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The earliest known fully quadrupedal sirenian

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Modern seacows (manatees and dugongs; Mammalia, Sirenia) are completely aquatic, with flipperlike forelimbs and no hindlimbs[1,2]. Here I describe Eocene fossils from Jamaica that represent nearly the entire skeleton of a new genus and species of sirenian—the most primitive for which extensive postcranial remains are known. This animal was fully capable of locomotion on land, with four well-developed legs, a multivertebral sacrum, and a strong sacroiliac articulation that could support the weight of the body out of water as in land mammals. Aquatic adaptations show, however, that it probably spent most of its time in the water. Its intermediate form thus illustrates the evolutionary transition between terrestrial and aquatic life. Similar to contemporary primitive cetaceans[3], it probably swam by spinal extension with simultaneous pelvic paddling, unlike later sirenians and cetaceans, which lost the hindlimbs and enlarged the tail to serve as the main propulsive organ. Together with fossils of later sirenians elsewhere in the world[1,4–7], these new specimens document one of the most marked examples of morphological evolution in the vertebrate fossil record.

Since 1990, abundant remains of sirenians, together with other marine taxa of early middle Eocene age (roughly 50 Myr ago), have been collected from Seven Rivers, Jamaica. The sediments (siltstones and sandstones) represent a lagoonal, estuarine or deltaic depositional environment. The age of the site was determined from molluscs (*Campanile*, *Eovasum*, *Paraseraphs*, *Velates*), and

corroborated by the presence of a primitive rhinoceros, *Hyrachyus* sp., of late early or early middle Eocene date[8]. The terrestrial fauna also includes an iguanian lizard[9] and possibly a primate[10]. The sirenian fossils are found in five distinct bone-beds within a 5-m stratigraphic section referred to the Guys Hill Member of the Chapelton Formation, and occur as isolated bones and associated partial skeletons, with the remains of several individuals commingled. In the lower three bone-beds, all the sirenian remains appear to represent a single taxon (described here: Figs 1 and 2). These provide the first view of the overall anatomy and mode of locomotion of sirenians during their evolutionary transition from land-dwelling to obligatorily aquatic life.

<div style="text-align:center">

Order **Sirenia** Illiger, 1811
Family **Prorastomidae** Cope, 1889
Pezosiren portelli, gen. et sp. nov.

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Etymology. Generic name from Greek *pezos* (on foot, walking) and *Seiren* (Latin *Siren*, f., siren). Specific epithet in honour of Roger W. Portell, discoverer and co-investigator of the site.

Locality and horizon. Known only from Seven Rivers (about 15 km south of Montego Bay), parish of St James, western Jamaica; Guys Hill Member, Chapelton Formation, Yellow Limestone Group (early middle Eocene).

Holotype. US National Museum of Natural History, Paleobiology collection (USNM), no. 511925 (Fig. 2a): pair of partial mandibles from Seven Rivers bone-bed II.

Referred material. Specimens illustrated here (Fig. 2b–h) comprise sacrum (associated with 7 thoracic, 4 lumbar and 1 caudal vertebrae), USNM 517463, bone-bed II; left and right innominates, USNM 517464, bone-bed II; left femur with separated distal epiphysis, USNM 517465, bone-bed II; left tibia, USNM 517466, bone-bed III; intermediate phalanx, USNM 517467, bone-bed II. The following description also draws on several hundred other cranial and postcranial elements from Seven Rivers bone-beds II–IV, not formally referred at this time, that remain to be catalogued in the USNM, University of the West Indies, and Florida Museum of Natural History collections.

Diagnosis. The diagnosis for the genus is the same as for the species until other species are described. *Pezosiren portelli* differs from *Prorastomus sirenoides*, the only other named member of the family, in having (1) a sagittal crest; (2) an auditory meatus that is about as wide anteroposteriorly as high; (3) a periotic that is not fused to the alisphenoid; (4) an unenlarged P₁; and (5) a horizontal mandibular ramus whose ventral border is turned down anteriorly. Character states 1 and 4 are primitive within the Sirenia; character states 2, 3 and 5 are considered derived[11].

Description. *Pezosiren* was a pig-sized quadruped (estimated total length 2.1 m) with a relatively short (but not extremely compressed) neck, a long, barrel-shaped trunk, short legs and a substantial (but not powerfully muscled) tail (Fig. 1). The skull (estimated condylobasal length 26.5 cm, zygomatic width 14.5 cm) is of clearly sirenian form, with a prominent although undeflected rostrum, large mesorostral fossa, large nasals, horizontally jutting supraorbital processes, and laterally projecting zygomatic arches. A weak sagittal crest is present; this appears to be absent in the holotype of *Prorastomus sirenoides* but may have been removed by erosion or preparation. The sphenopalatine region is primitively long, and lacks the enlarged, stout, ventrally projecting pterygoid processes characteristic of later sirenians. An alisphenoid canal is present, and the foramen ovale seems to be completely enclosed by bone.

The mandible (Fig. 2a) is long (19 cm) and slender, with its ventral border strongly turned down anteriorly; the symphysis is long, deep and mediolaterally compressed; the incisors and canines are arranged in parallel, parasagittal rows; several mental foramina are present; and the mandibular foramen is small, not exposing the dental capsule. The dental formula is uncertain (the toothrows are incomplete anteriorly) but was presumably 3.1.5.3 as in all other

Eocene sirenians[12]. The first upper incisor is enlarged to form a small tusk with subconical enamel crown. The alveolus interpreted as that of the lower canine is large, but not demonstrably divided for a two-rooted tooth as in *Prorastomus*. The first lower premolar alveolus is single and not enlarged, further contrasting with the large, two-rooted first premolar of *Prorastomus*. The tooth in front of M₁ is single-rooted, indicating replacement at the last (fifth) premolar locus.

The vertebral column (judging in part from two incomplete but overlapping series of associated trunk vertebrae) evidently comprised 7 cervical, 20 thoracic, 4 lumbar, 4 sacral, and probably a couple of dozen caudal vertebrae. The atlas has not been recovered. The axis and other cervical vertebrae grossly resemble those of Palaeocene condylarths such as *Ectoconus*[13], rather than being as compressed anteroposteriorly as in later sirenians. Anterior thoracics have tall neural spines, indicating the presence of a nuchal ligament that was able to support the weight of the head and neck on land. The thoracic, lumbar and sacral vertebrae are remarkable for
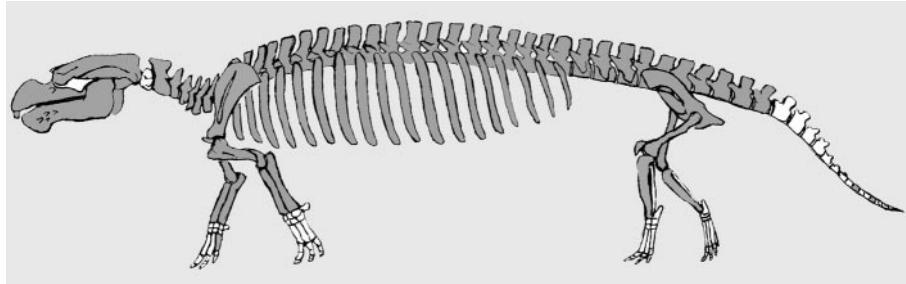

Figure 1 Reconstructed composite skeleton of *Pezosiren portelli*. Lateral view, length roughly 2.1 m. Shaded elements are represented by fossils; unshaded elements (jugal, atlas, fibula, most bones of the feet, and most caudal vertebrae) are not. The length of the tail, and the form and posture of the feet are partly conjectural.

Figure 2 *Pezosiren portelli*. **a**, Partial right mandible (holotype, USNM 511925); medial view, showing location of small mandibular foramen (white arrow). Approximate outlines of restored broken portions are shown. **b**, Dorsal view of sacrum (USNM 517463); pleurapophyses are missing on S3–S4. **c**, Right innominate (USNM 517464); ventromedial view. **d**, Right and left innominates (USNM 517464); ventral view. The apparently ventral direction of the acetabula is an artefact of dorsoventral crushing. **e**, Subadult left femur (USNM 517465); anterior view. **f**, Left tibia (USNM 517466); anterior view. **g**, Left tibia, (USNM 517466); lateral view. Note oblique, distolaterad-facing distal articular surface of tibia. **h**, Intermediate phalanx (USNM 517467); dorsal view. Scale bars, 5 cm (**a–g**); 1 cm (**h**).

having large, horizontally projecting flanges at the tips of the neural spines and prominent mammillary processes.

The transverse processes (pleurapophyses) of the (usually unfused) sacral vertebrae (Fig. 2b) are connected by rigid lateral articulations as in the cetacean *Rodhocetus*[14]. In older individuals the sacrals may be at least partly fused. The anterior sacrals bear large articular surfaces for the ilium, as in land mammals. Caudal vertebrae lack the enlarged transverse processes of later sirenians; the small transverse processes of the more anterior ones were pierced by foramina or notches, as in several other aquatic mammals but not in later sirenians. The ribs are swollen (pachyostotic) and composed wholly of dense bone (osteosclerotic), as in other sirenians; their shafts are subcylindrical and lack costal grooves. The sternum comprises at least three broad, dorsoventrally flattened elements, in contrast to the more primitive sternebrae seen in the otherwise more derived sirenian *Protosiren smithae*[4].

The scapular blade is broad, not sickle-shaped as in protosirenids and primitive dugongids. There is no clavicle. The humerus is remarkably broad distally. The ulnar shaft is flattened, and was evidently connected immovably (although not fused) to the radius. The radius apparently lay anteromedial to the ulna, but is not well preserved; its exact form and relationships are unclear, as are the structure and orientation of the wrist joint. The pelvis (Fig. 2c, d) is long and narrow (total length 243 mm), resembling those of primitive land mammals, with a moderately broad ilium and an elongate ischial tuberosity. The acetabulum, obturator foramen, and pubic symphysis are well developed. The femur (Fig. 2e; length 166 mm) is robust, with a distinct third trochanter.

The patella is large and shaped like a teardrop. The tibia (length 130 mm; Fig. 2f, g) greatly resembles those of *Ectoconus*[13] or other primitive ungulates, with a long and prominent cnemial crest, medial torsion of the shaft relative to the proximal end, and a distal articular surface that faces obliquely distolaterad[15]. Of the feet, only one metapodial, one proximal and one intermediate phalanx have been recovered; whether they represent the front or back feet is unknown. These bones are short and flattened like those of terrestrial ungulates, and show no signs of paddle-like elongation (Fig. 2h). The skeleton is shown here conjecturally with a digitigrade foot posture consistent with the presumed descent of sirenians from semicursorial "condylarths"[16,17]; however, a secondarily plantigrade posture such as that of otters (see 'Functional interpretation' below) cannot be ruled out.

Affinities. *Pezosiren portelli* is clearly a sirenian on the basis of its lack of paranasal air sinuses and its possession of a prominent rostrum, retracted and enlarged external nares, premaxilla-frontal contact, longitudinally aligned incisor arcades and extensive pachyosteosclerosis in the skeleton (see ref. 11 for relevant phylogenetic analysis). It is placed in the basal (and paraphyletic) sirenian family, the Prorastomidae, on the basis of its primitively undeflected rostrum, unenlarged pterygoid process and unexposed mandibular dental capsule. This hitherto monotypic family was erected for *Prorastomus sirenoides*, which was founded on a single skull, mandible and atlas vertebra from the parish of Trelawny, Jamaica, about 40 km east-southeast of Seven Rivers, in the earliest middle Eocene Stettin Member of the Chapelton Formation (a slightly earlier horizon than that of *Pezosiren*)[18]. Hardly any other remains (and no appendicular bones) referable to this family were discovered before the Seven Rivers finds. *Prorastomus* differs from *Pezosiren* most obviously in that the ventral border of the mandibular ramus is not downturned anteriorly (a primitive condition). Although *Pezosiren* seems to share some synapomorphies with more derived sirenians to the exclusion of *Prorastomus*, other character states are noncongruent and/or poorly understood, so a definitive conclusion on its phylogenetic position would be premature.

Functional interpretation. The tall anterior thoracic neural spines, multivertebral sacrum, strong sacroiliac articulation and robust appendicular elements with fully developed joint surfaces are exactly comparable to those of similar-sized land mammals, and show clearly that *Pezosiren* was capable of supporting its body weight out of water. It was a true sirenian, however, and its clear aquatic specializations (retracted nasal opening, lack of paranasal air sinuses and thorax with numerous heavy, pachyosteosclerotic ribs for ballast[19,20]) suggest that it spent most of its time in the water, probably feeding as well as resting there.

Unlike modern sirenians and cetaceans, it did not propel itself in the water by means of up-and-down undulations of a powerful tail. Its tail vertebrae lacked the broad transverse processes needed for large tail muscles, and the tail was probably otter-like, with some dorsoventral flattening but no distinct caudal fin or flukes. Main propulsion was apparently provided instead by forceful extension of the spine, and backward and upward thrusts of the hind feet together—in other words, simultaneous pelvic paddling combined with spinal undulation[21]. This mode of swimming is typical of otters and is also thought to have occurred in primitive whales such as *Ambulocetus*[3,22]. Strong spinal extension of this sort might explain the peculiar flanges on the tips of the thoracic, lumbar and sacral neural spines, as well as the large mammillary processes; powerful longissimus muscles would have inserted on both sites. □

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