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THE FIRST REPORTED *LEPTONECTES* (REPTILIA: ICHTHYOSAURIA) WITH ASSOCIATED EMBRYOS, FROM SOMERSET, ENGLAND

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ABSTRACT

A large but incomplete skeleton of an ichthyosaur (CAMSM J 13579) from Street, Somerset, in the Sedgwick Museum collection is associated with two embryos. The morphology of the pelvis and humerus indicate that the adult is *Leptonectes*. The elongated external naris, exclusion of the maxilla from the border of the external naris, notched radius of the embryo, and large size of the adult indicate that these specimens are most likely *L. tenuirostris*, a fairly common species from the Street location. The size of the head relative to the body in the more complete small skeleton (CAMSM J 35178), and its total length relative to the adult suggest that the small individuals are late term embryos rather than neonates.

INTRODUCTION

This paper describes a large, partial skeleton of an ichthyosaur (CAMSM J 35179) and a small associated skeleton (CAMSM J 35178), and will try to determine whether the smaller individual is an embryo or neonate. Because the two skeletons have been given two accession numbers, we follow Seeley (1880) in referring to CAMSM J 35178 as an embryo to avoid confusion with the numbers. We will show that his initial assessment was probably correct.

Live birth in ichthyosaurs had been suspected as early as 1846 (Pearce, 1846), although the argument for cannibalism rather than embryonic specimens persisted for more than a century (Benton, 1991). The current consensus is that most of the small individuals found within the body of larger ichthyosaurs are embryos (Böttcher, 1990; Benton, 1991). Specimens with embryos are known from *Mixosaurus* (Brinkmann, 1996) and *Besanosaurus* (Dal Sasso and Pinna, 1996) from the middle Triassic (Anisian), indicating that ichthyosaurs were viviparous early in their history. Camp (1980: 144) mentioned, but did not describe or figure, “embryonic material” within a *Shonisaurus* from the late Triassic (Carnian), although it is unclear whether more than one such skeleton was found. Jurassic specimens with embryos include only *Ichthyosaurus* (Pearce, 1846; Deeming et al., 1993) and *Stenopterygius* (McGowan, 1979; Böttcher, 1990), both common genera in the lower Jurassic. McGowan (1979) referred to a possible *Stenopterygius hauffianus* (now assigned to *Hauffiopteryx* in part) with embryos, but the specimen in question (GPIT 1491/1) is a *S. quadriscissus* (Maisch, 2008). Woodward (1906) and Swinton (1929) figured a specimen from Holzmaden, Germany with several embryos (NHMUK R 3300), and referred to it as *Ichthyosaurus acutirostris* (now assigned to *Temnodontosaurus*) but it is actually another *Stenopterygius* (*S. quadriscissus)*. Seeley (1880) mentioned another German specimen from Ohmden, *Ichthyosaurus tenuirostris* (now assigned to *Leptonectes*) as having an embryo. It is highly unlikely, however, that the specimen belongs to *Leptonectes* as the stratigraphy of Ohmden (Posidonia Shale) is Toarcian and *Leptonectes* is known only from the Rhaetian to Pliensbachian (McGowan and Motani, 2003). Thus including the specimen described here, three Jurassic genera have been found with preserved embryos. The geologically youngest specimen with an embryo is a *Maiaspondylus* from the early Cretaceous (Albian; Maxwell and Caldwell, 2003, 2006). Most finds are single individuals of a particular species, with the exception of *Stenopterygius* from the early Jurassic (Toarcian) Posidonia Shale of Holzmaden, Germany, where more than a hundred specimens with embryos have been found.

Ichthyosaurs with embryos or associated neonates are rare in the British Jurassic. Pearce (1846) wrote the first description of an ichthyosaur embryo, discovered between the ribs of an adult *Ichthyosaurus communis* from Somerset. This specimen (NHMUK R3372) was figured by Woodward (1906) and is presently on display at the Natural History Museum, London. Seeley (1880) mentioned two additional British specimens: one from the Lias of Lyme Regis which had “a number of embryos in the pelvic cavity” (Seeley, 1880: 69) and the small skeleton described herein. More recently, Deeming et al. (1993) described an *Ichthyosaurus ?communis* specimen with an associated embryo (BRSMG Ce 16611), which is from Kilve, Somerset. Interestingly, three of the four reported embryos are from Somerset rather than the more widely collected Lyme Regis area, west Dorset.

Abbreviations Used—BRSMG Bristol City Museum and Art Gallery, Bristol, UK; CAMSM Sedgwick Museum, Cambridge University, UK; GPIT Geologisch-Paläontologisches Institut der Universität Tübingen, Germany; MHH Museum Hauff, Holzmaden, Germany; NHMUK Natural History Museum, London, UK; SMNS the Staatliches Museum für Naturkunde, Stuttgart, Germany.

MATERIALS AND METHODS

The specimens of interest are CAMSM J 35178, a small individual comprising a skull, scapulae and a vertebral column, and an associated larger individual, CAMSM J 35179. Both specimens are encased in a similar tan matrix. They are preserved on separate blocks, but the blocks fit together to make a single, somewhat irregular, large slab.

Seeley (1880, pl. I, fig. 1) figured a small individual associated with a few caudal vertebrae of a larger one, and suggested that it was an embryo. The figure is very similar to CAMSM J 35178 in the orientation of the vertebral column, morphology of the skull, presence of disarticulated bones behind the skull, and in the number and orientation of the vertebrae of the larger individual so it is definitely the same specimen. In the text, Seeley (1880: 69) described a large slab with an “imperfectly preserved” specimen and a small skeleton “in the pelvic region”, which appears to refer to both CAMSM J 35178 and CAMSM J 35179. However, he did not give any information on the larger skeleton, perhaps because the paper focused on the mode of reproduction of ichthyosaurs. More than a decade later, in a catalogue of specimens in the Woodwardian Museum (precursor of the Sedgwick Museum), Woods (1891) listed an *Ichthyosaurus* sp. described as a young individual comprising a skull and vertebral column, which was donated by Thomas Hawkins. It is undoubtedly CAMSM J 35178 because Woods (1891: 171) cites Seeley (1880) as having figured it. It is possible that Woods did not mention the associated large individual because the catalogue focused on holotypes, figured specimens, and other important fossils in the collection.

Woods (1891) gave the provenance of CAMSM J 35178 as the Lias of Street, Somerset. The specimen was donated by Thomas Hawkins whose collection was largely from Street. The similarity of the matrix suggests that both CAMSM J 35178 and CAMSM J 35179 are from the same location. The color of the bone, state of preservation, and appearance of the matrix are consistent with a Street location. The strata exposed there are Upper Triassic (Rhaetian) to Lower Jurassic (Hettangian – Sinemurian) in age.

Both CAMSM J 35178 and CAMSM J 35179 are part of the historic Hawkins collection, identified through the label painted onto the matrix of the largest block and from the information on the small specimen given in Woods (1891). As a Hawkins specimen, the authenticity has to be considered because some Hawkins specimens are composites (McGowan, 1990). Although large parts of the matrix are covered by a medium gray plaster wash, it is a thin veneer and may have been applied for aesthetics. A cervical and smaller centrum (? distal caudal) adjacent to the skull seem to be imbedded in a thicker patch of plaster and may have been added. The dimensions of the cervical centrum indicate that it could belong to this individual (see below). Eleven articulated vertebrae seem to have been removed and reset. The first of these centra (centra 18-20), separated from the others by a crack, may be a continuation of the anterior series of centra. The remaining centra (21-28) are from the caudal portion of this or another vertebral column (see below). Within each large block, however, we cannot detect any other restoration or cracks that might indicate a composite.

At some time in the past, these specimens had been on display in the museum and mounted in plaster in a wooden frame. The embryo was placed to the right of the adult skeleton, along the top edge of the frame. The two blocks containing the embryo fit onto the larger blocks along what appears to be a cut edge. Thus, the embryo could have been shifted from its original position when framed for display. A fifth block, preserving fluke centra and a second series of small articulated centra, was also positioned to the right of the adult, but along the lower edge of the frame. Its original position with respect to the adult skeleton cannot be determined.

Measurements of the specimens were taken using digital calipers for features smaller than 15 cm, and recorded to the nearest 0.1 mm. For larger features, a measuring tape was used, and measurements were recorded to the nearest 1 mm.

FIGURE 1. Assembled blocks of the adult specimen, CAMSM J 35279. White arrow points to the isolated humerus. Black arrows identify both pelves. Scale bar = 20 cm. © 2012. Sedgwick Museum of Earth Sciences, University of Cambridge. Reproduced with permission.

DESCRIPTION

Although given two accession numbers, the material probably represents a single specimen. The large skeleton and associated smaller ones are preserved on five blocks of matrix. In addition there are three smaller blocks of matrix with no bones preserved. The two largest blocks, CAMSM J 35179, contain the adult specimen (Figure 1). CAMSM J 35178, the smaller individual, comprises two separate blocks that fit together (Figure 2). The block is broken between the jumble of bones at the back of the skull and the articulated vertebral column, although in Seeley (1880, pl. I, fig. 1) the specimen appears to be a single block. A fifth smaller block (Figure 3) contains fluke vertebrae of the adult and an articulated vertebral column of a second embryo.

Adult—The larger of the two blocks of the adult (CAMSM J 35179) measures 148.5 cm along its longest edge, and 59.5 cm along its front edge. It preserves a partial skull, a string of vertebrae, numerous ribs, a humerus, and pelvic bones. The poorly preserved skull is exposed ventrally, crushed, and missing most of the rostrum. It is disarticulated and lies 16 cm from the vertebral column. One of the quadrates has been displaced about 6 cm from the skull and is isolated in the matrix. The basioccipital is clearly visible and has a broad, arcuate extracondylar process. Because of the crushing, individual bones of the skull are broken, out of place, or covering one another. The second quadrate, both stapes, an exoccipital, a partial supratemporal and a partial parietal (with pineal foramen) are preserved (Figure 4). In the portion of the rostrum that is present, a few poorly preserved teeth are dislodged and are lying parallel to the rostrum. The teeth are long and slender, with smooth crowns and fluted roots.

An isolated humerus, probably preserved in ventral aspect, overlies the distal end of a few ribs. The humerus bears a slight constriction in the shaft, a greatly expanded distal end, and a distinct anterior facet. These features of the humerus are characteristic of *Leptonectes* (McGowan, 1996; McGowan and Motani, 2003).

The carcass probably landed on the seafloor on its ventral side (dorsal up), based upon the orientation of the ribs. The anterior portion of the vertebral column of the adult is twisted with respect to the skull, with ribs of the right side coming across the centra. Twenty-eight centra are on the larger block of the adult,

FIGURE 2. Assembled blocks of the embryo, CAMSM J 35278. Black arrow points to an isolated notched radius. Scale bar = 10 cm. © 2012. Sedgwick Museum of Earth Sciences, University of Cambridge. Reproduced with permission.

although the 17th centrum is probably buried underneath the ribs in the gap after the 16th centrum. The length of this portion of the vertebral column is 66 cm. The first 16 articulated centra are preserved in left lateral aspect, partially overlain by ribs. Four to six of them are cervicals, but we could not recognize an atlas-axis. The isolated cervical centrum near the skull is 3.34 cm wide and 2.88 cm high. The first articulated centrum is 3.27 cm wide and 2.60 cm high (although the next four centra are over 3.0 cm high). Allowing for some variation in shape due to deformation, the isolated cervical could belong to this specimen (Figure 5).

The last eleven vertebrae (18th – 28th) appear to be articulated in the correct order, but are upside down relative to the first series. From the edge of the block, one can see a groove that runs underneath these eleven centra, and they are surrounded by gray plaster. Cracks in the plaster, running across the vertebral column, suggest that three separate pieces have been reset. The diapophysis and parapophysis are touching on the 19th and 20th centrum, and have merged into a single, elongate articulation on the 21st centrum. As there may be one or two cervical vertebrae missing, single-headed ribs would have begun at the 22nd or 23rd vertebra. McGowan (1989) gave a presacral count of 45 for *L. tenuirostris*, thus the change from double-headed to single-headed ribs on this specimen is at least 20 vertebrae, or almost half of the trunk length, anterior to the pelvis. This would be highly unusual for a parvipelvian ichthyosaur (e.g., *Ichthyosaurus*, *Ophthalmosaurus;* Buchholtz, 2001). It is more likely that centra 18-28 do not belong to this individual or at least that they came from a more posterior section of the vertebral column. This is consistent with our previously mentioned observation that they appear to have been reset. Yet 28 ribs or impression of ribs are

FIGURE 3. Fifth block mounted with CAMSM J 35278 and 35279 is presumably part of the same specimen. Fluke vertebrae of the adult are scattered across an articulated vertebral column of another embryo. Arrows point to the anterior (white) and posterior (black) ends of the articulated vertebral column of the second embryo. Scale bar = 10 cm. © 2012. Sedgwick Museum of Earth Sciences, University of Cambridge. Reproduced with permission.

present ventral to the articulated centra on this block, indicating that the specimen may have originally had 28 articulated centra.

After the 28th centrum is a break in the matrix, and the orientation of the column changes by almost a 90º angle on the second block of the adult (Figure 1). The second adult block measures 73 cm along its longest edge and 52 cm along the back edge. It includes ribs from the right side of the anterior dorsal vertebrae from the larger slab, but few ribs from the vertebrae on the second slab itself. Nine articulated centra with partial neural spines are present. Four associated centra are disarticulated at the distal end, the last of which is lying flat on the matrix a few centimeters away from the other centra. The ventral side of the column is towards the skull. The length of this portion of the vertebral column is 33 cm. The single rib articulation is elongated on the first five of the centra in this series, and becomes round on the sixth. Given the morphology of the centra, this series is most likely from the anterior caudal region, thus on the order of fifteen posterior trunk centra may be missing between the two blocks. Towards the distal end of the vertebral column are four isolated, very small centra. One is clearly a fluke vertebra that likely belongs to the adult, but the others are probably from an embryo (Figure 6). The association of embryonic vertebrae with the right

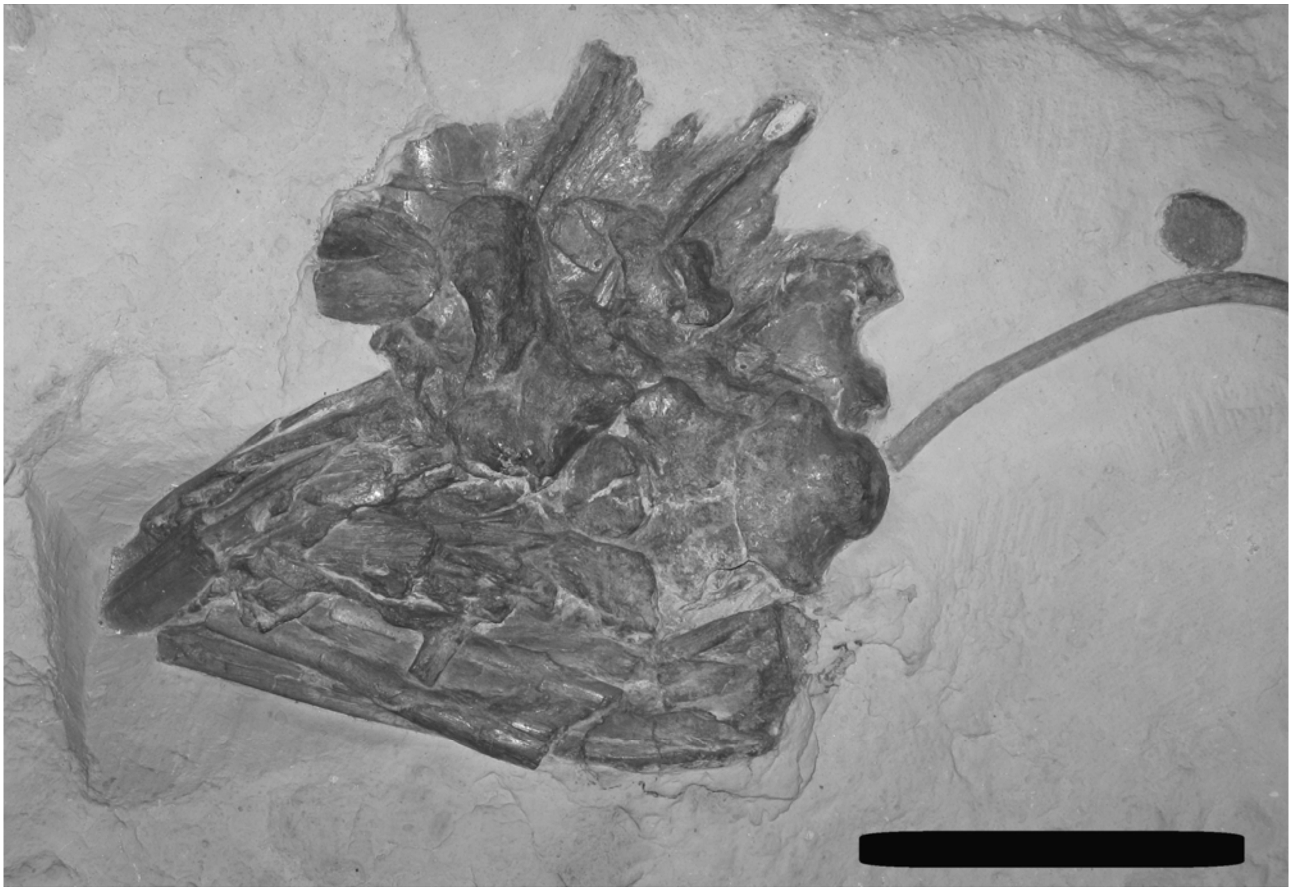

FIGURE 4. Ventrally crushed skull of the adult specimen, CAMSM J 35279. Scale bar = 10 cm. © 2012. Sedgwick Museum of Earth Sciences, University of Cambridge. Reproduced with permission.

pelvis and anterior caudal region of the adult vertebral column suggests that an embryo was somewhere nearby when the specimen was originally excavated. This would also explain the presence of adult caudal centra on the same block as CAMSM J 35178 (Figure 2).

The adult specimen includes all three bones of both pelves, one pelvis on each block. The left pelvis (on the larger block) is fused anteriorly, whereas the right pelvis (Figure 6) is fused at both ends. The fusion and the spatulate shape of the ischium and pubis is typical of *Leptonectes* (McGowan, 1996; McGowan and Motani, 2003). The ilium is a slightly curved bone that is widest in the middle. Short, elongate bones are scattered near the right pelvis and are probably caudal ribs (Figure 6). The sizes of the pelves are comparable, suggesting that they are from the same individual (Table 1).

Centrum Morphology of the Adult—The average height/length ratio for the 17 centra that could be measured (including both blocks) is 2.21, with a range of 1.75 to 2.61 (see Appendix). A small difference in the ratio occurs between centra with bicipital ribs (average 2.16, n=10) and those with unicipital ribs (average 2.30, n=7), but anterior caudal vertebrae tend to have a higher height/length ratio than dorsal vertebrae (Massare et al., 2006). The centrum height/length ratios of CAMSM J 35279 are comparable to those of presacral and anterior caudal vertebrae of *Opthalmosaurus natans*. The ratios are generally higher than those of *Suevoleviathan* and *Eurhinosaurus*, but lower than *Stenopterygius* and *Ichthyosaurus* (Massare et al., 2006, fig. 5).

Although the data are incomplete, the graph of centrum dimensions along the length of the vertebral column (Figure 5) suggests a highly unusual pattern in the length and height dimensions of the centra of the adult unless a portion of the presacral vertebral column is missing. Note that most of the measurements have been made on the posterior portion of the adult vertebral column (on the smaller, second block).

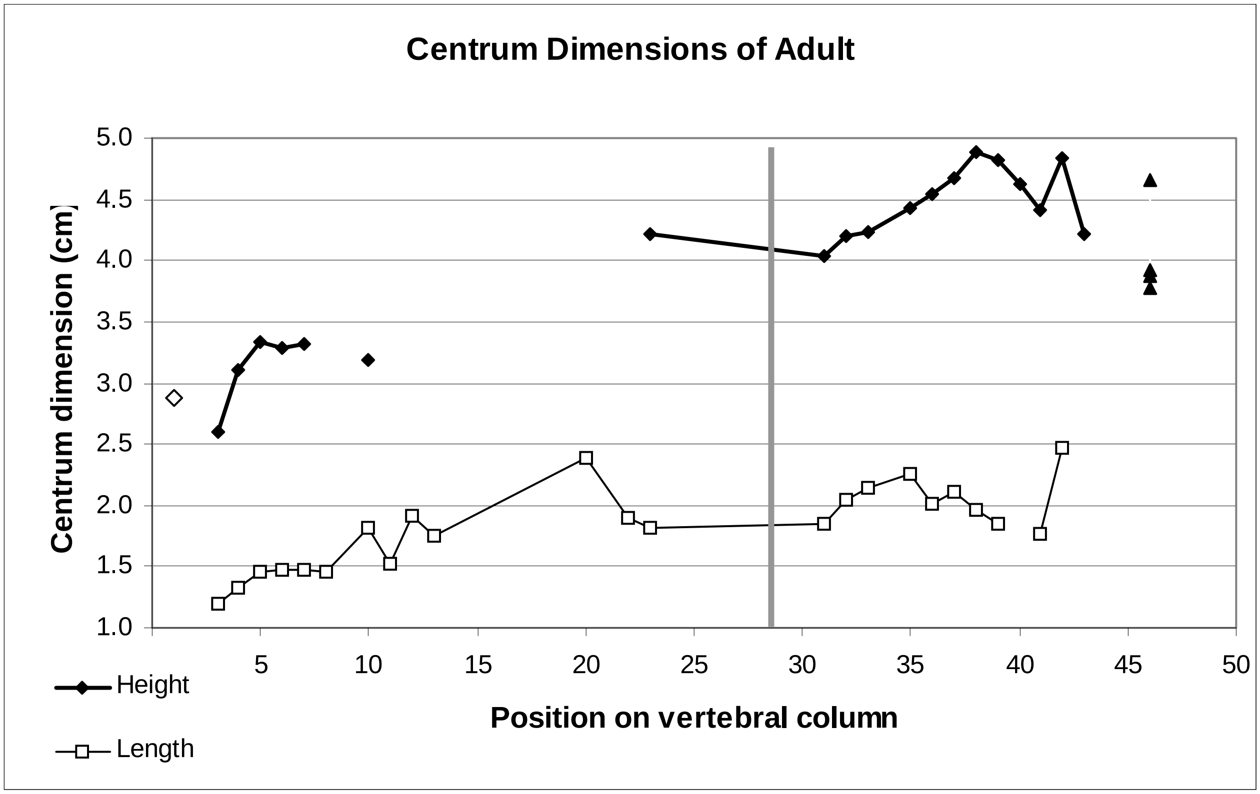

FIGURE 5. Plot of the height and length of measurable centra of the adult specimen, CAMSM J 35279. The open diamond to the left plots the height of the isolated cervical centrum near the skull. The closed triangles to the right plot four centra associated with the embryo, CAMSM J 35278. The vertical gray line indicates the approximate break between the two blocks of the adult.

A gradual increase in length of the centra can be seen from the anterior to the posterior of the preserved column, with perhaps a decrease in length beginning at the 35th centrum (accounting for a missing atlas and axis but not for missing posterior dorsals). This would be anterior to the pelvis using McGowan's (1989) presacral count of 45 for *Leptonectes tenuirostris*. Typically, (e.g., in *Ichthyosaurs communis* and *Temnodontosaurus trigonodon*) the decrease in length occurs at the pelvis, marking the separation between the trunk and anterior caudal region (Buchholtz, 2001). Centrum height in this specimen probably follows a similar trend, although even fewer measurements were possible. Height appears to decrease beginning at about the 38th centrum in CAMSM J 35279. In *I. communis*, the decrease in height begins at the pelvis, and in *T. trigonodon*, it begins well into the caudal region (Buchholtz, 2001, figs. 1B, 2B). These patterns provide further evidence that posterior dorsal centra are missing from where the column is broken in CAMSM J 35279.

Embryo—CAMSM J 35178 is composed of two small blocks that divide the skeleton into two pieces (Figure 2). The skull, several disarticulated centra, and other bones are on one block that measures 42 cm by 31 cm. The skull is lying with the right side exposed. It has a high crown and the large orbit is nearly circular, comprising almost the entire posterior portion of the skull. The snout appears relatively short, but the anterior end is broken so its exact length cannot be determined. The external naris is long, and widens posteriorly. The maxilla is low and separated from the external nares by the lachrymal and premaxilla. It extends slightly anterior to the external naris. No teeth are preserved within the snout.

Both scapulae are behind the skull, one partly overlaying the other. The shaft of the scapula is shorter and wider than that of the other common Lower Jurassic genus, *Ichthyosaurus*, and possesses a rounded articular edge (McGowan and Motani, 2003). The latter may be a juvenile characteristic. Next to the scapulae are eight disarticulated centra, three of which

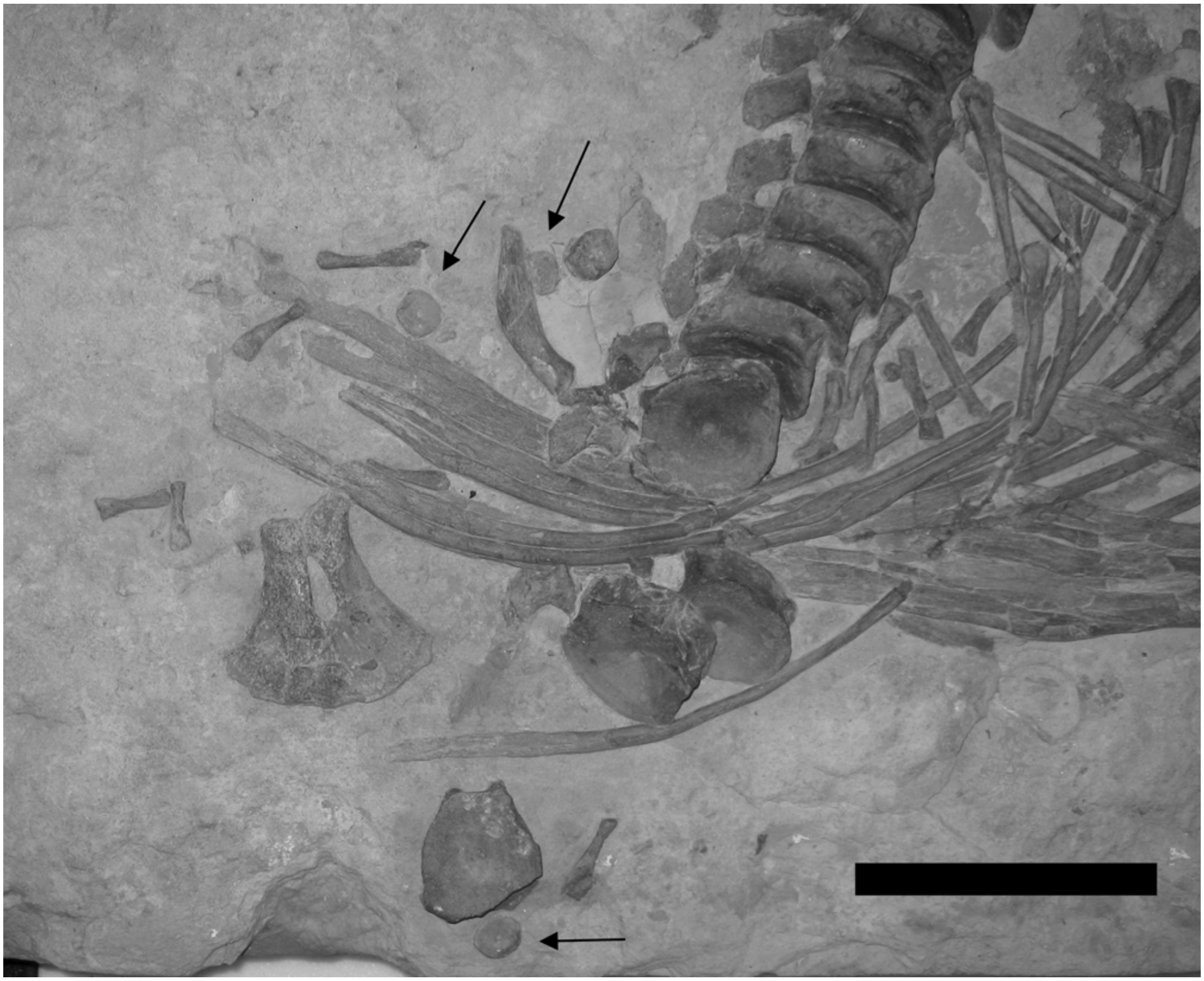

FIGURE 6. Posterior portion of the adult specimen, CAMSM J 35279, showing all three bones of the right pelvis which helps to identify the specimen as *Leptonectes*. Arrows point to isolated centra from an embryo. Scale bar = 10 cm. © 2012. Sedgwick Museum of Earth Sciences, University of Cambridge. Reproduced with permission.

are partially buried. At least three of the centra, and maybe as many as five, are cervicals. The height/width ratios of the three centra that could be measured range from 0.69 to 0.79 (see Appendix). The surfaces of the centra have uniformly and widely spaced 'pores', and may indicate that the centra were not fully ossified. One or two of them may still have an opening for the notochord. In addition to the centra, there are four short, possibly cervical ribs and four longer rib fragments, the longest of which is 4.11 cm.

The second block, which completes the embryo, is 40.5 cm long and has a maximum width of 37.5 cm. It preserves 54 articulated centra of the embryo, none of which show parapophyses or diapophyses. The 23 centra that could be measured, which included two of the cervicals, had an average height/length ratio of 2.55, with a range of 2.00 to 3.26 (see Appendix). In general, these centra are shorter and more disk-like than the centra of the adult, suggesting that centrum shape changes markedly with ontogeny.

In addition, five large centra are preserved at the distal end of the embryo. They are similar to the morphology of those at the posterior end of the adult vertebral column, as shown by their position on the graph of centrum height (Figure 5). Additionally two smaller centra with a more rounded shape are present. They are too large to belong to the embryo but could possibly be distal caudal centra of the adult. A third similar centrum may be the bone protruding from the matrix between the large vertebrae. A small phalanx of the adult is isolated in the matrix near the adult centra. A small, notched radius (length 0.89 cm; width 0.87 cm) belonging to the embryo, is at the distal end and dorsal to the vertebral column. This is clear evidence that notching of the radius is not an adult character, at least in this species.

A fifth block that also belongs with both specimens contains a series of 15 articulated centra that are similar in shape to those of the embryo. It is unlikely that this vertebral column is part of CAMSM J 35178. The posterior few centra of the more complete embryo are less than 1.3 cm high, whereas three of the four anterior-most centra of the second vertebral column have heights well over 1.4 cm (see Appendix). Thus the centra of the second column are too large to be a continuation of CAMSM J 35178, and must be a portion of a second embryo. Moreover, these small articulated centra could not be the distal centra of the adult, as the adult's fluke vertebrae, which are different in shape and size, are spread across the fifth block and overlay the small vertebral column. The five largest fluke centra that could be measured range in height from 1.69 to 1.90 cm, considerably larger than the aforementioned articulated centra. Also preserved are five isolated, very small teeth, the largest of which measures 0.38 mm high. Four of the teeth consist of just crowns; the other displays part of a fluted root. The teeth may belong to one of the embryos and must have dislodged from the dental groove as they are much too small to be from the adult.

TABLE 1. Measurements of the bones of the pelvis of CAMSM J 35279. The left pelvis is assumed to be the one on the larger block of the adult.

	left pelvis (cm)	**right pelvis (cm)**
pubis length	6.69	6.84
ischium length	6.01	6.09
ischium-pubis width	6.99	6.81

TABLE 2. Ratios of embryo and adult proportions for two genera of Jurassic ichthyosaurs, using measurements from Deeming, et al. (1993) for small skeletons associated with larger ones. Ratios for NHMUK R 3372 are calculated from measurements in Woodward (1906).
** Denotes specimens that may have died because of complications of the birthing process, and thus are full-term embryos according to Deeming et al. (1993).

	Embryo skull length to total length	**Embryo length to adult length**
STENOPTERYGIUS		
** GPIT Qu.1858 S219A	0.36	
GPIT 1491/1A	0.40	
** GPIT 1491/6A	0.42	
MMH Z21A	0.34	
SMNS 10460A	0.46	0.07
SMNS 10460B	0.48	0.10
SMNS 50963A	0.45	0.12
SMNS 52036A	0.39	0.31
SMNS 52036B	0.43	0.31
** SMNS 53001A	0.30	0.32
SMNS 6293A	0.33	0.34
Leipzig Embryo A	0.45	
ICHTHYOSAURUS		
BRSMG Ce 16611B	0.34	0.10
NHMUK R 3372	0.28	0.07

DISCUSSION

Based upon the humerus and pelvic girdle morphologies, we can confidently assign CAMSM J 35179 to the genus *Leptonectes*. Currently, three species of *Leptonectes* are recognized (McGowan and Motani, 2003). The first to be described and the most common is *Leptonectes tenuirostris*, a moderately sized, long-snouted species that is less than 4 m in length (Maisch and Matzke, 2000). *L. solei*, known only from two specimens, does not have quite as long a snout and is over 5 m in length (McGowan, 1993; Maisch and Matzke, 2000). The last species to be described, *L. moorei*, is known only from the holotype, a juvenile. It is characterized by a short snout and a high-crowned skull (McGowan and Milner, 1999).

We can rule out CAMSM J 35179 as a specimen of *L. solei* based on the pelvic girdle. *L. solei* possesses an unfused ischium and pubis, and the ischium has a rectangular shape rather than the spatulate form of this specimen (McGowan, 1993). *L. tenuirostris*, however, has a similarly shaped ischium and pubis, and they can be fused (McGowan, 1989). The pelvis of *L. moorei* is unknown (McGowan and Milner, 1999). The skull of CAMSM J 35178, the embryo, appears high-crowned, reminiscent of *L. moorei*, although Seeley (1880) suggested that a high crown was an embryonic characteristic. CAMSM J 35178 also appears to have a short snout, but the snout is broken and it is not possible to estimate its original length. The shape of the external naris and the exclusion of the maxilla from the border of the external naris suggest that this specimen could be a *L. tenuirostris*. In contrast, the maxilla forms part of the border of the somewhat rounded external naris in *L. moorei* (McGowan and Milner, 1999, text-fig 3). The notched radius associated with the skull and vertebral column

TABLE 3. Measurements and estimates of skull and vertebral column lengths and number of centra of the adult (CAMSM J 35279) and embryo (CAMSM J 35278).

	ADULT		EMBRYO	
	Measured	Estimated	Measured	Estimated
Skull length	22 cm	50 cm	19.2 cm	27.0 cm
Prenarial length			7.8 cm	
Presacral length of vertebral column	66 cm	106 cm		27.0 cm
Number of presacral centra	28	45		45
Vertebral column length to tailbend	99 cm	212 cm	32.4 cm	54.0 cm
Total number of centra	41		54	
Total length to tail bend	121 cm	262 cm	51.6 cm	81.0 cm

of the more complete embryo also suggests that these specimens belong to *L. tenuirostris*, as *L. moorei* does not have notching on the paddle elements (McGowan and Milner, 1999; McGowan, 1989). The adult is also within the size range of *L. tenuirostris*, and much larger than *L. moorei* (Maisch and Matzke, 2000).

Stratigraphic considerations also suggest that these specimens are more likely *Leptonectes tenuirostris*. Numerous specimens of *L. tenuirostris* are known from Street (McGowan, 1989). In fact, McGowan and Motani (2003) described the species occurrence as "primarily Street, Somerset". *L. moorei*, however, is known only from Lyme Regis, Dorset. *Leptonectes tenuirostris* has been documented from the Rhaetian through the Pliensbachian whereas *L. moorei* is known only from the Pliensbachian (Maisch and Reisdorf, 2006; McGowan and Milner, 1999). Pliensbachian strata are not exposed in the Street area, which has strata from the Rhaetian to Sinemurian age. Thus the probable age of the specimen indicates it most likely belongs to *L. tenuirostris*, whereas if it belonged to *L. moorei*, it would require a substantial revision of the geologic range of the species.

Embryo or Neonate?—Although originally the embryo was mounted to the right of the adult block in its frame, the three small isolated embryonic vertebrae near the right pelvis and the scattered posterior adult vertebrae near the embryo suggest that it was positioned at the end of the adult vertebral column, next to the disarticulated vertebrae of the adult. This would place the larger, more complete embryo near the pelvis, oriented with its head pointed away from the adult. Many embryos have been found in this position, although the normal birth position was probably tail-first (Böttcher, 1990). Additionally, Böttcher (1990) argued that ichthyosaurs had paired uteri and that twins were the common occurrence. The presence of a second small vertebral column suggests that these specimens are embryos rather than neonates.

Skull size is known to grow with negative allometry relative to the postcranial skeleton, such that juveniles have proportionately larger skulls than adults (McGowan, 1973). Deeming et al. (1993) reported an *Ichthyosaurus* embryo whose skull is about one third (0.34) of the length of the entire individual embryo (Table 2). The specimen was identified as a mid-term embryo based on the ontogeny of *Alligator* (Deeming et al., 1993). The embryo is posterior to the pelvic region of the adult, and shows a tightly curled position (Deeming et al., 1993). By comparison, data on small skeletons associated with *Stenopterygius* adults have skull length/total length ratios of 0.30 to 0.48 (Table 2; data from Deeming et al., 1993).

CAMSM J 35178, the embryo, is incomplete, but the preserved jaw is 19.2 cm long, and the vertebral column is 32.4 cm long (Table 3). The ratio of skull length preserved to total length preserved is thus 0.37. The vertebral column, however, includes 54 centra, so it extends beyond the pelvis but does not include most of the tail, assuming the vertebral count for *Leptonectes tenuirostris* (at least 45 but less than 50; McGowan, 1989; McGowan and Motani, 2003). Using 45 as the centrum count, only 83% of the measured length is the presacral portion (27.0 cm). If we assume that half of the prenarial region is missing from the snout (add an additional 7.8 cm to the skull length), and that the post-sacral length is at least as long as the pre-sacral length (double the estimated presacral length) the estimate of skull length is 27 cm and the vertebral column length is 54 cm (Table 3). For *Stenopterygius*, skull lengths above 29 cm are "free living" individuals, whereas skull lengths less than 16.5 cm are embryos; sizes in between include both (Deeming et al., 1993). The estimates place this specimen at the high end of the range that includes both small skeletons associated with larger ones and "free living" small specimens, as defined by

Deeming, et al. (1993, fig. 6). However, embryonic skull proportions may vary among genera and species, so the size ranges for *Stenopterygius* might not be the same for other taxa. Because *Leptonectes tenuirostris* has an unusually elongated skull, its embryos are likely to have relatively larger skulls than other species at the same ontogenetic stage. The estimated length of the skull and vertebral column give a skull to total length ratio of 0.33. This estimated ratio puts CAMSM J 35178, within the range of other embryos (Table 2).

Another approach is to look at the relative size of the associated skeletons, although the size of the embryo is related to the developmental stage. The preserved length of the adult *Leptonectes* is 121 cm, although most of the caudal region and a large portion of the snout are missing. The preserved length of the embryo, also missing most of the caudal region but with a more complete but broken snout, is 51.6 cm, about 43% the preserved length of the adult, but this estimate is high because both specimens are incomplete.

A better ratio can be calculated by estimating the complete size of the adult. Assuming that the anterior portion of the adult skeleton, with 28 centra, represents 62% of the 45 centra of the presacral column, the preserved length of 66 cm would mean a complete presacral length of at least 106 cm (Table 3). Assuming again that the caudal length is as large as the presacral length, the entire adult vertebral column would have been 212 cm long. For *Leptonectes tenuirostris*, the prenarial segment proportion of the rostrum is > 0.56 of the jaw length (McGowan, 1989). If we assume that the preserved skull of CAMSM J 35179 (the adult) is only the post-narial portion, the entire skull would have been 50 cm long (Table 3). Using the previous estimate for the total length of the embryo (81.0 cm), it would be 31% of adult length (262 cm). This is comparable to some of the *Stenopterygius* embryos in Table 2. O'Keefe and Chiappe (2011), however, suggested that for ichthyosaurs, as in extant r-selected reptiles, neonates were less than 30% of the adult size. Böttcher (1990) estimated that *Stenopterygius* neonates were about 25% of the adult length. From their estimates, CAMSM J 35278 is more likely a neonate than an embryo, although the measurements in Deeming et al. (1993) suggest a larger size for *Stenopterygius* embryos (Table 3). Brinkmann (1996) reported three late-term embryos of *Mixosaurus* that were approximately 40% of the adult size. Thus there may be considerable variation among genera. In particular, the exceptionally long rostrum of *Leptonectes tenuirostris* will result in an embryo being a larger percentage of the adult length than in other ichthyosaurs at the same ontogenetic stage. Although both of the skeletons discussed here are incomplete, the estimated ratios suggest that CAMSM J 35278 and the second small vertebral column are most likely late-term embryos.

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APPENDIX

Centrum measurements of CAMSM J 35279, the adult *Leptonectes tenuirostris*. Not all centra could be measured.
* indicates measurement is an estimate

Articulated centra on larger adult block

Position on specimen	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
1	3.27	1.19*	2.60
2		1.33*	3.11*
3		1.45*	3.33*
4		1.48*	3.28*
5		1.48*	3.32
6		1.45	
8		1.82	3.19
9		1.53	
10		1.92	
11		1.75	
18		2.39	
20		1.90	
21		1.82*	4.22
22		1.76*	4.12
23		2.14*	4.29
24		1.82*	4.06
25		2.08	4.29
26	3.61	1.82	4.35
28		2.27	4.01

Articulated centra on second adult block

Position on specimen	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
29		1.85	4.03
30		2.04	4.20*
31		2.14	4.24
33		2.25	4.43
34		2.02	4.54
35		2.11	4.68
36		1.97	4.89
37		1.85	4.82
38	4.44		4.63
39	3.40	1.76	4.41
40		2.47	4.83
41	3.80		4.22

Centra associated with CAMSM J 35278

	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
anterior	3.95		3.87
caudals	4.05		3.78
		1.93	4.65
		3.65	3.93
posterior	2.35		2.47
caudals	2.28		2.57

Adult fluke vertebrae in fifth block

	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
	1.46		1.86
		1.01	1.79
	1.32*	0.94	1.90
	1.34		1.79
	1.28		1.69*
	1.30		1.40*
		0.87	
		0.80	1.56
		0.87	1.54
	1.18		1.52
	1.07	0.81	1.57
	0.78	0.63	1.15
smallest		0.47	0.87
of the		0.55	0.86
articulated		0.53	0.90
fluke centra	0.73	0.57	0.88

Isolated centra near skull

	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
cervical	3.34		2.88
?distal caudal	2.47		2.35

Centrum measurements of the two embryos. Not all centra could be measured.

CAMSM J 35278

Disarticulated centra near skull

	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
cervical	1.37		1.08
cervical	1.32	0.42	0.91*
cervical	1.32	0.39	0.95

Articulated centra

Position on specimen	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
5	1.45		1.32*
7		0.39	1.27
8		0.43	1.20
9		0.46	1.22
10		0.50	1.16
11		0.55	1.19
12		0.49	1.09
13		0.51	1.14
14		0.54	1.08
15		0.56	1.26
18		0.53	1.37
19		0.63	1.49
22		0.67	1.54
30		0.55	1.44
31		0.59	1.54
32		0.58	1.48
33		0.58	1.57
34		0.51	1.49
35		0.55	1.52
36		0.47	1.44
37		0.45	1.37
38		0.48	1.23
49			1.22
53	1.11		1.28*
54	1.29		1.29*

SECOND EMBRYO

Articulated centra

	WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
1	1.26		1.51
2			1.46
3		0.41	1.29
4		0.41	1.46
9		0.43	1.29
10		0.38	1.36
12		0.39	1.36
last one		0.35	0.94*

Disarticulated embryonic centra

WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
1.17		1.45
1.15		1.43
1.14		1.31
1.03		1.22

Smaller, scattered embryonic centra

WIDTH (cm)	LENGTH (cm)	HEIGHT (cm)
0.69		0.77
0.57		0.64