstrate the undoubted scelidotheriine nature of the astragalus.

All the pedal ungual phalanges of *V. bucklandi* are preserved in MCL 4293, and their description below also applies to those known for MCL 4264. Claws were borne on digits 2–4, as Winge (1915:pl. 33, fig. 1) noted (Fig. 4D). Most scelidotheriines possessed a large claw only on digit 3, as occurs in *C. cuvieri* (McDonald, 1987) (Fig. 4H). The pes elements figured by Winge (1915:pl. 33, fig. 1) are morphologically identical to those known for MCL 4264, MCL 4293, and MCL 4294 except for the calcaneum and Mt V. In our opinion, based on comparison with the material available to us, the pes figured by Winge is composite and the calcaneum and Mt V belong to *C. cuvieri*. For example, Mt V bears a proximolateral projection that does not occur in any of the elements of *V. bucklandi* at our disposal, but is present in those that we have of *C. cuvieri*. The Mt V figured by Winge (1915:pl. 33, fig. 2) is morphologically different from that figured by Winge (1915:pl. 33, fig. 1) as part of the composite pes. The former Mt V (in Winge's figure 2) does indeed belong to *V. bucklandi*. The calcaneum illustrated in Winge's figure 1 (of the composite pes) is the only scelidotheriine calcaneum collected by Lund. As may be observed in Hoffstetter (1954:fig. 3), a large part of the tuber is missing, which renders its assignment uncertain because the lateral crest, so characteristic of *V. bucklandi*, is not preserved, as Winge (1915) also noted. The element was collected from Lapa dos Tatus, a locality from which other elements of *C. cuvieri* were also recovered. We compared the calcaneum figured by Winge (1915:pl. 33, fig. 1) and Hoffstetter (1954:fig. 3) with that of *C. cuvieri* MCL 4267. The proportions of the latter are nearly identical to those of the slightly larger calcaneum figured by these authors.

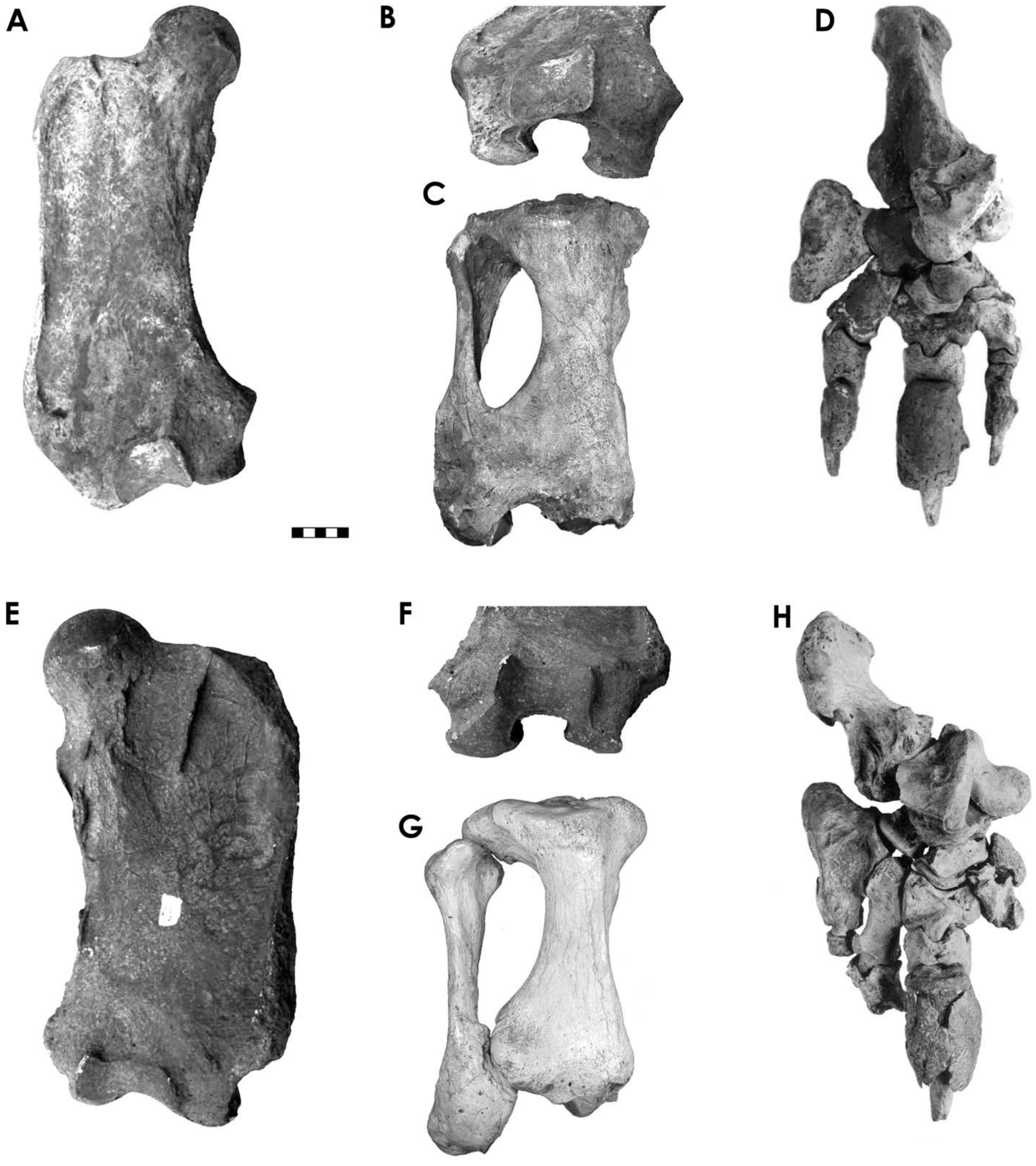

FIGURE 4. Lower limb elements of *Valgipes bucklandi* (above) and *Catonyx cuvieri* (below) including right femur in anterior view (**A**, **E**), distal extremity of right femur (**B**, **F**), right tibia-fibula in anterior view (**C**, **G**), and right pes in dorsal view (**D**, **H**). **A**, MCL 4293; **B**, MCL 4293, showing discontinuity of distal articular facets; **C**, MCL 4264; **D**, MCL 4293; **E**, MCL 4298 (reversed from the original left); **F**, MCL 4298, showing contiguous distal articular facets; **G**, MCL 4265; **H**, from Winge (1915:pl. 33, fig. 1). Scale bar equals 5 cm.

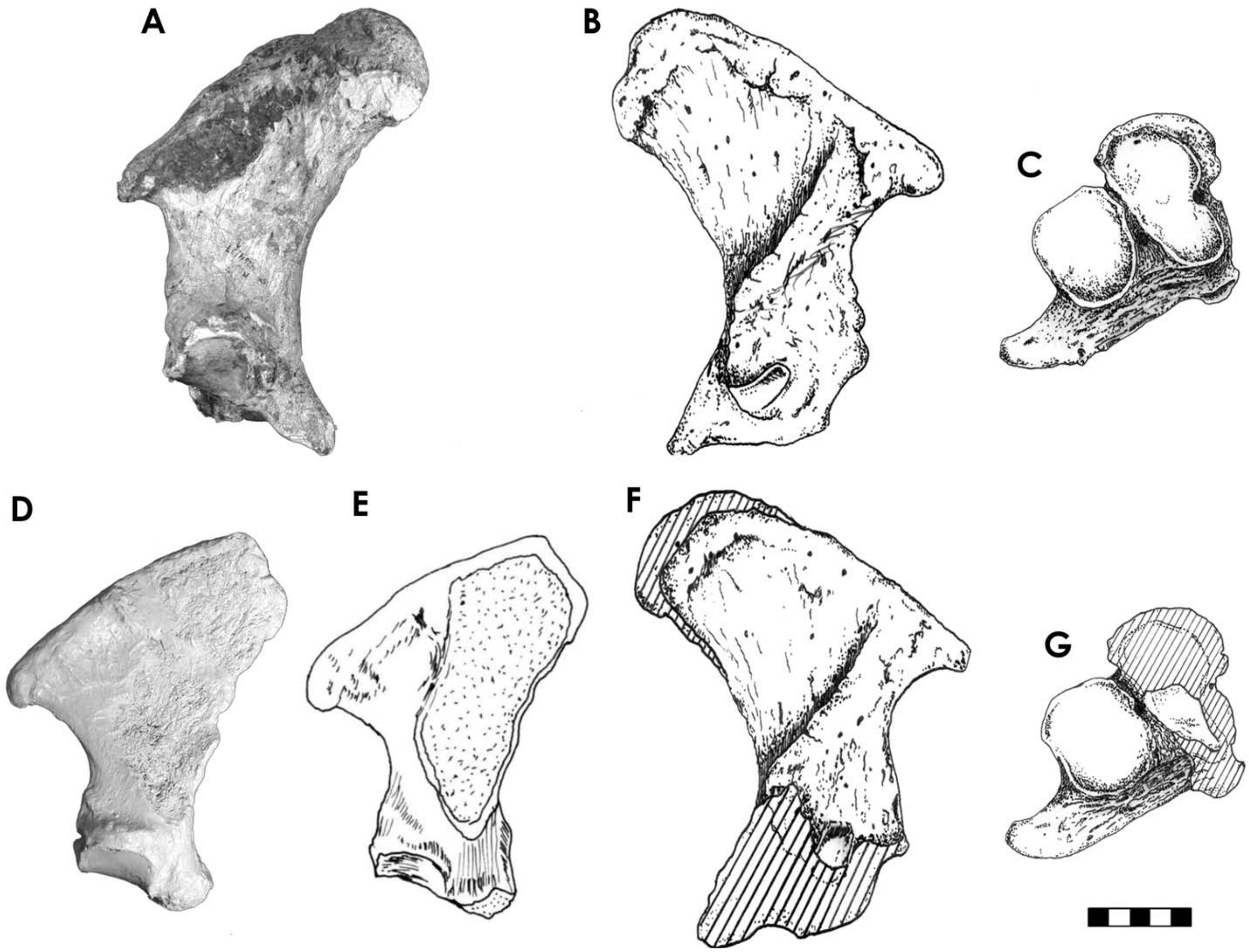

FIGURE 5. Right calcanea of *Valgipes bucklandi* including MCL 4264 (above) and MNHN 7384 (cast of holotype of *Valgipes deformis*, below). **A**, medial view; **B**, lateral view; **C**, proximal view; **D**, medial view; **E**, medial view reproduced from Hoffstetter (1954:fig. 4), with broken area stippled; **F**, lateral view, with cross-hatching indicating reconstructed portions; **G**, proximal view, with cross-hatching indicating reconstructed portions. Scale bar equals 5 cm.

DISCUSSION

The remains described here indicate the occurrence of two scelidotheriine species in intertropical Brazil during the Pleistocene, confirming the conclusions of Lund (1846) and Winge (1915). The species identified as *V. bucklandi* is undoubtedly a scelidotheriine, as shown by the morphology of the skull and dentition, as well as of the numerous postcranial remains, such as the manus (carpus) and pes (e.g., calcaneum, astragalus, cuboid and Mt III).

It is also apparent from our analysis that *V. bucklandi* should be considered generically distinct from *C. cuvieri*, based particularly on its upper dentition, postcranial morphology (Figs. 2–5), and phylogenetic position (see below; Fig. 6). Some of its elements caused several researchers to regard parts of this species as belonging to species of a different clade. In keeping with Paula Couto's (1973) reference to the taxonomy of Brazilian scelidotheres as a nomenclatural nightmare, it is difficult to determine the valid name for the species under consideration.

For the genus, it is clear that *Valgipes* Gervais, 1874 has priority over *Ocnopus* Reinhardt, 1875, given that the incomplete calcaneum, the holotype of Gervais' species, undoubtedly belongs to the species that Winge (1915) named *C. giganteus*, a synonym of Lund's (1846) *S. bucklandi*. Determination of the specific epithet is less straightforward.

Over several years, Lund (1839–1846) erected several poorly or insufficiently defined species that eventually fell as synonyms. Winge (1915), realizing the difficulties in choosing among Lund's names, opted for an incorrect solution: he decided on the first name given by Lund, *Myrmecophaga gigantea*. However, this name is clearly a nomen nudum because it is not accompanied by a description or a figure. One of the justifications that Winge (1915) cited for deciding on *giganteus* was that *bucklandi* was a barbaric name.

Hoffstetter (1954) proceeded on the mistaken assumption that only one scelidotheriine species was represented by the remains collected by Lund from Lagoa Santa. This author chose the specific epithet *gracilis* because the name *bucklandi* had been applied to a dentary that was scelidotheriine; in other words, he regarded it as a synonym of *C. cuvieri* (see above). We have demonstrated that this assumption is incorrect. The skull, dentition, and postcranial remains are clearly scelidotheriine

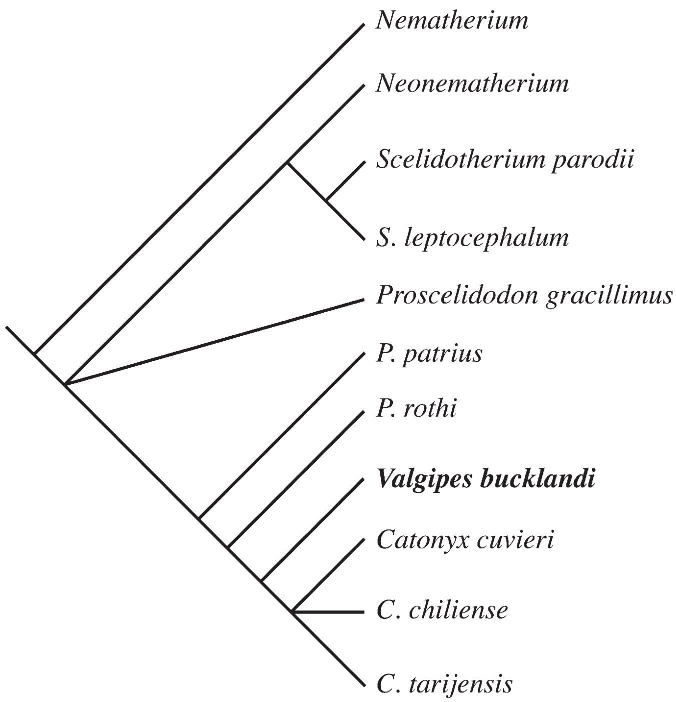

FIGURE 6. Strict consensus tree produced from two most parsimonious trees showing relationships among Scelidotheriinae.

(Figs. 1–5), even though some elements are somewhat reminiscent of megalonychid morphology.

Our solution on the correct specific epithet (*giganteus*, *gracilis*, or *bucklandi*) is to follow the International Code of Zoological Nomenclature (1999). In accordance with Article 24.2.1, we consider Lund to be his own first or, perhaps more appropriately, continued reviser. Rather than accepting his initial opinion, as many have done, it is necessary to consider his final word on the subject; a perfectly acceptable option. We may summarize the stages in Lund's self-correction process as follows:

(1) Lund (1839b,c). Among the limited material he had so far recovered, Lund noted three ground sloth species including *M. bucklandi*, which he based on a right dentary with m4 (ZMUC 526) and described as being about the size of a tapir. The three species were considered megalonychids. There is thus an illustration (dentary; Lund, 1839b) and even an attempt at diagnosis (size).

(2) Lund (1840a). In discussing the species *M. gracilis*, he stated "I now know in more detail one of the forms, *M. bucklandi*, noted in an earlier paper" (as quoted by Paula Couto, 1950:219; translated from Paula Couto's Portuguese). He was referring here to Lund (1839c). Lund (1840a) figured and thus continued to recognize *M. bucklandi*.

(3) Lund (1840b). In this work (written after publication of 1840a) he changed the genus from *Megalonyx* to *Platyonyx*. He eliminated *M. gracilis* from the extinct species from Lagoa Santa, but maintained *Platyonyx bucklandi*.

(4) Lund (1846). He arrived at the conclusion that there were two scelidotheriine species at Lagoa Santa: *Scelidotherium owenii* (that Winge (1915) would identify as *S. magnum*) and *Scelidotherium bucklandi* (which Winge (1915) would identify as *C. giganteus* and Hoffstetter (1954) as *O. gracilis*). Lund provided clear diagnostic figures of the two species. *S. bucklandi* is the only species he maintained throughout all the publications listed here.

It thus seems clear that: (1) despite the uncertainties related to the identification of species, Lund maintained one specific name, *S. bucklandi*, as valid; and (2) this species came to be defined gradually, so that although its first determination might be considered doubtful (as it was based on a juvenile jaw, even though such a specimen is technically acceptable; see Cartelle and De Iuliis, 1995), Lund's further work on this species leaves no doubt of its validity and provides sufficiently diagnostic characters based on several skeletal elements (e.g., left Mc III, right Mc IV, left Mt III–V, right Mt IV, right tibia-fibula).

Lund's (1846) effect as reviser is clear. He affirmed that there are two scelidotheriine species that can be differentiated on features of the manus, pes, and ribs. He also noted changes in ontogenetic stages and stated that he had erred in erecting the genus *Sphenodon* on juvenile teeth. Further, in this final work, he made no mention of megalonychids among his findings at Lagoa Santa. It is notable that Lund (1846), in his last scientific publication, illustrated a scapula of *S. owenii* and a tibia-fibula of *S. bucklandi*, as though emphasizing that the longstanding uncertainty over these two species had been resolved.

In conclusion, the solution supplied by Lund (1846) rectifies the nomenclatural nightmare, is preferable to the proposals of later researchers, and justifies the new combination proposed here: *V. bucklandi*. The specific epithet is in homage to William Buckland, from whom Lund adopted the concept of the diluvium, an idea that was very important to him. The name *S. owenii* is not valid, given that the epithet *cuvieri* has priority. Lund, therefore, should not have altered this species' name, and *cuvieri* is the one that should be maintained.

From the descriptions above, it is clear that two scelidotheriine species existed in intertropical Brazil, and that they may be distinguished on cranial, dental, and postcranial features. The postcranial skeleton of *V. bucklandi* includes elements that Hoffstetter (1954) erroneously considered as belonging to a megalonychid, such as the calcaneum of Gervais' (1874) *V. deformis*.

We corroborate Winge's (1915) conclusion, as opposed to Hoffstetter's (1954), that the material recovered by Lund from Lagoa Santa represents two scelidothere species: *C. cuvieri* (following McDonald (1987) for the valid generic name) and *V. bucklandi*. These species are strongly similar in form of the lower dentition, but their marked differences in several aspects support their generic and specific separation, as Winge (1915) argued. There are no characteristics diagnostic of Megalonychidae to support Hoffstetter's (1954) contention that the postcranial skeleton of *C. giganteus* belongs to a megalonychid. Winge's (1915) observations on the scelidotheriine nature of these postcranial remains are correct. Among these elements, the humerus (Fig. 3A), femur (Fig. 4A), astragalus and cuboid are undoubtedly scelidotheriine.

V. bucklandi is clearly distinct from *C. cuvieri* and exhibits a mosaic of plesiomorphic (e.g., number and form of the digits and phalanges, humerus with an entepicondylar foramen (lacking in *C. cuvieri*), and metapodial morphology) and derived (e.g., form of the dentition, distal articular facets of the femur, fusion of the tibia and fibula, calcaneal morphology) characters. The fact that fusion occurs in all adult tibiae-fibulae known for *V. bucklandi* indicates that it is a diagnostic character rather than, as suggested by Hoffstetter (1954), a pathological condition.

Although there are some superficial resemblances to megalonychids, *V. bucklandi* is clearly scelidotheriine in form of the dentition, skull and mandible, humerus, distal part of the tibia-fibula, calcaneum as well as other parts of the manus and pes, vertebrae, and scapula. McDonald's (1987:163) view that "the concave cuboid surface of the scelidothere astragalus and that of *Ocnopus*. . ..to be convergent" cannot be maintained because *Ocnopus* (= *V. bucklandi*) is not a megalonychid.

Guérin and Faure (2004) recently described the species *Scelidodon piauiense* from the state of Piauí, Brazil, based on skull, mandibular, and humeral remains. The morphology and measurements given for this proposed species are nearly identical to those described here for *V. bucklandi*, as well as to those figured by Winge (1915), which were not considered by Guérin and Faure (2004). These authors also noted the presence of osteoderms from the locality from which the remains were discovered, but did not attribute them to their species. Such osteoderms are present in *V. bucklandi*, however, as noted above. It is clear from the morphology and size of the remains that *S. piauiense* is a junior synonym of *V. bucklandi*. This occurrence expands the known distribution of *V. bucklandi*, which extended from Minas Gerais to Piauí.

PHYLOGENETIC POSITION OF *V. BUCKLANDI* AMONG SCELIDOTHERIINAE

The phylogenetic position of *V. bucklandi* among Scelidotheriinae was analyzed based on the 27 characters used by McDonald and Perea (2002: appendix 1) for their analysis of relationships among 10 scelidotheriines. The character states for these taxa and *V. bucklandi* are presented in Appendix 1. Following McDonald and Perea (2002), *Nematherium* Ameghino, 1887 was utilized as the outgroup. The analysis was conducted using PAUP 4.0b 10 (Swofford, 2002) as an exhaustive search with the outgroup method and optimality criterion for maximum parsimony and equal weighting of characters. Of the 27 characters, 22 were phylogenetically informative. The strict consensus tree (Figure 6), produced from two most parsimonious trees (Tree Length = 44, Consistency Index = 0.614, Retention Index = 0.685, and Rescaled Consistency Index = 0.420) shows that *V. bucklandi* falls between *Proscelidodon rothi* Ameghino, 1908 and *Catonyx* as the sister group to *Catonyx*, which helps validate its recognition as a distinct genus. All other relationships are as in McDonald and Perea (2002).

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APPENDIX 1. Character-taxon matrix for scelidotheriine phylogenetic analysis.

	5	10	15	20	25	27
Nematherium	000??	00000	01000	00000	00000	00
Neonematherium	110??	0101?	0????	?0101	1?100	00
Proscelidodon gracillimus	00000	01010	00000	00011	0111?	?0
P. patrius	01000	00110	01001	00111	01110	?0
P. rothi	01000	10101	0000?	?1?11	01110	?0
Scelidotherium parodii	10111	00100	10110	01101	11110	?1
S. leptocephalum	10111	00100	10110	01101	11110	11
Catonyx cuvieri	01011	11111	01001	10111	01111	00
C. chiliense	01011	11111	01001	10101	01110	00
C. tarijense	01011	11111	01001	10111	01110	00
Valgipes bucklandi	11111	11111	00001	10011	01110	00