A new leptocentid ichthyosaur from the Lower Jurassic (Hettangian) of Nottinghamshire, England, UK, and the taxonomic usefulness of the ichthyosaurian coracoid

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Thousands of ichthyosaurs have been discovered from the rich Lower Jurassic deposits of the UK, with the majority collected from along the Lyme Regis-Charmouth area of the Dorset coast. Here, I describe a new leptocentid ichthyosaur, *Wahlisaurus massarae* gen. et sp. nov., based on a partial skull and an incomplete skeleton collected from the Lower Jurassic (Hettangian) of Nottinghamshire, England. *Wahlisaurus* can be referred to the Leptonectidae through the possession of an extremely slender and delicate snout, and a mandible shorter than the snout which produces an overbite. This referral is supported by a phylogenetic analysis. The new taxon is distinguished from other ichthyosaurs through a unique combination of characters and autapomorphies of the pectoral girdle including the presence of both a scapular-coracoid foramen and a large and roughly ovoid coracoid foramen. A coracoid foramen has only previously been reported in the Triassic ichthyosaur *Cymbospondylus*. The peculiar coracoid morphology further highlights the taxonomic utility of coracoids in ichthyosaurs. The aforementioned features demonstrate that *W. massarae* cannot be referred to any currently recognized leptocentid. *Wahlisaurus* is the ninth Lower Jurassic ichthyosaur genus to be recognized worldwide, and the fifth documented in the Lower Lias Group.

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Introduction

Lower Jurassic ichthyosaurs are presently represented by eight genera (*Ichthyosaurus*, *Leptonectes*, *Eurhinosaurus*, *Excalibosaurus*, *Suevoleviathan*, *Stenopterygius*, *Hauffiopteryx* and *Temnodontosaurus*), and all but one (*Suevoleviathan*) have been reported from the UK (Maisch & Matzke 2000; Williams et al. 2015), although one specimen previously identified as *Hauffiopteryx* may represent a new Lower Jurassic taxon (Marek et al. 2015). The wealth of Lower Jurassic ichthyosaur specimens in the UK has significantly contributed to our understanding of ichthyosaurs from this time interval (e.g. McGowan 1974, 1989a, 1993, 1996; Benton & Taylor 1984; Delair 1969).

The relatively recent recognition of a new genus and a new species from the extensively studied Lower Jurassic sites of both Holzmaden and Dorset, respectively, suggest that new ichthyosaur taxa may yet be discovered (Maisch 2008; Lomax & Massare 2015). This is further exemplified by Marek et al. (2015). The focus of the present study is the identification of a new leptocentid ichthyosaur from the Lower Jurassic (Hettangian) Lias Group of Nottinghamshire, England. *Ichthyosaurus*, *Leptonectes*, *Temnodontosaurus* and *Excalibosaurus* have been reported from the Lower Lias Group, although only the former three have been confidently recorded in the Hettangian. The stratigraphical details of many Lower Jurassic specimens in the UK are unknown because they are from historical collections (McGowan 1974; Benton & Taylor 1984; Chapman & Milner 2010).

*Wahlisaurus massarae* gen. et sp. nov. is distinguished from other ichthyosaur taxa by a unique combination of characters including autapomorphic features of the pectoral girdle. An examination of the taxonomic usefulness of the coracoid in ichthyosaur studies is also discussed.

Geological setting

In the UK, Lower Jurassic ichthyosaurs have been collected in abundance from the Lyme Regis-Charmouth area along the Dorset coast (Milner & Walsh 2010), from numerous quarries around the village of Street, Somerset (Delair 1969), and from the Whitby area along the Yorkshire coast.

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(Benton & Taylor 1984). They are also relatively well recorded from Barrow-upon-Soar, Leicestershire (Martin et al. 1986). Some specimens have also been reported from quarries in Warwickshire (Smith & Radley 2007) and from Strawberry Bank, Somerset (Williams et al. 2015). Ichthyosaurs were briefly reported from Nottinghamshire (see discussion in Lomax & Gibson 2015), but only recently has a compilation of Nottinghamshire ichthyosaur specimens, including those from the Lower Jurassic, been completed (Lomax & Gibson 2015). It was during that compilation that the studied specimen was first examined.

The specimen (LEICT: G454.1951.5) was purchased in 1951 and previously formed part of the collection of Mr Percy Faulks. It was collected from Normanton Hills, near Normanton on Soar in the district of Rushcliffe, Nottinghamshire (Fig. 1). The exact collection date of the specimen is unknown, but it was recorded as being collected from exactly the same locality and horizon as LEICT: G378.1953.11, an unprepared skull from the Lower Jurassic, collected from an ‘old quarry’ and from either the top of the Pre-planorbis beds or the base of the planorbis Zone (lowermost Hettangian: perhaps the Scunthorpe Mudstone Formation, Barnstone Member; Lomax & Gibson 2015).

**Institutional abbreviations**

BGS: British Geological Survey, Keyworth, Nottingham, England; BRLSI: Bath Royal Literary and Scientific Institution, Bath, England (specimens are presently in the care of NMW: National Museum of Wales, Cardiff, Wales); CAMSM: Sedgwick Museum, Cambridge University, Cambridge, England; DONMG: Doncaster Museum and Art Gallery, Doncaster, England; LEICT: Leicester Arts and Museums Service (New Walk Museum and Art Gallery), Leicester, England; NHMUK: Natural History Museum, London, England; WARMS: Warwickshire Museum Service, Warwick, England.

**Systematic palaeontology**

Order *Ichthyosauria* de Blainville, 1835  
Minorder *Parvipelvia* Motani, 1999b  
Suborder *Neoichthyosauria* Sander, 2000  
Family *Leptonectidae* Maisch, 1998  
Genus *Wahlisaurus* gen. nov.

**Type species.** *Wahlisaurus massarae* sp. nov.

**Diagnosis.** As for type and only species.

**Derivation of name.** In honour of William (Bill) Wahl for his contribution to the study of Mesozoic marine reptiles and for introducing the author to the study of the group.

*Wahlisaurus massarae* sp. nov.  
(Figs 2–7)

**Holotype.** LEICT G454.1951.5, a partial skull and an associated incomplete skeleton comprising the pectoral girdle, humeri, pelvic elements, partial hind fins, vertebrae and ribs. Only known specimen.

**Derivation of name.** In honour of Professor Judy Massare for her significant contribution to the study of Mesozoic marine reptiles, especially ichthyosaurs, and for introducing the author to the study of the group.

**Diagnosis.** Small-bodied leptonectid ichthyosaur with the following autapomorphies: coracoid with a large, ovoid foramen, a coracoid foramen is present in *Cymbospondylus* but it is much smaller in this genus (Merriam 1908; Sander 1989); presence of both a coracoid foramen and scapular-coracoid foramen (fenestra coracoscapularis), the latter formed by articulation of the coracoid and scapula; a coracoid with a posterior notch that is much more developed than the anterior notch. Three other features may be autapomorphies: humerus deltopectoral crest prominent and 2.5 times greater than the dorsal process; dorsoventral width of the humerus is greater than the anteroposterior width, which results in a D-shape in proximal view; and slender, long, needle-like teeth with marginally recurved crowns and large, bulbous infolded roots.  

*Wahlisaurus massarae* is also characterized by the following combination of features shared with other taxa: very slender, delicate and relatively long snout (as in all leptonectids) with mandible shorter than snout, which...
produces an overbite (shared with *Eurhinosaurus*, *Excalibosaurus* and some specimens of *Leptonectes tenuirostris*; McGowan 1989a, 1996, 2003); basioccipital with extensive extracondylar area (as in *Ichthyosaurus*, *Excalibosaurus*, *Eurhinosaurus* and *Leptonectes tenuirostris* and all other non-opthalmosaurid ichthyosaurs; McGowan 2003; McGowan & Motani 2003; Lomax & Massare 2012); coracoid anteroposteriorly longer than mediolaterally wide (as in some specimens of several taxa including *Stenopterygius*, *Hauffiopteryx*, *Leptonectes tenuirostris*, *Ichthyosaurus* and *Ophthalmosaurus*; Maxwell et al. 2012); extensive contact between the anterolateral border of coracoid (lateral scapular facet and medial scapular facet) and scapula forms a small, semi-circular scapulocoracoid foramen, similar contact has been reported in some specimens of *Stenopterygius* and *Paraophthalmostaurus* (Johnson 1979; Efimov 1999) and is here noted in some specimens of *Leptonectes tenuirostris* (e.g. McGowan 1974, fig. 11; BGS 51236; WARMS G10868), but the coracoid-scapular foramen is much larger, deeper and ovoid in those taxa; a small, emarginated anterior notch in coracoid (as in the holotype of *Excalibosaurus* and also in *Suevoleviathan*, McGowan 1989b; Maisch 1998); a well-developed posterior notch in the coracoid

**Figure 2.** Basioccipital, rostrum and dentition of LEICT G454.1951.5, *Wahlisaurus massarae* gen. et sp. nov. A, basioccipital in posterior view; note the extensive extracondylar area, fragment of the left stapes and portion of basisphenoid. B, ventral view of mandible and snout with anterior portion of dentary rotated (in dorsal view) and positioned adjacent (dashed line indicates point of fit); note the slenderness of the rostrum and the presence of an overbite. C, close-up of the large, long and robust teeth and some of the needle-like teeth positioned under the maxilla. D, close-up of three dentary teeth; note the ‘waisted’ morphology, recurved crown and infolded root. Abbreviations: bas, basisphenoid; den, dentary; mx, maxilla (right maxilla); pmx, premaxilla; sta, stapes. Scale bars: A = 5 cm; B = 10 cm; C = 3 cm.
Figure 3. Skull roof elements of LECT G454.1951.5, *Wahlisaurus massarae* gen. et sp. nov. A, photograph; B, interpretative illustration based on the preserved skull elements. Due to crushing and damage, some of the sutures are difficult to distinguish. Note, as the postorbital and ?jugal are exposed laterally, their contact with the postfrontal and supratemporal may not be genuine. Dashed line indicates a possible suture; diagonal lines indicate a broken edge; grey represents matrix exposed between the bones; black area includes pineal foramen and upper temporal fenestra. Abbreviations: f, frontal; ju, jugal; na, nasal; p, parietal; pf, postfrontal; pif, pineal foramen; po, postorbital; prf, prefrontal; qj, quadratojugal; st, supratemporal. Scale bar = 5 cm.
(as in *Ichthyosaurus*; McGowan & Motani 2003); long scapula with greatly expanded proximal region but without prominent acromion process (as in *Leptonectes moorei, Eurhinosaurus, Excalibosaurus* and *Ichthyosaurus*; Maxwell et al. 2012); long femur with thin, slender shaft and distal end wider than proximal (as in *Leptonectes tenuirostris*; McGowan 1989a); notched tibia (as in several Lower Jurassic ichthyosaurs including *Temnodontosaurus, Stenopterygius, Leptonectes tenuirostris* and *Ichthyosaurus conybeari*; McGowan 1974; 1989a, 1996; Johnson 1979); pelvis tripartite with pubis widely expanded distally and approximately equal in size.
to ischium (as in some specimens of *Ichthyosaurus* and *Leptonectes tenuirostris*; McGowan 1993; McGowan & Motani 2003).

**Occurrence.** Lower Jurassic, either the top of the *Preplanorbis* beds or the base of the *planorbis* Zone (lowermost Hettangian: perhaps the Scunthorpe Mudstone Formation, Barnstone Member). Normanton Hills, near Normanton on Soar, Nottinghamshire, England, UK.

**Description and comparisons**

**Taphonomy.** Originally, this specimen was preserved in several blocks of matrix, but they were both mechanically and acid prepared sometime between 1952 and 1981 by R. Appleby (Mark Evans, pers. comm. 2015). Currently, the specimen is in several pieces, but three moderately large blocks constitute the majority of the specimen and are in some parts three-dimensional. Many isolated fragments of associated matrix are also present. The preservation is exceptional in places with some areas fully articulated, yet other portions are not as well preserved and are damaged, which make detailed comparisons of certain elements of the skeleton difficult to impossible. Nothing suggests that the elements belong to more than one individual (Mark Evans, pers. comm. 2013). A gastric mass is present between some of the ribs but the contents cannot be identified as this portion requires further conservation.

**Maturity.** The specimen is probably a subadult if not an adult. Johnson (1977) showed that a smooth humeral shaft and convex humeral head were indicative of a mature individual, although McGowan (1995) pointed out that the convexity of the humeral head differs depending on the angle at which the humerus is viewed. These characters are present in the studied specimen. McGowan (1995) noted that the articular region of the humerus has a rugose surface in immature individuals and a smooth surface in mature individuals. In this specimen, the articular region has a combination of both relatively rugose and smooth surfaces. Maxwell *et al.* (2012) also mentioned the fusion of cranial sutures of the dorsal skull roof as indicative of a mature individual. Of what can be reliably interpreted, this specimen displays some fusion in the skull roof elements, but poor preservation prevents confirmation of the fusion of all elements. Johnson (1979) compared the point of contact between the medial scapular facet of the coracoid with the medial coracoidal facet of the scapula and found that in immature specimens of *Stenopterygius* it may have been bounded anteriorly by cartilaginous areas which would leave a gap between the contact, whereas in mature specimens the margins appeared to be fully ossified. In the studied specimen there is no gap between the two articulating facets.

**Skull.** The skull is dorsoventrally crushed and only some elements are preserved, including a portion of the right side of the skull roof.

The basioccipital, exposed in posterior view and partially visible in dorsal view, possesses a bulbous, circular occipital condyle which occupies half of the posterior surface. The extracondylar area is extensive, rounded and flared laterally (Fig. 2A). The shape is similar to *Ichthyosaurus* (McGowan & Motani 2003), *Excalibosaurus* (McGowan 2003) and all non-ophthalmosaurid ichthyosaurs (McGowan & Motani 2003). However, in *Ichthyosaurus*, the extracondylar area is dorsoventrally longer and approximately squared and in *Leptonectes* it is mediolaterally wider and more circular. A fragment of the left stapes is present on the lateral surface of the extracondylar area (Fig. 2A), the contact is fairly extensive and extends across roughly half the lateral surface, similar to *Ophthalmosaurus* (Kirton 1983, fig. 1). Another element may be a partial stapes, which is relatively large, widely flared and has a somewhat narrow shaft that is probably damaged. The exoccipital facets are roughly square. The floor of the foramen magnum is triangular and flat and there appears to be no indication of a basioccipital peg, unlike in *Ichthyosaurus* and *Excalibosaurus* (Motani 1999b; McGowan 2003), although this cannot be confirmed. In posteriorventral view, at the base of the basioccipital, the extracondylar region and the stapes articulate with a robust rectangular element that is a portion of the basisphenoid.
exposed from underneath; the opening of the carotid foramen is present. A single quadrate is preserved in three dimensions and is probably the left. It is a large and robust element that is roughly C-shaped. In lateral view, it is anteroposteriorly wide and curved, and the postero lateral portion forms a prominent, wide, robust bulge. In posterior view, the proximal portion is noticeably thin mediolaterally.

An articulated portion of the skull roof is exposed in dorsal view, but dorsoventrally flattened (Fig. 3). The articulated parietals are large elements that contact the frontal anteriorly, postfrontal laterally and supratemporal posteriorly. The extensive parietal is similar to that of some specimens of *Ichthyosaurus* and *Leptonecetes* (Maisch & Matzke 2000, fig. 11; Motani 2005). The parietal is roughly crescent-shaped and has a distinct contact with the supratemporal. The opening of the pineal foramen is oblong and is situated within thefrontals. This position is similar to *Ichthyosaurus* and *Eurhinosaurus* (Motani 1999b; Maisch & Matzke 2000; Motani 2005), unlike in other Lower Jurassic ichthyosaurs such as *Leptonecetes, Temnodontosaurus, Stenopterygius* and *Suevoleviathan* (Maisch 1998; Maisch & Matzke 2000; Maisch & Matzke 2003; Motani 2005). The frontals do not contact the postfrontals. The postfrontal is a large element that contacts the parietal anterolaterally, and may contact the nasal and prefrontal anteriorly, and the supratemporal posteriorly. The postfrontal forms much of the anterior and lateral portions of the upper temporal fenestra. The supratemporal appears to contribute minimally to the posterior portion of the upper temporal fenestra, but the suture contact with the postfrontal cannot be identified. The right postorbital and possibly the jugal are partially exposed, having been displaced laterally. The postorbital is fairly long, slender anteriorly and slightly wider towards what is presumably the centre, but it is probably damaged so its exact morphology cannot be determined. Only the anterior section of the jugal can be identified and it is exposed in

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**Figure 6.** Humeri of LEICT G454.1951.5, *Wahlisaurus massarae* gen. et sp. nov. A, left humerus, ventral view; note the prominent deltopectoral crest. B, left humerus, dorsal view. C, left humerus, proximal view; note the D shape. D, right humerus, anterior view. Abbreviations: adn, anterodorsal notch; Ant, anterior; Dor, dorsal; dp, dorsal process; dpc, deltopectoral crest; Pos, posterior; Ven, ventral. Scale bar = 3 cm.
right lateral view. The anterior process is thin and sharply pointed, positioned dorsal to the maxilla.

Portions of both maxillae are preserved and the right is the most complete (Fig. 2C). It is a long and slender element, about 9.2 cm long anteroposteriorly. The posterior end extends under the jugal and is sharply pointed. The highest point of the maxilla is slightly posterior to the centre of the bone, but it is damaged. The anterior process of the maxilla is long and narrow and extends significantly beyond what is probably the external naris. Only a small portion of the lowermost section of the possible external naris is preserved and it appears to be a small lateral opening.

The middle and anteriormost portions of the nasal appear slender and perhaps short, but this cannot be confirmed due to the damage. However, the posterior portion of the nasal is relatively wide, but is incomplete (Fig. 3).

The premaxilla is long and slender, but it is damaged posteriorly (Fig. 2B). At its widest point posteriorly, dorsal to the highest point of the maxilla, the two premaxillae measure 3.6 cm. They are 1.5 cm wide at their narrowest point anteriorly. The premaxillary length is approximately 20 cm; it is 0.52 of the jaw length (premaxilla segment/jaw length).

The tip of the snout extends beyond the tip of the mandible by approximately 4.5 cm, forming a noticeable overbite, although both the tip of the premaxilla and dentary may be missing – but probably no more than a centimetre (Fig. 2B). The overbite is not as extensive as in *Eurhinosaurus* and *Excalibosaurus* (McGowan 1989b, 1994a), but is more apparent than in some specimens of *Leptonycteris tenuirostris*, which sometimes display an overbite (McGowan 1989a; Motani 1999b; McGowan & Milner 1999). Only one small tooth crown can be positively identified in the snout beyond the dentary.

**Mandible and dentition.** The mandible is broken into numerous sections that can be pieced together, but both the anterior and posterior ends are probably missing a small amount (Fig. 2B). The mandible is relatively long, delicate and thin, similar to the premaxilla. The estimated jaw length is approximately 38 cm. In lateral view, the posterior section of the dentary is thin and delicate and extends to under the highest point of the maxilla. At this position, the surangular is a wider element and its tip is large and extends farther forward than the maxilla, but the posterior portion of the element is not preserved. The angular is marginally exposed in lateral view. In ventral view, the angular is a long and delicate element, but its anterior and posterior regions cannot be reliably identified as they are either damaged or missing.

Many teeth are preserved although most are lying dislodged and several are broken and missing the crown. The tooth morphology differs between the posterior maxillary teeth and the premaxillary and dentary segments. Some of the maxillary teeth are larger, longer and more robust (Fig. 2C) although the teeth in the dentary are largely different from the others (Fig. 2D). Many of the teeth are needle-like with slender, subtly (almost smooth) striated crowns and finely pointed apices that are marginally recurved, whereas the roots are large, bulbous and infolded. Some of the teeth, especially in the dentary, are waisted, where there is a rapid expansion of the diameter of the root relative to the crown (Fig. 2D). The dentary teeth have bulbous, infolded roots and subtly (almost smooth)
striated, very narrow crowns that are recurved (Fig. 2D). This morphology is unusual. Ichthyosaur tooth shape varies from slender and sharply pointed to large and robust, although most have the form of small, slightly curved cones (Massare 1987). The needle-like crown morphology in the studied specimen is most similar to leptonecids but it is also comparable to the anteriormost teeth seen in Ichthyosaurus conybeari (McGowan 1989a, 1996, 2003; Maisch & Matzke 2000; pers obs: BGS 956). However, the large and relatively long maxillary teeth and the unusual morphology of the dentary teeth of the studied specimen are not found in these species.

**Axial skeleton.** Twenty-two mostly disarticulated dorsal centra are associated with the skeleton. One of the most complete is an anterior dorsal that is 3.4 cm wide, 3 cm high and 1.8 cm long. The remaining centra are also wider than they are tall. Numerous rib fragments are associated with some worn posterior dorsal and anterior caudal centra (the transition from dorsal to caudal is identified by the merge of the rib articulations). The ribs become broader and flatter towards the rib head. One preserved rib is probably unicipital whereas the other identifiable rib head is bicipital. The ribs are round in cross section. Several other isolated rib fragments are broken and separated from the main blocks.

**Pectoral girdle and forefin.** Two articulating blocks include complete, articulated coracoids, scapulae, portions of the clavicle and interclavicle, and associated humeri. All of the elements are robust and are exposed in ventral view (Fig. 4).

The coracoid is anteroposteriorly longer than mediolaterally wide. An anterior notch is present as a very small, reduced semi-circular emargination. An anterior notch of the coracoid is found in many ichthyosaur taxa (Maxwell et al. 2012) but the shape of the notch is variable and ranges from a shallow or deep tightly curved C-shape to a widely open curve (Maisch & Matzke 2000; McGowan & Motani 2003; pers. obs., e.g. BRLSI M3556, CAMSM J35183, DONMG 1983.98, NHMUK PV R972, NHMUK PV R1124, NHMUK PV R2137, NHMUK PV R3300, NHMUK PV R5465, NHMUK PV OR28327, WARMS G10868). Some difference in shape of the anterior notch might be a result of intraspecific or ontogenetic variation (Johnson 1979). A shallow emargination as seen in the studied specimen is unusual, although a similar emargination was reported in the holotype specimen of Excalibosaurus costini (McGowan 1989b). In the studied specimen, articulation between the coracoid and scapula is extensive and encompasses the anterior notch, which produces a small scapular-coracoid foramen (the fenestra coracoscopularis). An anterior notch that is enclosed and locked by contact of the coracoid and scapula has only been reported in some specimens of Stenopterygius (Johnson 1979; Maxwell et al. 2012), Paraophthalmosaurus (Efimov 1999; Arkhangel-sky & Zverkov 2014) and Leptonecites tenuirostris (e.g. McGowan 1974, fig. 11; pers. obs., e.g. BGS 51236 and WARMS G10868), although the scapular-coracoid foramen is much larger, deeper and more rounded in these taxa than in Wahlisaurus. At least in Stenopterygius, a scapular-coracoid foramen might reflect ontogenetic variation, with its presence associated with mature individuals (Johnson 1979). In Wahlisaurus, positioned posterior to the anterior notch and entirely within the coracoid, is a large, roughly ovoid foramen. The only ichthyosaur reported with a coracoid foramen is Cymbospondylus from the Triassic, and in that genus it is considered to have taxonomic importance (Merriam 1908; Sander 1989; Maisch 2010). Compared to the studied specimen, the coracoid foramen in Cymbospondylus is much smaller and round (Merriam 1908, figs 76, 133; Sander 1989, fig. 7). In Wahlisaurus, the foramen in the right coracoid is complete, but damage of the anterolateral border of the element gives the appearance that it may not be fully within the coracoid. However, the outline of the foramen, which is encompassed in the coracoid, is complete irrespective of the surrounding elements that are damaged and crushed (Fig. 5). In addition, the right foramen is marginally larger than the left, although this could be due to damage or excessive preparation. The anterior portion of the coracoid is large, wide and trapezium-shaped. The proximal end appears to have a relatively squared edge, but this portion of both coracoids is damaged and may be incomplete. The anterolateral border of the coracoid is extensive, formed by the proximal squared edge and the coracoid scapular facets. The anterolateral border of the coracoid is approximately 1.5 times longer than the glenoid contribution of the coracoid. In other ichthyosaur taxa the glenoid contribution of the coracoid is either marginally shorter than, equal to, or greater than the anterolateral length, and possesses either a well-defined anterior notch or a curved edge (Maisch & Matzke 2000; Maxwell 2010; Maxwell et al. 2012). A well-developed, wide, posterior notch is present in Wahlisaurus, as in Ichthyosaurus, unlike other Lower Jurassic taxa in which the posterior notch is absent or markedly reduced (Johnson 1979; Maisch & Matzke 2000; Maxwell & Druckenmiller 2011; Maxwell et al. 2012). The posterior margin of the coracoid is fan-shaped and rounded, but the posteromedial edge is straight and some of it may be broken. Fragments of the clavicle are preserved but do not enable detailed description. Part of the anteriormost T-shaped section of the relatively robust interclavicle is preserved and articulated; the corresponding portion is preserved on a separate block. The interclavicle shaft is robust and extends approximately midway along the coracoids, but a portion of the middle is missing and the posterior end is probably incomplete (Fig. 4).

The scapula has a straight, thin shaft that is slightly flared distally and is thick and expanded (flared)
proximally (Fig. 4). The coracoid facet comprises almost the entire length of the proximal end of the scapula, resulting in extensive contact with the coracoid. The glenoid contribution of the scapula is minimal. Proximal expansion of the scapula is present, but a large acromion process is absent. Some specimens of *Leptonectes*, *Eurhinosaurus* and *Stenopterygius* display markedly wide contact between the scapula and coracoid facets, but the contact is not as extensive. Instead, the scapula and coracoid contact is separated in part by a wide anterior notch, or their contact is by the lateral scapular facet of the coracoid and the lateral coracoid facet of the scapula only (McGowan 1974, 1989a; Johnson 1979; Maisch & Matzke 2000; Maxwell et al. 2012). In the studied specimen the right scapula is nearly complete and measures 12 cm long, 3.4 cm wide at the distal end and 7.2 cm wide at the proximal end. Thus the proximal end is more than twice the size of the distal end.

Both humeri are preserved but the distal portions are missing (Fig. 6). The left can be examined in three dimensions, and the following description is of that element, unless otherwise stated. The humerus is massive and robust proximally with a relatively wide shaft, which is similar to that of Lower Jurassic ichthyosaurs including *Ichthyosaurus*, *Stenopterygius*, *Eurhinosaurus*, *Excalibosaurus* and *Leptonectes moorei*, rather than the more slender shafts of the humeri of *Leptonectes tenuirostris* and to a lesser extent *Temnodontosaurus* (e.g. Johnson 1979; McGowan 1989a, fig. 2, 1995; Motani 1999a; McGowan & Milner 1999). Measured from anterior to posterior, the head is 4.8 cm wide. The prominent deltopectoral crest is 2.5 times longer dorsoventrally than the dorsal process. This is best observed in proximal view, where the dorsoventral width of the humerus is noticeably greater than the anteroposterior width, which results in a D-shape in proximal view (Fig. 6C). In ventral view, the deltopectoral crest is slightly offset towards the anterior, and a well-defined lip runs around the crest (Fig. 6A). In dorsal view, the peak of the dorsal process is roughly anteroposteriorly centrally located (Fig. 6B). It appears slightly reduced, but possesses a large surface area with a marked trochanter dorsalis. On the articular surface and anterior to the dorsal process is a gently curved L-shaped ‘notch’, termed here the anterodorsal notch (Fig. 6C, D). The notch appears to be genuine, but could be an artefact of excessive preparation. When examined in articulation with the pectoral girdle, this notch contacts the glenoid contribution of the scapula (Fig. 4). In proximal view, both the dorsal and ventral processes are not as offset as in specimens of *Ichthyosaurus* (e.g. McGowan & Motani 2003, fig. 46). The humerus shaft is wide, slightly narrower than the proximal region with barely a constriction, but the humeri are incomplete; the narrowest section of the shaft, measured anteroposteriorly, is 3.6 cm wide. The distal portions of both humeri are missing, but the anterior side appears relatively straight, whereas the posterior is slightly flared (Fig. 6A, B).

**Pelvic girdle and hindfin.** An associated pubis and ischium are preserved and perhaps represent the left pelvis (Fig. 7A). Both elements are completely three-dimensional and unfused, but a proximal contact is evident, similar to that seen in *Temnodontosaurus*, *Leptonectes* and *Ichthyosaurus* (McGowan 1993, 1996; Maisch & Matzke 2000). The ischium is the more slender of the two elements. It has a relatively thick proximal end and a fairly slender shaft, but a portion of the anterodistal end is broken so its exact morphology cannot be determined. However, prominent medial and distal expansions of the ischium are not evident. A slight expansion at the middle of the element is present, but its full extent cannot be confirmed due to the broken edge. The proximal portion of the other ischium is also present, but it is poorly preserved. The pubis and ischium are approximately equal in length, although the pubis is marginally shorter. The proximal end of the pubis is relatively thick and bulbous. The shaft of the pubis is constricted but remains thick and it flattens and widens abruptly into a fan shape distally, similar to some specimens of *Ichthyosaurus* and to *Leptonectes tenuirostris* but without the fusion of the distal end (McGowan 1993; McGowan & Motani 2003; pers. obs., e.g. CAMSM J35183, NHMUK PV R1124, NHMUK PV R3372). Only a few fragments of both hind fins are preserved. The left hindfin is the more complete of the two but consists of only an almost complete femur and articulated notched tibia (Fig. 7). The right hindfin is represented by the distalmost portion of the femur with associated notched tibia. The femur has a robust head, long and slender elongate shaft, and a wider distal end than proximal end, which is similar to *Leptonectes* (McGowan 1989a), *Excalibosaurus* (McGowan 2003) and *Eurhinosaurus* (pers. obs., NHMUK PV R5465). The left femur is proximodistally 7.8 cm long. There is no distinct separation between the tibia and fibula facets. The tibia has a concave edge, a result of a broad, open notch which is similar to some specimens of *Leptonectes tenuirostris* (pers. obs., BGS 51236, BRLSI M3556, BRLSI M3568) and *Eurhinosaurus* (pers. obs., NHMUK PV R5465). All Lower Jurassic genera have at least one species with hindfin notching, although notch shape varies considerably among (and within) species (Massare & Lomax 2016).

**Phylogenetic analysis**

In order to explore the phylogenetic position of *Wahlisaurus massarae*, it was added to the data matrix of Maxwell et al. (2012; Supplemental Material 1). However, some of the coding in Maxwell et al. was modified for *Leptonectes tenuirostris* (see Supplemental Material 2). Character 23...
can be coded as the basioccipital is preserved in one specimen identified as probably *L. tenuirostris* (Lomax & Massare 2012). Prior to this, the basioccipital morphology of *L. tenuirostris* was unknown. Character 26 was also modified because some specimens of this species display an overbite (McGowan 1989a; McGowan & Milner 1999).

The analysis was performed using the implicit enumeration (exact search) in TNT v. 1.1 (Goloboff et al. 2008). Sixteen of the 60 characters (27%) could be coded in *W. massarae* (Supplemental Material 3). The analysis produced six most parsimonious trees of 142 steps (consistency index (CI) = 0.479; retention index (RI) = 0.608). Maisch (1998) defined the Leptonectidae as a monophyletic group formed by *Eurhinosaurus* and *Leptonectes* and stated that the family contained the genera *Eurhinosaurus*, *Excalibosaurus* and *Leptonectes*. A strict consensus tree shows that *W. massarae* groups with other leptonectids and is recovered as a member of the family Leptonectidae (Maisch 1998) (Fig. 8; Supplemental Material 4). *Wahlisaurus massarae* is a sister taxon to *Excalibosaurus costini* and *Eurhinosaurus longirostris*, but their exact relationship cannot be resolved (Fig. 8; Supplemental Material 4). These three taxa are more basal than *L. moorei* and *L. tenuirostris*, but more derived than *L. solei*. The strict consensus tree was bootstrapped with 1000 replicates; support values are very low at most nodes, and values of less than 25% are not shown (Fig. 8). With the inclusion of *W. massarae*, the tree topology of Maxwell et al. (2012) altered slightly, with *Ichthyosaurus communis* and *Leptonectes solei* recovered as sister taxa (Fig. 8). This demonstrates that *W. massarae* has some phylogenetic implications for parvipelvian phylogeny. However, a reanalysis of parvipelvian phylogeny is beyond the scope of this paper.

The following characters are present in *W. massarae* and are shared with several leptonectids, which further strengthens the results of the analysis. *Wahlisaurus massarae* possesses an extremely slender and delicate snout which is found in all leptonectids. The basioccipital with ventral extracondylar area smaller than condyle but still extensive is shared with all leptonectids, but is unknown in *Leptonectes moorei* and *L. solei*. The pineal foramen is situated well anterior to the anterior edge of the upper temporal fenestra (char. 15), which is shared with *Eurhinosaurus* and *L. tenuirostris*, but is the opposite in *L. solei* and unknown in *Excalibosaurus* and *L. moorei*. The position of the pineal foramen is, however, situated between the frontals and is shared with *Eurhinosaurus* but not *Leptonectes tenuirostris*. An overbite (char. 26) is shared with both *Eurhinosaurus* and *Excalibosaurus*, but the overbite in *W. massarae* is not as extensive; some specimens of *Leptonectes tenuirostris* display an overbite (McGowan 1989a; McGowan & Milner 1999). The anterior process of the maxilla extends at least 1.5 or more narial lengths beyond the external naris (char. 2), which is shared with *Eurhinosaurus* but no other leptonectid. The absence of a large acromion process, but anterior expansion of the proximal portion of the scapula present (char. 31), is shared with all leptonectids, but is different in *L. tenuirostris* and unknown in *L. solei*. A reduced anterior notch in the coracoid (char. 33) is only shared with some specimens of *Eurhinosaurus*. A notched tibia (char. 58) is found in all leptonectids, although it is sometimes absent in *Eurhinosaurus*; it is unknown in *L. moorei* and

![Figure 8](image_url)  
*Figure 8.* Results of the phylogenetic analysis. A strict consensus of six most parsimonious trees was produced using a modification of the matrix of Maxwell et al. (2012) (CI = 0.479; RI = 0.608). Bootstrap support values of greater than 25% are presented above the branches. *Wahlisaurus massarae* gen. et sp. nov. was recovered as a leptonectid.
L. solei. Features shared only with L. tenuirostris and no other leptonectid include approximately equal size of ischium and pubis (char. 49); coracoid anteroposteriorly longer than mediolaterally wide (char. 32); and the presence of a scapular-coracoid foramen which is only found in some specimens of L. tenuirostris. This unique combination of characters demonstrates that W. massarae can be reliably distinguished from all other leptonectids.

Features that are not shared with any leptonectid include a well-developed posterior notch in the coracoid (char. 34; as in Ichthyosaurus) and parietal with a minor contribution (less than half) to the anterior edge of the upper temporal fenestra (char. 14), although this is unknown in L. moorei, L. solei and Excalibosaurus. A large, ovoid coracoid foramen and the presence of both a coracoid foramen and scapular-coracoid foramen are presently unknown in any ichthyosaur.

The taxonomic usefulness of coracoids in ichthyosaurs

The coracoid is one of the largest, and in some cases one of the most robust, elements of the ichthyosaurian skeleton. Due to its size and position, the coracoid is often preserved in complete or fragmentary skeletons, and as an isolated element. The shape of the coracoid, presence/absence/size of anterior and posterior notches, the relative sizes of the scapular and glenoid facets, contact between the coracoid and scapula, and presence of a coracoid foramen have all been used to differentiate between ichthyosaur genera (e.g. Maisch & Matzke 2000; McGowan & Motani 2003). As for the posterior notch, it is absent in Excalibosaurus, Eurhinosaurus, Temnodontosaurus, Suevoleviathan and most species of Stenopterygius (McGowan 1989b; McGowan & Motani 2003; Maisch 2008), although S. aalenensis and some specimens of L. tenuirostris display a shallow concavity or slightly emarginated posterior notch (McGowan 1989a, 1989b; Maxwell et al. 2012). The only genus to possess well-developed anterior and posterior notches is Ichthyosaurus (McGowan 1989b; Maxwell et al. 2012).

In some specimens of Stenopterygius, Paraophthalmosaurus and Leptonectes tenuirostris, the anterior notch forms part of the scapular-coracoid foramen. Johnson (1977) noted that a scapular-coracoid foramen was preserved in mature individuals of Stenopterygius, but, irrespective of whether its presence is ontogenetically dependent, a large, circular scapular-coracoid foramen is taxonomically useful in these taxa.

The most variable aspect of the coracoid in Lower Jurassic taxa appears to be the overall shape (Johnson 1979; Maxwell & Druckenmiller 2011), which can be rounded, rectangular or square, with the posterior margin often fan-shaped (Maisch & Matzke 2000; McGowan & Motani 2003). The posterior margin of the coracoid in Leptonectes solei is considered unusual for being scalloped, with only one other individual (CAMSM 8372, a specimen of L. tenuirostris) having a similar morphology (McGowan 1993). Coracoid shape has even been used to distinguish among Cretaceous genera (Fischer et al. 2011a, 2012). However, using coracoid shape to distinguish between species within a genus is problematic because the shape may reflect intraspecific or ontogenetic variation (Johnson 1979; Efimov 1999; Maxwell & Druckenmiller 2011).

Wahlisaurus massarae possesses several features of the coracoid that are unreported in any leptonectid. The morphology of the coracoid, with its wide, trapezium-shaped anterior portion and extensive anterolateral border, could be argued simply to represent variation. However, in addition to the unusual shape, the coracoid has several differences. The combined presence of both a small anterior notch, which forms a scapular-coracoid foramen, and a coracoid foramen are features that are not found in any leptonectid (McGowan 1989a, 1989b, 1993, 1994a, 1996, 2003; Vincent et al. 2014), or indeed any ichthyosaur (Maisch & Matzke 2000; McGowan & Motani 2003; Eurhinosaurus) and some species of Stenopterygius and Temnodontosaurus, the notch is usually a C shape that is deep, prominent and narrow (McGowan 1974, 1989a, 1994a, 2003; Johnson 1979; Maisch & Matzke 2000; Maisch 2008; Vincent et al. 2014), although the holotype of Excalibosaurus possesses a slight, incipient notch (McGowan 1989b), similar to that of Suevoleviathan (Maisch 1998). In specimens of Ichthyosaurus the anterior notch is most often a broad and open C shape (Maisch & Matzke 2000; McGowan & Motani 2003).
Palaeontology, University of Bath, with an eye to the discovery of new taxa. These features, together with the morphology of the coracoid foramen, are unique to *W. massarae*. In addition, the presence of a well-developed posterior notch in *Wahlisaurus is found in only one other genus, Ichthyosaurus*. The posterior notch in *Wahlisaurus* is considerably more developed than the small anterior notch, the reverse of that seen in other ichthyosaurs. The substantial difference in the coracoid morphology of *Wahlisaurus* in comparison with other leptonectids is as distinct as the differences among the coracoids in other Lower Jurassic ichthyosaur genera. Thus the combination of features in the coracoid of *Wahlisaurus* does not represent morphological variation of a currently recognized leptonectid and is sufficiently different to be considered a new genus.

Conclusions

*Wahlisaurus massarae* gen. et sp. nov. is a new leptonectid ichthyosaur from the Lower Jurassic (lower Hettangian) of Nottinghamshire, England. It possesses a unique combination of characters that distinguish it from all other ichthyosaurs, including autapomorphic characters of the pectoral girdle such as a large, ovoid coracoid foramen and the combined presence of a coracoid foramen and scapular-coracoid foramen. These features further highlight the taxonomic utility of pectoral girdle elements in ichthyosaurs.

The recognition of *Wahlisaurus massarae* as a leptonectid adds to the currently valid taxa that form the family Leptonectidae (Maisch, 1998) – *Leptonectes* (*L. temiurostris, L. solei* and *L. moorei*), *Excalibosaurus costini* and *Eurhinosaurus longirostris* – and unequivocally adds an additional region for the geographical occurrence of leptonectids. Presently, leptonectids are confidently identified from the following locations: *Leptonectes temiurostris* from Dorset, Somerset, Leicestershire, Warwickshire (England: McGowan 1996; Smith & Radley 2007), Dusslingen (Germany: Maisch 1999) and Unter Hauenstein (Switzerland: Maisch & Reisdorf 2006); *Leptonectes moorei* from Dorset (England: McGowan & Milner 1999); *Leptonectes solei* from Dorset (England: McGowan 1993); *Excalibosaurus costini* from Somerset (England: McGowan 2003); and *Eurhinosaurus longirostris* from Yorkshire (England: McGowan 1994a), Holzmaden and surrounding areas (Germany: McGowan 1979), Staffellegg (Switzerland: Reisdorf et al. 2011), Dudelange (Luxembourg), Noirefontaine and Marcoux (France: Fischer et al. 2011b). Including *Wahlisaurus*, a total of nine ichthyosaur genera are recognized from the Lower Jurassic. The discovery of a new ichthyosaur from the well-studied British Lower Jurassic demonstrates that new taxa may yet be found through detailed re-examination of museum collections as well as new discoveries.

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Supplemental material

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