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The hindlimbs of *Sobrarbesiren cardieli* (Eocene, northeastern Spain) and new insights into the locomotion capabilities of the quadrupedal sirenians

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Abstract

In the transition from a terrestrial to an aquatic environment, sirenian marine mammals reduced and lost their hindlimbs and developed a horizontal tail, the main propulsive organ in extant sirenians. Quadrupedal forms are only known from the Eocene and are represented by three different taxa: the amphibious prorastomids, the aquatic quadrupedal protosirenids and *Sobrarbesiren cardieli*, a four-legged sirenian from the middle Eocene of Spain, considered the sister taxon of the aquatic Dugongidae. This ecological shift was naturally associated with adaptations, among others, of the skeleton. However, sirenian hindlimb bones have been poorly studied because of the scarce material available in the fossil record. Here we describe in detail the hindlimb bones of *Sobrarbesiren*, analyzing their functional morphology and comparing them with other basal sirenians and cetaceans. *Sobrarbesiren* had strong control of its hindlimbs, which were capable of a great variety of movements. Based on the presence of a strong sacroiliac articulation, we propose that it swam by dorsoventral pelvic undulation combined with pelvic paddling analogous to some protocetid archaeocete whales. We also conducted the first microanatomical analysis of hindlimb bones of an Eocene sirenian. Data reveal extreme inner compactness in the *Sobrarbesiren* innominate bone and femur, with the first description of

osteosclerosis in an amniote innominate bone combined with the highest degree of osteosclerosis observed in amniote femora. The results confirm that the microanatomical changes precede the external morphological changes in such ecological transitions. The process of adaptation of sirenians to an aquatic life was thus a more complex process than previously thought.

Keywords (4 a 6): Marine mammals, aquatic adaptation, microanatomy, functional morphology.

INTRODUCTION

The transition of mammals from land to sea has occurred in independent mammalian lineages including cetaceans, sirenians, desmostylians, pinnipeds, the sea sloth, mustelids (the sea otter, the South American marine otter and the extinct sea mink) and the only marine-living ursid, the polar bear (Berta et al. 2015). This transition implies great skeletal and physiological modifications. Extant sirenians and cetaceans are the only obligate aquatic mammals nowadays, and they share several morphological features, such as a fusiform body, a short neck, paddle-like forelimbs, the loss of hindlimbs (except for a vestigial innominate bone present in extant species, with no bony connection to the vertebrae in the case of sirenians), and horizontal tail fins as the main organ of propulsion (Domning 2000). These morphological traits for the adaptation of whales and sirenians to aquatic life illustrate one of the classic examples of convergent evolution. The evolutionary history of both sirenians and cetaceans began in the Paleocene, but the variation in the morphologies and ecological niches reached by cetaceans in the fossil record and today is much greater than that of sirenians. The extant species of manatees and the dugong are classified as vulnerable fauna by the IUCN (International Union for Conservation of Nature) and are limited to shallow coastal environments at tropical latitudes (except for the giant Steller's sea cow *Hydrodamalis gigas* (Zimmermann, 1780) Palmer, 1895, which was adapted to cold climates (Domning 1978) before falling victim to the Earth's sixth extinction).

By far the best-known evolutionary history of a mammalian transition from land to sea is that of the cetaceans. Among the Eocene basal cetaceans, five families in the suborder Archaeoceti have been described, including semiaquatic (Pakicetidae, Ambulocetidae, Remingtonocetidae and Protocetidae) and completely aquatic forms (Basilosauridae) (Uhen 2008a; Berta et al. 2015 and references therein). All of them preserve the hindlimbs. Less attention has been paid to the study of the first stages in the adaptation of sirenians to aquatic life. In the Eocene three basal sirenian families are known, including semiaquatic and aquatic quadrupedal (Prorastomidae, Protosirenidae and *Sobrarbesiren*) and completely aquatic forms (Dugongidae). Comparisons of Eocene sirenian hindlimbs are scarce in the literature (e.g., Abel 1904; Stromer von Reichenbach

1921; Zalmout and Gingerich 2012), probably because of the scarcity of non-vestigial (i.e. still functional) elements in the fossil record. Nevertheless, hindlimbs, in particular the innominate bones, are considered to be a key trait in basal sirenian evolution (Gingerich et al. 1995a; Domning 2000; Zalmout and Gingerich 2012).

This paper includes the first in-depth morphofunctional interpretation of basal sirenian hindlimbs, with the aim of providing key insights into the earliest stages of the evolution of locomotion in these marine mammals. To this end, we here examine the morphology and joints of the hindlimbs of *Sobrarbesiren cardieli* Díaz-Berenguer, Badiola, Moreno-Azanza and Canudo, 2018, the oldest sirenian species in western Europe, and compare them with the other genera of Eocene quadrupedal sirenians known, *Pezosiren* and *Protosiren*. Moreover, this study includes for the first time 3D microanatomical data from a sirenian (*Sobrarbesiren*) innominate bone and femur.

BACKGROUND

(a) On the Eocene sirenian hindlimbs

Sirenians originated in Africa during the Paleogene from an indeterminate clade of afrotherian mammals (Domning et al. 1982; Hautier et al. 2012; Benoit et al. 2013, among others), and as early as the middle Eocene were widely distributed across the western and eastern Atlantic coasts and across the Tethyan Realm (e.g., Gingerich et al. 1995a; Domning 2001a; Bajpai et al. 2009; Astibia et al. 2010; Domning et al. 2010; Díaz-Berenguer et al. 2018). Domning (2000) proposed three different stages of adaptation to aquatic life, represented by the families Prorastomidae, Protosirenidae and Dugongidae.

The prorastomids (*Prorastomus* Owen, 1855 and *Pezosiren* Domning, 2001b) are the most primitive sirenians and are considered semiaquatic animals. The most complete prorastomid, *Pezosiren portelli* Domning, 2001b, from the Lutetian of Jamaica, combines aquatic skeletal characteristics, such as retracted nares and pachyosteosclerotic bones, with features of terrestrial mammals, such as a multivertebral sacrum, a weight-bearing sacroiliac articulation and well-developed hindlimbs. *Pezosiren* was an amphibious animal capable of locomotion on land, and

probably used its hindlimbs as the main propulsive organ for swimming, combined with spinal undulation (Domning 2000). The protosirenids (*Protosiren* Abel, 1907, *Ashokia* Bajpai, Domning, Das and Mishra, 2009 and *Libysiren* Domning, Heal and Sorbi, 2017) are aquatic quadrupedal sirenians which have hindlimbs that are well developed though reduced in size, and only one sacral vertebra, and which use the tail as their main propulsive organ. In the Old World, protosirenids are found in the middle Eocene of the South Tethyan coasts; no protosirenid fossils are known in Europe, with the exception of isolated remains of uncertain affinities (Hooijer 1952; Kordos 2002). Protosirenid hindlimbs have only been described for the genus *Protosiren*. Abel (1904) was the first to describe a *Protosiren* innominate bone. This Lutetian fossil, found in Egypt, was first identified as “*Eotherium*” and later assigned to *Protosiren fraasi* (Sickenberg 1934). Abel (1904) recognized the primitive characteristics of the innominate bone, including a large and deep acetabulum, and proposed the existence of a still functional femur for this taxon. The most complete *Protosiren* skeleton known is that of *Protosiren smithae* Domning and Gingerich, 1994, from the late Bartonian-early Priabonian of Egypt. This specimen preserves cranial, axial and limb elements, including for the first time the patella, femur, tibia and fibula. *Protosiren sattaensis* Gingerich, Arif, Bhatti, Raza and Raza, 1995, from the Bartonian of Pakistan, is described from a quite complete vertebral column, ribs and innominate bones. Gingerich et al. (1997) published new remains assigned to *P. sattaensis* from the same stratigraphic level as the type specimen, including one innominate bone and a left femur. The only protosirenid fossil found in the New World is a partial innominate bone from the Bartonian of the USA (South Carolina) assigned to the genus *Protosiren* (Beatty and Geisler 2010).

Eocene dugongids (*Halitherium* Kaup, 1838, *Prototherium* de Zigno, 1887, *Eotheroides* Palmer, 1899, *Eosiren* Andrews, 1902, *Sirenavus* Kretzoi, 1941, *Paralitherium* Kordos, 1977 and *Anisosiren* Kordos, 1979) are already fully aquatic animals, which lack external hindlimbs and used the tail as the main propulsive element for swimming (Domning 2000). Only vestigial innominate bones and femora are known for this family. From Africa (Egypt), hindlimb bones and femora are known in the early Priabonian species *Eotheroides sandersi* Zalmout and

Gingerich, 2012 and in the late Priabonian species *Eosiren libyca* Andrews, 1902 (Andrews 1906; Stromer von Reichenbach 1921; Siegfried 1967; Zalmout and Gingerich 2012). *Eotheroides clavigerum* Zalmout and Gingerich, 2012, from the early Priabonian of Egypt, preserves the innominate bones. In Europe, sirenian innominate bones and femora are known in the taxon “*Halitherium*” *taulannense* Sagne, 2001 from the Priabonian of France, and in *Sirenavus* sp. from the late Eocene of Hungary (Kordos 2002). Incomplete innominate bones are also described in *Prototherium intermedium* Bizzotto, 1983, from the Priabonian of Italy, and in *Prototherium? montserratense* Pilleri, Biosca and Via, 1989, from the Bartonian of Spain, the latter considered *Prototherium intermedium* by Domning (1996). Stromer von Reichenbach (1921) described the innominate bones of *Prototherium veronense* de Zigno, 1887 from the late Lutetian of Italy, but the origin and age of this material are not clear. From the New World, only the partial left innominate bone of an Eocene dugongid from North Carolina has been identified as *Eotheroides* sp. (Zalmout and Gingerich 2012), having previously been assigned to *Protosiren* sp. (Domning et al. 1982).

All the European Eocene sirenians are assigned to the family Dugongidae, with the exception of various specimens of uncertain affinities (Hooijer 1952; Kordos 2002). In the Pyrenean region, Eocene sirenian remains are scarce and fragmentary, and the most complete fossils are assigned to the genus *Prototherium* (e.g., Pilleri et al. 1989; Balaguer and Alba 2016). The exception is the sirenian fossil remains found in the middle Lutetian site of Castejón de Sobrarbe-41 (Huesca, Spain), which were described as *Sobrarbesiren cardieli* (Díaz-Berenguer et al. 2018) (Fig. 1). This is the oldest sirenian from western Europe and has been recovered phylogenetically as a sister taxon to Dugongidae. This stem sirenian from the northeastern Atlantic coast (Bay of Biscay) is represented by a very complete skeleton including the skull, ribs, vertebrae, pectoral and pelvic girdle bones, and fore and hindlimb elements. To date, *Sobrarbesiren* is the first adequately known quadrupedal sirenian from Eurasia, and has been hypothesized to represent a transitional stage of adaptation to aquatic life between the amphibious prorastomid *Pezosiren* and the aquatic quadrupedal protosirenid *Protosiren* (Díaz-Berenguer et al. 2018). This paper presents

a microanatomical and morphofunctional analysis of the hindlimbs of *Sobrarbesiren* in order to test this hypothesis.

(b) On the histology and microanatomy of the sirenian skeleton

The microanatomy of mammals secondarily adapted to aquatic life has been studied in many groups, highlighting the link between bone microstructure and the aquatic lifestyle and locomotion abilities of the taxa, and thus these data are relevant to understanding how the process of return to an aquatic life occurred in the various lineages concerned (Houssaye et al. 2016 and references therein). According to the fossil record, microanatomical changes in bone tissue occur before the external morphological changes in aquatic amniotes (Gray et al. 2007; Houssaye 2013). The occurrence of bone mass increase, essentially as pachyosteosclerosis, i.e. the combination of pachyostosis (increase in cortical bone deposits engendering a change in morphology) and osteosclerosis (increase in bone inner compactness), is considered an autapomorphy of the order Sirenia (Kaiser, 1960; Savage 1976; Domning and Buffrénil 1991; Buffrénil et al. 2010). This osseous specialization occurs mainly in cephalic and thoracic regions in sirenians and is regarded as enabling hydrostatic control of buoyancy and body trim in poorly active swimmers (Domning and Buffrénil 1991). According to Buffrénil et al. (2010), pachyostosis is the first process to appear and is already present in middle Eocene sirenian taxa, whereas osteosclerosis is incipient in basal sirenians such as *Pezosiren* but not strongly developed until the late Eocene. (Domning 2000). Protosirenid ribs show osteosclerosis, much stronger than in *Pezosiren*, but not pachyostosis, which is already present in the Jamaican taxon (Buffrénil et al., 2010). The internal structure of extant and fossil sirenian bones has previously been studied for the axial skeleton and humeri (Astibia et al. 2005; Buffrénil et al. 2008, 2010; Dumont et al. 2013; Laurin et al. 2011; Hayashi et al. 2013, among others) and for cranial remains (Gingerich et al. 1994a), but nothing is known about the microanatomy of sirenian hindlimbs. This contribution presents, for the first time, the results of X-ray computed microtomography (μ CT) of a sirenian innominate bone and femur.

MATERIAL AND METHODS

The type locality of *Sobrarbesiren*, Castejón de Sobrarbe (province of Huesca, Spain), crops out in the Ainsa Basin (South Pyrenean Central Unit; Mochales et al. 2012). The sirenian bonebed (CS-41) is located in the uppermost part of the Sobrarbe Formation, which is interpreted as a deltaic plain related to the Sobrarbe Deltaic Complex (Dreyer et al. 1999). According to the magnetostratigraphic and paleontological data, the CS-41 site is dated as middle Lutetian (middle Eocene) and has been placed within Chron C19r and the biozone SBZ 15 (Díaz-Berenguer et al. 2018). The macrofossils of the vertebrate assemblage are dominated by complete and well-preserved sirenian bones, although some pleurodiran turtle shell plates and eusuchian crocodylomorph teeth and bones have also been collected in the excavation campaigns.

Two innominate bones (MPZ 2017/47, MPZ 2017/48), three femora (MPZ 2017/53, MPZ 2017/55, MPZ 2018/520), two patellae (MPZ 2017/51, MPZ 2017/52) and two fibulae (MPZ 2017/56, MPZ 2018/521) are here studied. The fibula of *Sobrarbesiren* is the oldest sirenian fibula known. Some of the specimens included in this study (MPZ 2017/47, MPZ 2017/48, MPZ 2017/51, MPZ 2017/52, MPZ 2017/53, MPZ 2017/55, MPZ 2017/56) were preliminarily described in Díaz-Berenguer et al. (2018). In the present paper, extensive descriptions of these pieces and comparisons with other Eocene sirenian fossils are carried out. In addition, new specimens are added to the study (MPZ 2018/520 and MPZ 2018/521). All the *Sobrarbesiren* fossils described here are housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain (Canudo 2018).

In this study, different hindlimb bones such as the innominate bones, femur, patella, tibia and fibula of different Eocene sirenians are compared. Most of the comparative taxa have been studied at first hand, including *Pezosiren portelli*, *Protosiren sattaensis*, *Protosiren smithae*, *Eosiren libyca*, “*Halitherium*” *taulannense*, *Prototherium? montserratense*, *Prototherium intermedium* and *Sirenavus* sp (see Table 1 for detailed material). The innominate bones and femora of

Protosiren fraasi, *Eotheroides clavigerum* and *Eotheroides sandersi* and the femur of *Eosiren libyca* are studied from the literature (Abel 1904; Sickenberg 1934; Gingerich et al. 1995a; Zalmout and Gingerich 2012; Siegfried 1967, respectively).

The names of the muscles mentioned in this paper, as well as their origins, insertions and actions, come from Getty and Sisson (1975), unless otherwise noted. The key to the measurement of fibulae and patellae used in this study is provided in Fig. 2. For the remaining bones, see the corresponding references in the table captions.

For the microanatomical section we studied one of the innominate bones (MPZ 2017/48) and the femur (MPZ 2017/53,) of *Sobrarbesiren cardieli*. These bones were scanned using high-resolution computed tomography (GEphoenix|X-ray v|tome|xS 240) at the AST-RX platform at the Museum National d'Histoire naturelle, Paris (France); reconstructions were performed using datox/res software. Voxel size is 68.2 µm for the innominate and 42.3 µm for the femur. Image visualization and virtual thin sections were performed using VGStudioMax 2.2 (Volume Graphics Inc., Heidelberg, Germany).

Institutional abbreviations – **CGM**, Cairo Geological Museum (Egypt); **GSP**, Geological Survey of Pakistan; **MÁFI**, Geological Institute of Hungary; **MGP-PD**, Museum of Geology and Paleontology, University of Padua (Italy); **MGSB**, Geology Museum of the Seminary of Barcelona (Spain); **MPZ**, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, (Spain); **NHM**, Natural History Museum, London; **RGHP**, Réserve Géologique de Haute Provence (France); **USNM**, US National Museum of Natural History (USA).

RESULTS

(a) Morphological features

Description

Innominate bones. MPZ 2017/47 is a left innominate bone that lacks part of the pubic symphysis (Fig. 3a- d). It can be assumed to pertain to an adult specimen because the suture lines have been

obliterated. It is elongated and narrow with a total length of 240 mm (more measurements in Table 2).

The **ilium** is rod-like and triangular in cross section. It has a well differentiated lateral spine that appears abruptly (Fig. 3b: lilsp). The ventrolateral surface of the spine is narrow (6 mm wide) and flattened, and tapers towards the anterior edge of the ilium. On the medial side, the sacroiliac articular surface is large (Table 2), rugose and slightly concave (Fig. 3c, d). This surface is well delimited by an irregular lip. There is a blunt ridge in the middle of this surface parallel to the dorsoventral borders. The ilium narrows towards its anterior edge, which is triangular in outline, slightly concave and rugose. On the dorsal (external) side of the ilium, at the level of the posterior edge of the lateral spine, there is a protuberance projecting dorsally, identified as the posterior iliac spine (Díaz-Berenguer et al. 2018) (Fig. 3b: pilsp). This is composed of three isolated and blunt protuberances forming an isosceles triangle. The ilium widens towards the acetabulum. On the ventral margin of the innominate bone and anterior to the acetabulum, the iliopectineal eminence (iliopubic eminence in Getty and Sisson 1975) for the attachment of the pectineus muscle (sensu Uhen 2014) is present (Fig. 3b: ie). It projects ventrally and shows a slightly depressed and rugose surface. Just anterior to the acetabulum there is a roughened subtriangular depression for muscle attachment. This probably corresponds to the area for the origin of the m. rectus femoris (Fig. 3b: mrf).

The **acetabulum** is rounded, large and deep (see Table 2). The anterior border of the acetabular lip is sharp and high, whereas the dorsal and ventral borders are low and the dorsal one slightly concave. The acetabular notch is broad (18 mm wide) and opens posteroventrally. The lunate surface is circular in outline and well-defined. It overhangs the acetabular notch dorsally. In its anterior part, there is a shallow hollow. The acetabular fossa, for the attachment of the round ligament, is very well marked and subtriangular in shape (Fig. 3b: af).

The **obturator foramen** is opened and large (Fig. 3d: of; see Table 2). Its outline is D-shaped, and its longer axis is proximolaterally-mediolaterally oriented. In medial view, there is a groove at the point where the anterior pubic ramus and the ischial ramus join, which ends at the pointed

anterior border of the obturator foramen. This is probably the obturator groove (Fig. 3d: og), related to the obturator nerve and vessels. The distance between the proximal edge of the obturator foramen and the beginning of the sacroiliac joint is 70 mm.

The **ischium** is broad, flattened, curved dorsally and directed dorsolaterally with respect to the long axis of the innominate bone (Fig. 3a-d). It forms an angle of 160° with the long axis of the ilium, and 140° with the pubic bone. The ischium is 94 mm long as measured from the center of the acetabulum, and its maximum dorsoventral breadth is 45 mm. The thickness of the ischial ramus behind the obturator foramen is 23 mm. Its medial and lateral sides are smooth, except at its distalmost edge, where it is slightly striated. The distal edge is swollen and asymmetrical in outline. Its surface is slightly concave and rugose.

The **pubis** is long and flattened (Fig. 3a-d). The pubic ramus behind the obturator foramen is flat in lateral view and rounded in medial view. Its thickness is 24 mm. The pubic ramus in front of the obturator foramen is oval in cross-section and narrower than the other ramus (13 mm wide). The pubic bone is strongly turned ventromedially. The partially preserved symphysis is long, with an estimated length of 35 mm. It is straight and rugose, as expected for a symphyseal fibrocartilage attachment.

The right innominate bone MPZ 2017/48 belongs to a subadult (see Table 2 for measurements). The proximal edge of the ilium, the distal edge of the ischium, the pubic symphysis and the acetabular lip are missing. The suture lines are still visible (Fig. 3e-h). Its general morphology is similar to that of MPZ 2017/47 but shows some differences. The posterior iliac spine (Fig. 3f: pilsp) is flattened, triangular, and pointed, with a rugose external border lacking the blunt protuberances observed in MPZ 2017/47. The **ischium** is directed posteriorly with no deviation from the long axis of the innominate bone. The **acetabulum** is rounded and large (see Table 2), and the lunate surface is circular. The anterior and higher part of the acetabular lip is missing, so its real depth is not clear. It measures 14 mm in depth from the preserved border of the lip to the acetabulum surface. The acetabular notch measures 17 mm. The roughened, subtriangular depression anterior to the acetabulum for the origin of the m. rectus femoris is more marked in

this specimen (Fig. 3f: mrf). There is a rounded protuberance on the lateral side of the ischial ramus at the level of the distal end of the obturator foramen, which is absent in MPZ2017/47.

Femora. The most complete femur (MPZ 2017/53) corresponds to a subadult individual (Fig. 4a-f). It lacks the proximal epiphysis, which was not fused, and the distal epiphyseal suture is still conspicuous. It is a robust femur and has a total length of 134 mm (see Table 3 for more measurements). The **lesser trochanter**, for the insertion of the iliopsoas muscle, is prominent, flange-like, pointed and directed posteromedially (Fig. 4a: lt). Parallel and anterior to this trochanter, and in medial view, there is a deep elongated furrow (25 mm long) that extends to the midshaft. A rudimentary **third trochanter** is present for the insertion of the gluteus superficialis muscle (Fig. 4a: tt). It is a swelling 10 mm long on the lateral surface of the shaft and is situated slightly below the level of the lesser trochanter. A protuberant **intertrochanteric crest** encloses a deep trochanteric fossa (Fig. 4d: ic). The **shaft** is straight and slightly flattened anteroposteriorly. Its cross section is subrectangular at midshaft and expands towards the distal end. In lateral view a very low lateral keel is present just below the midshaft, which probably corresponds to the insertion for the m. adductor magnus (sensu Bebej et al. 2012). The distal part of the shaft bulges anteriorly slightly and shows a torsion of 14° directed medially with respect to the frontal plane of the proximal shaft. The **patellar surface** is angled toward the lateral condyle. It is 20 mm wide and covers the anterior and distal portion of the epiphysis. The lateral epicondyle is slightly projecting laterally. It has one small rounded fossa, probably for the insertion of the lateral collateral ligament, and underneath which there is an elongated fossa following the distal border of the epicondyle, probably the popliteal fossa for the popliteus muscle (Fig. 4b: pf). The medial epicondyle has a suboval fossa (9 mm in width), probably for the insertion of the medial collateral ligament (Fig. 4e: mcl). The ventral surface of the trochlea is inclined 12 degrees with respect to the shaft axis. The **condyles** are well developed. The medial femoral condyle is larger (18 mm in height x 14 mm in width) than the lateral condyle (17 mm in height x 11 mm in width) and extends forward posteriorly. The articular surfaces of the condyles are convex to flat and face posteriorly relative to the femoral shaft. The **intercondyloid fossa** is deep (13 mm, measured from the

posterior end of the patellar trochlea to the posterior surface of the condyles) and has two deep oval depressions. The larger depression takes up the medial part of the lateral condyle. This structure is interpreted as the insertion of the anterior cruciate ligament (Fig. 4d: acl), which attaches to the medial surface of the lateral femoral condyle and inserts on the intercondylar eminence of the tibia. The smaller depression is situated in the upper part of the fossa, close to the medial side of the medial condyle, coinciding with the expected insertion point of the posterior cruciate ligament (Fig. 4d: pcl), which is attached to an eminence at the popliteal notch of the tibia and ends in the anterior part of the intercondyloid fossa of the femur.

MPZ 2018/520 is identified as a right distal epiphysis because of the size of the condyles (Fig. 4g, h). The medial condyle (17 mm in height x 11 mm in width) is larger than the lateral (14 mm in height x 11 mm in width) and extends forward posteriorly, as in MPZ 2017/53. The dorsal surface of the bone is rugose, and its profile is consistent with the conspicuous fusion line observed in MPZ 2017/53. Its general morphology is like that of MPZ 2017/53 but the size is smaller (Table 3), and the muscle scars on the medial and lateral epicondyles, though present, are less marked, in accordance with what would be expected for a specimen younger than MPZ 2017/53.

MPZ 2017/55 is an isolated **femoral head** (Fig. 4i-k; Table 3)). The articular surface of the head is symmetrical and rounded. It is 9 mm in height. This femoral head is the right size to articulate with the acetabulum of the innominate bones MPZ 2017/47 and MPZ 2017/48, described above. The presence of a fovea capitis is not clear, because the area where it would be located has been eroded by plants, hampering its identification. Nevertheless, the large and strongly marked acetabular surface of the innominate bones indicates that the round ligament anchoring the femoral head in the acetabulum was probably present.

Patellae

Two specimens (MPZ 2017/51 and MPZ 2017/52) are preserved (Fig. 5). They are large and pointed-oval to teardrop-shaped in anterior view. The proximal edge (or patellar base) is higher

anteroposteriorly than the distal edge, making the bone wedge-shaped in lateral view. In both patellae, the base has a deep furrow parallel to the posterior border, probably for the attachment of the quadriceps tendon (Fig. 5b, e: qt). The apex is thin and rounded. There is a horizontal notch in the apex, interpreted as an insertion area for patellar ligaments that connect the patella with the tibial tuberosity. The posterior (femoral) side is gently concave, with a single femoral facet (Fig. 5c, f: ff)). There is a thin furrow on this side, which surrounds the distal border, probably for the attachment of the articular cartilage. Although the two patellae are similar in shape, they show some differences. MPZ 2017/52 is larger than MPZ 2017/51 (Table 4), and the perimeter of the femoral facet is better marked and slightly protuberant in this patella. Its articular surface is oval, with the larger axis directed diagonally (20 mm in height x 15 mm in width) and occupies almost the whole posterior side of the patella. By contrast, this facet is proportionally smaller (14 mm in height x 13 mm in width) and rounded, and positioned more dorsally, in MPZ 2017/51. These differences are interpreted as ontogenetic variability; the smaller patella, MPZ 2017/51 (Fig. 5a-c), is assigned to a younger individual, with scars for the attachment of the articular cartilage and the femoral facet less marked.

Fibula

MPZ 2017/56 is a left fibula that lacks the epiphyses (Fig. 6a-e), and MPZ 2018/521 is the proximal diaphyseal fragment of a right fibula that also lacks the epiphysis (Fig. 6f-i). The fibula is not fused to the tibia. MPZ 2017/56 is a slender bone and has a total length of 65 mm (see Table 5 for other measurements). The dorsal surface is rugose for the fusion of the proximal epiphysis, and although slightly broken, it preserves a subrectangular shape. The proximal edge shows a small blunt protuberance on the medial side, followed by a shallow depression located towards the posterior side. This depression is limited by a posterolaterally-projected crest, which disappears gradually towards the midshaft. The lateral side has a low ridge, which is more developed in MPZ 2018/521. The fibular shaft is arched in anterior view (Fig. 6a). The proximal midshaft is broad and lateromedially flattened. It gets narrower towards the distal midshaft, which is anterolaterally rotated with respect to the sagittal plane of the proximal midshaft. In addition, the distal

midshaft is triangular in cross-section, with the medial side flattened. In posterior view, the distal edge of the fibula broadens slightly and has an elongated shallow furrow bordered by a prominent distolateral crest, which is 10 mm long and was interpreted as the processus lateralis fibulae in Díaz-Berenguer et al. (2018) (Fig. 6c: plf). In ventral view, the fibula shows a triangular rugose surface anteriorly angled.

Comparisons

Innominate bones. The *Sobrarbesiren cardieli* innominate bones resemble those of the other basal sirenians, the prorastomids and protosirenids, in having a deep acetabulum, a large obturator foramen and a long pubic symphysis (Fig. 7); the exception is *Protosiren sattaensis*, which has a pointed pubic bone and lacks a pubic symphysis (Gingerich et al. 1995a). However, there are important differences among the quadrupedal sirenian innominate bones. *Sobrarbesiren* has an autapomorphic lateral iliac spine (“crista lateralis” in Abel 1904 and “dorsal iliac spine” in Gingerich et al. 1995a and Zalmout and Gingerich 2012) that appears abruptly on the lateral surface of the ilium and presents a flattened and rugose ventrolateral surface (Fig. 3b, f and Fig. 7b: lilsp). In the process of reduction and modification of the sirenian innominate bones, the ilia become narrower lateromedially and expand dorsoventrally, and the proximal iliac crest turns into the lateral spine present in *Sobrarbesiren*. This spine is also present in protosirenids (Abel 1904; Gingerich et al. 1995a) (Fig. 7c- e). The *Pezosiren* ilia are thin, flattened dorsoventrally and lateromedially expanded, especially on their anterior edge, which is pointed and ventrolaterally directed. *Pezosiren* preserves a well-developed iliac crest like that of terrestrial mammals, with a flattened and rugose proximal surface (Fig. 7a). This surface is similar to that observed on the lateral iliac spine of *Sobrarbesiren* (Fig. 7b). By contrast, the protosirenid lateral iliac spine rises gradually from the ilion surface and lacks a flattened dorsal surface, at least in *P. fraasi* and *P. smithae*. This structure is broken in *P. sattaensis*. *Protosiren fraasi* has a lateral iliac spine that begins just anterior to the acetabulum, whereas it begins in the middle of the iliac ramus in *P.*

smithae, *P. sattaensis* and *Sobrarbesiren* (Fig. 7b-e). The lateral spine is absent in Eocene dugongids (e.g., Zalmout and Gingerich 2012: fig. 77).

Another autapomorphic feature of the *Sobrarbesiren* ilia is the presence of a **posterior iliac spine** (Díaz-Berenguer et al. 2018) (Fig. 3b,f: pilsp). This spine probably corresponds to the sacral tuber in Getty and Sisson (1975), or “*épine iliaque dorso-caudal*” in Barone (1976), a structure related to the sacral articulation present in extant mammals such as horses, pigs and dogs (Getty and Sisson 1975) or humans (Barone 1976). In pigs and dogs, the sacral tuber articulates directly with the sacrum; it is divided into two eminences in the latter; and in horses it is the highest part of the skeleton and does not make contact with the sacrum (Getty and Sisson 1975). This structure thus shows great morphological variability. However, the sacral tuber is the attachment area of some accessory ligaments to the sacroiliac articular surface, though not directly connected with this surface; examples include the dorsal sacroiliac ligament that joins the sacral tuber to the top of the sacral spines (Getty and Sisson 1975). Therefore, although the exact role of the posterior iliac spine in *Sobrarbesiren* is not clear, its presence reinforces the idea of a strong connection between the innominate bones and the sacrum of this stem sirenian. The posterior spine is present in both *Sobrarbesiren* innominate bones MPZ 2017/47 and MPZ 2017/48, but they show different morphologies. MPZ2017/47 has a posterior spine composed of three isolated and blunt protuberances forming an isosceles triangle that is consistent with a syndesmotomic articulation, whereas MPZ 2017/48 has a flattened, triangular and pointed posterior spine. This difference is interpreted as an intraspecific variation in an element that is undergoing a process of modification. The posterior iliac spine is absent in all other sirenians.

The sacroiliac articular surface of Eocene sirenian innominate bones is gradually reduced in the process of adaptation to aquatic life, as is the number of sacral vertebrae. *Sobrarbesiren* has a large and rugose sacroiliac articular surface (Fig. 3d, h: sas), and the distance between this surface and the obturator foramen is similar to that in *Pezosiren* (Díaz-Berenguer et al. 2018). The amphibious proramphid *Pezosiren* has a sacroiliac joint similar to that of terrestrial mammals (Domning 2001b), but it lacks a prominent posterior iliac spine like that in *Sobrarbesiren*. Instead,

the medial side of the *Pezosiren* ilium bends and expands mediolaterally at the level of the base of the sacroiliac articular surface and continues to the anterior edge of the ilium (Fig. 7a-b). Protosirenids have already lost the sacroiliac articulations (Gingerich et al. 1995a), although the holotype of *Protosiren sattaensis* (Fig. 7d) shows a marked expansion of the dorsal margin of the proximal part of the ilium in medial view, and the innominate bone of *Protosiren smithae* shows a gentle deviation of the dorsal border of the ilium near its distal edge at the level of the beginning of the lateral iliac spine (Fig. 7e). These are probably a remainder of the sacroiliac surface observed in the bent ilia of *Pezosiren*. Gingerich et al. (1995a) argued that despite the absence of a sacroiliac joint, the *P. sattaensis* ilia were probably connected to the transverse processes of the sacral vertebrae, via ligaments attached to the rugose surface of the anterior edge of the ilium. This rugose surface is also present in the *Sobrarbesiren* ilia, so there is an extra connection between the ilia and the sacral vertebrae in addition to the sacroiliac joint in the Spanish taxon. Eocene dugongids lack well-developed sacroiliac articular surfaces, with the exception of the late Eocene Egyptian taxon *Eotheroides clavigerum*, which has a concave and rugose sacroiliac articular surface, indicating a robust attachment between the ilia and the sacral vertebra through ligaments and cartilage (Zalmout and Gingerich 2012).

The *Sobrarbesiren* innominate bones preserve the **iliopectineal eminence** on the ventral surface of the bone, just anterior to the acetabulum (Fig. 3b, f: ie). Abel (1904, pl. 7, fig. 1) describes the iliopectineal eminence (or “tuberculum iliopectinum”) on the innominate bone of *Protosiren fraasi*. It is more pronounced and pointed in *P. fraasi* than in *Sobrarbesiren* (Fig. 7b-c). The Pakistani protosirenid *Protosiren sattaensis* shows a distinct gentle bulge on the ventral side of the innominate bone, just anterior to the acetabulum, which is probably a reduced iliopectineal eminence, but it lacks rugosities for muscle insertion or a lateral projection. The iliopectineal eminence is not present on the innominate bone of any other sirenian, including the Eocene quadrupedal sirenians *Pezosiren* and *Protosiren smithae*.

The subtriangular roughened area for the attachment of the m. rectus femoris observed in the *Sobrarbesiren* innominate bones, especially in specimen MPZ 2017/48 (Fig. 3b: mrf), is also

present in the protosirenid *Protosiren fraasi* (Fig. 7c). Andrews (1906) described the presence of a roughened area for the attachment of the rectus femoris muscle on the innominate bone of the Eocene dugongid *Eosiren libyca*, but it has not been possible to confirm its presence, on account of the preservation of the specimen.

With respect to the **acetabulum**, *Sobrarbesiren* has a very deep acetabulum that is rounded in shape and with a horizontal acetabular surface similar to the *Pezosiren* acetabulum. However, its lip is very high in its anterior part and low in the dorsal and ventral parts, as in *Protosiren fraasi* (Hautier et al. 2014), whereas it maintains the same height throughout its perimeter in *Pezosiren*. As a result of this acetabulum morphology with its elevated lip, *Sobrarbesiren* would have had the proportionally deepest acetabulum of all basal sirenians. Protosirenids also show a higher acetabular lip in their anterior part, but the acetabulum is shallower (ratio between the acetabulum depth and the acetabulum diameter is 0,37 in *P. fraasi* (measurements in Abel 1904), 0,36 mm in *P. smithae* and *P. sattaensis*, and 0,65 in *Sobrarbesiren*) and exhibits a crescent-shaped morphology with its longer axis directed anteroventrally-posterodorsally, except in *P. fraasi*, which also has a rounded acetabulum. *P. sattaensis* shows the most opened acetabular notch, with a ratio of “acetabular notch width to acetabulum diameter” of 0.68. In *P. fraasi* and *P. smithae* the ratio is 0.54, which is similar to that of *Sobrarbesiren*. Nevertheless, the *Sobrarbesiren* acetabular fossa is larger than that of protosirenids and occupies almost the whole anteroposterior diameter of the acetabulum. Among protosirenids, *P. fraasi* shows the largest acetabular fossa. The acetabular notch separating the ends of the lunate surface within the acetabulum thus tends to be more opened, and the acetabular fossa is less clearly defined and anteroposteriorly lower, a condition consistent with the loss of the fovea capitis observed in protosirenid femora (see below for comparison of femora). Further, the acetabular surface is angled towards the obturator foramen in protosirenids. All these features are also observed in Eocene dugongid innominate bones, which show a crescent-shaped acetabulum with a higher anterior part of the lip, a shallow acetabulum, an acetabular fossa that is barely marked or is lost, and an acetabular surface that is verticalized.

The latter feature is especially marked in the late Eocene Hungarian innominate bone MÁFI V.15366, belonging to *Sirenavus* sp.

One of the structures that undergo the greatest changes in the process of reduction of the innominate bones is the obturator foramen. Other marine mammals that also modify the pelvis, such as cetaceans or pinnipeds, show a tendency to enlarge the obturator foramen, at least in the basal taxa (Uhen 2014; Bebej et al. 2015; Berta and Ray 1990). In contrast, sirenians reduce this foramen to the point of disappearance. *Pezosiren* has an obturator foramen whose greatest diameter is directed anterodorsally-posteroventrally (Fig. 7a), as in many terrestrial mammals, such as deer, goats, rhinoceroses, horses, buffaloes and pigs (Pales and Lambert 1971). The teardrop-shaped morphology of the large *Sobrarbesiren* obturator foramen is similar to that of *Pezosiren*, but proportionally reduced in size (Fig. 7a-b; Table 2). In addition, in *Sobrarbesiren* the pointed anterior margin of the obturator foramen and the presence of the obturator groove provide evidence that the obturator nerve and vessels are still present in this taxon. Protosirenids show a different morphology. The maximum diameter of the obturator foramen is directed dorsoventrally as a horizontal oval in *Protosiren fraasi*; it is anteroposteriorly directed in *P. sattaensis* and anteroventrally-posterodorsally in *P. smithae* (Fig. 7c-e). The *Sobrarbesiren* obturator foramen is proportionally smaller than that of *P. fraasi* and *P. sattaensis* (and bigger than that of *P. smithae*) (Fig. 7b- e) (Table 2). In the innominate bones of the Eocene dugongids, the obturator foramen is reduced to a tiny hole.

The innominate bone of *Pezosiren* has narrow ischia. This bone tends to expand dorsoventrally in protosirenids (Zalmout and Gingerich 2012). *Sobrarbesiren* also has an expanded ischium, but its general morphology resembles that of *P. fraasi*, with a straight distal border, unlike the rounded ischium edge of *P. smithae* and *P. sattaensis* (Fig. 7d-e). The ischia of the Eocene dugongids are more elongated and narrower.

Gingerich et al. (1995a) highlight differences in the width of the pubic ramus behind the obturator foramen in the *Protosiren* spp. The pubic ramus is very thin in *Protosiren sattaensis* and

Protosiren fraasi and much broader and more robust in *Protosiren smithae* (Fig. 7c-e). The *Sobrarbesiren* pubic ramus is even broader than that of *P. smithae* but the pubic ramus in front of the foramen is more gracile in the Spanish taxon (Fig. 7b). The posterior pubic ramus is also wider than the anterior one in Eocene dugongids such as *Eotheroides* spp. and “*Halitherium*” *taulannense*, in spite of their greatly reduced obturator foramen. The *Sobrarbesiren* pubic bone is dorsoventrally expanded and elongated in the space where the two pubic rami contact, more so than in *Pezosiren* or in the *Protosiren* spp.

The *Sobrarbesiren* pubic symphysis is long and rugose, as expected for a symphyseal fibrocartilage attachment. The *Sobrarbesiren* innominate bones would probably thus have been strongly connected to one another, and probably also in *P. fraasi* and *P. smithae*. By contrast, the end of the pubic bone is pointed in *P. sattaensis* and there is no pubic symphysis, indicating that the connection between the two innominate bones would have been weak (Gingerich et al. 1995a).

The *Sobrarbesiren cardieli* innominate bones are very primitive compared with those of Eocene dugongids. The innominate bones of *Sobrarbesiren* differ from the latter mainly in having a well-developed and deep acetabulum, a large obturator foramen and an elongated pubic symphysis.

Femora. The general morphology of the *Sobrarbesiren* femora resembles that of basal sirenians such as the prorastomid *Pezosiren portelli* and the protosirenid *Protosiren smithae* in having a pronounced lesser trochanter, a prominent intertrochanteric crest, a deep trochanteric fossa, a distal epiphysis with robust condyles, and a wide patellar surface (Fig. 8). Nevertheless, there are important differences between the bones of the three taxa. The isolated femoral head MPZ 2017/55 of *Sobrarbesiren* is hemispherical (Fig. 8d-e), with an articular surface diameter of 12 mm. The *Pezosiren portelli* femur (USNM 517465; Fig. 8a-b) has a spherical femoral head, and the articular surface is taller than in the Spanish taxon. By contrast, the holotype femur (cast, USNM 94810) of *Protosiren smithae* has an asymmetrical head that narrows towards the notch between the head and the greater trochanter (Fig. 8h-i). It is very flattened and has a proportionally smaller (5 mm in height) articular surface. When observed in anterior view, this articular surface

is limited to the more medio-dorsal part of the head, but in posterior view the articular surface occupies almost the entire surface from the notch that separates it from the greater trochanter to the medial border of the head. It is clearly displaced medially and posterodorsally in comparison with the dorsomedially directed femoral head of *Pezosiren*. The *Pezosiren* femoral head preserves the fovea capitis, as is the case in terrestrial mammals, and is separated from the shaft by a prominent neck, whereas the *P. smithae* femur lacks the fovea capitis and has a short neck. Furthermore, the femoral head is above the greater trochanter in *Pezosiren* and at the same level as the trochanter in *P. smithae* (Fig. 8a-b, h-i). According to Gingerich et al. (1997), the general morphology of the femur of the protosirenid *Protosiren sattaensis* is similar to that of *P. smithae*, apart from its more slender and longer diaphysis. This taxon also has a femoral head positioned above the greater trochanter, although in this case it is because the trochanter is reduced and the notch between the femoral head and the trochanter is very low (Gingerich et al. 1997: fig. 13B), as in the femora of Eocene dugongids. This feature is unknown in *Sobrarbesiren*. The lesser trochanter of *Sobrarbesiren* is of the same size as that of *P. smithae*, but it is more pointed (Fig. 8f, i: lt). Both are relatively smaller than the enlarged sheet of bone that forms the lesser trochanter in the femur of *Pezosiren* (Fig. 8b: lt). The lesser trochanter of *P. sattaensis* is broken but present (Gingerich et al. 1997: fig. 13B). The third trochanter is a small protuberance in *Sobrarbesiren* (Fig. 8f: tt) similar to that described by Gingerich et al. (1995b, fig. 15) for the archaeocete *Remingtonocetus* cf. *R. harudiensis* from the early Lutetian (middle Eocene) of Pakistan. It is very reduced compared with the sheet-like, laterally expanded third trochanter of *Pezosiren* (Fig. 8b: tt). It is absent in the *Protosiren* spp. (Domning and Gingerich 1994; Gingerich et al. 1997) (Fig. 8i). The intertrochanteric crest is low in *Sobrarbesiren* and *P. smithae* and is pronounced in *Pezosiren*. The trochanteric fossa is significantly shorter and deeper in *Pezosiren* than in the other basal sirenians.

The *Sobrarbesiren* femoral midshaft is rounded and narrow at the level of the lesser trochanter like that of *Pezosiren*, and maintains a constant diameter as far as its distal extremity, where it broadens. The shaft of *P. smithae* has an hourglass-like general morphology and is broad and

anteroposteriorly very flattened at the level of the lesser trochanter, narrows just in the midshaft, and broadens again toward the distal end. The femoral shaft of *Sobrarbesiren* shows a medial torsion of the distal end of 14° with respect to the frontal plane of the proximal edge. This torsion is more pronounced (50°) in the femur of *P. smithae* (Fig. 8g, j) and seems also to be present in the *P. sattaensis* femora (Gingerich et al. 1997: fig. 13 B). However, *Pezosiren* has a straight femoral shaft (Fig. 8b, f, i).

Although the patellar trochlea and condyles are well developed in the *Sobrarbesiren* and *P. smithae* femora, there is a clear decrease in the size of the femur's distal extremity compared with the proximal part (Table 3). By contrast, the proximal and distal extremities are of approximately the same size in *Pezosiren* (Fig. 8b, f, i). In addition, there are some differences with respect to the femur distal extremity of the non-prorastomid taxa. The width of the distal end is proportionally greater in *P. smithae* (length of the femoral body: 139 mm; greatest width of the distal end: 42 mm) than in *Sobrarbesiren* because of the presence of a very pronounced medial epicondyle that projects posteromedially in *P. smithae*, which is scarcely marked in *Sobrarbesiren* (Fig. 8g, j: mc). Moreover, the patellar trochlea of *P. smithae* significantly overhangs anteriorly in lateral view in comparison with the trochleae of the other quadrupedal sirenians. The internal distance between the condyles (the width of the intercondyloid fossa) is proportionally greater in *Pezosiren* (the ratio between the width of the intercondyloid fossa and the length of the femoral body is: 0.11) than in *Sobrarbesiren* (0.06) and slightly smaller in the Egyptian taxon (0.05) (Table 3). The medial condyle is larger than the lateral in the *Sobrarbesiren* femur. Both condyles are similar in size in the *Pezosiren* femur. In the *P. smithae* femur the lateral condyle is the larger.

The *Sobrarbesiren* femur is very different from the reduced femora of the Eocene dugongids (e.g., Zalmout and Gingerich 2012: fig. 64). It differs in having a well-developed head, a prominent lesser trochanter, a third trochanter and an intertrochanteric crest, a deep trochanteric fossa, and a still functional distal extremity.

Patellae. These bones are known in the three quadrupedal sirenians under consideration. The general morphology of the *Sobrarbesiren* patella MPZ 2017/52 is similar to DPD UNNUM of the Jamaican taxon *Pezosiren portelli*. Both bones are teardrop-shaped in anterior view and have a concave posterior side in lateral view (Fig. 9a, d and b, e). Nevertheless, the patella of *Pezosiren* is trapezoidal in lateral outline, with a thicker and more rounded apex than that of *Sobrarbesiren*. In *Pezosiren*, the femoral facet is elongated, covering the entire length of the posterior side, and very concave, which is different from the more rounded and flattened femoral facets of *Sobrarbesiren* and *Protosiren smithae* (Fig. 9d, e, f). The *Sobrarbesiren* and *Pezosiren* patellae are very different from the holotype patella CGM 42292 (cast, USNM 94810) of *P. smithae*. This patella is rounded in outline (Fig. 9c, f), with its total length equal to its maximum width, and its posterior side is slightly convex in lateral view. Further, the articular surface of the *P. smithae* patella is divided into two clearly discernible femoral facets separated by a low ridge (Fig. 9f: mff, lff), whereas there is a single femoral facet in *Sobrarbesiren* and *Pezosiren* (Fig. 9d, e: ff). One femoral facet is bigger than the other in the *Protosiren* patella; probably the lateral one is bigger in accordance with the size of the femoral condyles (Fig. 8j). In addition, *Sobrarbesiren* has a dorsal furrow for the attachment of the quadriceps tendon, which is absent in *Pezosiren*. *P. smithae* shows a dorsal flange, but not a furrow, probably also related with the quadriceps tendon (Fig. 9b, c: qt).

Fibulae. The fibulae described in *Sobrarbesiren* (MPZ 2017/56, MPZ 2018/521; Fig. 6) are the oldest sirenian fibulae known (Díaz-Berenguer et al. 2018). Domning and Gingerich (1994: fig. 11G) figured the fibula of the protosirenid *Protosiren smithae* from the Bartonian-Priabonian of Egypt, but no other fibulae are known from the sirenian fossil record. As in *Sobrarbesiren*, this fibula is not fused to the tibia and its general morphology is similar, although there are differences between the two fibulae. In the holotype right fibula of *P. smithae* (cast, USNM 94810), the cross-section is rounded throughout the shaft, whereas in the *Sobrarbesiren* fibula MPZ 2017/56 (Fig. 6a-e) it is lateromedially flattened in the proximal midshaft and triangular in its distal part. Ac-

cordingly, the distal or ventral surface of the fibula is rounded in *Protosiren* but bears a longitudinal ridge in *Sobrarbesiren*, with the medial side flattened. The posterolateral crest present at the proximal end of the *Sobrarbesiren* fibula MPZ 2017/56 is less marked in the *Protosiren* fibula, but the Egyptian specimen has a low keel along its medial side. However, the processus lateralis fibulae described in *Sobrarbesiren* (Díaz-Berenguer et al. 2018) is absent in the Egyptian taxon.

(b) Functional morphology

Hip joint. The hip joint is formed by the articulation between the pelvic acetabulum and the head of the femur. The acetabular fossa and the femoral head of the basal sirenians show important differences related to their capacity for hindlimb movement. The *Sobrarbesiren* innominate bones preserve a deep acetabulum that is rounded in shape, a large acetabular fossa, and a narrow acetabular notch, in accordance with the rounded morphology of the femoral head MPZ 2017/55 (Fig. 4i-k). Nevertheless, the acetabular lip is higher in its anterior part. A hemispherical femoral head suggests that the femur is capable of rotation and provides evidence for broad motion at the hip joint. The *Sobrarbesiren* hip joint is capable of flexion and extension movements in the parasagittal plane, evidenced by the elevated anterior lip of the acetabulum, and abduction movements, thanks to the low and slightly concave dorsal border of the acetabulum. In addition, the *Sobrarbesiren* innominate bones and femur preserve several insertions for muscle attachment that testify to powerful control of the hip joint and thigh movements. The roughened area just anterior to the acetabulum observed in the *Sobrarbesiren* innominate bones (Fig. 3) is the point of origin of the **rectus femoris** (one of the four quadriceps muscles), which would be attached to the deep furrow at the base of the *Sobrarbesiren* patella (Fig. 5) via the quadriceps tendon (Getty and Sisson 1975). The iliopectineal eminence also present on the *Sobrarbesiren* innominate bones (Fig. 3b, f: ie) is where the **pectineus muscle** originates (Uhen 2014). This muscle attaches to the medial side of the femoral shaft. The presence of the lesser trochanter and a rudimentary third trochanter in the *Sobrarbesiren* femur (Fig. 4a: tt) indicates that the **iliopsoas** and the **gluteus superficialis** muscles are still present. All these muscles are involved in the flexion of the hip joint, and moreover, the iliopsoas takes part in the lateral rotation of the thigh. The pectineus

muscle also takes part in the adduction of the thigh, and the gluteus superficialis muscle in the abduction of the limb. The presence of the **adductor magnus** muscle is also proposed. This muscle inserts along the lateral surface of the femur, and it is involved in the extension and adduction of the hip joint (Bebej et al. 2012). It has been associated with the strong lateral keel observed in the remingtonocetid femora (Bebej et al. 2012). The lateral side of the *Sobrarbesiren* femur has a very small and low lateral ridge (Fig. 4b) in comparison with the strong lateral keel of remingtonocetids, but the existence of the adductor magnus muscle in *Sobrarbesiren* cannot be ruled out. However, some of the structures, such as the lesser and third trochanters, where some of these muscles must have inserted, are reduced in size in *Sobrarbesiren* in comparison with the quadrupedal amphibious *Pezosiren* (Fig. 8a-b, d-f), which displays a mediolaterally-shorter articular surface of the femoral head. There is thus a decrease in the capacity for motion of the hip joint compared with the Jamaican taxon.

In turn, protosirenids show a crescent-shaped, shallower acetabulum, except for *Protosiren fraasi* (Fig. 7c-e), and a smaller acetabular notch in addition to a flattened femoral head that lacks the fovea capitis. According to Adam (2009) the absence of a **fovea capitis femoris** is evidence of the loss of the round ligament “which normally maintains the femoral head within the acetabulum of the pelvis in mammals that have weight-bearing hip joints”. The absence or reduction of the fovea capitis femoris, like the modification of the acetabular fossa, is an argument broadly used as evidence of adaptation to aquatic life in marine mammals such as Archaeoceti (e.g., Gingerich et al. 2001; Gingerich and Cappetta 2014; Bebej et al. 2015). Nonetheless, various graviportal mammals such as desmostylians and proboscideans (Domning 2002; Shil et al. 2013, respectively) lack the fovea capitis, indicating that it is possible to do without this structure and still support one’s weight on land. However, the absence of the fovea capitis in the *Protosiren smithae* femur is clearly a derived condition from the femur of the prorastomid *Pezosiren*. In protosirenids, moreover, the reduction in size of the acetabular fossa, where the round ligament is anchored, is evidence of a reduction in control of hindlimb movement in this sirenian family. Whether the fovea capitis is present or absent in the *Sobrarbesiren* femora is unknown, but the

acetabular fossa of the *Sobrarbesiren* innominate bones is proportionally bigger than that of protosirenids (Fig. 7b-e), occupying almost the entire anteroposterior length of the acetabulum. Therefore, the presence of the round ligament in the Spanish taxon cannot be ruled out.

A different morphology of the femoral head articular surface implies a different capacity for hindlimb movements. *Pezosiren* has a spherical femoral head and *Sobrarbesiren* a hemispherical one, and both have deep acetabula (Fig. 8a, b and d, e), evidencing a wide variety of thigh movements. By contrast, the *Protosiren smithae* femoral head is flattened and lateromedially elongated, in accordance with the acetabular morphology of the innominate bone (Fig. 8h, i). This indicates that *P. smithae* was capable of a smaller variety of limb movements in comparison with *Pezosiren* and *Sobrarbesiren*. Indeed, the morphology of the femoral head of *P. smithae*, together with its inclined acetabulum, its long axis directed anteroventrally-posterodorsally and its low dorsal and ventral acetabular borders, implies a tendency for movement of the hip joint in one direction. If, as proposed by Gingerich et al. (1997), the morphology of the femur of *P. sattaensis* is similar to that of *P. smithae*, a similar capacity for limb movement can be inferred. The form of the femoral head in mammals reflects the position of the femoral long axis relative to the body axis (Jenkins and Camazine 1977). There is a significant difference in the angle formed by the femoral neck with the femoral long axis between *Pezosiren* (47°) and *P. smithae* (65°), indicating a more abducted position of the femur in the latter. The absence of a complete femur of *Sobrarbesiren*, including a femoral head, prevents us from inferring the femur position in relation to the body axis.

Knee joint. The bones involved in the knee joint are the femur, the tibia and the patella. The small fossae for the insertion of the **medial and lateral collateral ligaments, the cruciate ligaments** and the **popliteus muscle**, which control the stability of the knee, are present in the *Sobrarbesiren* femur. This, in conjunction with a broad patellar surface, the presence of a large patella with an insertion area for the patellar ligaments, and the well-developed femoral condyles, indicates that *Sobrarbesiren* had a heavily muscled knee.

The articular condyles of the femur are directed posteriorly in *Sobrarbesiren*, *Pezosiren* and *Protosiren*. This indicates that the knee always remained flexed (Gingerich et al. 1990). According to Court (1994), “in medial view, a line drawn from the posterior-most extent of the inner condyle to its anterior margin, when orientated in the horizontal plane, reflects the position of maximum articular congruence at the knee and the likely habitual posture of the femur”. This method has been used to infer the femur posture in different quadrupedal animals, such as *Numidotherium koholense* (Court 1994) and *Desmostylia* (Domning 2002), among others. By this criterion, the femur of *Sobrarbesiren* would have habitually inclined about 51° from the vertical in resting posture. Similar angles are recovered for *Pezosiren* (53°) and *Protosiren smithae* (49°), indicating a similar normal resting posture of the femur. *Sobrarbesiren* and *P. smithae* share a feature not observed in the proramphid *Pezosiren*: a torsion of the femoral shaft (Fig. 8c, g, j). Other taxa with a distal torsion of the femur are the marine sloth *Thalassocnus* Muizon and McDonald, 1995 (Amson et al. 2015) and the Eocene archaeocete whale *Basilosaurus isis* Beadnell, 1904 (Gingerich et al. 1990). Both are similar in having an abducted position of the knee. When the femur of *P. smithae* is positioned with its distal extremity parallel to the frontal plane, then the proximal extremity is turned laterally and the long axis of the femoral head is directed anteromedially-posterolaterally in accordance with the long axis of the acetabulum. The result is a knee abducted in the normal resting posture. Even in the absence of a complete femur, a similar posture can be inferred for the *Sobrarbesiren* knee. The only dugongid that shows a medial femoral torsion is *Eotheroides sandersi* (Zalmout and Gingerich 2012, fig. 64).

Tibiae are only preserved in *Pezosiren* and *Protosiren smithae*, but there are also some differences between the tibiae of these taxa. The *Pezosiren* tibia (USNM 517466) has a prominent and elongated cnemial crest and the shaft shows a medial torsion (Domning 2001b). The cnemial crest of the *Protosiren* tibia (CGM 42292) is shorter and is limited to the first third of the shaft, and the distal midshaft is directed laterally and shows a lateral torsion relative to the proximal end. By contrast, the *Pezosiren* distal midshaft is slightly directed medially. This difference in the torsion direction of the tibia, in conjunction with the torsion of the *Protosiren* femur, brings to light a

different position of the limb with respect to the sagittal body axis from that in *Pezosiren*. Although the tibia of *Sobrarbesiren* is not known, the fibula shows a lateral torsion of its distal extremity (Fig. 6). This, together with the lateral torsion of the *Sobrarbesiren* femora when it is positioned with its distal extremity parallel to the frontal plane, albeit less strong than in *Protosiren*, suggests a position of the hindlimb similar to that of *P. smithae*.

The tibia of *P. smithae* (specimen CGM 42292, cast) is surprisingly long with respect to the femur, considering that the zeugopodium of this animal is in a process of reduction. The estimated ratio between the tibia total length and the femur total length is 0.94, even though the *Protosiren* tibia lacks the distal epiphyses. If this proportion is accurate, it suggests the hypothesis that prior to the incipient process of reduction in the sirenian zeugopodium, there was an elongation of the tibia in protosirenids related to adaptation to aquatic life. A tibia proportionally longer relative to the femur is a feature found in mammals secondarily adapted to aquatic life, such as marine sloths (Muizon and McDonald 1995) or pinnipeds (Berta and Ray 1990). The *Pezosiren* femur and tibia were recovered as isolated fossils in two different bonebeds from the same stratigraphic section (Domning 2001b), so they pertain to different individuals and comparisons can't be made to test this initial hypothesis.

The femoral facet of the patella is subdivided into medial and lateral facets by a more or less salient ridge for articulation with the femur in many mammals, such as proboscideans (Shil et al. 2013), artiodactyls and perissodactyls (Pales and Lambert 1971), among others. Patellae with a single femoral facet, like those in *Pezosiren* and *Sobrarbesiren* (Fig. 9), have been described in the basilosaurid archaeocete whales (Gingerich et al. 1990; Uhen 2004). Gingerich et al. (1990) described the hindlimbs of the Egyptian middle Eocene basilosaurid *Basilosaurus isis*. This archaeocete had a highly modified distal extremity of the femur with two well-differentiated positions for the patella separated by a cylindrical ridge. This feature indicates that there was only one alternative position to the normal resting posture (Gingerich et al. 1990). It is not observed in the sirenian femora, so its implication for the sirenian knee is unknown.

Ankle joint. No elements of the sirenian tarsus and back foot are known, so the characteristics of the sirenian ankle articulation remain a mystery. Nevertheless, Díaz-Berenguer et al. (2018) described the presence of the processus lateralis fibulae in the fibula of *Sobrarbesiren* as a plesiomorphy and as evidence of the retention of a mobile foot in this taxon. According to Davis (1964), this process “separates the peroneal tendons into two groups: the long peroneal tendons lie immediately anterior to the process, while tendons of the brevis and tertius lie immediately behind it”. This process is also present in other taxa such as the quadrupedal proboscidean *Numidotherium koholense* Jaeger, 1986 (Court 1994), ursids and phocines (Berta and Ray 1990), and in pakicetid whales (Madar 2007), among others. All of the above are animals with a mobile foot implied in walking and/or swimming. The *Protosiren smithae* fibula lacks this process, but the presence of a functional foot has also been proposed for this taxon related with the presence of the fibula (Domning and Gingerich 1994). Nevertheless, this hypothesis could not be tested due to the absence of the distal epiphysis of the fibula, where articular facets with the tarsus are located, or more distal elements, which could clarify whether the animal might have had real control of its foot. The interpretation of the processus lateralis fibulae as a plesiomorphy in *Sobrarbesiren* implies that it was also present in more basal sirenians or previous ancestors. Thus, if we consider its absence in *Protosiren* as a derived condition, this indicates less control of the foot in this sirenian.

(c) Microanatomical features

Description

The **innominate bone** MPZ 2017/48 is extremely compact, whereas it is spongy in the other taxa where it is known. We thus made several transverse sections in order to gain an idea of the distribution of the osseous tissue along this bone (Fig. 10). The compactness appears rather homogeneous along the bone, with only small cavities rather randomly distributed and with slightly larger ones in the core of the bone. It is indeed the first time that osteosclerosis is observed in an innominate bone.

The **femur** is strongly compact, as shown by the longitudinal and transverse sections performed on the bone (Fig. 11). In this bone, the growth center is at midshaft. Its location is determined following the layers of primary cortical bone, which attain their maximal thickness at the growth center and decrease proximally and distally away from the growth center. The midshaft is strongly compact with a cavity in the core of the section that probably represents the nutrient canal (Fig. 11b). Other cavities are just vascular spaces that are much smaller. Around the growth center, in the centralmost part of the bone (constituting about 18% of its length), compactness remains extremely strong. Away from the midshaft the compactness decreases, forming a spongiosa with rather large trabecular spaces surrounded by a compact cortex (Fig. 11a, c). Towards the epiphyses, the intertrabecular spaces become smaller and thus more numerous.

Comparisons

Innominate bone sections are extremely rare. To our knowledge, the inner structure of innominate bones has been investigated mainly in humans (Cunningham and Black 2009; Abel and Macho 2011), also in monkeys (Volpato et al. 2008), and apart from primates only in an archaeocete whale (Hautier et al. 2014). The protocetid archaeocete innominate sections show large inner cavities connected by thin trabeculae (Hautier et al. 2014: fig.4), whereas the cavities are really small in *Sobrarbesiren* and the spongiosa is strongly compacted. An innominate bone as compact as that of *Sobrarbesiren* has never before been described. Due to the absence of comparative data, especially for taxa displaying a strong increase in bone mass, it is difficult to draw functional inferences based on such a peculiar pattern. Comparisons with other primitive sirenians and with other archaeocete whales and cetaceans with an unfused sacrum would be of great interest in order to better document the possible occurrence of this specialization in the innominate bone in lineages in the process of a secondary adaptation to an aquatic life.

The femur of *Sobrarbesiren* is extremely compact and thus osteosclerotic. Very few femur longitudinal sections exist, and comparisons can primarily be drawn with previously published mid-diaphyseal sections, the usual reference plane for transverse sections. The midshaft section is extremely compact, even more so than in other osteosclerotic amniotes. To our current

knowledge, it is similar only to what is observed in the aquatic sloth *Thalassocnus carolomartini* McDonald and Muizon, 2002 (Amson et al. 2014; Houssaye et al. 2016). Unfortunately, only a mid-shaft transverse section is available for this taxon and longitudinal sections would be required to verify if this high compactness is general to the bone as in *Sobrarbesiren*. The conspicuous variations along the shaft in *Sobrarbesiren*, rare in terrestrial mammals but recently highlighted in several aquatic amniotes (Houssaye et al. 2016), evoke what is observed in the femora of the protocetid whale *Rodhocetus* Gingerich, Raza, Arif, Anwar and Zhou, 1994 and *Maiacetus* Gingerich, Ul-Haq, von Koenigswald, Sanders, Smith and Zalmout, 2009 and the sea otter, but with a significantly higher compactness (Houssaye et al. 2015, 2016; Houssaye and Botton-Divet 2018). Indeed, *Rodhocetus* shows a strongly compact cortex at midshaft, but the medullary area displays an open medullary cavity surrounded by small cavities, unlike the extremely compact structure observed in *Sobrarbesiren*. Similarly, away from the growth center, the medullary area is much lighter. The midshaft section of the whale *Maiacetus* is more compact than in *Rodhocetus* but also shows a much lighter organization than in *Sobrarbesiren*. As for the sea otter femur, it shows an extremely compact mid-shaft as in *Sobrarbesiren* but the overall compactness of the bone is much less compact (Houssaye and Botton-Divet 2018). The extremely compact inner structure of the *Sobrarbesiren* femur thus documents the strongest osteosclerosis observed so far in an amniote femur.

DISCUSSION

Anatomical differences in the hindlimbs of the three quadrupedal sirenians under consideration (*Pezosiren*, *Protosiren* and *Sobrarbesiren*) (Table 6) reveal that these mammals did not swim in an identical fashion, and that some variability in locomotor capabilities existed during the first stages of the evolution of sirenians. Three different evolutionary stages in the adaptation to aquatic life have been described in the Eocene sirenians (Domning 2000), in accordance with the model of transition from terrestrial to aquatic animals based on swimming modes proposed by Fish (1996). Prorastomids exemplify the most primitive condition. They are represented by the Jamaican Lutetian taxon *Pezosiren portelli*, for which the postcranial skeleton is mostly known.

Pezosiren has a normally unfused sacrum (although partly fused in old individuals) composed of three or four vertebrae connected by rigid articulation of the pleurapophyses, a still strong sacroiliac articulation and caudal vertebrae that lack broad transverse processes (Domning 2001b). *Pezosiren* probably had an otter-like tail but with some dorsoventral flattening (Domning 2001b). Prorastomids are considered amphibious quadrupeds that combined dorsoventral spinal undulation with simultaneous pelvic paddling for swimming (Domning 2000, 2001b). The next stage is represented by the protosirenid *Protosiren smithae* from the Bartonian-Priabonian of Egypt. Protosirenids have a single sacral vertebra with elongated pleurapophyses, already lack a sacroiliac joint, and have well-developed hindlimbs and caudal vertebrae with broad, dorsoventrally flattened transverse processes, evidencing the presence of an at least incipient tail fin (Domning and Gingerich 1994; Gingerich et al. 1995a). *Protosiren fraasi* was probably also a quadrupedal sirenian with a functional femur (Gingerich et al. 1995a), but hindlimb elements of this taxon are unknown. Protosirenids are interpreted as aquatic quadrupeds that swam by dorsoventral undulation of the enlarged tail and reduced hindlimbs (Domning 2000). The third stage is represented by Eocene dugongids, which lacked external hindlimbs and were obligate aquatic animals that swam exclusively with the tail (Domning 2000). The dugongids *Eotheroides sandersi* and *Eotheroides clavigerum* from the Priabonian of Egypt are considered already to have had a tail fluke (Zalmout and Gingerich 2012).

Within this evolutionary framework, an intermediate stage of adaptation to aquatic life between the amphibious prorastomids and the aquatic quadrupedal protosirenids was proposed for *Sobrarbesiren* by Díaz-Berenguer et al. (2018). This is supported by the results described in this paper. *Sobrarbesiren* presents a combination of different morphological features not described to date: an unfused sacrum composed of an indeterminate number of sacral vertebrae, with short anteroposteriorly and dorsoventrally expanded pleurapophyses; a strong connection between the sacrum and the ilia; functional hindlimbs; and probably a horizontally-flattened tail, in accordance with the dorsoventrally flattened transverse processes of the caudal vertebrae.

Sirenians and cetaceans share several morphological traits adapted to a completely aquatic life style, such as a reduction in the number of sacral vertebrae and the loss of the connection between the ilium and the sacrum, among others. The presence or absence of a connection between the sacrum and the ilium is considered evidence of different swimming modes in the archaeocete whales (Uhen 2014 and references therein). Pakicetids, ambulocetids and remingtonocetids have a multivertebral sacrum that is solidly fused (e.g., Thewissen et al. 2001; Madar et al. 2002; Madar 2007; Bebej et al. 2012), whereas protocetids show a great variety of stages in the sacral region. Protocetids with a solidly fused sacrum such as *Maiacetus inuus* are considered to swim by alternate pelvic paddling (Gingerich et al. 2009). Protocetids such as *Rodhocetus* and *Natchitochia* Uhen, 1998, with an unfused multivertebral sacrum that is articulated with the innominate bones, are considered to swim by simultaneous pelvic paddling, in other words, with an active role played by the posterior limbs (Uhen 2014). This assumption is based on the fact that they possess a strong sacroiliac articulation between the sacral vertebrae and the innominate bones, independently of their number of sacral vertebrae (four vertebrae in *Rodhocetus* and two sacral vertebrae and two sacrocaudals in *Natchitochia*). Other protocetids such as *Georgiacetus* Hulbert, Petkewich, Bishop, Bukry and Aleshire, 1998, which lack the sacroiliac articular surface, are considered as swimming by dorsoventral pelvic undulation (Uhen 2014). The more derived basilosaurid archaeocetes have innominate bones disconnected from the vertebral column and a caudal fluke, and they are considered to have swum by caudal oscillation (Uhen 2014). The hindlimbs of basilosaurids are very small relative to their body size and have been interpreted as copulatory guides (Gingerich et al. 1990).

The decrease in articulation between sacral vertebrae happens before the loss of the sacroiliac articulation in Eocene cetaceans (Buchholtz 1998). This assumption is also consistent with the evolution of the sacral region in sirenians according to the fossil record. As proposed by Domning (2000), prorastomids such as *Pezosiren* possess an unfused multivertebral sacrum, like that of *Rodhocetus* from the middle Eocene of Pakistan (Gingerich et al. 1994b), and a strong sacroiliac joint. *Sobrarbesiren* has an unfused sacrum composed of at least two vertebrae, in accordance

with the triangular facet observed in the anteroventrally-shortened and dorsoventrally-swollen sacral transverse processes (Díaz-Berenguer et al. 2018), and it preserves the sacroiliac articulation, whereas *Protosiren* spp. lack a real sacroiliac articulation (Gingerich et al. 1995a). Domning (2000) proposed that the *Pezosiren* sacrum is similar to that of the protocetid *Rodhocetus* and that *Pezosiren* also swam by simultaneous pelvic paddling, though in this case combined with dorsoventral pelvic undulation (Domning 2001b). Accordingly, when compared with cetaceans, the most primitive sirenians known are in a similar stage of adaptation to aquatic life as derived protocetids, at least in the evolution of the sacral region. When *Sobrarbesiren* is compared with the archaeocete whales, it could also coincide with derived protocetids, which have a reduced number of unfused sacral vertebrae and preserve the sacroiliac articulation, as *Natchitochia* does (Uhen 2014). Nevertheless, the auricular process of the sacral vertebrae of *Sobrarbesiren* is reduced compared with that of protocetids.

A strong sacroiliac articulation, evidenced by a large articular surface and the presence of the posterior iliac spine, thus indicates that *Sobrarbesiren* was capable of simultaneous pelvic paddling. Although the *Sobrarbesiren* hindlimbs are reduced in size compared to their forelimbs, its hip and knee joints testify to strong control of the hindlimb and a capacity for making a great variety of movements. In addition, the presence of an unfused multivertebral sacrum in *Sobrarbesiren* is evidence of a flexible lumbocaudal region (Uhen 2014). The *Sobrarbesiren* post-sacral vertebrae recovered to date are scarce, and it is not possible to hypothesize about the presence or absence of a fluke. However, the caudal vertebrae show dorsoventrally flattened transverse processes (Díaz-Berenguer et al. 2018), indicating that *Sobrarbesiren* had an at least incipient horizontal tail fin. *Sobrarbesiren* probably combined dorsoventral pelvic undulation with simultaneous pelvic paddling to generate propulsion during swimming. If this is so, the development of a horizontal tail fin begins before the loss of the sacroiliac joint in sirenians, by contrast with what happens in the archaeocete whales. Protocetids are thought to have lacked a tail fluke, and the development of tail fins appears in the more derived archaeocetes of the family Basilosauridae (Uhen 2014 and references therein).

Sobrarbesiren shows an expanded ischium compared with *Pezosiren*, similar to that of protosirenids. In spite of the general reduction in the innominate bone structures observed in non-prorastomid sirenians, exemplified by rod-like ilia or decrease in size of the obturator foramen, curiously the ischia tend to expand. Bebej et al. (2015) proposed that in semiaquatic archaeocetes an expanded ischiatic table is related to the presence of powerful muscles for the retraction of the hindlimbs during swimming. This might also be an explanation for the expansion of the ischia in non-prorastomid quadrupedal basal sirenians.

With respect to protosirenids, several previous authors have discussed the theoretical locomotor capabilities of their hindlimbs in both terrestrial and aquatic locomotion. Domning and Gingerich, 1994 proposed that *Protosiren smithae* was still an amphibious animal, but with functional short limbs relative to its body and a weak sacroiliac joint, which moved on land in a manner similar to pinnipeds and “it merely slid or rested on its belly when out of the water”. Domning (2000) suggested that the tail was the main propulsive organ in swimming in protosirenids and added that the hindlimbs were probably also involved in swimming. Zalmout and Gingerich (2012) argued that a sacrum composed of only one vertebra and the absence of a real sacroiliac articulation implied that *P. smithae* was not an amphibious animal but a quadruped that used its legs “to crawl on the sea bottom while feeding”, reinforcing the hypothesis of dorsoventral caudal undulation as the principal swimming mode of *Protosiren*, and ruling out the idea that hindlimbs had an important role in swimming.

When compared with *Sobrarbesiren*, protosirenids show less control of their hindlimbs. In addition to the absence of the sacroiliac joint, they have a crescent-shaped acetabulum (except for *Protosiren fraasi*), a shallower acetabulum, a modified obturator foramen and a flattened femoral head, evidencing a lesser variety of movements of the limb, with movement of the hip joint reduced to only one direction. Furthermore, the absence of the processus lateralis fibulae indicates less control of the foot. In the middle Eocene, the locomotor capabilities of protosirenid hindlimbs were more reduced than in *Sobrarbesiren*. According to the hypothesis that a lack of sacroiliac articulation rules out an active role of the hindlimbs in swimming, as has been interpreted for the

protocetid *Georgiacetus* (Uhen 2014), protosirenids would not have been capable of controlling the movements of their hindlimbs. The connection between the protosirenid innominate bones and the vertebral column has been lost or is limited to a ligamentary connection between the anterior edge of the ilium and the sacral vertebra(e), as proposed by Gingerich et al. (1995a) for the Pakistani taxon *Protosiren sattaensis*. Even though protosirenids show a stage of sacral reduction and a lack of the sacroiliac joint similar to more derived sirenians such as dugongids, they still preserve well-developed hindlimbs. *P. smithae* shows hindlimb features not described to date, such as a torsion of the distal femoral shaft and a hypothetical elongated zeugopodium, as suggested by the proportions of the femur and tibia of the CGM42292 specimen. Nevertheless, the autopodial elements of the holotype of *P. smithae*, interpreted as metacarpals and manual phalanges by Domning and Gingerich (1994), show no evidence of the elongation described in other aquatic mammals (Gingerich 2003). Further, *P. smithae* has caudal vertebrae with broad transverse processes (Domning and Gingerich 1994), so that a horizontal tail is at least incipient (Domning 2000). As discussed previously, the torsion of the *Protosiren* femur results in an abducted position of the knee, with the limb deviating outside the body wall. Together with the elongation of the zeugopodium, this can result in a hindlimb whose role is to increase the propulsive surface. The *Protosiren* hindlimb could thus improve the efficacy of a still-incipient horizontal tail and enhance lift-based propulsion by dorsoventral caudal undulation. *Sobrarbesiren* also shows a torsion of the femur, although less than that observed in *P. smithae*, so the hindlimbs probably also complemented the surface of the incipient tail fin. The *P. smithae* hindlimbs were thus involved in swimming, but not with an active role given that there is no real sacroiliac articulation. A similar situation has been proposed for the protocetid *Georgiacetus*, which lacks a connection between the sacral vertebrae and the innominate bones but is thought to preserve an elongated femur (Uhen 2014). The hindlimbs of this protocetid contributed to the propulsive surface during swimming and moved thanks to an axial undulatory wave from the post-thoracic vertebrae (Uhen 2008b). Nevertheless, *Georgiacetus* is considered to have swum by pelvic undulation because a horizontal tail is absent in this taxon (Uhen 2014), whereas a horizontal tail is at least incipient in *P. smithae*.

As regards the microanatomical features of *Sobrarbesiren*, the micro-CT analysis of its innominate bone and femur reveals an extremely strong osteosclerosis in the hindlimb bones of this middle Eocene (middle Lutetian) basal sirenian; these bones are extremely compact, even though they are involved in a process of reduction through their disappearance.

The microanatomical features of *Sobrarbesiren* suggest an exclusively aquatic lifestyle based on the major increase in mass observed in these bones. Indeed, compact bones are brittle (Watkins 1999) and thus not ideal for terrestrial locomotion. This is notably highlighted by the absence of trabecular organization in the femoral head and the pelvis and also around the knee joint, that was specifically adapted to absorb impacts in terrestrial locomotion. The degree of osteosclerosis in the *Sobrarbesiren* femur is much greater than in pinnipeds or even than in the sea otter, which is almost exclusively aquatic and whose terrestrial locomotion is thus complicated (Bodkin 2001). It is also much greater than that of the protocetid whales *Rodhocetus* and *Maiacetus*. The comparison of the microanatomical characteristics of the *Sobrarbesiren* femur with those of these protocetids is in accordance with our observations on its osteology, which reveal that the Spanish taxon was at a stage of adaptation to aquatic life similar to some derived protocetids that exhibit unfused sacral vertebrae but a still-strong sacroiliac connection. For the moment, microanatomical data on femora of protocetids are only known for *Rodhocetus* and *Maiacetus*. New data about the femora of more derived protocetids such as *Natchitochia* or *Georgiacetus* would be very useful for comparisons.

As previously mentioned, changes in inner bone structure may appear prior to changes in the bone's outer shape during an ecological shift (Gray et al. 2007; Houssaye 2013). This probably results significantly from the plasticity of the inner bone structure. A taxon may thus show limited changes in its gross anatomy, but more marked changes microanatomically. In such cases, that is when gross morphology remains unclear/ambiguous, microanatomy provides a very efficient tool in amniotes for drawing ecological inferences and highlighting the various steps in a process such as adaptation to an aquatic lifestyle. In the present case, pronounced osteosclerosis of the innominate bone (the first observation of osteosclerosis in this element in amniotes) suggests an

exclusively aquatic lifestyle, but the absence of comparative microanatomic data prevents more precise inferences about the locomotor abilities of *Sobrarbesiren*. Microanatomic comparisons with other sirenians such as prorastomids, protosirenids and Eocene dugongids, as well as archaeocetes including derived protocetids, would be required in order to further discuss this morphofunctional question.

Díaz-Berenguer et al. (2018) proposed that *Sobrarbesiren* shows a combination of aquatic adaptations, such as retracted nares, pachyosteosclerotic ribs, an unfused sacrum and relatively short posterior extremities, with terrestrial features, such as a strong sacroiliac joint and an anterior thoracic vertebra with a long neural spine. Accordingly, an amphibious lifestyle was proposed for this taxon. The morphofunctional interpretations undertaken in the present paper reveal that, though reduced in size, the posterior hindlimbs of *Sobrarbesiren* were functional and capable of a great variety of movements when swimming, exemplifying a stage of evolution similar to some semiaquatic archaeocete whales, whereas the microanatomical data obtained from the innominate bone and femur of *Sobrarbesiren* testify to a high degree of aquatic adaptation.

CONCLUSIONS

The evolution of sirenians towards a completely aquatic mode of life entails, among other adaptations, an extreme reduction of the innominate bones, the disappearance of the hindlimbs, and the development of a powerful horizontal tail. The Eocene sirenian taxa evidence different steps in this process, ranging from the primitive semiaquatic prorastomids to the derived dugongids clearly adapted for an exclusively aquatic life. Nevertheless, the basal sirenian hindlimbs have been poorly known to date. A study of the osteology, functional morphology and microanatomy of the recently described Spanish taxon *Sobrarbesiren cardieli* in comparison with various other basal sirenians, suggests that the reduction of the limbs in sirenians was a more complex process than previously thought. The hindlimbs underwent not only a reduction of the structures, but modifications such as torsion of the femur and/or a hypothetical elongation of the zeugopodium, as proposed for the Egyptian taxon *Protosiren smithae*. Such modifications were

probably related to different swimming modes in these basal sirenians. *Sobrarbesiren cardieli* represents a new combination of features not previously known in sirenians. These include an unfused sacrum composed of an indeterminate number of sacral vertebrae with anteroposteriorly-short and dorsoventrally-expanded pleurapophyses, a strong connection between the sacrum and the ilia, functional hindlimbs with strong hip and knee joint muscles capable of a great variety of movements, and probably a horizontal tail in accordance with the dorsoventrally-flattened transverse processes of the caudal vertebrae. It is proposed that this taxon swam mainly by dorsoventral pelvic undulation, but combined this with simultaneous pelvic paddling, as shown by some protocetid archaeocetes. Furthermore, the microanatomical data on the hindlimb bones of *Sobrarbesiren* indicate an exclusively aquatic way of life for this sirenian.

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