A marine reptile fauna from the Early Jurassic Saltford Shale (Blue Lias Formation) of central England

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SUMMARY: A previously undocumented marine reptile fauna comprising well-preserved ichthyosaur and plesiosaur remains is described from the Early Jurassic Saltford Shale Member within the Blue Lias Formation of central England. Two ichthyosaur genera are recognized, namely *Leptonectes* and *Ichthyosaurus*, as well as generically indeterminate remains of plesiosaurs. The specimens include partly-articulated skeletons, reflecting preservation in dysaerobic argillaceous sediment in a dominantly low-energy setting on the English East Midlands Shelf.

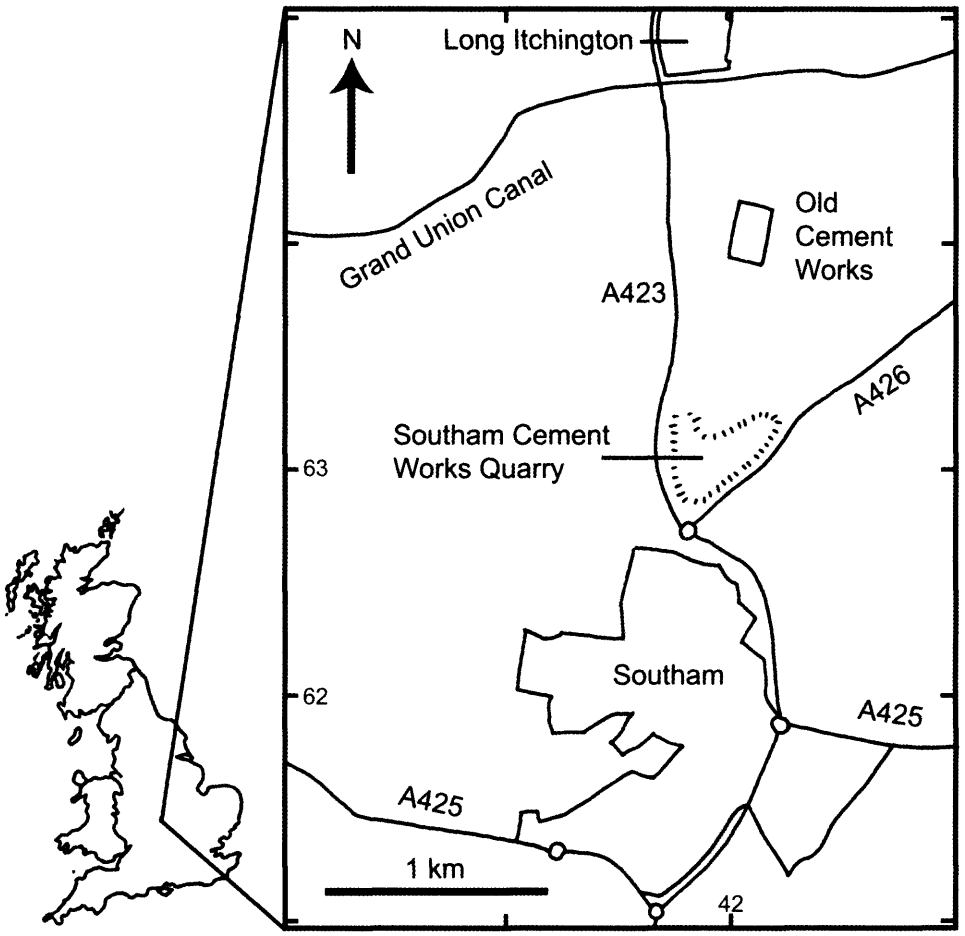

Fig. 1.
Location of Southam Cement Works quarry [SP 421 631 – 418 629], Warwickshire, England.

The latest Triassic to Early Jurassic Lias Group succession in central England comprises mudstone-dominated strata of epicontinental marine origin, yielding rich macrofaunas at many levels (Arkell 1933; Hallam 1968; Simms *et al.* 2004). Today, much of the succession is very poorly-exposed, following the closure of numerous stone, cement and brick-clay quarries. Southam Cement Works quarry, eastern Warwickshire [SP 421 631 – 418 629] (Fig. 1), still exposes mudrocks and limestones assigned to part of the latest Triassic – Early Jurassic Blue Lias Formation (the Saltford Shale and Rugby Limestone members; Hettangian to Sinemurian; Liasicus to Bucklandi Chronozones; Fig. 2). Descriptions of the succession are given for example by Old *et al.* (1987), Radley (2002) and Martill (2005).

Until 2006, the quarry provided a complete section through the Saltford Shale Member (Liasicus to Angulata Chronozones; Radley 2002), which is otherwise very poorly-exposed in central England (Ambrose 2001). However, the quarry is now disused and exposures of the Saltford Shale are largely flooded and inaccessible. At Southam, the Saltford Shale

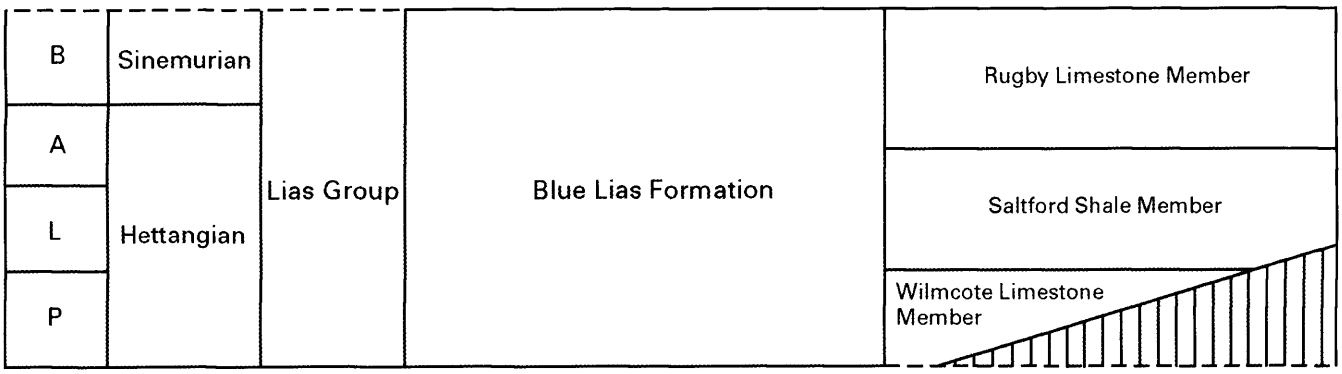

Fig. 2. Outline lithostratigraphy and biostratigraphy of the Lower Jurassic Blue Lias Formation, Warwickshire, England. Chronozones are indicated in the left-hand column. P = Planorbis; L = Liasicus; A = Angulata; B = Bucklandi.

comprises approximately 17 m of dark-grey, laminated to blocky mudstone enclosing limestone nodules and interspersed with thin limestone beds. Macrofossils are rare. Laminated limestone nodules occasionally preserve concentrations of schlotheimiid ammonites and fish debris (Radley 2002; Martill 2005) and, rarely, reptile remains (this account). Overlying the Saltford Shale, the lower part of the Rugby Limestone Member (Angulata to Bucklandi Chronozones) marks the development of macrobenthos-rich bioturbated limestone, shale and mudstone beds (Ambrose 2001).

1. REPTILE MATERIAL FROM WARWICKSHIRE, CENTRAL ENGLAND

Parts of the Blue Lias Formation were extensively quarried in south-western and eastern Warwickshire during the nineteenth and early twentieth centuries as raw material for the Rugby cement industry, for building and paving stone, and for agricultural lime (Williams & Whittaker 1974; Old *et al.* 1987). The quarries yielded numerous reptile remains, principally of ichthyosaurs and plesiosaurs (Old *et al.* 1987; Benton & Spencer 1995 and references therein). Many were collected from laminated calcilutites of the Rhaetian–Hettangian (Planorbis Chronozone) Wilmcote Limestone Member (Old *et al.* 1991; Benton & Spencer 1995; Warwickshire Museum collection; JDR, personal observations), developed below the Saltford Shale on the margin of the East Midlands Shelf and Worcester Basin in the Avon Valley of south-western Warwickshire (Ambrose 2001; Radley 2003; Simms *et al.* 2004). Additionally, there are numerous records of near-complete ichthyosaur and plesiosaur skeletons from large cement quarries in eastern Warwickshire, as at Harbury, Long Itchington and Stockton (e.g. Spens 1899; Drinkwater 1912; Swinton 1930), which appear to have been excavated largely, or possibly wholly, within the Rugby Limestone Member (Old *et al.* 1987; Ambrose 2001).

To our knowledge, there are no published descriptions of marine reptile assemblages formally ascribed to the intervening Saltford Shale in central England. Here we report a fossil assemblage collected from the Southam Quarry during the 1990s, now held within the collections of the Warwickshire County Museum. The collection includes well-preserved ichthyosaur and plesiosaur remains, partly prepared mechanically from the pale grey, laminated, fine-grained, silty limestone nodules that characterize the Saltford Shale at that site (Radley 2002; Martill 2005). The bones are predominantly pale to medium-brown in colour, more-or-less uncompacted, free of obvious macrobioerosion and bioencrusters, and internally mineralized by calcite. Voids within the vertebral centra of a partial ichthyosaur skeleton (Warwickshire Museum specimen G15647; see below) enclose geopetal fills of pale calcilutite below partial void-fills of sparry calcite. Pyrite is rare, occurring as a localized 'skin' on a few bones and as a heavy overgrowth on the partial vertebral column of G15647. This paper provides an inventory of the reptile remains, with notes on their taxonomy and palaeoenvironmental significance.

2. SYSTEMATIC PALAEONTOLOGY

The remains described are of two ichthyosaur taxa and indeterminate plesiosaurs (Table 1). The partial skeletons of two juvenile plesiosaurs within the Southam collection (specimens G15650 and G15651) are thought to have originated from the slightly younger Rugby Limestone Member (JDR, personal observations) and are not discussed in this account.

Table 1
Inventory of reptile fauna from the Early Jurassic Saltford Shale (Blue Lias Formation) of Southam Cement Works quarry, central England

Warwickshire Museum specimen	Brief description and identification
G15643	Skull of *Ichthyosaurus communis* Conybeare (Fig. 3D–E)
G15644	Limestone nodule containing incomplete disarticulated ichthyosaur bones and tooth (Fig. 4B)
G15645	Ichthyosaur jaw with associated teeth, two parts, incomplete (not figured)
G15646	Partial forelimb of *Ichthyosaurus* sp. (Fig. 4A)
G15647	Partial ichthyosaur skeleton. *Leptonectes tenuirostris* (Conybeare) (Fig. 3A–C)
G15648	Partial plesiosaur skeleton, pectoral region in three parts (Fig. 5C–D)
G15649	Partial plesiosaur skeleton, sacral region in a limestone nodule (Fig. 5A–B)

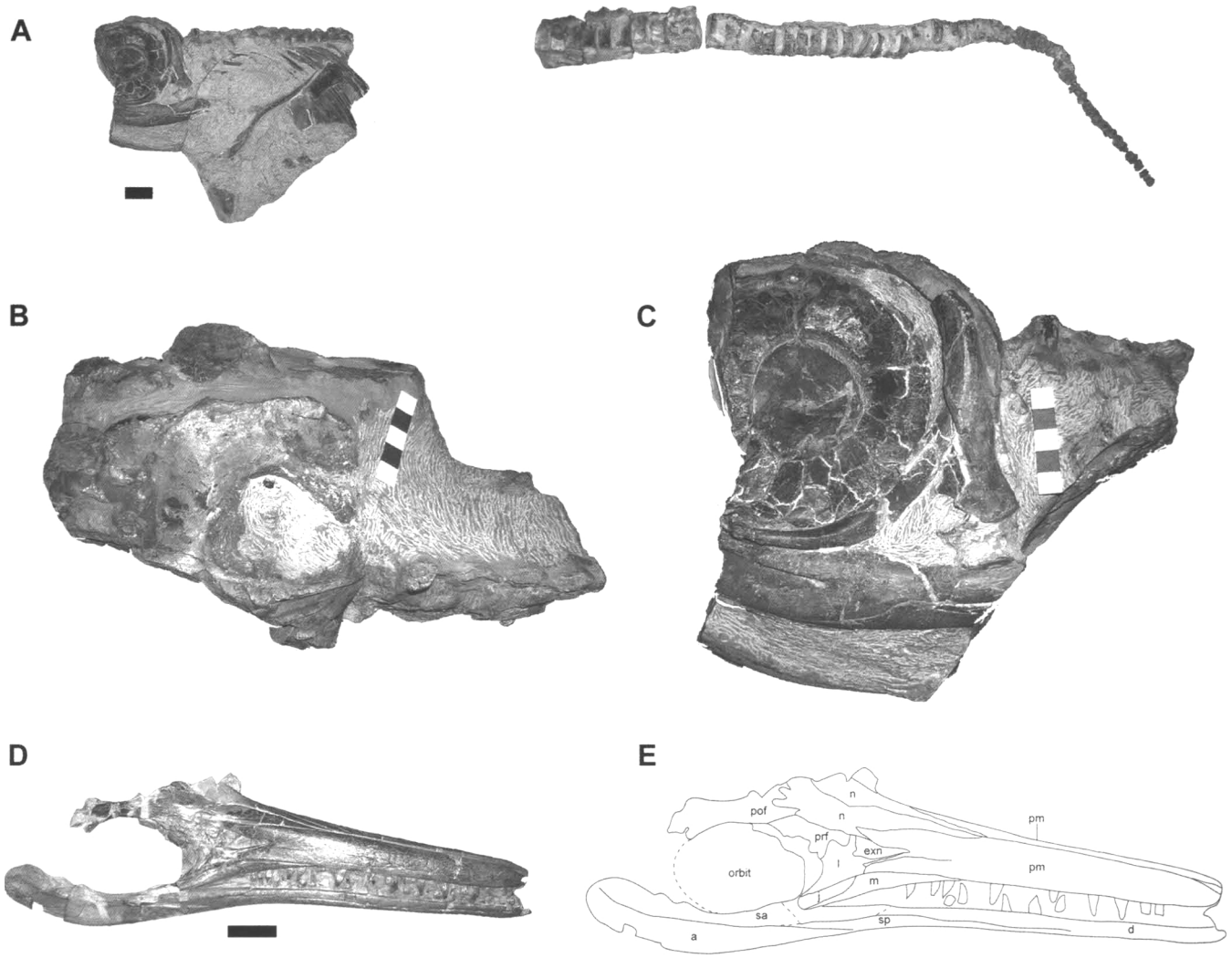

Fig. 3. Ichthyosaur remains from the Saltford Shale Member (Hettangian; Liasicus to Angulata Chronozones) of Southam Cement Works quarry, Warwickshire, England. (**A**) *Leptonectes tenuirostris* (Conybeare) (Warwickshire Museum specimen G15647). Arranged in approximate inferred life position. The gap in the vertebral column represents a number of missing vertebrae. Scale bar = 5 cm; (**B–C**) Detail of the skull of *Leptonectes tenuirostris* (Conybeare) (Warwickshire Museum specimen G15647). (B) Dorsal view; (C) Left lateral view, as seen in Fig. 3A, to show details of the cranium and provide a comparison of the orbit and temporal fenestra. Scale bar = 5 cm; (**D**) Skull of *Ichthyosaurus communis* Conybeare (Warwickshire Museum specimen G15643). Scale bar = 5 cm; (**E**) Interpretation of the skull of *Ichthyosaurus communis* Conybeare (Warwickshire Museum specimen G15643, see Fig. 3D). Right lateral view, showing the position of sutures. Abbreviations: a, angular; d, dentary; exn, external naris; j, jugal; l, lachrymal; m, maxilla; n, nasal; pm, premaxilla; pof, postfrontal; prf, prefrontal; sa, surangular; sp, splenial. Dotted lines indicate unknown/uncertain regions.

Class **REPTILIA**
Order **ICHTHYOSAURIA** Blainville, 1835
Family **LEPTONECTIDAE** Maisch, 1998
Genus ***LEPTONECTES*** McGowan, 1996

Leptonectes tenuirostris (Conybeare, 1822) (Fig. 3A–C)

Material. Partial skeleton; Warwickshire Museum specimen G15647.

Description. The largest and most complete of the reptile specimens is a partial ichthyosaur skeleton comprising the posterior portion of a skull and a near-complete vertebral column associated with a partial pectoral girdle and rib cage (Table 2). The anterior portion of the skull and mandible is broken off at the anterior border of the orbital sclerotic ring. The left temporal and cheek region is preserved in 3D whereas the bones on the right side are displaced ventrally. The medial border of the right upper temporal fenestra is visible but the lateral temporal region is broken off, the fracture running through the temporal arch. The post-temporal region is short with a postero-laterally facing cheek, extremely large eyes (132 mm diameter), and a small upper temporal fenestra approximately one third the size of the orbit. All characters are diagnostic of the leptonectid taxon *Leptonectes tenuirostris* (Conybeare, 1822), and the latter character (size of upper temporal fenestra) has been considered apomorphic for this species (Maisch & Matzke 2003). Four cervical vertebrae are associated with the skull, occurring in their natural articulated position.

The postcranial skeleton is preserved as five fragments. The most anterior fragment comprises ten vertebral neural spines, a partial rib cage, a complete left scapula and clavicle, and possibly both humeri (visible in cross section). This fragment

Table 2
Characterization of *Leptonectes tenuirostris* (Conybeare): Warwickshire Museum specimen G15647

Character	Measurement/count
Observed length of vertebral column	135.50 cm
Total estimated length of vertebral column	192.50 cm
Total estimated length of animal	247.00 cm
Observed number of vertebrae to tail bend	55
Orbital diameter	13.20 cm
Diameter of sclerotic ring (internal circumference)	5.30 cm
Left supratemporal fenestra – length	6.80 cm
– width	4.50 cm
– average diameter	5.65 cm
Temporal fenestra average diameter/orbit	0.43
Temporal fenestra width/orbit	0.34 (fenestra width approx ⅓ size of orbit)
Observed length of mandible	16.00 cm
Estimated total length of mandible based on the proportions of OUMNH J10305 (McGowan 1989)	54.80 cm

cleanly adjoins the skull segment along a sharp fracture and, when restored, contributes the posterior tip of the retroarticular process to the left mandibular ramus. With the exception of the possible humeri, fore- and hind limbs are missing. The scapula is strongly curved with the concave surface facing towards the ribs, which are unremarkable. The remaining sections consist of vertebrae, including twenty loose vertebrae attributed to the tail fluke. The vertebral count (55) to the tail bend contrasts with the diagnostic count (>79) for *L. tenuirostris* (McGowan 1989), indicating that a significant number of dorsal vertebrae are missing. The identification of this late Hettangian specimen as *L. tenuirostris* is consistent with the Rhaetian to Pliensbachian range of that taxon (Maisch & Reisdorf 2006). Two other species of *Leptonectes* are discounted. *Leptonectes solei* McGowan, 1993, has been recorded from strata of the same age, but is larger and has relatively smaller orbits (McGowan 1993). *Leptonectes moorei* McGowan & Milner, 1999, is known from younger, Pliensbachian strata and differs from *L. tenuirostris* in possessing a particularly short stout rostrum (McGowan & Milner 1999).

Genus ***ICHTHYOSAURUS*** de la Beche & Conybeare, 1821

Ichthyosaurus communis Conybeare, 1822 (Fig. 3D–E)

Material. Skull of a relatively small animal (Warwickshire Museum specimen G15643) lacking the posterior cranium but otherwise well-preserved in 3D. Associated remains include teeth and indeterminate small bone fragments.

Description. The right ramus of the mandible is complete (58 cm long). The snout length is 35 cm; the width across the temporal region is 7 cm. The cranial morphology, position of the sutures and late Hettangian age are consistent with the genus *Ichthyosaurus*, which ranges from the Rhaetian to the Sinemurian (Motani 1999). Furthermore, the teeth are robust, curved and blunt, characteristic of *Ichthyosaurus communis* Conybeare, 1822 (Maisch & Matzke 2000). However, it should be noted that the taxonomic diversity of Early Jurassic ichthyosaurs is under-represented (Motani 1999): *Ichthyosaurus* is historically something of a 'waste-basket' taxon, and as such this diagnosis remains tentative.

Indeterminate ichthyosaurian remains (Fig. 4A–B)

Material. A partial forelimb (Warwickshire Museum specimen G15646), lacking the proximal half of the humerus and distal phalanges; two jaw fragments containing teeth (G15645) (the fragments cannot be confidently reunited but are considered to belong to the same individual); a limestone nodule (G15644) containing a concentration of small bones including eight vertebrae, a recurved tooth and a caudal rib.

Description. Specimen G15646 (forelimb) is distinguished from the limb of contemporaneous *Leptonectes* by the angular and tightly packed (rather than discoidal and well-spaced) phalangeal configuration, the absence of a notch on the preaxial surface of the radius and lack of the foramen between the radius and ulna (McGowan 1989). These characters (or lack thereof), especially the tightly packed angular mesopodials, are characteristic of *Ichthyosaurus* (see Maisch & Matzke 2000, fig. 35). On this basis, the specimen is assigned to *Ichthyosaurus* sp.. The tooth shape and ornament of teeth preserved within the two jaw fragments (G15645) is typical for the Ichthyosauria but the material is too fragmentary to allow confident identification. Vertebrae preserved within the limestone nodule G15644 are deeply amphicoelus; a typically ichthyosaurian character. The associated tooth is slender and recurved and probably ichthyosaurian. This association, and the confused arrangement of the bones, leads us to interpret the accumulation as a scour fill.

Order **PLESIOSAURIA** Blainville, 1835 (Fig. 5A–D)

Material. Two incomplete plesiosaur skeletons, neither retaining a skull (Warwickshire Museum specimens G15648, G15649).

Description. G15649 comprises the semi-articulated trunk and sacral region of a small plesiosaur, preserved within a limestone nodule. It includes a sequence of 12 vertebrae exposing their right sides (6 of which are cleanly exposed), an almost complete (partially-exposed) pelvic girdle including both pubes and ischia, and an ilium. The vertebrae preserved within G15649 bear small nutritive foramina high upon the lateral surfaces of the centra. A single phalange abuts the right femur and there is a near complete pelvic girdle, with the flat surfaces of the pubic blades folded to face each other. Much of the bone remains to be prepared from the matrix. The nutritive foramina on the vertebral centra, expanded

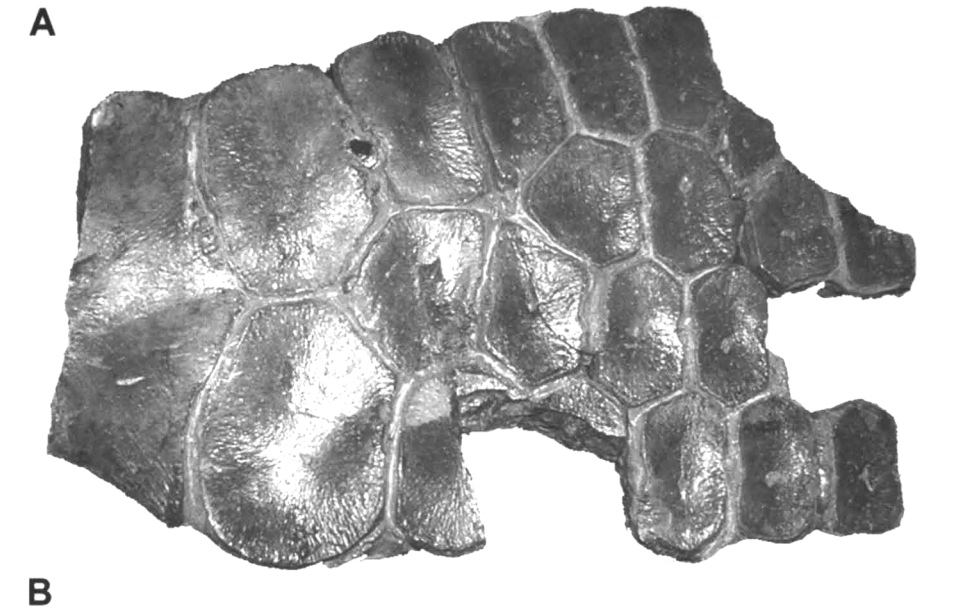

Fig. 4.
Ichthyosaur remains from the Saltford Shale Member (Hettangian; Liasicus to Angulata Chronozones) of Southam Cement Works quarry, Warwickshire, England. (**A**) Partial forelimb of *Ichthyosaurus* sp. (Warwickshire Museum specimen G15646). Length of specimen = 78 mm; (**B**) Accumulation of ichthyosaur vertebrae, probable ichthyosaur tooth (white arrow) and an ichthyosaur caudal rib (black arrow), tentatively interpreted as a scour-fill (Warwickshire Museum specimen G15644). Scale bar = 5 cm.

plate-like pelvic elements, and elongate dorsoventrally flattened propodial (in this case the femur) are characteristic of plesiosaurs (Brown 1981). Further taxonomic clarification would require a systematic revision of Early Jurassic plesiosaurs.

G15648 comprises three parts. Two of these join to form a complete left coracoid, together with a number of cervical vertebrae. The third part, a left scapula, does not show any indication of its exact position relative to the other fragments, though it is inferred to have been closely associated with the coracoid with which it would have articulated in life. The coracoid bears a close resemblance to that of *Plesiosaurus* (Storrs 1997, fig. 10), with an elongate median symphysis, because it is greatly expanded posteriorly (as is typical of plesiosaurs; Brown 1981). However, given the lack of additional material, any referral of G15648 to this genus should be considered extremely tentative.

3. DISCUSSION

The Rhaetian (Late Triassic) to Sinemurian (Early Jurassic) Blue Lias Formation was deposited in epicontinental marine environments influenced by sea-level fluctuations and a warm, generally humid climate (Hallam 1975; Hesselbo & Jenkyns

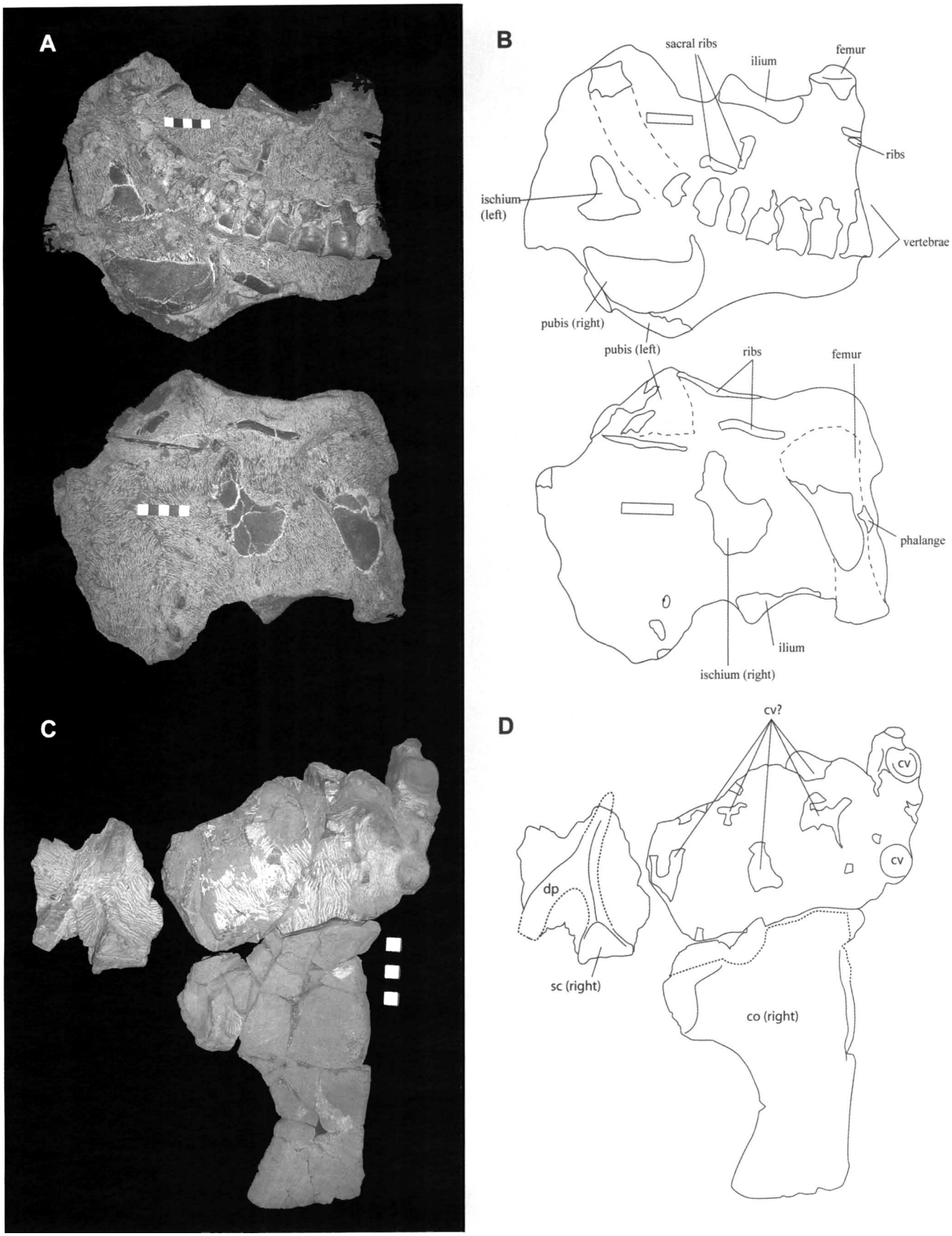

Fig. 5. Plesiosaur remains from the Saltford Shale Member (Hettangian; Liasicus to Angulata Chronozones) at Southam Cement Works quarry, Warwickshire, England. (**A**) Indeterminate plesiosaur sacral region (Warwickshire Museum specimen G15649), photographs of the flattened nodule seen from two aspects. Scale bars = 5 cm; (**B**) Interpretation of plesiosaur sacral region (Warwickshire Museum specimen G15649); (**C**) Indeterminate plesiosaur pectoral region (Warwickshire Museum specimen G15648). Scale bar = 5 cm; (**D**) Interpretation of plesiosaur pectoral region (Warwickshire Museum specimen G15648). Abbreviations: co, coracoid; cv, cervical vertebra; cv?, indeterminate bones – probably cervical vertebrae; dp, dorsal process of scapula; sc, scapula. Dotted lines indicate unknown/uncertain regions.

1998; Simms *et al.* 2004). In Warwickshire, central England, the Blue Lias Formation was deposited in a mud-dominated mid to outer ramp setting near the southwestern end of the English East Midlands Shelf, NW of the partly emergent London–Ardennes Landmass (Donovan *et al.* 1979; Simms *et al.* 2004). The Saltford Shale Member marks a Hettangian marine transgressive pulse onto the London Platform (Donovan *et al.* 1979). The dark colour, widespread fine lamination and virtual absence of macrobenthos indicates deposition in a low-energy, predominantly dysaerobic setting (Wignall & Hallam 1991; Radley 2003). Linear to lenticular concentrations of imbricated ammonite conchs, figured by Martill (2005), are interpreted as distal storm-flow gutter and scour fills (Radley 2002, 2003).

Radley (2003) inferred a setting below maximum storm wave-base, at depths of at least a few tens of metres. Some of the reptile remains represent partially disarticulated skeletons, providing further evidence for pre-burial disturbance by weak currents and/or perhaps scavengers. At least one accumulation of disarticulated bones is interpreted as a scour-fill (G15644, see above, Fig. 4B). The absence of obvious macrobioerosion and bioencrustation affecting the bones probably reflects the oxygen-poor conditions. A preliminary survey of the Wilmcote Limestone reptile fauna from the Avon Valley (see above) indicates a similar preservation mode, comprising well-preserved, partially disarticulated remains, lacking obvious evidence for post-mortem degradation on the sea-floor (Warwickshire Museum collection; JDR, personal observations). This is also thought to reflect a low-energy, partly dysaerobic environment (Simms 2004), similar to that inferred for the Saltford Shale. In contrast, reptilian remains from the relatively fossiliferous Rugby Limestone Member, which overlies the Saltford Shale at Southam, are commonly oyster-encrusted and of degraded, chemically corroded and/or microbioeroded appearance (Warwickshire Museum collection; JDR, personal observations). This clearly reflects increased benthic oxygenation, possibly associated with prolonged exposure at the sediment-water interface (Martill 1987, 1995) and/or relative shallowing (Radley 2003).

British Early Jurassic marine reptile faunas, such as the Hettangian example documented herein, are dominated by ichthyosaurs (Benton & Spencer 1995). Significant faunas have been documented from Hettangian mudrock-dominated formations throughout Britain, including sites in Somerset, Warwickshire, Leicestershire and Nottinghamshire. At Barrow-upon-Soar, Leicestershire, 57 km NNE of Southam, Hettangian (Planorbis Chronozone) limestones and mudstones of the Wilmcote Limestone Member, slightly older than the Southam beds, yielded a fauna that includes *I. communis*, *L. tenuirostris* and the plesiosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Martin *et al.* 1986; Cruickshank 1994; Storrs & Taylor 1996).

Additionally, in Warwickshire, notable ichthyosaur and plesiosaur faunas have been collected from partly older strata of latest Triassic (upper Rhaetian) to Hettangian age in the Avon Valley (Wilmcote Limestone Member; Simms *et al.* 2004 and above; Fig. 2) and the slightly younger (Hettangian–Sinemurian; Angulata to Bucklandi Chronozones) Rugby Limestone Member of the Rugby district in eastern Warwickshire (see above and Fig. 2). The Wilmcote Limestone yielded a near-complete plesiosaur referred to *R. megacephalus* (Cruickshank 1994). At Harbury, 5 km SW of Southam, strata of Angulata Chronozone age appear to fall wholly within the Rugby Limestone (Ambrose 2001) and yielded the holotype of the plesiosaur *Macroplata tenuiceps* (Swinton) (Swinton 1930).

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