The oldest fossil record of the extant penguin genus \textit{Spheniscus}—a new species from the Miocene of Peru

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Described here is a partial postcranial skeleton and additional disarticulated but associated bones of the new fossil penguin \textit{Spheniscus muizoni} sp. nov. from the latest middle/earliest late Miocene (11–13 Ma) locality of Cerro la Bruja in the Pisco Formation, Peru. This fossil species can be attributed to the extant genus \textit{Spheniscus} by postcranial morphology and is the oldest known record of this genus. \textit{Spheniscus muizoni} sp. nov. is about the size of the extant Jackass and Magellanic penguins (\textit{Spheniscus demersus} and \textit{Spheniscus magellanicus}). Beside \textit{Spheniscus urbinai} and \textit{Spheniscus megaramphus} it is the third species of \textit{Spheniscus} represented in the Pisco Formation. This study contains morphological comparisons with Tertiary penguins of South America and with most of the extant penguin species.

Key words: Spheniscidae, Pisco Formation, Miocene, Peru.

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Introduction

The fossil record of penguins in South America comes from both Atlantic and Pacific coasts and is restricted to findings in Argentina, Chile, and Peru; their stratigraphic distribution ranges from the late Eocene–early Oligocene (Acosta Hospitalche 2005) to the late Pliocene (Emslie and Correa 2003). Most of the described fossil species come from the early Miocene of Patagonia, Argentina (see Ameghino 1891, 1895, 1899, 1901, 1905, 1920; Moreno and Mercerat 1891; Simpson 1972, 1975a). Recently, the South American fossil penguins have been taxonomically revised (e.g., Acosta Hospitalche et al. 2005) to the late Pliocene (Emslie and Correa 2003). The following taxa are known from Peru: a Spheniscidae indet. (late Eocene–early Oligocene, Otuma Formation), \textit{Palaeospheniscus} sp. (lower middle Miocene, Chilcatay Formation), \textit{Spheniscus urbinai} Stucchi, 2002 and \textit{S. megaramphus} Stucchi, Urbina, and Giraldo, 2003 (both from the upper Miocene–lower Pliocene of the Pisco Formation).

Thus, findings of fossil representatives of the extant penguin genus \textit{Spheniscus} are restricted to Peru and Chile and have been known from the late Miocene to late Pliocene hitherto. For the Pisco Formation of Peru, Noriega and Tambussi (1989) and Cheneval (1993) already mentioned probable new taxa of Spheniscidae, but did not name them; recently they have been described by Stucchi (2002) and Stucchi et al. (2003) as \textit{Spheniscus urbinai} from different sites of late Miocene to early Pliocene age and as \textit{S. megaramphus} from the upper Miocene of the Montemar locality. In Chile, fossils of \textit{Spheniscus} are described as cf. \textit{Spheniscus} by Walsh and Hume (2001) from the middle Miocene–lower Pliocene Bahía Inglesa Formation and as \textit{S. chilensis} Emslie and Correa, 2003 from the late Pliocene (Mejillones Formation) of Cuenca del Tiburón, Península de Mejillones.

Herein a new fossil species of \textit{Spheniscus} is described again from the Pisco Formation in Peru, but coming from older deposits at the Cerro la Bruja locality of latest middle/earliest late Miocene (11–13 Ma) age.
Institutional abbreviations.—LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; MNHN, Muséum National d’Histoire Naturelle, Paris, France; SAPM, Staatsammlung für Anthropologie und Paläoanatomie, Munich, Germany; UCBL, Université Claude Bernard, Lyon 1, France; UF, University of Florida, Florida Museum of Natural History, USA.

Geological setting

The locality of Cerro la Bruja, Department of Ica, is situated in the marine Pisco Formation (Fig. 1). The age of the Pisco Formation ranges from the middle Miocene to early Pliocene (Muizon and DeVries 1985). The deposit of Cerro la Bruja is dated on biostratigraphic data to be of latest middle Miocene to earliest late Miocene age (13–11 Ma; Muizon 1988), and therefore represents the oldest deposit within the Pisco Formation.

The Pisco Formation corresponds to a marine transgression along the southern coast of Peru during the Neogene and is known for its abundant marine vertebrate fauna. Its geology and palaeoecology in the Sacaco area were studied by Muizon and DeVries (1985). The marine bird fauna is one of the richest known from the Neogene of South America. Beside Cerro la Bruja other fossil penguin bearing localities in the Pisco Formation are: El Jahuay (ELJ), ca. 9 Ma, late Miocene; Aguada de Lomas (AGL), ca. 7–8 Ma (Muizon et al. 2003), late Miocene; Montemar (MTM), ca. 6 Ma, late Miocene; Sacaco Sud (SAS), ca. 5 Ma, early Pliocene; Sacaco (SAO), ca. 3.5 Ma, early Pliocene ( datings from Muizon 1984, 1988; Muizon and DeVries 1985). For additional vertebrate faunas see Conclusions.

Material and methods

The osteological terminology used here follows Baumel et al. (1993) but terms are translated into English. Measurements were taken after von den Driesch (1976) and Stephan (1979). For metrical comparisons, using published data, it has to be considered that different authors (e.g., Simpson 1946, 1975b, 1979a, b), had slightly deviating ways of measuring the greatest lengths of some limb bones; often they measured the functional lengths, taking recessed points or sulci between condyles (e.g., for femur, distal tibiotarsus, distal tarsometatarsus) as landmarks. However, the differences in the values are never more than a few mm.

The penguin material of Cerro la Bruja described here comes from excavations of Christian de Muizon and belongs to MNHN, but is temporarily housed in the collections of UCBL. For morphological comparisons with the fossil Chilean species, Spheniscus chilensis, parts of the paratype material (UF 143295, 143299, 144112, 144134, 144148, 144149, 144154, 144168, 144169) were at disposal by loan. Morphological comparisons with extant penguins are based on following specimens provided by the collections of SAPM and UCBL: Spheniscus humboldti (SAPM 5 ♂, 12 ♀; UCBL 25588), S. demersus (SAPM 12 ♂, 13 ♀), S. magellanicus (SAPM 8 ♂, 9 ♀), Eudyptes chrysochome (junior synonym E. crestatus), (SAPM 6 ♂, 5 ♀), E. chrysolophus (SAPM 1 ♂), Aptenodytes patagonicus (SAPM 6 ♂, 8 ♀), Pygoscelis papua (SAPM 12 ♂, 3 ♀), and Py. adeliae (UCBL XII 1978). Metric data of extant penguin species were acquired on the aforementioned specimens as well as additional material from the SAPM. Measurements of S. mendiculus are based on specimens at the LACM and were provided by Kenneth Campbell.

Systematic palaeontology

Sphenisciformes Sharpe, 1891
Spheniscidae Bonaparte, 1831
Genus Spheniscus Moehring, 1758
Type species: Spheniscus demersus (Linnaeus, 1758).

Remarks.—Based on the following osteological features the postcranial penguin material of Cerro la Bruja, presented here, can be affiliated to Spheniscus on generic level.

Humerus with humeral head barely swollen proximally (more swollen in Aptenodytes, Pygoscelis, and Eudyptes), proximal outline of humerus without proximal notch between
dorsal tubercle and the head (notched in Aptenodytes, Pygoscelis, and Eudyptes, slightly notched in Palaeospheniscus); bipartite pneumatic fossa with a deep cranial fossa (non-bipartite in Paraptenodytes and Arthropytes); proximal border of pneumatic fossa in ventral view straight and almost horizontally (proximally concave in Apytenodytes and Eudyptes); caudal-most process of the ventral epicondyle hardly surpassing ventral margin ofdistal humerus shaft (in cranial/caudal view; clearly surpassing in Aptenodytes and Pygoscelis). Coarcoindic probably closed supracoracoid foramen(openin Pygoscelis,Eudyptula, and Apytenodytes and probably in Palaeospheniscus). Femoral head and trochanter proximally at same level (trochanter higher in Eudyptes, Pygoscelis, and Apytenodytes). Tarsometatarsus quite elongate, with an elongation index (maximal length/proximal width) of 2.07, thus smaller than in Palaeospheniscus (elongation index: 2.2–2.4); extensor sulci long and deep (shallower in Eudyptes, Pygoscelis, and Apytenodytes); trochlea II and trochlea IV of about same length distally (unlike in Palaeospheniscus, Eudyptes, Pygoscelis, and Apytenodytes, where trochlea IV is somewhat shorter than trochlea II); the position and arrangement of the two proximal vascular foramina and of the very pronounced impressions of the extensor retinaculum corresponds best with Spheniscus; lateral intertrocchlear incision deeper incised proximally than medial one.

Spheniscus muizoni sp. nov.

Figs. 2, 3, 4A, C, E, G, I, 5A.

Holotype: Partial postcranial skeleton MNHN PPI 147: subcomplete left and right coracoid (147a); cranial end of left and subcomplete right scapula (147b); subcomplete left and right humerus (147c); left complete ulna (147d); proximal and distal end of right femur (147e); complete right and proximal end of left tibiartarsus (147f); proximal end of left fibula (147g); right complete tarsometatarsus (147h), cranial portion of sternum with articular sulcus for coracoid and fragment of the cranialateral process (147i); two fragmentary thoracic vertebrae (147j) from the caudal region; seven caudal vertebrae (147k); fragmentary synsacrum (147l);

Paratypes: Additional isolated bones from the type locality (MNHN PPI 148–153): distal fragmentary half of left coracoid, worn (148); right subcomplete coracoid (153); left complete ulna (149); left complete radius (150); right complete carpometacarpus (154); distal end of right femur (151); cranial end of pyostyle (152); rib fragment without ends (153).

Derivation of the name: Named after Christian de Muizon (MNHN) who collected the studied material and graciously placed it at my disposal; and in recognition of his efforts and paleontological investigations on the vertebrate fauna of the Pisco Formation in Peru.

Type locality and horizon: Cerro la Bruja, Department of Ica, Peru; Pisco Formation, latest middle/earliest late Miocene, ca. 13–11 Ma (Muizon 1988).

Diagnosis.—Small-sized fossil Spheniscidae; similar in size to extant Spheniscus magellanicus (Forster, 1781) and S. demersus (Linnaeus, 1758), slightly smaller than S. humboldti Meyen, 1834, but larger than S. mendiculus Sundevall, 1871. Distinctly smaller than the fossil species S. urbinai and S. megaramphus, but of similar size to S. chilensis (Tables 1, 2 and Fig. 6).

Carpometacarpus with distinct step between the proximal carpal trochlea and the extensor process of the alular metacarpal (step weaker or absent in extant species of Spheniscus), an almost complete fusion of proximal alular digit with the major metacarpal (fusion less advanced in S. chilensis), and an open spation without ossified synchondroses (unlike S. chilensis with synchondroses).

Humerus with humeral head barely swollen proximally, proximal outline without proximal notch between dorsal tuberculum and the head, but proximal outline less steep (in caudal view) than in all compared extant species of Spheniscus; proximal border of pneumatic fossa forms no ventrocaudally projecting lip, a feature shared with S. urbinai and S. chilensis, but unlike in extant species of Spheniscus and Pygoscelis; proximal border of pneumatic fossa in ventral view straight and almost horizontally like in extant Spheniscus species (unlike in S. chilensis, S. urbinai, Dege hendeyi, and extant species of Apytenodytes and Eudyptes where it is proximally concave); distinct concave indentation of bicpital crest between ventral tuberculum and shaft, but which is absent in S. chilensis; preaxial angle situated more proximally than in other penguin taxas, at about mid of shaft length; caudal-most tip at the ventral epicondylus (process-like crest caudally bordering the humerotricipital sulcus) slightly oriented upwards (ventroproximally); cranial-most tip at ventral epicondylus (process-like crest caudally bordering the scapulotricipital sulcus) projecting ventrodistally somewhat longer and oriented slightly more distally than in S. chilensis.

Femoral head and trochanter at about the same level proximally; medial condyle cranially very low and hardly projecting (unlike in all other compared extant and fossil penguins), lateral condyle prominent and reaching further proximally than medial one.

Tibiotarsus characterized by its straight (not mediadally deflected) and relatively narrow (in cranial/caudal view) distal end; distinct and deep mediad impression of the medial collateral ligament situated mediadally on proximal end.

Tarsometatarsus quite elongate and slender; proximal end relatively narrow; elongation index (2.07) higher than in S. urbinai, but smaller than in Palaeospheniscus; extensor sulci long and deep; extremely deep dorsal infracotylar fossa; proximal vascular foramina on different level (same level in Palaeospheniscus), medial proximal vascular foramina small and situated very proximomedially; hypotarsus with medial hypotarsal crest oriented medioplantarly and bent medially; medial hypotarsal crest divided in two crests, with lateral one being very weak, thin, and shorter; lateral hypotarsal crest blunt and low; lateral intertrocchlear incision longer proximally than medial one; trochlea II and IV of about same length distally (unlike in Palaeospheniscus); lateral condyle of trochlea III (in distal view) at same level dorsally as trochlea IV (plantarily recessed in extant Spheniscus and S. chilensis); lateral and medial condyle of trochlea III (in distal view) dorsally at about same (medial one dorsally more swollen in extant Spheniscus and S. urbinai); trochlea...
II oriented somewhat obliquely; lateral condyle of trochlea IV (in distal view) plantarly tapering.

**Description and comparisons**

**Remarks.**—For measurements of *Spheniscus muizoni* sp. nov. see Table 1. The material represents bones of at least two individuals. None of the bones provides any indication that the studied individuals of the new species are juveniles. No cranial material is preserved; for this reason comparisons with *S. megaramphus* are impossible, which is only known by its skull and mandible. However, *S. muizoni* sp. nov. is distinctly smaller than both *S. megaramphus* and *S. urbinai* (Fig. 6). In the following, comparisons are priorly made with both extant and fossil species of *Spheniscus*, but also with extant taxa, with fossil South American taxa (*Palaeosphe−

**Table 1. Measurements of *Spheniscus muizoni* sp. nov. from Cerro la Bruja in the Pisco Formation; n, number of specimens; parentheses indicate estimated values.**

<table>
<thead>
<tr>
<th>Skeletal elements and measured sections</th>
<th>Measurements (mm)</th>
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<tr>
<td>scapula</td>
<td>greatest length</td>
<td>–</td>
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<tr>
<td></td>
<td>maximal diagonalcranial end</td>
<td>20.4</td>
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<td>smallest width of neck</td>
<td>10.9</td>
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<td>coracoid</td>
<td>greatest length (medial)</td>
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<tr>
<td></td>
<td>length, lateral</td>
<td>76.3</td>
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<tr>
<td></td>
<td>width, distal</td>
<td>23.9</td>
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<td></td>
<td>width of distal facies</td>
<td>23.7</td>
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<tr>
<td></td>
<td>smallest width of shaft, including foramen nervi supracoracoidei</td>
<td>11.9–14.4</td>
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<tr>
<td>humerus</td>
<td>greatest length including ventral epicondylus</td>
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<td>length (from head to condylus ventralis)</td>
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<td>greatest width of proximal end</td>
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<td>15.0–15.6</td>
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<td></td>
<td>smallest width of shaft</td>
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<tr>
<td></td>
<td>greatest diagonal width of distal end</td>
<td>24.0</td>
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<td>ulna</td>
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<td></td>
<td>depth of proximal facies articulareis</td>
<td>(7.1)</td>
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<tr>
<td></td>
<td>greatest width of shaft</td>
<td>17.7</td>
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<td></td>
<td>greatest diagonal of distal end</td>
<td>7.1–8.2</td>
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<tr>
<td>radius</td>
<td>greatest length</td>
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<td>depth of proximal facies articulareis</td>
<td>5.6</td>
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<tr>
<td></td>
<td>width of proximal end</td>
<td>(8.1)</td>
</tr>
<tr>
<td></td>
<td>greatest width of shaft</td>
<td>11.6</td>
</tr>
<tr>
<td></td>
<td>diagonal of distal facies articulareis</td>
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<td>carpometacarpus</td>
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<tr>
<td></td>
<td>diagonal width of distal facies articulareis</td>
<td>12.5</td>
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Dege, Inguza, and ?Palaeosphe−

**Scapula** (Fig. 2A).—Two fragmentary scapulae, a cranial end of a left scapula and a damaged cranial half of a right scapula, lacking most of the cranial end, are preserved (MNHN PPI 147b1–2). In cranial view, the cranial end is mediolaterally narrow; specifically the ventral part is slightly narrower than in *S. humboldti* and *S. demersus*, and more closely resembling *S. magellanicus*. The coracoid tubercle is elliptical and also mediolaterally narrow. The acromion is broken off in both specimens (which is of different length and direction within extant genera). Medially on the cranial end, a distinct but low crest runs from the acromion diagonally ventrocaudally to below the coracoid tubercle; such a distinct crest could not be observed in any of the compared...
extant penguin taxa. The glenoid process is mediiodistally oblate. The medial articular facet for the coracoid on the glenoid process is bordered medially and ventrally by a weak edge. The collum is quite mediolaterally flattened; the ventral margin of the scapular blade carries a little projection about 20 mm caudally the cranial end.

Coracoid (Fig. 2F).—Fragmentary left and right coracoid of the partial skeleton (MNHN PPI 147a/1-2) and a distal fragmentary half of a worn left coracoid (MNHN PPI 148) are present. The left coracoid lacks the procoracoid process and the lateral angle of the distal end, the right one lacks the proximal end. The coracoid corresponds well with the morphology of the extant species of Spheniscus and of S. urbinai and S. chilensis. The acrocoracoid process is long and angled rectangular to the bone; its distal margin is almost straight in dorsal/ventral view. In proximal view, the ventral inflexion of the procoracoid process is a little less close than in the extant species of Spheniscus. The scapular cotyla is round and relatively large; the articular facet for the humerus is oval and flat and not well defined. Despite the procoracoid process is lacking in both specimens, the fracture at the right coracoid

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Fig. 2. Spheniscid penguin Spheniscus muizoni sp. nov. from Cerro la Bruja, latest middle/earliest late Miocene, Pisco Formation, Peru. A. Left scapula (MNHN PPI 147b) cranial end, in medial (A1) and lateral (A2) views. B. Left ulna (MNHN PPI 147d), in ventral (B1) and dorsal (B2) views. C. Left humerus (MNHN PPI 147c), in caudal (C1), cranial (C2), and distal (C3) views. D. Left radius (MNHN PPI 150), in dorsal (D1) and ventral (D2) views. E. Cranial portion of sternum (MNHN PPI 147i), in cranial (E1) and ventral (E2) views. F. Left coracoid (MNHN PPI 147a), in ventral (F1), ventrolateral (F2), and dorsal (F3) views. G. Right carpometacarpus (MNHN PPI 154), in ventral (G1) and dorsal (G2) views.
indicates a closed supracoracoid foramen as in all extant Spheniscus; its length can be estimated as about 6 mm. There is no osteological indication if there was a second foramen, larger and distally to the first one, as often developed in extant Spheniscus; however, its presence or absence can vary intraspecifically, following own observations. The distal end of the coracoid is dorsally strongly concave; the lateral process is short and thin, and forms laterally a concave margin. The medial angle is thickened, proximodistally elongated and forms a pin-like process in proximal direction. Ventral to the medial angle, the surface of the coracoid forms a concavity. The articular facet for the sternum is separated from the medial angle by a little indentation on the distal margin.

The coracoid of Spheniscus muizoni sp. nov. distinguishes from the fragmentary preserved coracoid of S. chilensis (Emslie and Correa 2003: fig. 2B) only by a somewhat shorter supracoracoid foramen. However, its length is variable in extant Spheniscus species and therefore probably not diagnostic.

The closed supracoracoid foramen distinguishes S. muizoni sp. nov. from Palaeospheniscus, in which it is open, as suggested by Simpson (1946: 49). In contrary to Ps. patagonicus and Ps. bergi (figured in Moreno and Mercerat 1891: pl. 1: 23, 25), the coracoid of S. muizoni sp. nov. is smaller and more slender, especially at the level of the foramen.
Fig. 3. Spheniscid penguin *Spheniscus muizoni* sp. nov. from Cerro la Bruja, latest middle/earliest late Miocene, Pisco Formation, Peru. A. Right tibiotarsus (MNHN PPI 147f), in medial (A₁), caudal (A₂), lateral (A₃), and cranial (A₄) views. B. Right femur (MNHN PPI 147c), distal end, distal view (B₁), proximol end, caudal view (B₂), distal end, caudal view (B₃), proximal end, cranial view (B₄), and distal end, cranial view (B₅). C. Right tarsometatarsus (MNHN PPI 147h), in dorsal (C₁) and plantar (C₂) views. D. Synsacrum (MNHN PPI 147l), in dorsal (D₁) and caudal (D₂) views. E. Pygostyl (MNHN PPI 152), in lateral view. F. Thoracic vertebrae T3-7? (MNHN PPI 147), in lateral view. G. Thoracic vertebra T4? (MNHN PPI 147), in caudal (G₁) and cranial (G₂) views. H. Cervical vertebra C12? (MNHN PPI 147), in caudal (H₁) and dorsal (H₂) views.
Humerus (Figs. 2C, 4A).—Left and right humeri (MNHN PPI 147c1+2) are preserved; the right one is quite complete; only the cranial surface of the proximal end and the caudal surface of the shaft are damaged and the cranial edge of the ventral epicondylus is broken off; the left humerus lacks the ventral epicondylus and the caudal and ventral walls of the pneumatotricipital fossa are broken off. As is typical for fossil and extant species of Spheniscus, S. muizoni sp. nov. has a weakly proximally swollen humeral head, and also lacks the proximal notch between dorsal tubercle and humeral head (in caudal view; present in Palaeospheniscus); in both S. muizoni sp. nov. and S. urbinai the proximal outline from the head to the dorsal edge is less steep than in all compared extant species of Spheniscus. The pneumatotricipital fossa is bipartite, with the cranial fossa being deep; this contrasts the genera Paraptenodytes and Arthrodytes, which fossa is non-bipartite (Simpson 1972: 18; Acosta Hospitaleche 2005: 407). The proximal border of the pneumatotricipital fossa is in ventral view relatively straight and horizontal; this is also typical for the extant Spheniscus species, but contrasts the development of the fossil Spheniscus species, S. urbinai and S. chilensis, as well as Dege hendeyi and the extant penguins Eudyptes chrysoceome, E. chrysolophus, and Aptenodytes patagonicus, where this border is concave proximally. Furthermore, in S. muizoni sp. nov. this margin, proximally bordering the pneumatotricipital fossa, forms no ventrocaudally projecting lip (Fig. 5) separated from the head by an extended capital groove. As a result, the caudal surface of the proximal humerus end of S. muizoni sp. nov. is planar and shows no notch in dorsocaudal view. The lack of this ventrocaudally projecting lip is a common feature of S. muizoni sp. nov., S. urbinai, and S. chilensis, but contrasts all extant species of Spheniscus as well as those of Pygoscelis. The preaxial angle is weak (but stronger than in ?Palaeospheniscus huxleyorum and D. hendeyi) and situated about the mid-point of the shaft and thus is placed more proximally than in all other species of Spheniscus, Palaeospheniscus, Eudyptes, Pygoscelis, or Aptenodytes.

The ventral tubercle is strong and protruding, separated by a broad capital groove. S. muizoni sp. nov. differs from S. chilensis by a distinct concave indentation in the bicipital crest between ventral tubercle and shaft (Fig. 4A1, B1). This indentation is also present only in S. magellanicus, hinted in S. demersus and slightly in Pygoscelis adeliae, but is lacking in S. humboldti, Eudyptes, Py. papua, A. patagonicus, and Ps. huxleyorum. In proximal view, the sulcus for the transversal ligament is short and deep; dorsal to it, a small, shallow dent is present like in Spheniscus, but which can vary in depth in other recent penguins and which can also form a short sulcus running distally, like in A. patagonicus or Py. papua. The fossa on the proximal caudal surface is as shallow as in all studied Spheniscus species, but is deeper when compared to Eudyptes, Pygoscelis, and Aptenodytes.

As is typical for Spheniscus, the line defined by ventral and dorsal condyle (in cranial/caudal view) is steeper than in Eudyptes, Pygoscelis, and Aptenodytes. On the ventral epicondylus, the tip of the caudal-most process, caudally bordering the humerodtricipital sulcus, is slightly rising upwards (ventroproximally), most notably its distal margin; this differs from the ventral orientation in Spheniscus chilensis (Fig. 4A2,
B2). The tip of the caudal-most process barely surpasses the ventral margin of the distal shaft (in cranial/caudal view), which corresponds to extant Spheniscus and Eudyptes species; it is longer and strongly surpassing in Aptenodytes patagonicus, moderately long in Pygoscelis papua, and shorter in Inguza predemersus. The middle process-like crest, caudally bordering the scapulotricipital sulcus, is slender, slightly pointed, and extends relatively far distoventrally; it is somewhat longer and oriented slightly more distally than in S. chilensis (Fig. 4A2, B2). The cranial-most process-like crest, cranially bordering the scapulotricipital sulcus, is incomplete and missing its tip; however, the distal margin of the preserved part ends more proximally than that of the caudal process-like crest, unlike in S. chilensis (Fig. 4A1, B1). In distal view, the dorsal end of the scapulotricipital sulcus is curved caudally (Figs. 2C3, 4A4).

Ulna (Fig. 2B).—Preserved are a complete left ulna (MNHN IPP 147d), belonging to the associated skeleton, and a slightly smaller fragmentary left ulna (MNHN IPP 149), with damaged proximal end and proximal caudal margin. They show no important differences from those of extant Spheniscus. The bone is flattened and expanded caudally into a crest-like flange; the ulna of S. muizoni sp. nov. is like the extant species of Spheniscus and like Eudyptes, relatively broader than the more slender ulnae of the representatives of Pygoscelis and Aptenodytes. In several extant penguin taxa the flange-like caudal margin shows in ventral or dorsal view in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in its distal half a slight indentation to which distally the bone becomes more slender; this recess is very weak in S. chilensis (Fig. 4A1, B1). In distal view, the dorsal end of the scapulotricipital sulcus is curved caudally (Figs. 2C3, 4A4).

Carpometacarpus (Figs. 2G, 4C).—An almost complete right carpometacarpus (MNHN PPI 154) is morphologically very similar to that of extant Spheniscus. Concerning limb bone length relations (Fig. 6), S. muizoni sp. nov. has a relatively short carpometacarpus, but which is relatively long for S. chilensis. The carpometacarpus of S. muizoni sp. nov. differs from S. humboldti and S. demersus by a short but distinct step between the proximal carpal trochlea and the extensor process of the alular metacarpal; such a step is low but present in S. magellanicus, and well developed in the compared species of Eudyptes, Pygoscelis, and Aptenodytes. The caudal margin of the minor metacarpal is less recessed below the carpal trochlea (Fig. 4C) in S. muizoni sp. nov. than in S. chilensis. In S. muizoni sp. nov. the line of fusion between alular digit and the major metacarpal is marked only by one foramen dorsally and none ventrally; thus, the fusion of these bones seems to be more progressive than in extant Spheniscus and also S. chilensis, which show at least two but often more foramina on both the ventral and dorsal side (Fig. 4C). The carpometacarpus is broadest at its distal shaft. The spatium is narrow and open, and shows no synchondroses, but which are present at least in both specimens of S. chilensis that were available for comparisons (UF 144110 figured in Emslie and Correa 2003: fig. 2C, and UF 144112). However, this character is more constant in extant species (own observation), but is observed to be variable, e.g., for S. urbinai.

Femur (Figs. 3B, 4I).—The right femur is represented by a proximal portion and a distal end (MNHN PPI 147e); in addition, there is a distal end of a right femur of another individual preserved (MNHN PPI 151). Both distal ends are slightly damaged. The femur corresponds well with those of the extant species of Spheniscus. The proximal portion of the femur is relatively straight, in contrast to that of Py. papua whose proximal half is curved medially. The femoral head and trochanter reach the same level in proximal direction as typical for all fossil and extant species of Spheniscus, but unlike in Eudyptes chrysolophus, E. chrysolophus, Py. papua, Py. adeliae, and A. patagonicus, in which the trochanter surpasses the head more or less distinctly. The trochanteric crest projects cranially but not proximally on the trochanter. A large and deep obturator impression is laterally bordered by a prominent crest. The depth and size of this impression seem to vary within the compared extant species. The neck of the head is, in distal view,
Fig. 6. Simpson’s (1941) ratio-diagram of the main long bones of all extant and fossil Spheniscus species and some more fossil penguin species. The differences of the limb bone measurements, converted into logarithms, are shown in ratio to those of the chosen standard, Spheniscus humboldti. The horizontal distance between the points, marking the same bone elements of different taxa, is proportional to the ratio of their real dimensions. It is essentially: log (mean of measurement of compared taxon) – log (mean of measurement of standard taxon) = log (mean of measurement of compared taxon / mean of measurement of standard taxon). L, length; GL, greatest length. Fossil taxa are indicated by an asterisk.

slightly thinner than in all compared extant specimens. Characteristic for S. muizoni sp. nov. is the cranially very low, barely projecting medial condyle (in distal and medial view; Fig. 4I), lower than in the compared extant species of Spheniscus as well as in S. chilensis (Fig. 4J) and S. urbinai. As in extant and fossil Spheniscus species, the lateral condyle cranially reaches further proximally than the medial one, whereas the condyles reach about equally far proximally in most of the compared specimens of Eudyptes, Pygoscelis, and Aptenodytes. In distal view, the tibiofibular crest of the lateral condyle caudally projects relatively high and is sharp-crested; its medial flank is steep like in extant Spheniscus, but steeper compared to Eudyptes, Pygoscelis, and Aptenodytes specimens. The sulcus of the fibular trochlea is relatively deep. There is a deep cranial impression for the attachment of the cruciate ligament in the intercondylar sulcus.

Tibiotarsus (Figs. 3A, 4E).—The right tibiotarsus is almost complete, only the proximal end of the lateral and cranial cnemial crest are somewhat damaged, the left tibiotarsus is represented by its proximal end, with also damaged crests (MNHN PPI 147f-1+2). The proximal end is caudally characterized by two fossae, separated by a longitudinal crest, which is relatively sharp-edged and proximally quite thin. The lateral longitudinal flexor fossa is also more or less developed in extant penguins; however, characteristic is the deep and distinct medial fossa (impression) of the collateral ligament (Fig. 4E1); it is mostly not or only very weakly developed in most compared extant species (weak in S. magellanicus and in one of the two compared specimens of Py. papua). Also characteristic is a distinct furrow along the lateral side of the distal shaft, starting on the caudal side distal to the fibular crest and turning to the laterocranial side in distal direction; this furrow is much weaker in all of the compared extant penguin specimens.

Remarkable is the straight distal end of the tibiotarsus of S. muizoni sp. nov., contrasting most extant and fossil penguins (S. urbinai, Palaeospheniscus), which distal end is bent medi-ally (in cranial view). Furthermore, the medial condyle is vertical in S. muizoni sp. nov. and not laterally inclined and lacks a swollen tubercle for the retinaculum of the fibularis muscle forming the lateral bulge on the distal shaft (Fig. 4E1, E2); instead of the latter there is only a very weak vertical line. In contrast, this lateral bulge is present in most extant Spheniscus species, Pygoscelis, Eudyptes, and Aptenodytes. Only S. magellanicus and S. chilensis also show a quite straight distal end of the tibiotarsus, provoked by very weak lateral tubercle for the retinaculum of the fibularis muscle, but differ by an inclined medial condyle (Fig. 4F1).

Unlike extant and other fossil penguin taxa, the distal end of the tibiotarsus of S. muizoni sp. nov. lacks the furrow between the tubercle for the retinaculum of the fibularis muscle and the extensor sulcus, and both the medial and lateral tuberosity for the extensor retinaculum on both sides of the extensor sulcus; the latter distinguishes S. chilensis, which has a distinct lateral tuberosity for the extensor retinaculum (Fig. 4E1, E2, F1, F2). The medial border of the extensor sulcus is relatively thin and straight. Like other fossil and extant species of Spheniscus, S. muizoni sp. nov. lacks the craniolaterally protruding lip-like crest (tuberositas retinaculi extensoris medialis), but which is present in Eudyptes and also sometimes in Pygoscelis and Aptenodytes. The lateral condyle is sub-rounded, the medial one is more longer...
Fibula.—The fibula is represented by a proximal portion of a right specimen (MNHN PPI 147g). The proximal articular facet for the femur is slightly damaged but was cranio-cranially concave. The proximal articular facet for the tibia is flat. The fibula of S. muizoni sp. nov. is characterized by a distinct and very deep concavity on the caudal side, which is less deep or almost absent in the extant species. The proximal shaft of the fibula is laterally marked by a distinct furrow running obliquely from proximocranial to distocaudal. This furrow is very well developed and also present in all compared species but can vary intraspecifically.

Tarsometatarsus (Figs. 3C, 4G).—One complete right tarsometatarsus (MNHN PPI 147h) is present. Fig. 6 shows that the tarsometatarsus of S. muizoni sp. nov. is relatively long in comparison with most extant Spheniscus species. It is slender and extends especially distally.

The elongation index of S. muizoni sp. nov. (2.07) is higher than that of S. urbinaí (1.7–1.95; see Table 2), below that of Palaeospheniscus, which is diagnostically about 2.2–2.4 (Simpson 1972: 8) and distinctly below that of E. tomnii (elongation index: 2.66, Acosta Hospitalchele et al. 2004: 235), but is in the range of that of Parapatennodytes (elongation index: 1.8–2.1). However, Pa. robustus and Pa. antarcticus are distinctly larger species. The elongation index of S. chilensis is not known, but its ratio of length/least breadth of shaft (length: 33.5 mm, least breadth of shaft: 16 mm, unpublished data provided by Steve Emslie) is 2.09, whereas that of S. muizoni sp. nov. is 2.24.

The extensor sulci in S. muizoni sp. nov. are long and deep, as in Spheniscus. In contrary, both sulci are shallower in Eudyptes, Pygoscelis, and Aptenodytes and in Palaeospheniscus (Ps. patagonicus and Ps. bergi) the medial sulcus is shallower. However, the medial sulcus of S. muizoni sp. nov. is in its distal part deeper than in extant species of Spheniscus. Emslie and Correa (2003) described the extensor sulci of S. chilensis as shallow below the proximal foramen; from own observations, I would surmise that they are deep proximally but shallow only in their distal half. However, this is different from S. muizoni sp. nov., in which the sulci are also deep distally (Fig. 4G1, H1).

There are very probably two proximal vascular foramina, unlike in the smaller-sized species E. tomnii (Acosta Hospitalchele et al. 2004: 235) and N. insolitus (from the early Pliocene of Duinfountain, South Africa [Simpson 1979a]), which are characterized by only one foramen. In S. chilensis the medial proximal foramen of the tarsometatarsus is described as “...greatly reduced or absent...” (Emslie and Correa 2003: 313). In S. muizoni sp. nov. the lateral proximal vascular foramen is probably situated in the middle of the lateral dorsal extensor sulcus, but where the bone is damaged; the medial one is small, situated more proximally than the lateral one in the most proximomedial edge of the infracotylar fossa and opens plantarly on the medial surface of the hypotarsus. The arrangement of the proximal foramina corresponds more to that of Spheniscus than to any other extant genus, but the medial foramen is situated more proximal than in extant species. The position and size of these foramina also differs from Inguza predemersus.

The dorsal infracotylar fossa is very deep in that the proximal portion of the metatarsal III is distinctly lower than that of metatarsals II and IV. The proximal end of the metatarsal II dorsally carries a very pronounced impression of the extensor retinaculum (defining a distinct fossa) and a little distally to another small muscle or tendon scar; the arrangement and distinctiveness of these impressions and scars also corresponds mostly with the genus Spheniscus, whereas it is much weaker in Eudyptes chrysolophus, E. chrysochome, Py. papua, and A. patagonicus. The metatarsal III carries dorsally a long tuberosity for the attachment of the tibialis muscle.

The hypotarsus is relatively weak in comparison with extant Spheniscus species. The medial hypotarsal crest is relatively thin and oriented medioplantarly (not lateroplantarly as in Palaeospheniscus); in proximal view it is bent hook-like medially with a concave furrow along its medial side; laterally attached to it (along its distal half) is a second very weak crest. The lateral hypotarsal crest is very weak and hardly projecting; laterally it is limited by a ridge, which runs distally passing medially to the lateral proximal foramen. Lateral to the ridge, the plantar surface of the proximal shaft is concave.

The medial metatarsal (II) is more slender than the middle (III) and the lateral one (IV). In lateral view, a plantarily concave ridge borders the lateroplantar side of the metatarsal IV.

As typical for all extant and fossil Spheniscus species, the lateral intertrocchlear incision is longer (deeper incised proximally) than the medial one (in dorsal view), whereas in A. patagonicus, E. chrysochome, and Py. papua they incise about the same length.

In S. muizoni sp. nov. as well as in all extant and fossil species of Spheniscus, the trochlea II and IV are of about equal length distally; this is different in extant Eudyptes, Pygoscelis, and Aptenodytes and fossil Palaeospheniscus (Ps. patagonicus and Ps. bergi), which trochlea VI is somewhat shorter than II.

Trochlea III is very robust and swollen dorsally. In distal view, trochlea III reaches dorsally at the same level as the lateral condyle of trochlea VI or slightly surpasses it (also in lateral view). S. muizoni sp. nov. shares this feature with S. urbinaí (and with E. chrysolophus), but differs from S. chilensis and all extant species of Spheniscus, which trochlea IV dorsally surpasses the lateral condyle of trochlea III (Fig. 4G3, H3). Additionally, the lateral bulge of trochlea IV is dorsoplantarly lengthened and clearly surpasses trochlea III.
in plantar direction. The medial and lateral condyle of trochlea III are dorsally about the same level, whereas in extant Spheniscus species, the medial one is clearly surpassing the lateral one. In lateral view, the lateral condyle of trochlea IV is distally somewhat flattened and shorter than the medial one (like in Pygoscelis papua and Aptenodytes), unlike in extant Spheniscus. Trochlea II is oriented relatively obliquely, so that the medial fovea is apparent in dorsal view.

Sternum (Fig. 2E).—Only a small, cranial-most center portion of the sternum with both sulci for the coracoid articulation is present. The cranial spines (spina interna and externa) and the carina are broken off.

Cervical vertebrae (Fig. 3H).—The probable two caudal-most cervical vertebrae (C12, C13) are represented. C12 is quite complete, but lacking the transverse processes, of C13 only the body is preserved. Both vertebrae are strongly heterocoel and characterized by deep lateral dents on the lateral concavities of the body, as typical for these vertebrae positions. C12 has a short spinous and ventral processes.

Thoracic vertebrae (Fig. 3F, G).—Seven thoracic vertebrae out of normally eight are preserved; they probably represent the cranial-most ones (T1–T7). All of them show the lateral depressions for the rib articulation. First and second vertebrae (T1, T2) are preserved fragmentary; T1 lacks the dorsal arc, T2 its caudal half. T3–T7 (Fig. 3F) are more complete, but lack all ventral or dorsal spines and the transverse processes; the cranial and caudal zygapophyses are mostly preserved. The first two vertebrae, even if fragmentary, show moderate heterocoel articulation facets, whereas the further five vertebrae are opisthocoel.

Synsacrum (Fig. 3D).—The synsacrum is represented by two fragments, a short portion of the cranial end and the rest of the fragmentary synsacrum, but both portions lack contact. The cranial portion is represented only by the laterally strongly flattened body with a worn convex cranial articular facet and ventrally forms a longitudinal crest. The larger caudal portion lacks the body of the synsacrum, thus the vertebral canal is open; additionally, both lateral edges of the synsacrum are badly damaged; in its cranial half the spinous crest is preserved, which becomes higher in the cranial direction. The sinoid structure forming the iliosynsacral suture is only partly preserved by their caudal portions, which are laterally concave. The number of vertebrae involved in the synsacrum is not reconstructible.

Pygostyle (Fig. 3E).—About the cranial half of the pygostyle is preserved. It is laterally strongly flattened. The cranial articulation is oval and higher than broad. The basis of the pygostyle is damaged.

Estimating the living weight based on the relationship of the body mass of birds with some hindlimb measurements (circumference of the shafts of femur and tibiotarsus), a method presented by Campbell and Marcus (1992), the femur leads to a weight of about 3500 g, and the tibiotarsus to a weight of about 3800 g for S. muizoni sp. nov.; these calculations were made by considering penguins as swimmers (SW in Campbell and Marcus 1992). The estimated living weight of S. muizoni sp. nov. corresponds well with the body mass of S. demersus, 3310 g for males and 2960 g for females, but is somewhat smaller than that for S. magellanicus (4500 g) and distinctly smaller than that for S. humboldti (4500 g), but is larger than that for S. m. mendiculus (2500 g; body masses by Dunning 1993).

Stratigraphic and geographic distribution.—Only known from the latest middle or earliest late Miocene of the type locality Cerro la Bruja.

Conclusion

Detailed comparisons with extant and fossil species of Spheniscus suggest that the available postcranial bones of S. muizoni sp. nov. morphologically correspond best with those of S. urbinai, aside from that the latter is distinctly larger. Some shared features are found to be exclusive for these two species within Spheniscus, such as the lack of a ventrocaudally projecting lip proximally bordering the pneumotricipital fossa on the humerus, or a tarsometatarsus which trochlea III is dorsally at about the same level as the lateral condyle of trochlea VI or slightly surpasses it. Although of almost identical size, S. muizoni sp. nov. can be distinguished by several osteological features from S. chilensis, such as the limb bone proportions of the carpometacarpus (Fig. 6) and morphological differences at the humerus, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. Based on the morphological similarity of S. m. mendiculus sp. nov. and S. urbinai and their stratigraphical succession within the Pisco Formation, it can be supposed that the first gave directly rise to at least the latter.

S. muizoni sp. nov. is the only known penguin species from the Cerro la Bruja locality and is unknown from any older or younger deposit in or outside the Pisco Formation. As penguins are shorebirds—breeding on land (or ice) and feeding in fairly adjacent marine waters (del Hoyo et al. 1992), the penguin fossils complement the exclusively marine vertebrate fauna represented at Cerro la Bruja, comprising fossil taxa of marine fishes (Teleostei) and sharks (Selachii), a turtle and a crocodile, different marine mammals such as fossil odontocetes (Kentriodontidae, Pontoporiidae), mysticetes (Cetotheriidae, Balaenopteridae), pinnipeds (Phocidae), and a booby (Aves, Sulidae; Muizon 1988: table 1).

To date, all fossil penguins reported from the different levels of the Pisco Formation belong to the extant genus Spheniscus. The today living species of Spheniscus include: S. m. mendiculus (Galapagos), S. humboldti (coast of Peru and Chile), S. magellanicus (coast of Chile and Argentina, Islas Malvinas or Falkland Islands), and S. demersus (coast of South Africa and Namibia; del Hoyo et al. 1992).

However, S. muizoni sp. nov. from the latest middle/earliest late Miocene of Cerro la Bruja is not only the most ancient
penguin species in the Pisco Formation, but also the stratigraphically oldest record for the extant genus Spheniscus in general.

The fossil record indicates a faunal change of Spheniscus species within the stratigraphically older sequence of the Pisco Formation. S. muizoni sp. nov., exclusive in the oldest deposits (latest middle/earliest late Miocene, 13–11 Ma) is replaced by the persistant S. urbinai, existing from the late Miocene to the early Pliocene (9 to 3.5 Ma) deposits (S. megaramphus is only known from a 6 Ma old locality). This replacement might be linked to changes of the climatic conditions at the Pacific coast of South America during the latest middle Miocene. Tsuchi (2002: 269) dated a short warm episode in between cool episodes of the surface marine climate of the latest middle Miocene. Extant penguins (on a species level) require a relatively stable water temperature (del Hoyo et al. 1992: 144) and change of water temperature (e.g., as in the phenomenon known as El Niño) is known to have far reaching effects on the Humboldt and Galapagos Penguin. It is not known yet, if there is a faunal consequence also within some other fossil vertebrate groups represented in Cerro la Bruja and younger localities in the Pisco Formation because the vertebrate fauna of Cerro la Bruja has not been studied in detail as yet.

Apart from Spheniscus, there is only very scanty penguin material known from other Peruvian localities, which is described as Palaeospheniscus sp. and Spheniscidae indet. (Acosta Hospitaleche and Stucchi 2005). However, the latter comes from deposits older than the Pisco Formation, the lower middle Miocene Chilcatay Formation and the upper Eocene–lower Oligocene Otuma Formation, respectively.

Outside the Pisco Formation, fossil representatives of Spheniscus have been reported only from Chile: S. chilensis from the late Pliocene and Spheniscus sp. from the late Miocene–early Pliocene. There was only one report on a fossil Spheniscus outside of South America, S. predemersus Simpson, 1971 described from South Africa. This species was, however, later referred by Simpson (1975b) to the new genus Inguza.

Thus, the fossil record of Spheniscus is restricted to the latest middle/earliest late Miocene to the late Pliocene of South America, more precise to the Pacific coast of South America (Peru and Chile). The modern distribution of Spheniscus correlates with cold marine currents—the west–east directed Circumpolar Antarctic Current and their northern upturns along the west–coasts of South America (Humboldt Current) and southern Africa (Benguela Current). However, the restriction of the Mio–Pliocene record of Spheniscus to the Pacific coast of South America was not due to a geographic barrier, as the Drake passage was already open by the late middle Eocene around 40 Ma ago (Scher and Martín 2006). However, no record of Spheniscus is known along the Atlantic coasts of South America or southern Africa during the Neogene. However, the presence of this genus cannot be ruled out if their restriction to the Pacific coast during the Neogene is linked to other ecological or alimentary factors—perhaps interrelated to the still open Panama Isthmus (closure starts during the early Pliocene, about 4–3 Ma, Kameo and Sato 2000) and thus corresponding marine currents, which might have had an effect on the distribution of potential prey. In all extant Spheniscus species pelagic school fish (mostly anchovies) is the dominant prey; cephalopods and crustaceans are subordinate (del Hoyo et al. 1992). Because the skull of S. muizoni sp. nov. is lacking, no information is available on the shape of the bill, which varies at least in some extant penguin genera and their preferred diet. Neither fossil nor extant Spheniscus species show any obvious interrelation of body size and latitude of their habitat.

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